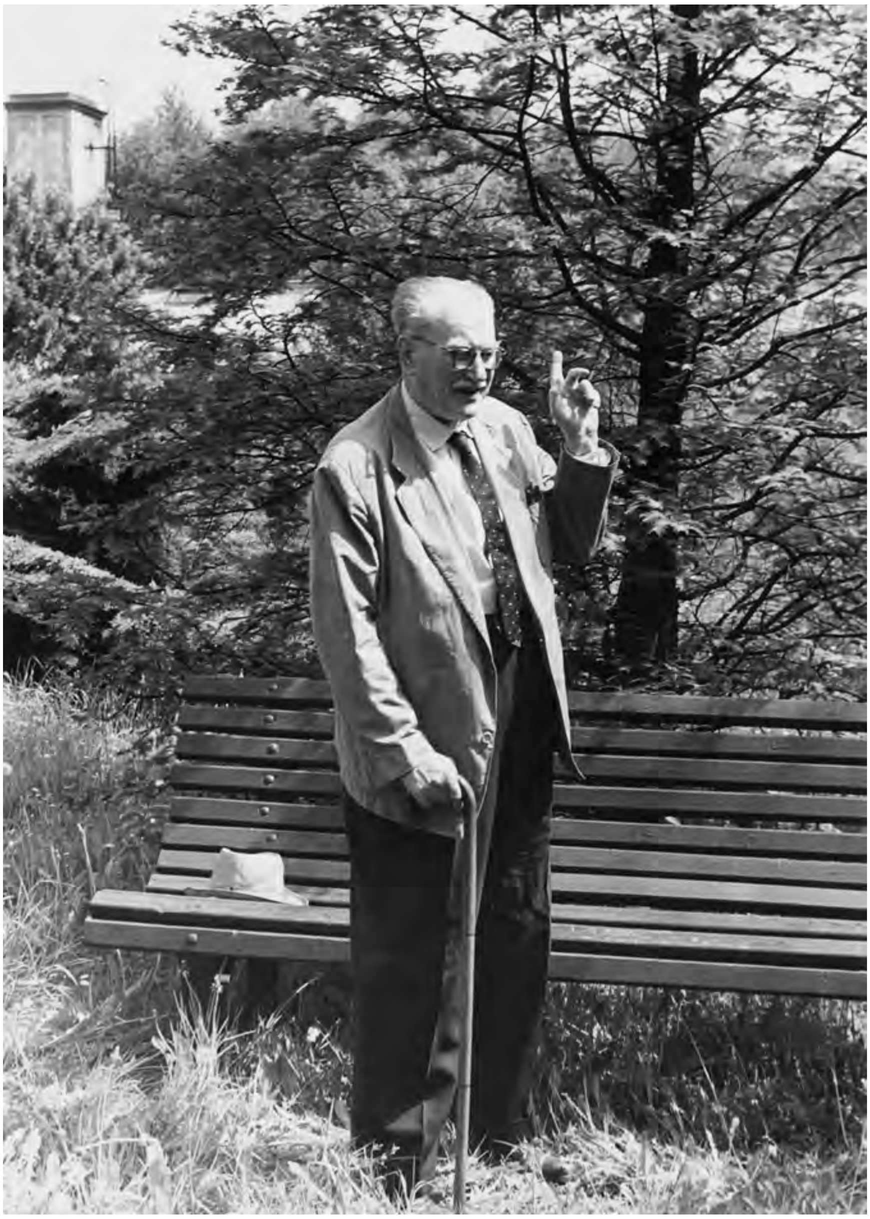
LATE GLACIAL AND HOLOCENE HISTORY OF VEGETATION IN POLAND BASED ON ISOPOLLEN MAPS



This book is dedicated
to the Memory of ***Professor Władysław Szafer,***
who invented and applied for the first time
the isopollen method in 1935

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Edited by

Magdalena RALSKA-JASIEWICZOWA

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Małgorzata LATAŁOWA, Krystyna WASYLIKOWA, Kazimierz TOBOLSKI,
Ewa MADEYSKA, Herbert E. WRIGHT Jr., Charles TURNER

Original computer programs and editing of maps
Dorota NALEPKA & Adam WALANUS

W. Szafer Institute of Botany, Polish Academy of Sciences
Kraków 2004

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Preface

Five decades have passed since Professor Władysław Szafer established the Institute of Botany of the Polish Academy of Sciences, thus setting up in Kraków a centre for studies and documentation of the biodiversity in respect to the flora and vegetation of Poland. Taking up the task of his mentor, Professor Marian Raciborski, W. Szafer made palaeobotany one of the principal aspects of botanical studies in the Institute, to complement the taxonomic/evolutionary and plant geographical/ecological approaches. A recapitulation of these 50 years of the Institute's work as well as that of botanists from other research centres in Poland is represented, *inter alia*, by a series of publications called *Biodiversity of Poland* – the first comprehensive documentation of the current state of biodiversity in all groups of the Polish flora: slime moulds, fungi, lichens, algae, mosses, liverworts, pteridophytes, and flowering plants.

The present volume, *Late Glacial and Holocene history of vegetation in Poland based on isopollen maps* supplements the aforementioned series *Biodiversity of Poland* by presenting the palaeobotanical perspective of the history of biodiversity development from the last glaciation to the present, thus covering more than thirteen thousand years. The work was completed by a group of more than twenty researchers from all over Poland, led by W. Szafer's former student Professor M. Ralska-Jasiewiczowa in cooperation with K. Wasylikowa and M. Latałowa. At the editing stage a significant input was also brought by two outstanding scientists from abroad: Charles Turner (Open University Cambridge) and Herbert E. Wright Jr. (University of Minnesota), who not only provided the linguistic corrections of English translation but furnished critical perspectives on substantive issues as well. We are very grateful to all of those who contributed their time and effort towards the completion and publication of this work.

This book comes out exactly 70 years after the publication of the Szafer's original isopollen method, which now has a great comeback. In addition to improved methods for identifying taxa and dating, enormous advances in computer techniques as well as in statistical and cartographic software has allowed Szafer's isopolls maps to be turned into a precision tool to study the historical development of the present biodiversity at the level of whole floras. So it is not surprising that with this method Polish and other European palaeobotanists have now succeeded in making syntheses in the field of historical plant geography. Advances in many branches of environmental sciences have markedly enhanced the interpretive potentials of palaeobotany and palaeoethnobotany. This work employed the original POLPAL software developed in the Institute for gathering, processing, and presenting isopollen maps. It is now widely accepted and used by palaeobotanists in several different countries.

Late Glacial and Holocene history of vegetation in Poland based on isopollen maps is a synthesis of the palaeophytogeography and palaeoecology. This publication will be a key to understanding the multidimensional and varied history of vegetation as well as to untangling the development of biodiversity in the flora and landscapes. It also offers a way for comprehending the historical roots of Poland's natural history – thus providing a solid basis for rational environmental management and conservation of the natural heritage. This work examines many hypotheses of importance to the biological sciences or even broadly termed natural sciences by showing the migration routes of particular elements of the flora and their relations to climatic changes and to human impact throughout millennia. At the same time, this book is a starting point to develop new hypotheses by utilizing *inter alia*, state-of-the-art methods and techniques of molecular palaeobotany and molecular evolutionary taxonomy and plant geography.

It should be emphasised that the book pertains to a particularly important part of Europe. Poland is situated perfectly in the transition zone between the atlantic and continental climates, as well as between the north and south of Europe.

Recognising and understanding the present biodiversity and its origins is important in the biological sciences as well as in nature conservation and management concerned with sustainable development. At the same time it has become a focus of interest of culture broadly defined.

Late Glacial and Holocene history of vegetation in Poland based on isopollen maps, like its predecessor, *Vegetation of Poland* (Oxford University Press) edited by W. Szafer, should be a valuable reference in English for many European regional syntheses in the field of environmental change and the emergence of contemporary natural/cultural landscapes.

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Kraków, 21 July 2004

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ISOPOLLEN HISTORY OF HERBACEOUS PLANTS

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INTRODUCTION

The book we are offering to those people who are interested in changes of the Holocene palaeoenvironment is the third attempt of Polish palynologists to reconstruct the plant-migration patterns on the territories of Poland from the Late Glacial to modern times on the basis of isopollen maps.

The first effort on this subject, published in 1935 by Professor Władysław Szafer – the originator of the isopolls method – introduced the idea of isopollen maps and presented migration maps for two tree species on the interwars area of Poland. The maps, based on 152 sites, were constructed for several arbitrarily defined periods of the Late Glacial-Holocene climatic cycle, as in those days there were no methods of absolute age determination.

The second project, issued in 1983 by M. Ralska-Jasiewiczowa, was based on 64 sites, but only 14 of them had more than two ^{14}C dates, and 29 were not dated at all. The maps of 9 major tree and shrub genera were presented, excluding pine and birch, for time intervals of 1000 years. These maps were hand-drawn. They were based on intercorrelations of sites supported by poor dating, as well as on the general knowledge of the subject.

Since then, for more than 20 years substantial progress has been made in the studies of Polish vegetation history during the last 15,000 years. The number of sites investigated by pollen analysis increased considerably, and, what is the most important, many of them have been much better radiocarbon dated. After a discussion within a group of Polish palynologists it has been agreed that the input of new data is good enough to try to present the history of vegetation applying the isopollen method to our up-to-date results, both published and still under study. The idea led to high interest among colleagues, and 27 people have offered their contribution to the project. The Holocene palynological database available at the W. Szafer Institute of Botany of the Polish Academy of Sciences in Kraków was a base of gathering material to this project. More than 250 profiles investigated by pollen analysis, including those still unpublished, have come into the new database. The 190 profiles were qualified as useful for the construction of the maps.

The project as a whole is based on numerical methods. Various applications of the POLPAL program (Walanus & Nalepka 1999, Nalepka & Walanus 2003a, b) have been applied to elaborate raw data and to construct maps. The maps have been produced by D. Nalepka on the basis of programs prepared by A. Walanus, and in constant contact with all the authors. All the most important tree genera have been included as well as some taxa of shrubs and herbs interesting for pollen-analytical studies. The status of dating of the profiles and other more precise methodical data are presented in the chapters describing the methods (Nalepka & Walanus, Walanus & Nalepka, this volume).

The sets of dot and isopollen maps for particular taxa illustrate both changes in their distribution and in their importance in plant communities within the time scope between 14,000 and 100 ^{14}C yr BP. The maps for the majority of taxa were originally drawn for all time-cuts, starting from 14,000 yr BP. Later, however, it was decided to exclude the maps which presented only single pollen finds (one or a few sites), obviously rebedded or coming from long distance transport. The set of maps for every taxon is described as one figure. The isopollen maps are provided with the text chapters discussing presented taxa. The texts include the maps of present-day distribution of corresponding species in Poland according to Zając A. and Zając M. (eds) (2001), if the discussed taxon is represented in Poland by no more than 3 species. The chapters have been prepared by small groups of authors, and almost all of the contributors to the project participated in this task. D. Nalepka, as the maps maker, has been included as a co-author for these all chapters. The extensive summary, containing conclusions from the analyses of isopollen maps for the main phases of the Holocene interglacial cycle, prepared as the individual author's contributions (M. Latałowa, M. Makohonienko, M. Ralska-Jasiewiczowa, and K. Tobolski), completes the text part. Throughout the whole text all dates are given as radiocarbon years BP unless it is otherwise stated. In order to facilitate the orientation in geographical regions of Poland a physical map is attached at the end of the book.

This monographic study is an accomplishment of a certain stage of research, and it will need to be brought up-to-date as our knowledge expands. This particularly concerns those areas of our country that are ‘white spots’ at present. Uneven distribution of sites has caused some inevitable falsifications resulting from extrapolation over a relatively large radius of impact.

We hope that this new study on the migration histories of selected trees, shrubs, and herbaceous plants will be received with appreciation and bring a lot of positive results.

Acknowledgments

We are very grateful to Professor A. Zając (Jagiellonian University) for making access to the maps of the present distribution in Poland of the taxa studied and to Professor Emer. W. Matuszkiewicz for providing us with the map of potential vegetation of Poland and with many other illustrations. Professor J.M. Matuszkiewicz (Institute of Geography and Spatial Organization, Polish Academy of Sciences) kindly made the correction of the English names of the forest associations, and Dr. R. Bednarek (Nicolaus Copernicus University) provided us with the map of Polish soils. Figures in chapter ‘Present-day natural vegetation of Poland’ are included in the text with permission of the publisher Wydawnictwo Naukowe PWN S.A. We wish to express our thanks to E. Malata and B. Biernat for their efforts in the English translation of the whole text.

Professor Emer. H.E. Wright Jr. (Limnological Research Center, University of Minneapolis, U.S.A.), and to Dr. Ch. Turner (Department of Earth Sciences, The Open University, Cambridge, U.K.), assumed the duties of critical reading and linguistic correction of the manuscript.

Magdalena Ralska-Jasiewiczowa
Krystyna Wasylikowa

PRESENT-DAY NATURAL ENVIRONMENT OF POLAND

Krystyna Wasylikowa

Poland is located in the geographical centre of Europe (14°07′–24°08′E, 49°00′–54°50′N), and components of its relief contribute to the natural environment of the transition between western and eastern part of the continent.

Topography and soils

The relief of Poland is characterised by a latitudinal sequence of the main orographical units. From south to north, they are the Carpathian Mountains and subcarpathian valleys along with the Sudetes and Sudetian foothills, then a belt of uplands, followed by the lowland of the old-glacial area, and finally the lowland of the young-glacial area, stretching from the southernmost terminal moraines of the last glaciation to the Baltic Sea (Fig. 1) (Gilewska 1991a). The basic relief features of southern Poland had been formed by the end of the Tertiary, and in the Quaternary they were only modified under the influence of glacial-interglacial climatic changes. The relief of central and northern Poland was formed in the Quaternary. Pleistocene glaciations produced outwash gravel and sands of proglacial stream

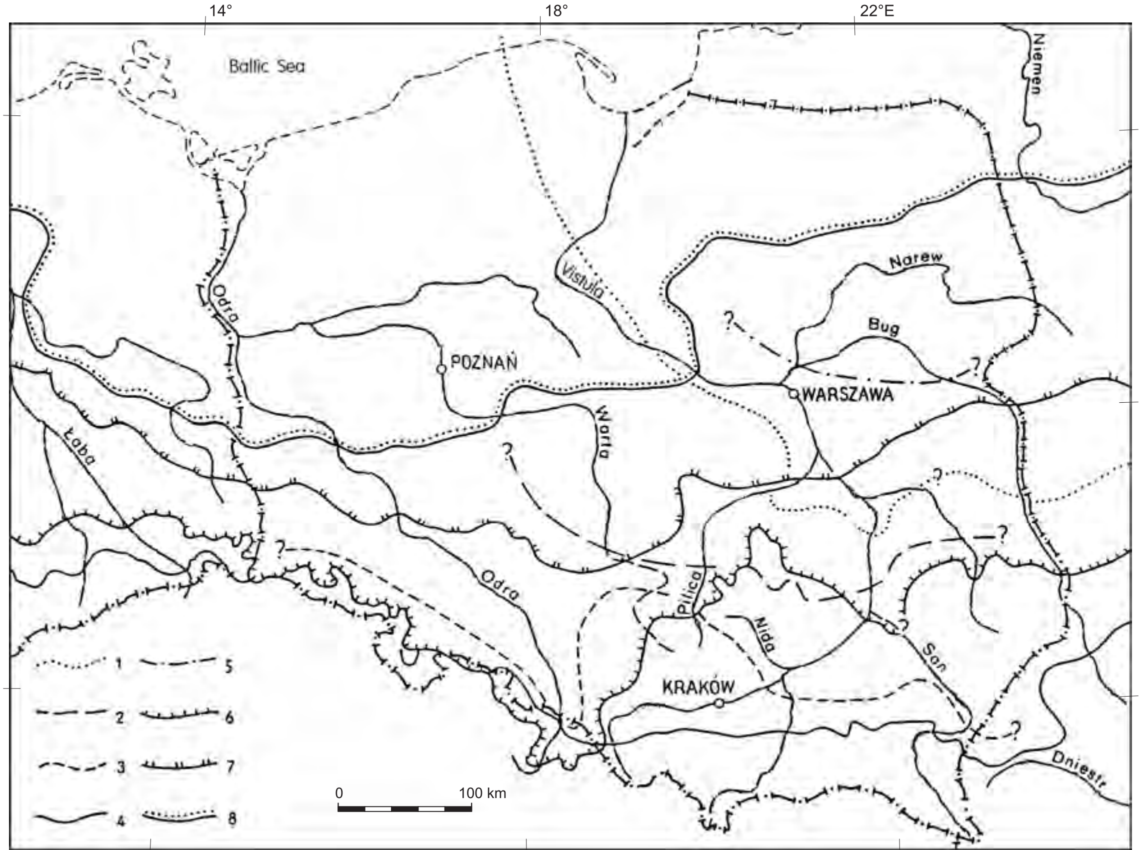


Fig. 1. Maximal extents of Pleistocene glaciations in Poland: 1 – Narew river, 2 – Nida river, 3 – San river 1, 4 – San river 2, 5 – Liwiec river, 6 – Odra river, 7 – Warta river, 8 – Vistula river (Lindner 1992, simplified)

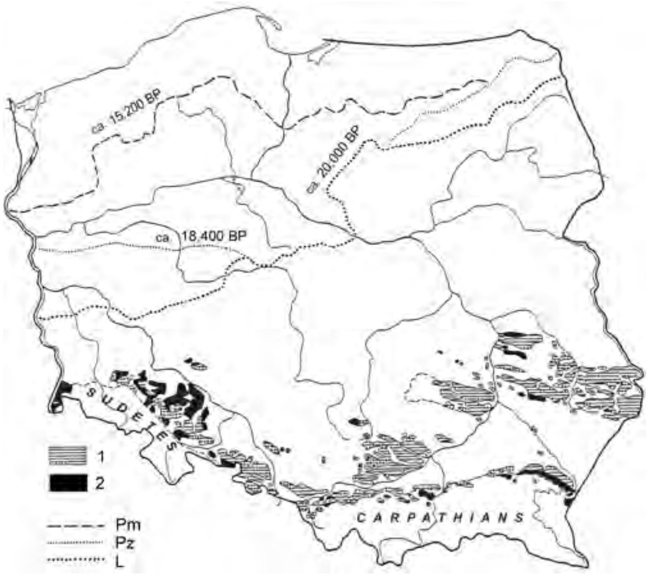


Fig. 2. Distribution of loess in Poland and the extent of continental glacier during the main phases of the Vistula glaciation: 1 – relief forms of loess, 2 – periglacial muck and clayey deposits with patches of loess. L – Leszno phase, Pz – Poznań phase, Pm – Pomeranian phase (Kozarski 1991, slightly altered)

valleys, silty clay formations of aquatic origin, and loesses (Fig. 2) and dune sands (Fig. 3), forming the parent materials from which the soil cover developed. The history of vegetation in the last 15 thousand years was determined by processes caused by climatic changes of the Vistulian glaciation.

Most of the Polish land is covered by zonal brown soil types (brown and lessivé soils, covering about 50% of the surface) and podzolic soil types (rusty soils, podzolic soils, and podzols, covering 25% of the surface) (Fig. 4). Brown soil types occur more commonly in southwest Poland, and among podzolic soil types the contribution of podzol soils increases to the east and north east, as elsewhere in Europe (Fig. 5). Patches of chernozem soils appear extrazonally, scattered in the south of Poland (about 1% of the area) and having no contact with the main chernozem area in the southeast of Europe (Prusinkiewicz & Bednarek 1991). Some pedologists distinguish grey forest soils, characteristic of forest steppe. Intrazonal soils include alluvial soils covering about 5% of the Polish area, hydrogenic soils formed under high moisture conditions and covering about 7.8% (e.g. peaty soils, mucky soils, gley soils, black earth) and rendzinas, as well as salt marshes covering small areas. A separate category is constituted by azonal soils, in which the soil profile has not yet been formed, including incipient and weakly developed soils and anthropogenic soils (Prusinkiewicz & Bednarek 1991, Bednarek 1996).

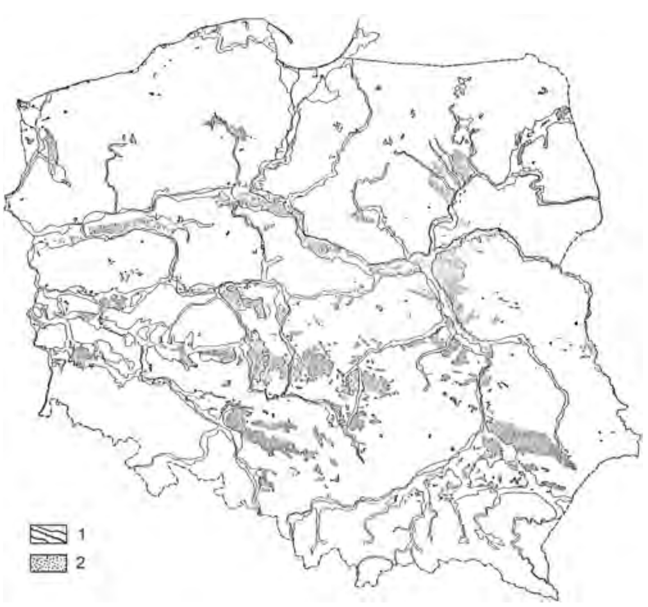


Fig. 3. Distribution of inland dunes and cover sands in Poland: 1 – river valleys, 2 – dunes and sandy areas (Galon 1958)

CLIMATE

Poland lies in the zone of warm temperate climates. The country's low relief north of the mountains causes the climate to be determined mainly by air masses coming from the west and to a lesser extent from the east. This results in the transitional character, between the oceanic climate of western Europe and the continental climate of the east, with distinct modifications caused by the land-relief, elevation, the distance from the Atlantic Ocean and the Baltic Sea, as well as influences from the Asian continent. The existing climate classifications of Europe either emphasise this transitional type of the Polish climate, marking the borderline between the temperate and rainy climate in the west and the boreal snowy-forest climate in the east, or they distinguish a separate type of Polish continental climate. Isotherms of the coldest month in the lowlands have a distinct meridional course (Fig. 6A), and the mean temperature in January decreases from –1°C in the west to –5°C in the north-east (Suwałki Lake District) (Paszyński & Niedźwiedź 1991). The mean annual temperature decreases from over 8.5°C in southwest Poland to 6.5°C in the northeast (Fig. 6C). In the Carpathians the mean annual temperature declines by about 0.5°C for every 100 m of altitude, and in the Sudety Mountains the mean annual temperature is more than 0.5°C lower than in the Carpathians at the same elevation. The mean temperature in July is less well differentiated in the lowland area of the country than the mean temperature in January, and its isotherms have more or less a longitudinal course, from over 18.5°C in the south, to about 16.5°C in the north (Fig. 6B).

Annual precipitation is largely dependent on the relief and elevation. Most of the country has a mean annual precipitation between 500 and 700 mm. The lowest precipitation occurs in Wielkopolska and Kujawy Lowland. It is higher in lake districts and highest in the mountains

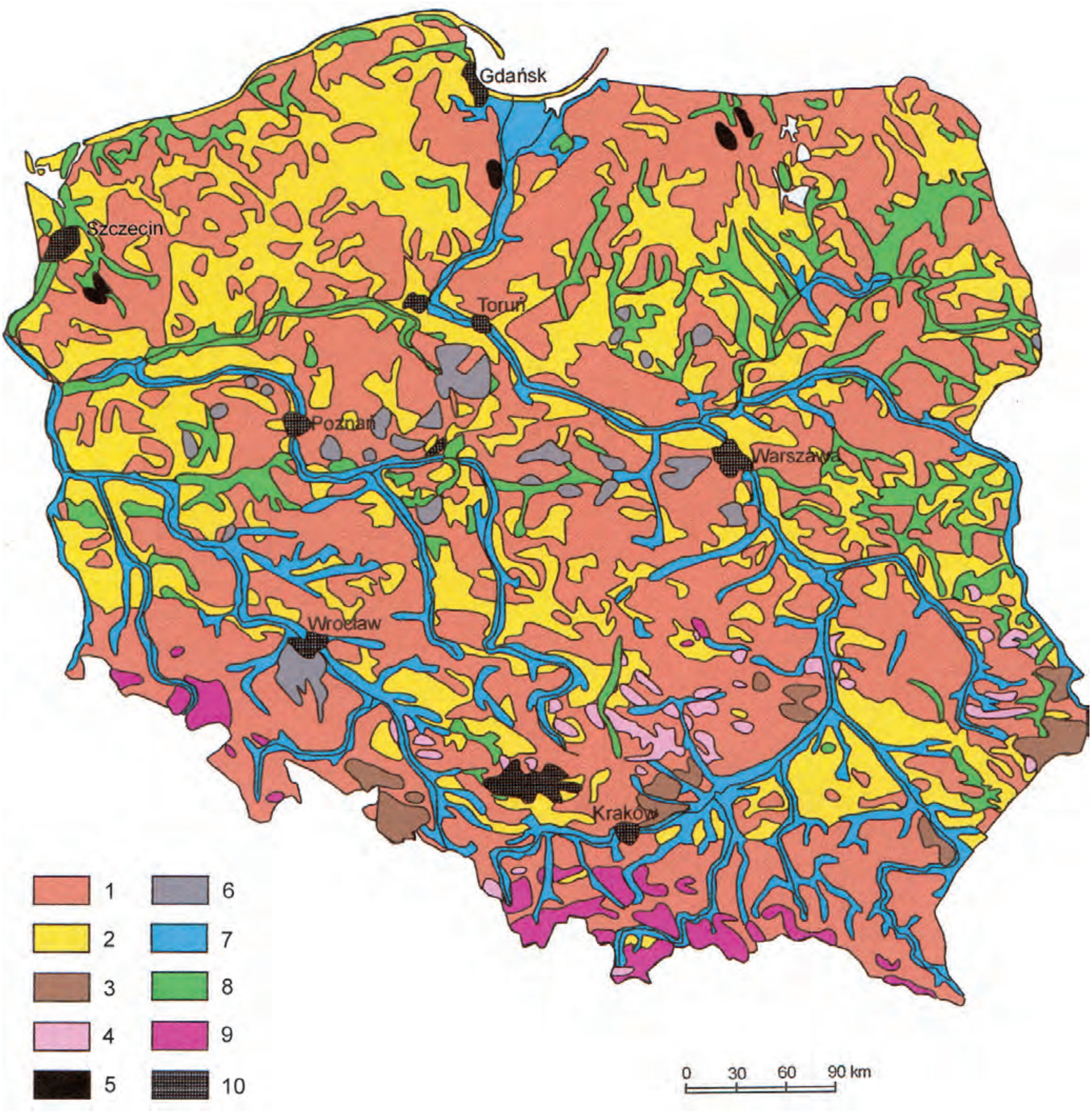


Fig. 4. Map of soils of Poland. Zonal soils, typical for the moist warm-temperate zone: 1 – brown and lessivé soils (Cambisols and Luvisols), 2 – rusty and podzolic soils and in places podzols (Arenosols and Podzols). Extrazonal soils: 3 – chernozems (Chernozems). Intrazonal soils: 4 – rendzinas (Rendzic Leptosols), 5 – vertisols (Vertisols), 6 – black earths (Mollic Gleysols), 7 – alluvial soils (Fluvisols), 8 – peaty soils and associated soils (Histosols and associated soils). Azonal soils: 9 – initial and weakly developed soils (Leptosols and Regosols), 10 – anthropogenic soils (Anthrosols) (after Bednarek 1996; names in brackets according to soil classification by FAO/UNESCO, 1988, and World Reference Base for Soil Resources – FAO, ISRIC, ISSS 1998, after Bednarek, oral inf.)

(Fig. 6D). Most of the precipitation falls in summer (mainly July), which is characteristic of continental climates, and the predominance of autumn precipitation over spring precipitation is a feature of oceanic climates. The average number of days with the snow cover in non-mountainous areas rises from about 40 in the lower Odra river valley to over 100 in the Suwałki Lake District (Paszyński & Niedźwiedź 1991).

The vegetation period, that is the number of days from the beginning of thermic spring, when the mean 24-hour temperature reaches at least 5°C, to the end of thermic autumn, when the mean 24-hour temperature falls below 15°C, fluctuates between 220 days in the west and 190 in the north-east (Fig. 7).

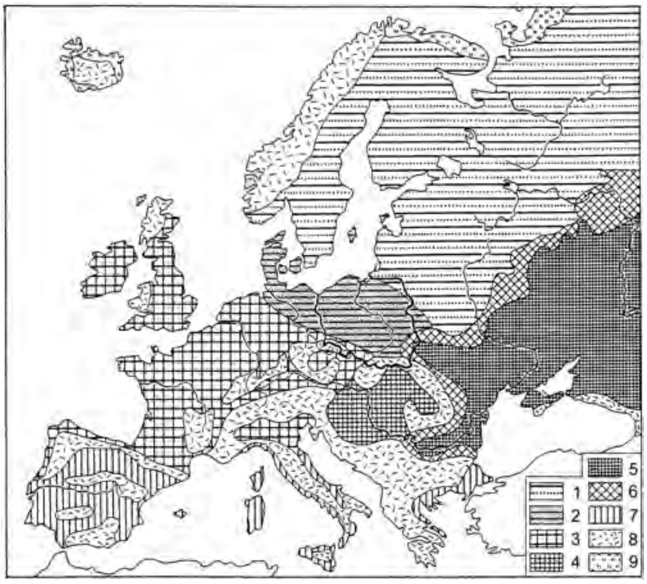


Fig. 5. Location of Poland on the map of European soils: 1 – zonal brown and podzolic soils with eastward increase in podzolic soils, 2 – zonal brown and podzolic soils, 3 – zonal brown type soils with the dominance of brown soils, 4 – brown soils and chernozems, 5 – chernozems, 6 – grey forest soils, 7 – cinnamon and grey cinnamon soils, 8 – montane soils, 9 – tundra soils (Gilewska 1991b)

VEGETATION

Poland lies within the Euro-Siberian Region of the kingdom of Holarctis (Medwecka-Kornaś 1972). Most of the area of Poland belongs to the Central European Lowland-Upland Province, characteristic of deciduous and mixed forests. The mountains lie within the Central-European Mountain Province (Fig. 8). The mountains are distinguished by a relatively rich flora and vegetation. Although they cover only 3% of the country's area, 20% of all species are composed of strictly montane species, and mountain plant associations constitute 20.8% of the total (Matuszkiewicz W. 1991). The plant cover of lowland and upland Poland is far less differentiated.

Similar to other components of the natural environment, a transitional location of Poland is also demonstrated in flora and vegetation by the penetration of northern and southern elements as well as eastern and western ones (Fig. 9). In the lowlands and uplands the majority of species (53.7%) and syntaxa belong to a transgressive element, i.e. to the units that have no geographical range limits in Poland (Matuszkiewicz W. 1991). In the forest vegetation of Poland there is a considerable reflection of

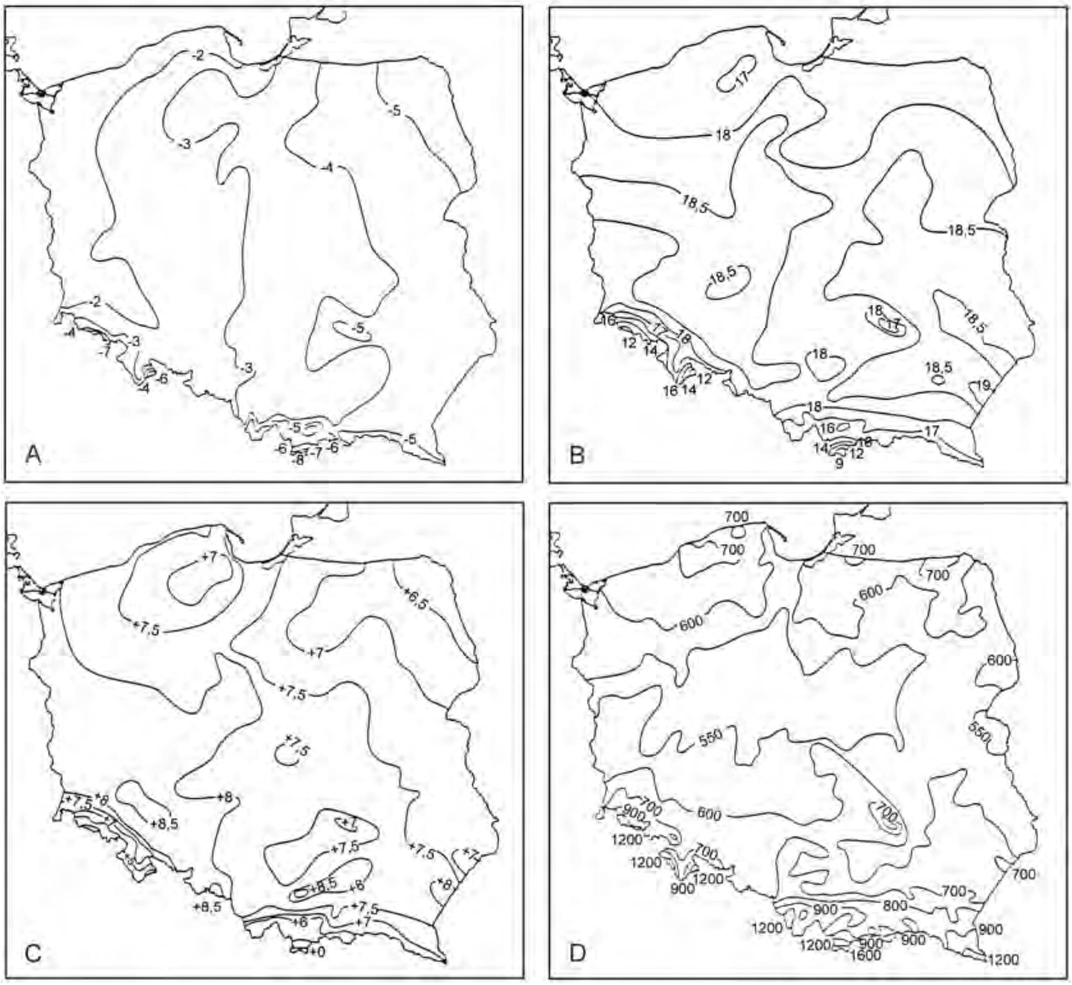


Fig. 6. A – mean January temperatures, B – mean July temperatures, C – mean annual temperatures, D – total mean annual precipitation (mm) (after Atlas Klimatyczny Polski IMiGW, for 1951–1960, changed by Z. Kuroś; in Zając A. & Zając M. 2001)

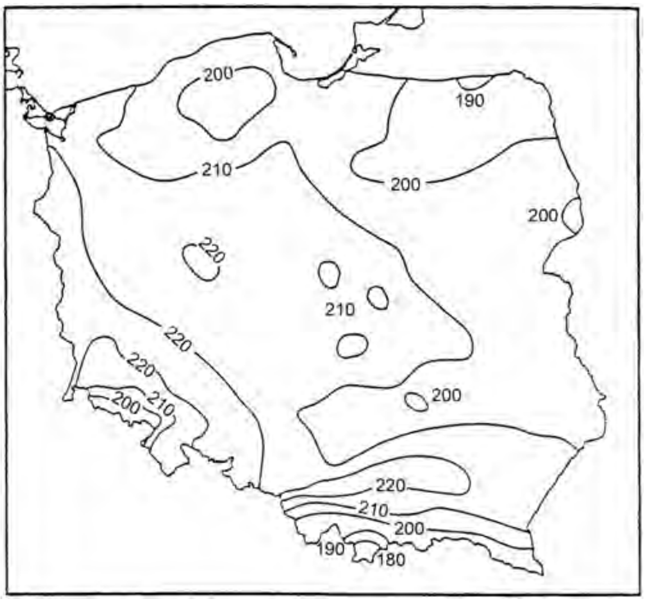


Fig. 7. Average length of vegetation period (after Atlas Klimatyczny Polski IMiGW, for 1951–1960, changed by Z. Kuroś; in Zając A. & Zając M. 2001)

the increase of climatic continentality from west to east. It is well demonstrated by the continentality index ‘K’, defined by Ellenberg’s method for *Quercus-Carpinus* forests on the basis of their floristic composition (Fig. 10). As regards the general distribution of forests in Poland, it has been observed that communities typical for the oceanic climate are disappearing eastward, whereas communities characteristic of continental climate are disappearing westward (Fig. 11).

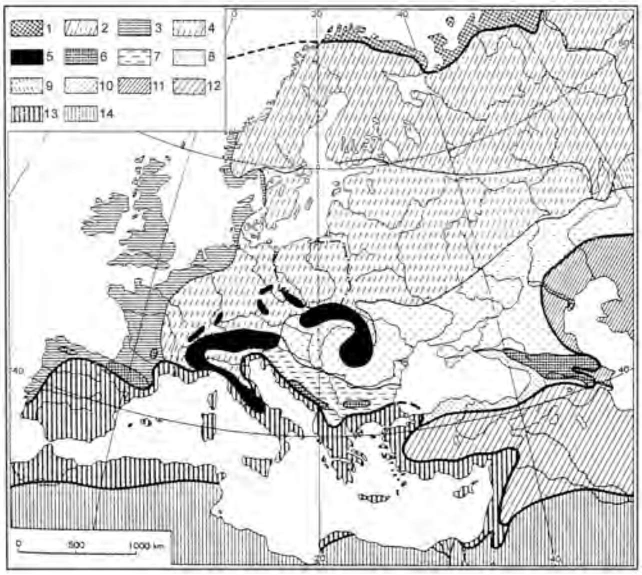


Fig. 8. Poland on a phytogeographical map of Europe. BOREAL SUBKINGDOM: 1 – the Arctic Region; 2–10 – Euro-Siberian Region: 2 – Northern Province, 3 – Atlantic Province, 4 – Central European Lowland-Upland Province, 5 – Central European Montane Province, 6 – other montane provinces, 7 – Illyrian Province, 8 – Pontic-Pannonian Province, 9 – South Siberian Province, 10 – Ponto-Hirkany Province. IRANO-TURANIAN SUBKINGDOM: 11–12 – Irano-Turanian Region: 11 – Turanian Province (Caspian-Aral), 12 – Iranian Province. 13 – MEDITERRANEAN SUBKINGDOM and Region. 14 – SAHARO-SINDIAN SUBKINGDOM and Region (Medwecka-Kornaś 1972, slightly modified)

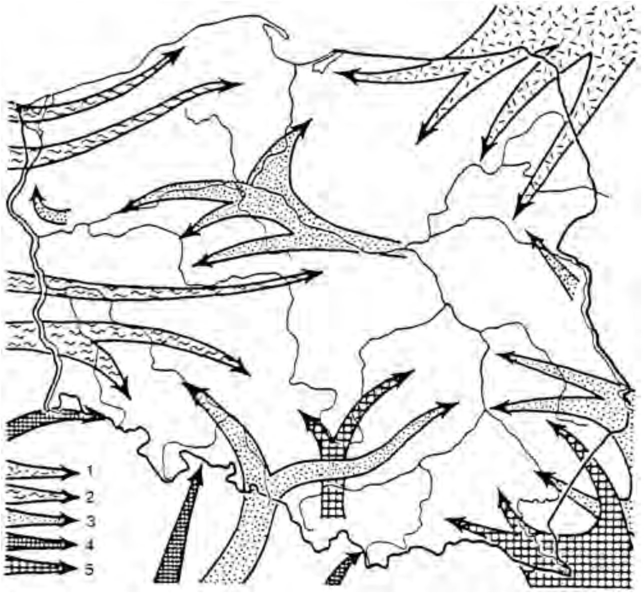


Fig. 9. Directions of migration of geographical components of vegetation in Poland: 1 – boreal, 2 – oceanic, 3 – continental (Pontic-Pannonian and others), 4 – Alpine, 5 – Carpathian (Matuszkiewicz W. 1991)

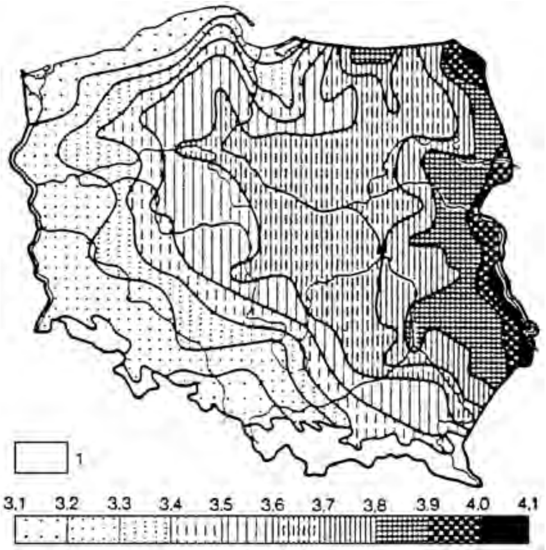


Fig. 10. Changes of the index of continentality ‘K’ in Poland after Degórski 1984 (quoted from Matuszkiewicz W. 1991)

In the present-day landscape of Poland, about 28% of the area is covered with forests, but the forest cover of mountain regions is higher (up to 40–50%) than that of lowlands. The remaining 72% of the area consist of fields, meadows, and urban areas (Fig. 12). Lowland areas are dominated by coniferous forests (85% of the forest area), which mostly are semi-natural or planted (Fig. 13). Climatic and habitat conditions of the development of forest communities currently appearing in Poland have been widely discussed by J.M. Matuszkiewicz (2002).

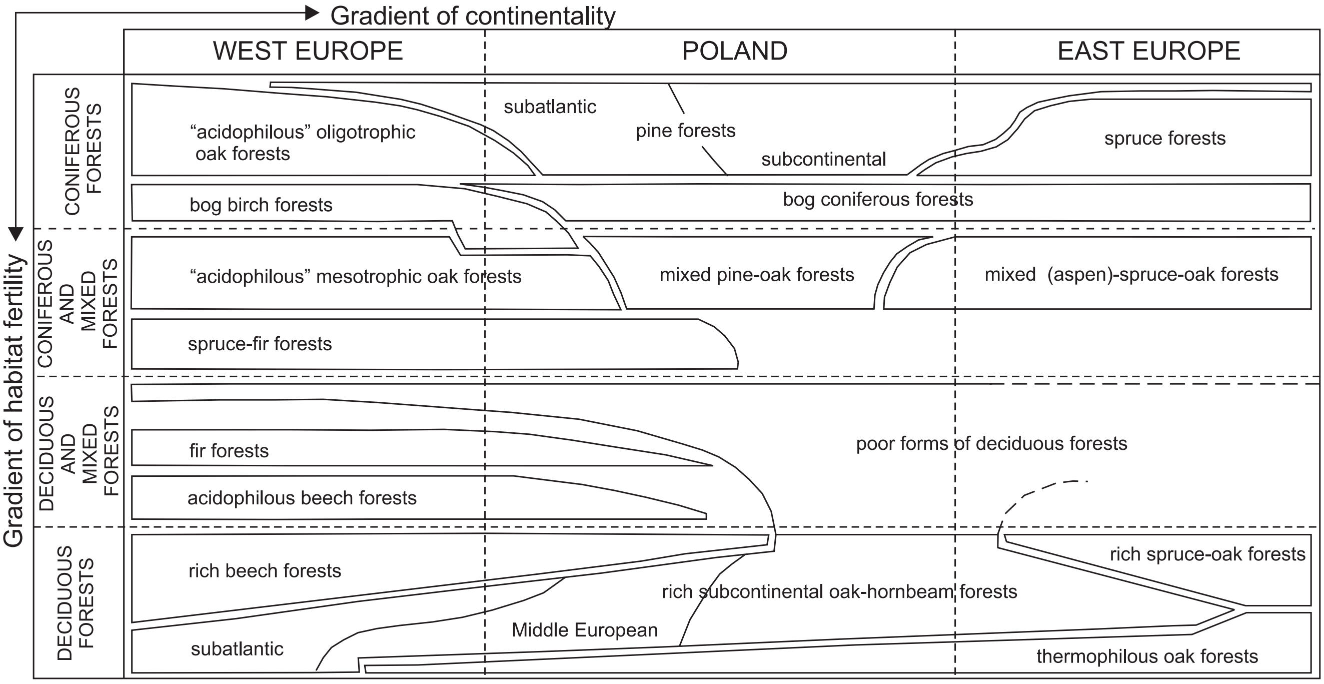


Fig. 11. Differentiation of lowland-upland forest communities in Poland in relation to fertility of habitats and degree of continentality (Matuszkiewicz W. 1991)

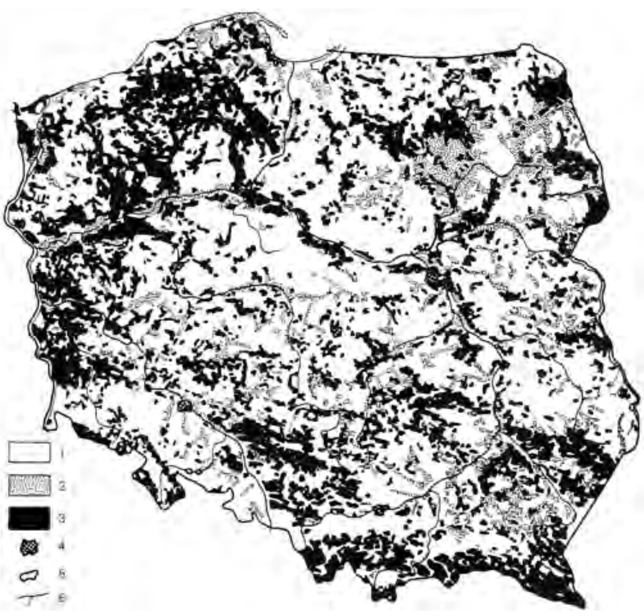


Fig. 12. Land use in Poland: 1 – arable land, 2 – grass land, 3 – forests, 4 – towns, 5 – reservoirs, 6 – rivers (Breymeyer 1991)

The present-day vegetation of Poland is mostly changed by human activity. If human interference were stopped, according to today's ecological potential of the physiographic environment (Fig. 14), mesophilous deciduous forests would cover more than half of the country's surface (58.1%). The most widespread potential natural community would be *Quercus-Carpinus* forests (41.6%). *Fagus* forests would cover 13.6%, thermophilous well-lighted *Quercus* woods 2.9%, mixed forests 19.1%, and coniferous forests (mainly *Pinus*) 11.4%. Azonal communities, such as different carrs, *Alnus* swamps and peats would find habitats suitable for them on 10.9% of the area. Only a tiny percentage would be taken by maritime and high mountain vegetation (Matuszkiewicz W. 1991).

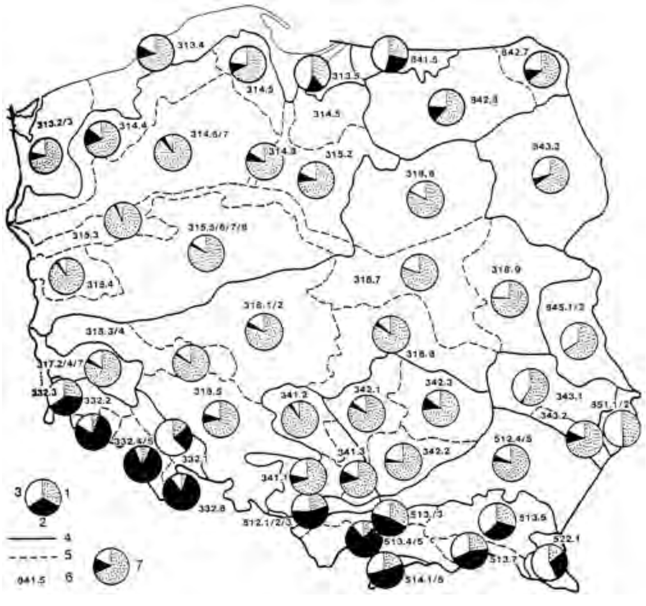


Fig. 13. Areas occupied by different tree stands in proportion to the total forest area in physiographical macroregions: 1 – pine, 2 – other coniferous trees, 3 – deciduous trees, 4 – subprovince limits, 5 – region limits, 6 – numbering of macroregions according to Kondracki 1988, 7 – average for the whole country (after Breymeyer 1991)

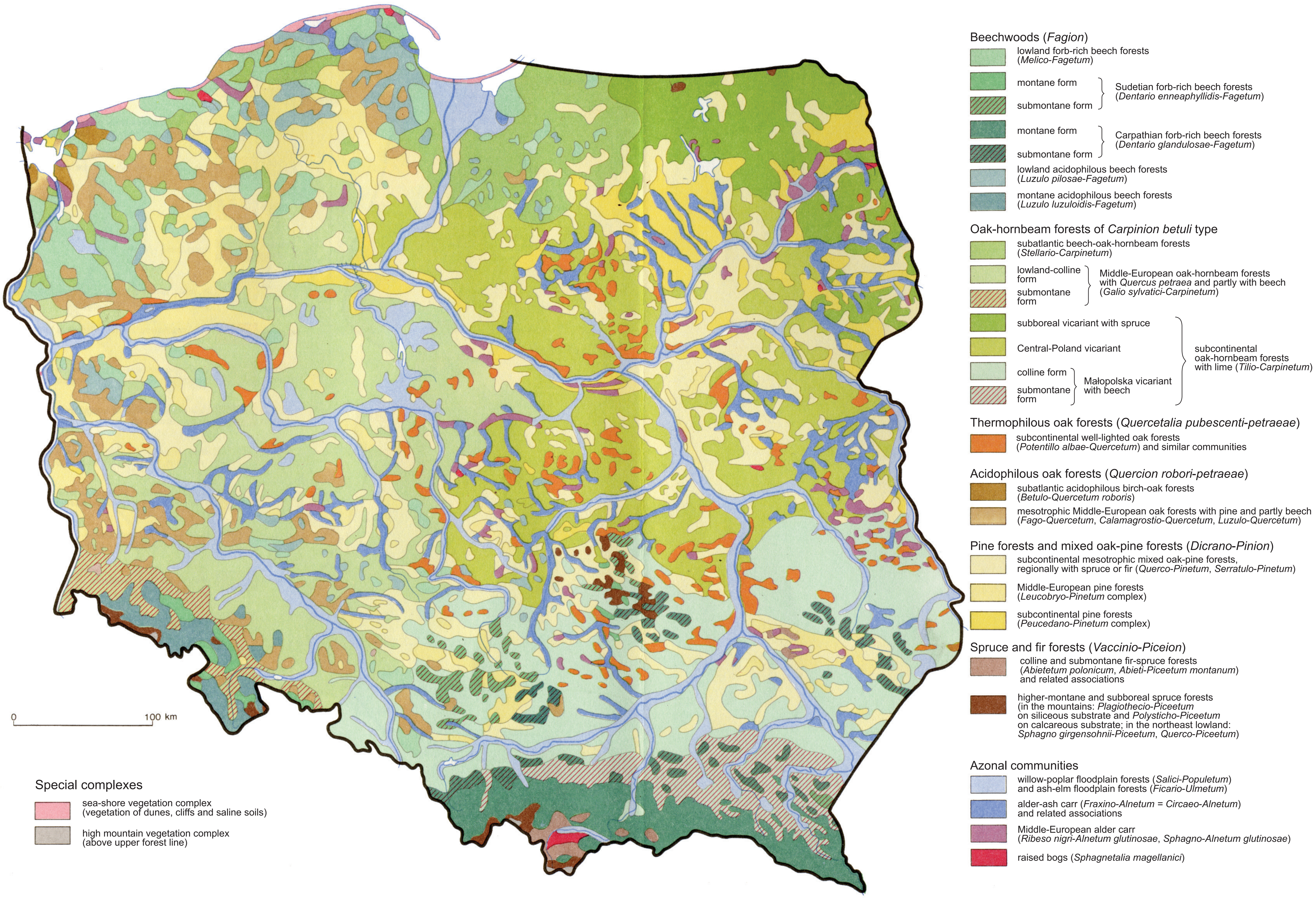


Fig. 14. Reconstruction of potential natural vegetation in Poland (Matuszkiewicz W. 1991)

ON HISTORY OF MAPPING THE PALYNOLOGICAL DATA

Magdalena Ralska-Jasiewiczowa

The first attempts to map palynological data were undertaken early in the development of pollen analysis and involved different methods. The earliest type of pollen maps included circle diagrams, where the size of circles represented pollen values for a taxon at a particular site (von Post 1924). Another type of circle pollen map shows the tree taxa dominating at a site, with different sections of the circle corresponding to the percentage contribution of particular taxa (Neushtadt 1957). The other kinds of pollen maps are described in the Textbook of Pollen analysis, 4th ed. (Faegri et al. 1989).

The method of isopollen maps was developed by Professor Władysław Szafer in early thirties of 20th century and described for the first time in 1935 (Szafer 1935). In this type of maps, produced for the particular time horizons (intervals), synchronous lines connect sites with the same pollen percentages of a taxon (Fig. 15). In his first paper Szafer attempted to show the migrations of *Picea* and *Fagus* during the Holocene on maps for five periods of vegetation development: '1. subarctic period, 2. the oncoming warmer period characterized by appearance of thermophilous trees, 3. the time of maximal expansion of those trees, 4. their decrease resulting from the rising moisture and coolness of the climate, and the expansion of the Sub-Atlantic species – *Fagus* and *Abies*, 5. decrease of these forest elements and the expansion of subcontinental species such as *Picea*'. Szafer gave the name 'isopollen maps' (isopolls) to this type of iso-frequency contour map.

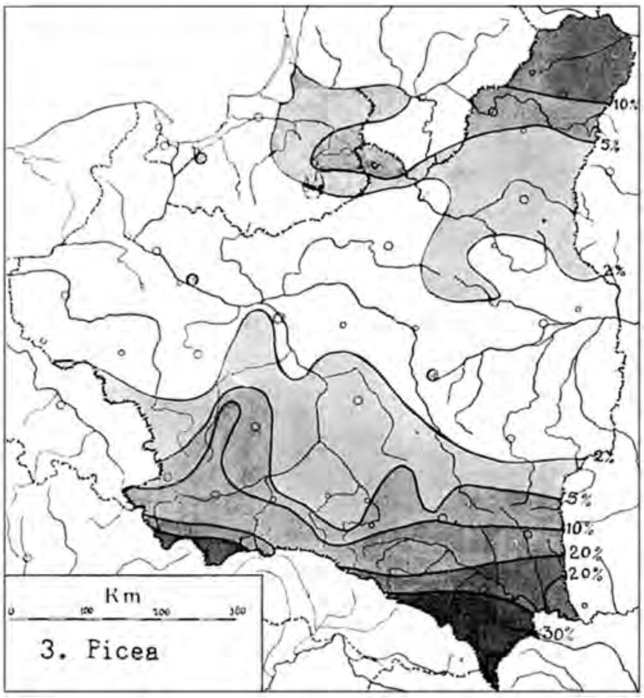


Fig. 15. Isopollen map of *Picea* migration in Poland for the period of Holocene 'culmination of warmth-requiring trees' from Szafer 1935 (Poland's boundaries from before the World War II)

This method of presenting tree migrations was then used by Sauramo (1940) for Finland and by Firbas (1949) and Bertsch (1953) for central Europe. However, in all those cases the correlation of sites was based on biostratigraphy, because maps were constructed before the introduction of the radiocarbon method of dating organic fossils and sediments at the beginning of the 1950s, before the chronostratigraphy based on this method was introduced into palynological research.

The setting up of many radiocarbon laboratories in Europe and North America provided researchers with chronologies and stimulated the introduction of another cartographic method into palynological studies of vegetation history – the isochrone map. In this method the isolines separate the areas with sites where the presence or absence of a pollen taxon occurred at the same (similar) time (or within the same time interval). Such maps were published both in Europe (e.g. Donner 1963, Moe 1970), and in North America (e.g. Davis M.B. 1976, Bernabo & Webb 1977).

Szafer's isopollen method was later used in Europe by Birks et al. (1975) in constructing maps for the British Isles and by Birks and Saarnisto (1975) for Finland. At the same time, this method was applied in the United States for comparing maps of modern pollen spectra with subfossil vegetation maps (Davis R.B. & Webb 1975). Other

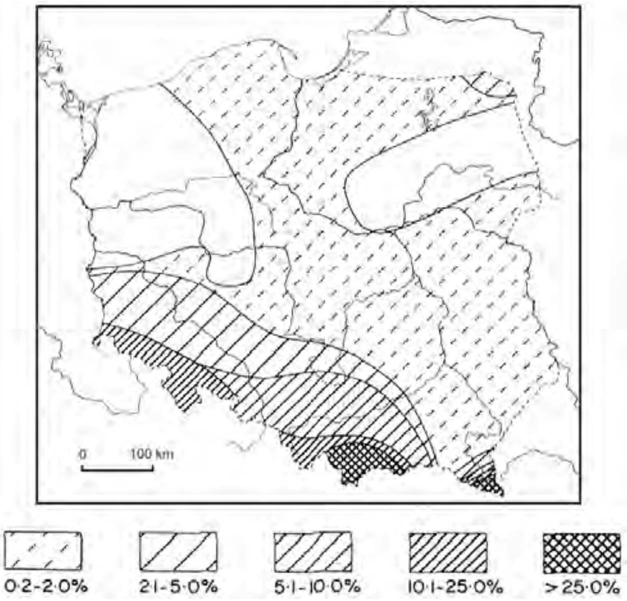


Fig. 16. Isopollen map of *Picea* migration in Poland for the time-horizon 6000 ^{14}C BP – a hand-drawn map from Ralska-Jasiewiczowa (1983)

studies followed, e.g. an attempt to compare very simplified isopollen maps with the model results for 18,000–500 BP for eastern North America (Webb et al. 1987).

The most important achievement of the early 1980s was 'An Atlas of isopollen maps for Europe' by B. Huntley and H.J.B. Birks (1983). The atlas contained present-day and fossil pollen maps for 0–13,000 years ago for trees and selected shrubs and herbs. It included principal component analyses to provide a basis for the reconstruction of the main vegetation types. Since then the atlas has been used by researchers from different scientific disciplines.

At the same time, another paper following Szafer's idea of showing the dynamics of tree migrations in Poland by isopollen maps was published by Ralska-Jasiewiczowa (1983), showing the history of the 9 most important forest tree taxa for 0–11,000 years ago in 1000 yr intervals (Fig. 16).

At the end of 1980s the European Palynological Database in Arles, affiliated with the University of Marseilles, was developed on the basis initially of data from the IGCP-158 B programme 'Palaeohydrological changes in the temperate zone in the last 15,000 years: lake and mire environments', completed in 1988. The data assembled made it possible to show changes in the distribution of basic types of vegetation in Europe for 0–13,000 years ago on maps prepared by means of numerical methods (Huntley 1988, 1990a, b, and others). The European Palynological Database is still developing, and it serves researchers from many countries. It is helpful not only in producing papers on the European scale but also in elaborating the detailed isopollen maps for limited regions and time intervals (e.g. a map atlas for Holland 13,000–9500 BP; Hoek 1997a, b). Recently isopollen maps have assisted more and more studies on refugial centres and routes of migration of forest trees after the last glaciation (e.g. FOSSILVA Project of the EU 5th Programme). The pollen maps transformed into palaeovegetation maps (e.g. Bradshaw & Holmqvist 1999, Lindbladh et al. 2000) may help to develop our research studies in completely new and fascinating directions.

METHODS USED FOR THE CONSTRUCTION OF ISOPOLLEN MAPS

Dorota Nalepka and Adam Walanus

In the years 2000–2003 the palynological database for the Late Glacial and Holocene was established, and it has served as a basis for constructing isopollen maps. Some of data were taken from the Polish Palynological Database (PPDB) available at the W. Szafer Institute of Botany, Polish Academy of Sciences in Kraków, but most of the data were provided by the authors of pollen diagrams. Some of them were unpublished or are still in the course of interpretation. The data for a few sites were derived from published diagrams by digitalisation.

Initially 257 pollen profiles were assembled, and after some were excluded because they appeared to be useless for map construction, 190 profiles remained (see Appendix, this volume). Each profile containing counts of all the sporomorphs is described by the following data: site name, geographic coordinates, and sample numbers, which correspond to their depth in the profile. These quantitative data as well as the radiocarbon dates are provided with textual description (site specification form).

Numerical data are stored in the POLPAL system (Walanus & Nalepka 1999, 2004, Nalepka & Walanus 2003a). Before supplying data to the PPDB all the authors had to unify nomenclature of the taxa occurring in the submitted tables. This was achieved with the help of special application POLPAL TabCom. The format of numerical data included in both the tables and the textual description was unified in the course of work on the chronology of the samples.

Descriptive data are registered as text files (*.txt). They contain lithological characteristics (depths of the layer boundaries and layer description) as well as conventional radiocarbon dates with laboratory error and the depth ranges from which the dated samples were taken. Apart from the radiocarbon dates the site specification forms are provided with the dates proposed by the palynologists studying the particular sites, designated here as estimated dates. The estimated dates are based both on palynological correlation with the nearest dated profiles and on the author's background knowledge of the general vegetation history and site lithology. Among the profiles used in the construction of the isopollen maps, 17 are dated exclusively by radiocarbon measurements (^{14}C BP) and 79 profiles are also provided with the estimated dates in addition to the ^{14}C dates (Fig. 17). 92 profiles have only estimated dates (Fig. 18). Altogether 171 profiles contain estimated dates (Fig. 19). One profile, from Lake Gościąż (G1/87), has varve dates for all the counted

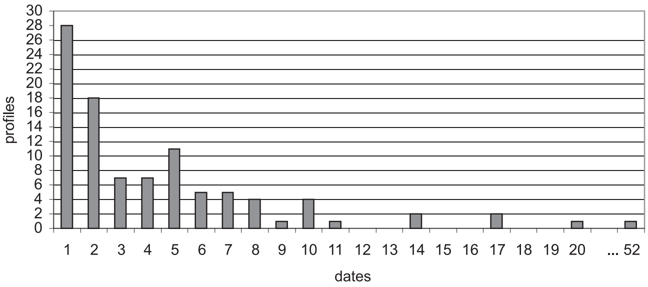


Fig. 17. Number of profiles with ^{14}C dates

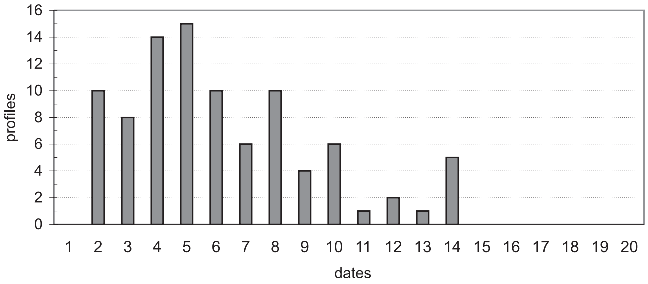


Fig. 18. Number of profiles with only estimated dates

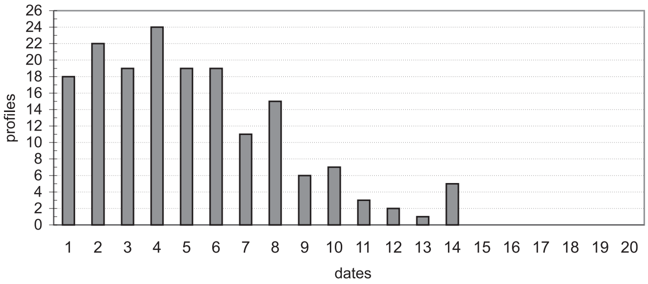


Fig. 19. Number of profiles with estimated dates in a profile

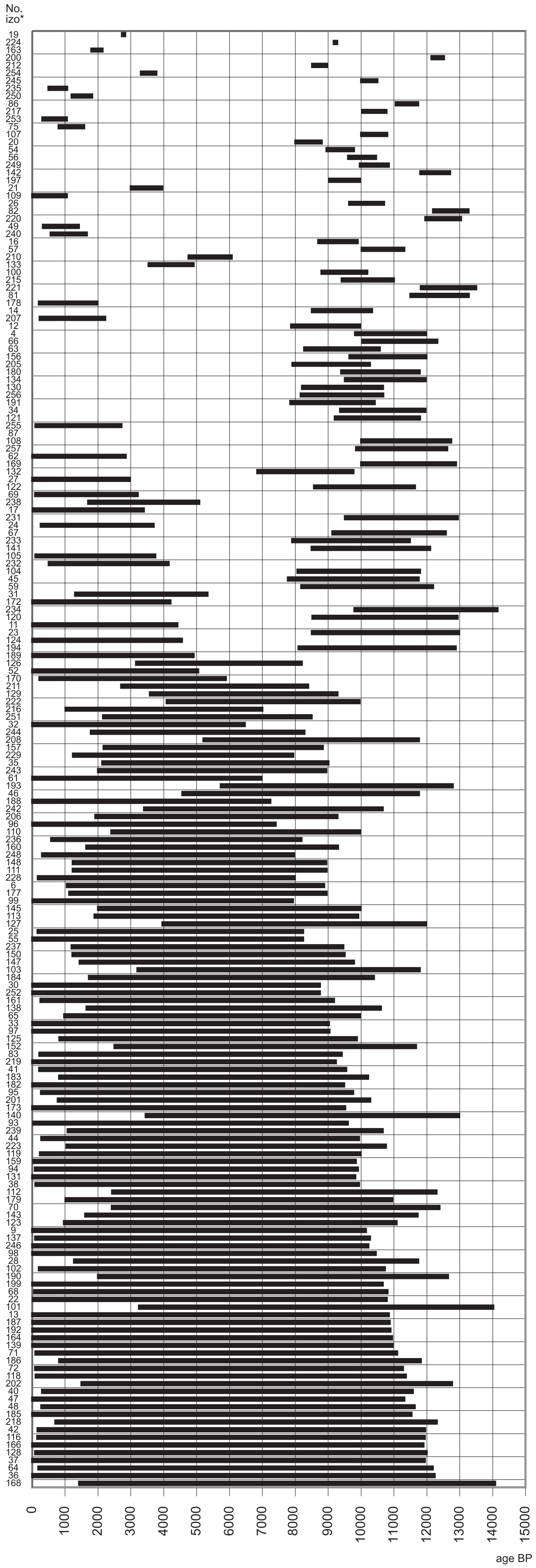


Fig. 20. Diagram illustrating time range of particular profiles; * identification number of profile in the isopollen data base and on the maps (see Appendix, this volume)

pollen samples, and these dates are correlated with several dozen ^{14}C AMS dates based on terrestrial macrofossils (Ralska-Jasiewiczowa et al. 1998). Altogether 454 radiocarbon (^{14}C BP) dates, 894 estimated and 310 varve dates (calendar dates of varve sediments converted to ^{14}C BP age) were included in the project. The scope of dates for all the profiles used for maps construction is 14,149 ^{14}C yr BP to –50 ^{14}C yr BP. The time range of each profile is presented in Figure 20.

Three mathematical models of the depth-age relation were applied in all the profiles to date each pollen sample. This dating was made by computer with the Age application created in the POLPAL system (Nalepka & Walanus 2003b). Dating was based on approximation with use of interpolation algorithms: a broken line connecting dates with straight lines, cubic spline function connecting dates, polynomial (of any degree, cubic recommended) as well as approximation of depth-age relation through a hand-drawn broken line, considering lithology and other data. Each result of mathematical dating was verified by the author of the pollen diagram. The results of mathematical chronology were added to the pollen tables (as archival material), but only one of them (after verification) was used to draw isopollen maps.

In the next stage a summary table was prepared from the POLPAL BDI application. It contains percentage values of pollen/spores taxa selected for the maps construction, for each time horizons for all the sites whose positions on the map are specified by their geographic coordinates. The table is registered as *.csv file in MS Excel format. The maps are drawn for 29 time horizons. The missing spectra for the needed time horizons in the palynological continuous profiles were interpolated.

The maps are drawn for the following 24 tree and shrub taxa: *Abies alba*, *Acer*, *Alnus*, *Betula*, *Carpinus betulus*, *Corylus avellana*, *Ephedra* (= *Ephedra* undiff. + *E. distachya*-type + *E. fragilis*-type), *Fagus sylvatica*, *Fraxinus excelsior*, *Hedera helix*, *Hippophaë rhamnoides*, *Juniperus communis* (= *Juniperus* undiff. + *J. communis*), *Larix decidua*, *Picea abies*, *Pinus cembra*, *Pinus* subgen. *Pinus*, *Populus*, *Quercus*, *Salix* (= *Salix* undiff. + *S. glauca*-type + *S. pentandra*-type), *Taxus baccata*, *Tilia* (= *Tilia* undiff. + *T. cordata*-type + *T. platyphyllos*), *Ulmus*, *Viscum*, and *Vitis vinifera* subsp. *sylvestris.* Herbaceous plants include 14 taxa: *Artemisia*, Cerealia excl. *Secale* (= Cerealia undiff. + *Triticum*-type + *Hordeum*-type + *Avena*-type), Chenopodiaceae (= Chenopodiaceae + Chenopodiaceae/Amaranthaceae), Cyperaceae, *Dryas octopetala*, *Filipendula*, Poaceae (Gramineae) (= Gramineae + *Phleum*-type + *Phragmites*-type), *Helianthemum* (= *Helianthemum* + *H. alpestre*-type + *H. canum*-type + *H.* cf. *alpestre* +

H. nummularium-type + *H. oelandicum*-type), *Plantago lanceolata*, *Pteridium aquilinum*, *Rumex* (= *Rumex* + *Rumex acetosa/acetosella* + *Rumex acetosa*-type + *Rumex acetosella*-type + *Rumex/Oxyria*), *Secale cereale*, *Selaginella selaginoides*, and *Typha latifolia*.

A pollen sum of trees, shrubs, and terrestrial herbs (Σ P) is the basis of calculation of percentage pollen values. Cyperaceae pollen is excluded because of its mostly local character in the majority of sites. The isopollen maps for the pollen sum of the herbaceous plant taxa (NAP) were drawn in two ways including and excluding Cyperaceae pollen. For a few taxa selected isopollen maps with Cyperaceae pollen in a total sum were also included. These maps have different legend background colour. In the case of one site, Kunice (No. 180) the isopollen maps of herbaceous plants were constructed without this site, because herb pollen was available only as NAP sum. Percentage values of *Typha latifolia* pollen were calculated on the basis of the sum (Σ P) + pollen of all aquatic and telmatic plants. Percentages of *Pteridium aquilinum* and *Selaginella selaginoides* spores were calculated from the basic sum (Σ P) + the sum of all Pteridophytes (Berglund & Ralska-Jasiewiczowa 1986).

The following time horizons in conventional ^{14}C years were accepted for drawing the isopollen maps: from 14,000 BP to 500 BP every 500 years plus the top 100 BP. To all the horizons were assigned equal ranges of ±100 years (for example, the horizon of 5000 has the range of 4900–5100, thus 4899 and 5101 are beyond this horizon). The possibility to express boundaries of time horizons in the calendar scale is presented in the chapter by Walanus & Nalepka (this volume).

Next the application of the POLPAL Map was applied to construct the isopollen maps from the data in the summary table discussed above. The maps are registered in bitmap (*.bmp) format. Their dimension is 2200×2200 pixels. In the Map application the contour map of Poland was used with marked parallels of latitude and longitude (every 2°) as well as the more important rivers and state boundaries. On this map the percentage pollen values were calculated on the square grid of 2 km intervals.

Drawing of the maps was preceded by testing of the mathematical algorithms used in their construction, i.e. a weighting function was chosen. Such a function describes the degree of dependence of the site on a distance. Percentage values in a particular point are influenced by pollen percentage values from all the sites, but the nearby sites have the greatest influence, decreasing with distance. The weighting function determines how the influence of the site decreases with distance. From four proposed alternatives (inverse distance with dead field, square inverse distance with dead field, Gaussian function, and exponential function) the square function has been selected in which weight (influence) decreases with the square of the distance, i.e. a site situated at a two times greater distance will have four time smaller weight (influence).

Two parameters were used for drawing the maps: maximal radius and smoothing radius. A maximal radius describes the maximal distance to the nearest site at which the drawing of the isopollen line seems to be sensible. It is accepted that for the sites situated farther from the nearest site than a maximal radius, the percentage pollen values of a particular taxon will not be presented (white spot will be left). After many attempts the maximal radius of 200 km is established for drawing the maps. Because of this no white spots appear on most of the maps. However, it should be borne in mind that extrapolation of the data has been applied for a distance up to 200 km from the nearest site.

A smoothing radius describes a rate of decreasing influence of neighbouring sites with a distance on percentage values at a specified site. A smoothing radius of 30 km is used for the maps.

For trees and shrubs as well as for herbaceous plants various extensions of percentage ranges and various palettes of colours have been applied. For tree and shrub pollen the following percentage ranges have been accepted: 0.01, 0.1, 0.5, 1, 2, 3, 5, 7, 10, 15, 20, 25, 30, 40, 60%, and for sporomorphs of herbs: 0.01, 0.2, 0.5, 0.7, 1, 2, 3, 5, 7, 10, 20, 30, 40, and 60%. The maps of trees and shrubs have been drawn in colours from yellow to brown and of herbs in graded green colours. The lowest percentage values (0–0.01%) have been marked in light-grey colour in both scales, and the values >60% in black.

Most maps are presented in a form of isoline maps. Each map is provided with a fragment of legend containing a palette of those colours that are used in its construction.

Maps for taxa displaying low representation and occurring only sporadically have been presented in a form of dot maps provided with percentage values of a given taxon. Points without percentage values mark those profiles in which a specified taxon was absent in spite of the fact that the sediments of a particular age were present.

CALENDAR AGES OF THE TIME HORIZONS PRESENTED ON THE ISOPOLLEN MAPS

Adam Walanus and Dorota Nalepka

The isopollen maps have been constructed for 500-year time intervals chosen as even dates from 14,000 yr BP to the present-day (Nalepka & Walanus, this volume). These horizons are expressed in the scale of conventional radiocarbon age. For the horizons an equal range of ±100 years has been accepted, so the assigned time horizons include 200 years (0±100 yr BP, 500±100 yr BP, 1000±100 yr BP, etc.). The range of ±100 does not mean a measurement error. For example, the range of the time horizon 3000±100 years means that those spectra have been used to draw the map whose calculated dates were included in the time interval from 2900 to 3100 yr BP. In other words, all the pollen spectra dated within the limits of ±100 are included in the range of this time horizon.

Dating of spectra from the particular profiles may contain some errors. These dates result from the interpolation (less frequently from extrapolation) of radiocarbon and other dates, thus a few kinds of error are superimposed on each other (Nalepka & Walanus 2003a, b). The errors (uncertainties) in dating of spectra are different for particular sites, being the greatest for profiles without radiocarbon dates. The character of these errors does not allow them to be described by normal distribution, unlike the case for conventional radiocarbon dates (Walanus & Goslar 2004). Moreover, it is almost impossible to give a quantitative estimation of accuracy of dating. This results from applying the broad range of information from natural sciences such as biostratigraphy and lithology of sediments (Hoek 1997a, b) in assigning ages of the palynological zones. To include this type of qualitative knowledge in an estimation of the error in a final result, it would be necessary to present subjective probabilities of possible deviations from a situation accepted for a particular dating, and this would not provide much greater precision.

The time scale is the radiocarbon conventional age. Most of the dates are given in the conventional scale (Nalepka & Walanus, this volume). To calibrate ages of horizon boundaries used to construct isopollen maps, the commonly available programme OxCal v3.8 (Copyright Bronk Ramsey 2001) established in the Radiocarbon Laboratory of Oxford University has been applied. Figure 21 presents a calibration curve.

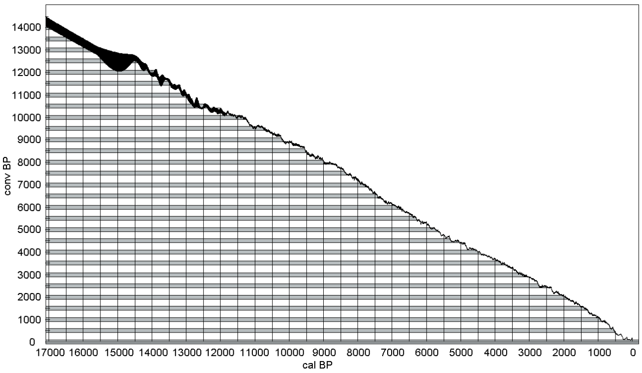


Fig. 21. Time horizons referring to the calibration curve. Calibration of particular time horizons is presented in Figs 22 and 23. The calibration curve is provided by the OxCal v3.8 programme

A basic result of calibration of time horizon boundaries is a set of diagrams (Figs 22 and 23) comprising appropriate fragments of a calibration curve, in which the limits of horizons are drawn as horizontal lines.

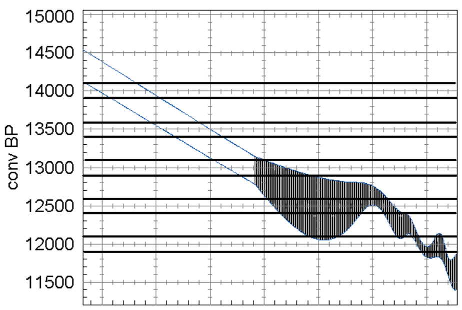
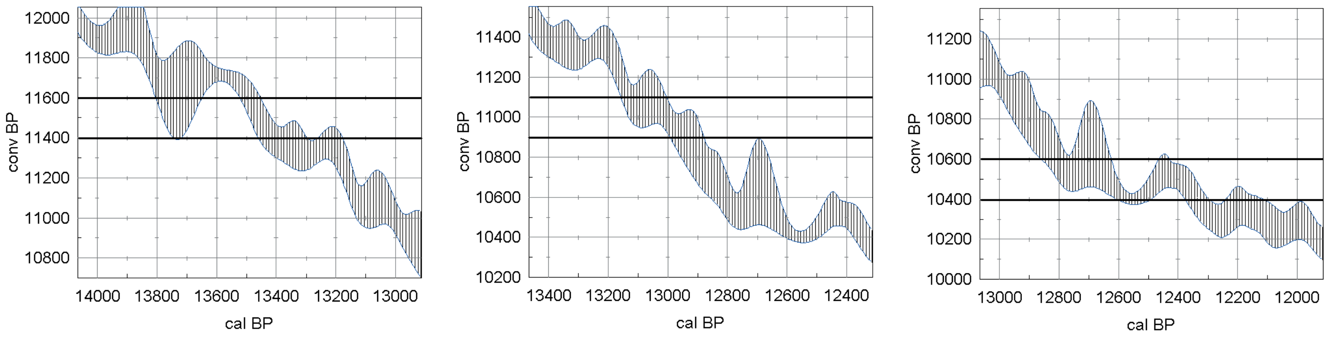


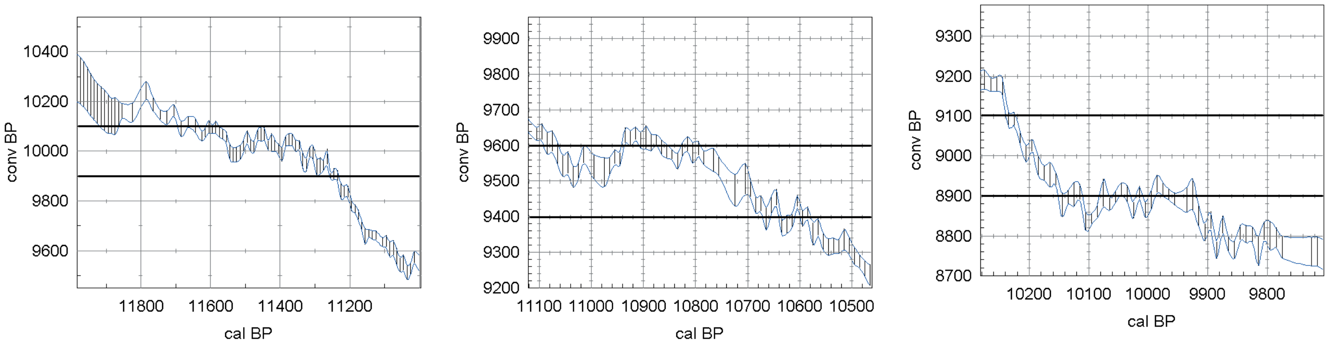
Fig. 22. Calibration of time horizons from14,000 to 12,000 yr BP used for drawing the isopollen maps



Time horizon of 11,500 yr BP

Time horizon of 11,000 yr BP

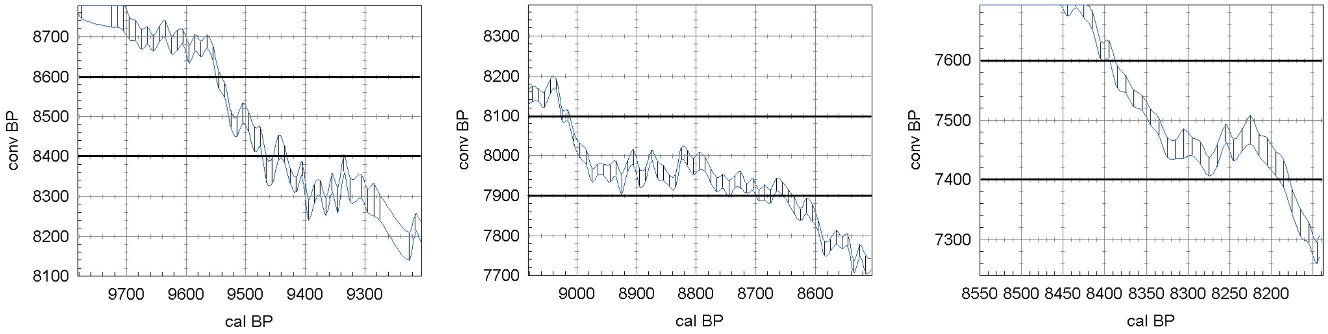
Time horizon of 10,500 yr BP



Time horizon of 10,000 yr BP

Time horizon of 9500 yr BP

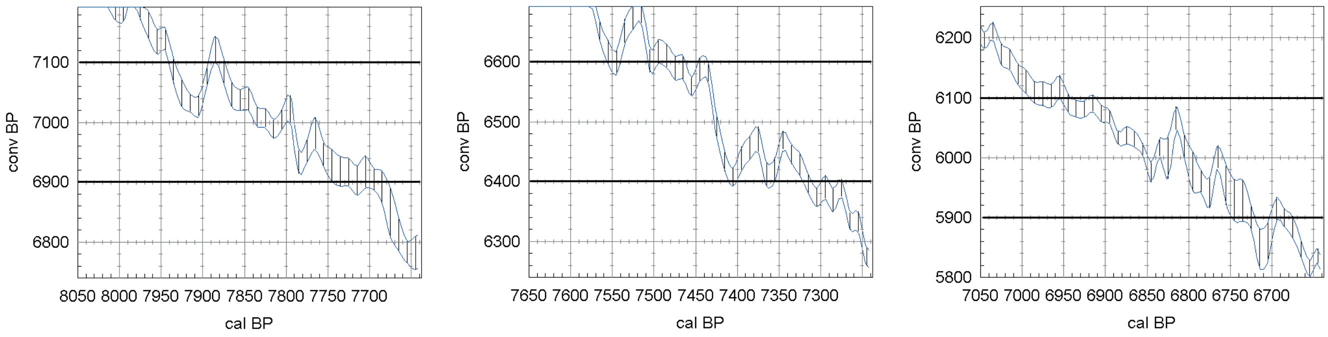
Time horizon of 9000 yr BP



Time horizon of 8500 yr BP

Time horizon of 8000 yr BP

Time horizon of 7500 yr BP

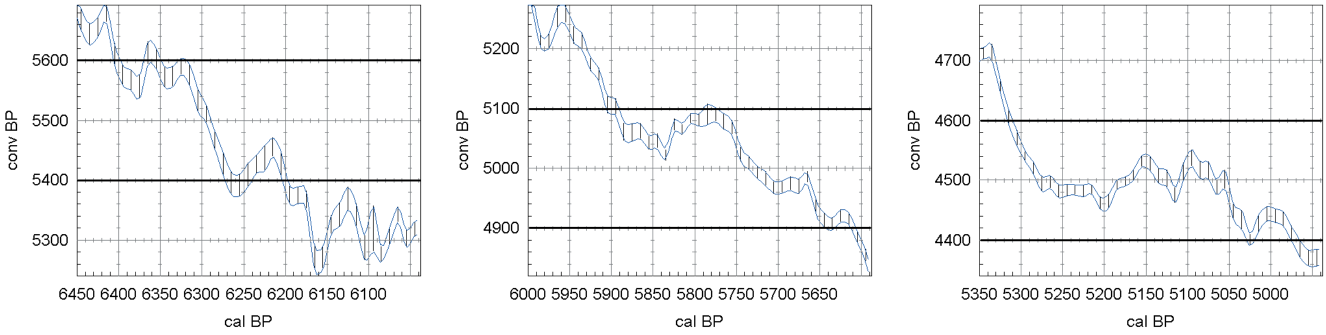


Time horizon of 7000 yr BP

Time horizon of 6500 yr BP

Time horizon of 6000 yr BP

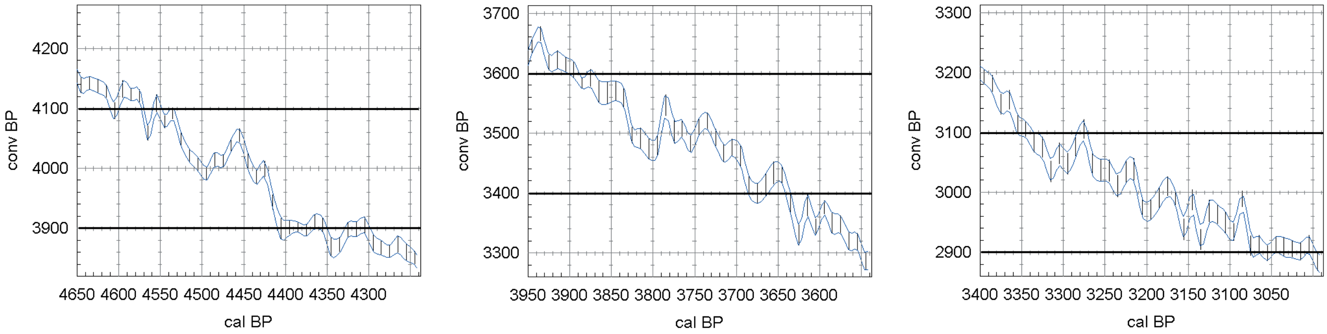
Fig. 23. Calibration of time horizons from 11,500 to 100 yr BP used for drawing the isopollen maps



Time horizon of 5500 yr BP

Time horizon of 5000 yr BP

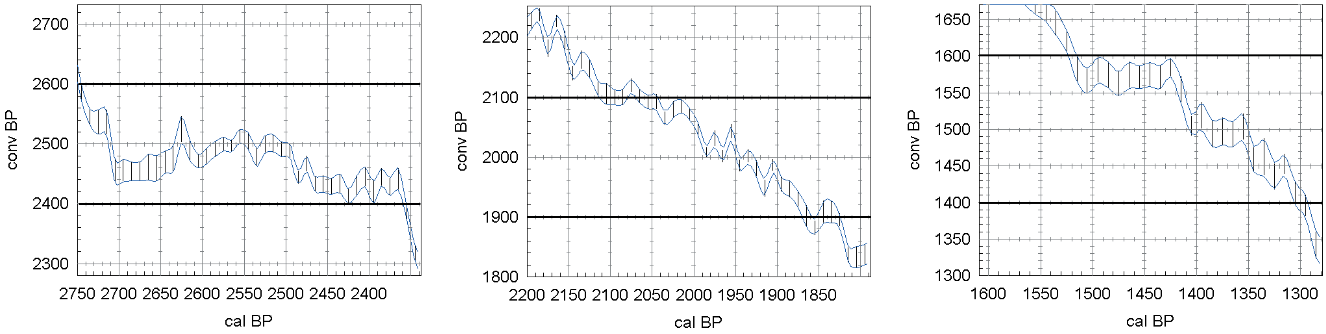
Time horizon of 4500 yr BP



Time horizon of 4000 yr BP

Time horizon of 3500 yr BP

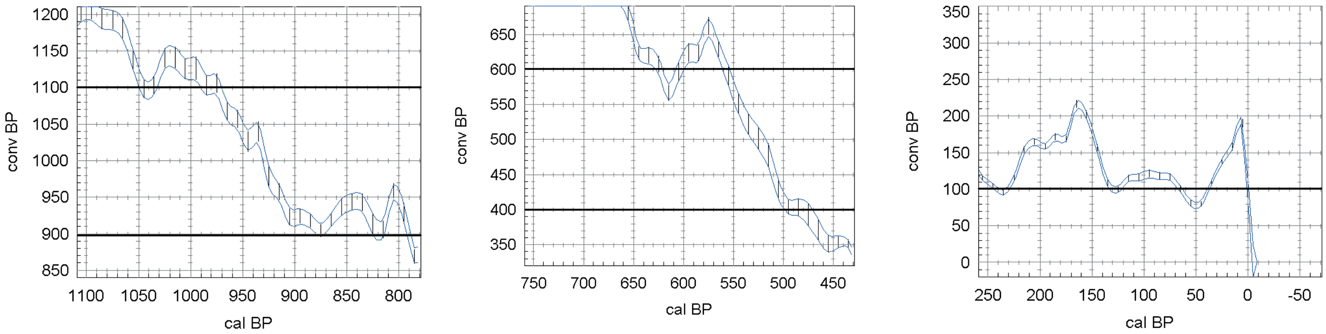
Time horizon of 3000 yr BP



Time horizon of 2500 yr BP

Time horizon of 2000 yr BP

Time horizon of 1500 yr BP



Time horizon of 1000 yr BP

Time horizon of 500 yr BP

Time horizon of 100 yr BP

Fig. 23. Cont.

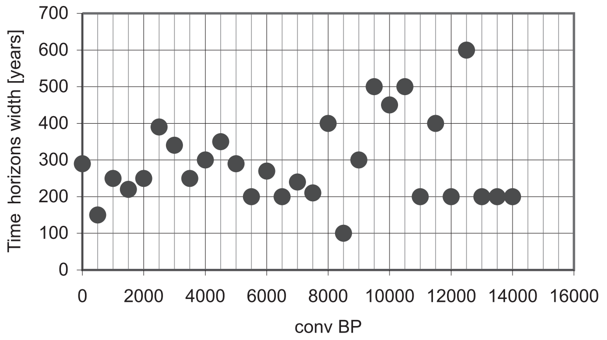


Fig. 24. The width of time horizons after calibration (in a scale of conventional radiocarbon years the width of all the horizons equals 200 years)

Calibrated (=calendar) dates are given along the horizontal axis. Diagrams allow some leeway because of the shape and limited accuracy of a calibration curve. The widths of the time horizons after calibration are presented in Figure 24.

Proposals of the authors of this chapter concerning expression of the ages of boundaries of time horizons in calendar scale are presented in Table 1. However, it should be emphasized that due to the lack of the unequivocal nature and certainty of the radiocarbon calibration curve it is not possible to precisely determine the calendar age of the boundaries of time horizons.

Interpretations given in Table 1 are based on two assumptions:

1. calendar age of a boundary should not differ much from the most probable age (or from the median),

2. the width of a horizon expressed in calendar years should not differ much from the width resulting from the mean inclination of the calibration curve close to the horizon, which is usually 200 years.

Table 1. Calendar age of limits of time horizons (interpretation according to Figs 22 and 23)

Conventional age yr BP			Calibrated age yr BP	
centre of horizon	upper limit	lower limit	upper limit	lower limit
0	–100	100	–50	240
500	400	600	480	630
1000	900	1100	790	1040
1500	1400	1600	1300	1520
2000	1900	2100	1850	2100
2500	2400	2600	2360	2750
3000	2900	3100	3000	3340
3500	3400	3600	3640	3890
4000	3900	4100	4300	4600
4500	4400	4600	4970	5320
5000	4900	5100	5610	5900
5500	5400	5600	6200	6400
6000	5900	6100	6680	6950
6500	6400	6600	7300	7500
7000	6900	7100	7700	7940
7500	7400	7600	8180	8390
8000	7900	8100	8650	9050
8500	8400	8600	9450	9550
9000	8900	9100	9950	10,250
9500	9400	9600	10,600	11,100
10,000	9900	10,100	11,250	11,700
10,500	10,400	10,600	12,300	12,800
11,000	10,900	11,100	12,900	13,100
11,500	11,400	11,600	13,300	13,700
12,000	11,900	12,100	13,900	14,100
12,500	12,400	12,600	14,500	15,100
13,000	12,900	13,100	15,400	15,600
13,500	13,400	13,600	16,100	16,300
14,000	13,900	14,100	16,700	16,900

ISOPOLLEN HISTORY
OF
TREES AND SHRUBS

Abies alba Mill. – **Fir**

ANDRZEJ OBIDOWICZ, KAZIMIERZ SZCZEPANEK, EWA MADEYSKA, AND DOROTA NALEPKA

The genus *Abies* includes evergreen, long-lived trees, growing for up to 700–800 years, reaching a maximum height of up to 70–80 m (Boratyński 1983). In Europe this genus is represented by six species: *Abies alba* Mill., *A. borisii-regis* Mattf., *A. cephalonica* Loud., *A. nebrodensis* (Lojac.) Mattei, *A. pinsapo* Boiss., and *A. sibirica* Ledeb. (Lang 1994).

PRESENT DISTRIBUTION IN EUROPE

Fir (*Abies alba*) is a central European, montane species descending to the lowlands in the northern parts of its range. The range of *Abies alba* is divided into smaller and larger fragments, which follow the distribution of the mountain ranges and massifs. Its European area of occurrence includes the central and southern parts of the continent (Fig. 25). The western limit of the distribution of fir includes the Black Forest, the Vosges, the Swiss Jura, the Alps and in the south the Apennines, the Dinarid Alps and the Balkans.

PRESENT DISTRIBUTION IN POLAND

The north-eastern limit of the fir range runs across Poland (Fig. 26). Apart from small, isolated patches such as in the eastern part of the Białowieża Forest, its occur-

Fig. 25. *Abies alba* – map of present-day distribution in Europe: ● – native isolated occurrence, ◒ – status of site unknown or uncertain (after Jalas & Suominen 1973 and Boratyński 1983)

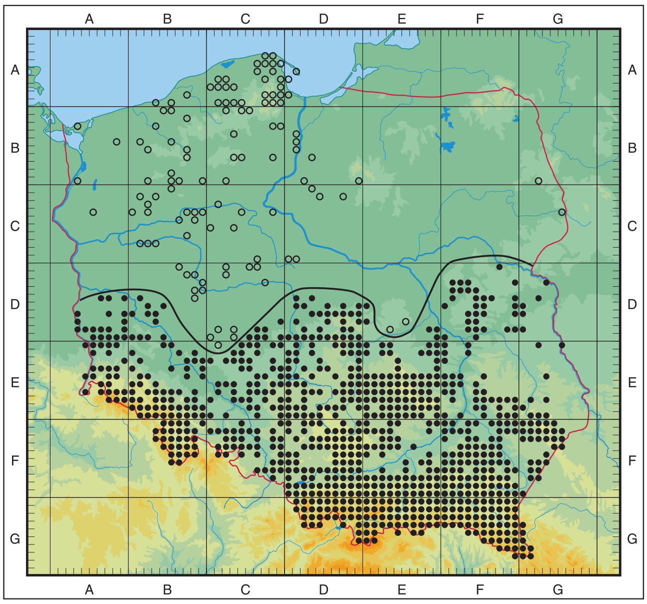


Fig. 26. Present-day distribution of *Abies alba* Mill. in Poland: ○ – synanthropic sites (after Zając A. & Zając M. 2001)

rence is associated with the mountainous areas and their forelands, mainly with the Carpathians, the Sudetes and the Świętokrzyskie Mountains. The highest occurrence of *Abies alba* is in the Tatra Mountains (at 1450 m a.s.l.). In other ranges of the Polish mountains its highest sites reach from 1050 m a.s.l. (the Western Beskidy Mountains), through 1260 m (the Western Bieszczady Mountains) up to 1322 m (Babia Góra Mountain) (Boratyński 1983). Its eastern limit follows the arc of the Eastern Carpathians (Komornicki 1974).

ECOLOGY

The ecological requirements of fir can be described as intermediate between the requirements of beech and spruce. A mean January temperature of –4.5°C and a mean July temperatures of 15°C are the limiting factors for the optimum development of fir (Jaworski & Zarzycki 1983). In all the areas with considerable air humidity, fir tolerates very low temperatures well. The northern limit of its range is associated with annual isohyet of 600 mm, whereas optimum conditions for fir in the Carpathians are associated with an annual precipitation of 700 mm or more. Drought during the growing season may often result in the death of trees. Fir is a shade-tolerant species, however, it shows better tolerance of shade when young, and on fertile soils. It occurs primarily on all fertile, deep and moist soils. It grows well on cryptopodsolic and gley soils as well as on humic pararendzinas. Less favourable habitats occur on sandy loam soils or on strongly skeletal soils. Fir grows and regenerates well on highly acid soils and on the neutral soils if they are sufficiently humid. Deficiency of nutrients or their excess may cause death of firs (Jaworski & Zarzycki 1983). The adverse influence of industrial air pollution on fir was already observed in the 1930s.

The age when fir first produces cones with seeds varies from 30 to 100 years depending on the situation of the tree, either on the edge of the forest or in the middle of it. Fir regenerates only from seeds (Suszka 1983).

Forest communities in which fir is present vary according to the region. This tree occurs in associations belonging to two classes *Querco-Fagetea* and *Vaccinio-Piceetea*. In general *Abies alba* finds better conditions for regeneration in mixed woods rather than in monospecific ones. It develops best in the Carpathian *Dentario glandulosae-Fagetum* association, at altitudes of 800 to 1200 m a.s.l., although there are considerable differences within sub-associations. In the Sudetes the optimum conditions occur in the *Dentario enneaphyllidis-Fagetum* association.

POLLEN PRODUCTION AND DISPERSAL

Firs are monoecious trees, having unisexual wind-pollinated flowers. *Abies alba* is an inefficient pollen producer. Female inflorescences, borne in large cones are produced almost exclusively at the top of the tree. Male flowers, usually very numerous, grow singly in the axils of needles, on the lower side of the previous year's shoots. *Abies alba* flowers from April to May. Due to the considerable density of its pollen grains and high speed of pollen fall in air the effective distance of transport of individual grains is small (Suszka 1983). However, when strong stormy winds occur during flowering periods, fir pollen can be transported for long distances. According to Kulczyński (1930) its long-distance transport can exceed 200 km.

EXPANSION IN EUROPE DURING THE LATE GLACIAL AND HOLOCENE

Some of the refugial areas of *Abies alba*, that migrated to Poland, were probably located in the mountains of north-western Greece (Willis 1992). After the beginning of the Holocene this species migrated northwards across the Dinarid Alps, the Eastern Alps, the Bavarian Forest and further to the Carpathians (Lang 1994). Thus, in its migration fir was bound to the mountains. Genetic research indicates that fir came to the Carpathians from the Balkan refugia and from northern Italy. The Sudetes and the Western Carpathians were areas of introgression where firs coming from these two different centres met and mingled (Konnert & Bergmann 1995).

MIGRATION PATTERN IN POLAND (Fig. 27)

9000 – 5500 BP

On the 9000 BP to 5500 BP maps, quite numerous sites, scattered throughout the country, show very low values of fir pollen. Only on the 6500 BP map, at the site of Kunice in the vicinity of Legnica (south-western

Poland), *Abies* pollen values reach 2.5%, which results from a very low pollen sum.

5000 BP

At about 5000 BP, in pollen diagrams from the southern side of the Sudetes and of the Western Carpathians, fir is represented by high values (ca. 20%). Late- and even early-Atlantic sites with macrofossils of fir are known also from this area (Opravil 1976). Probably already by the end of the Atlantic period this tree may have contributed to the forests of the southern ranges of those mountains.

The 5000 BP map for Poland shows that *Abies* was already present in the Western Carpathians. Based on investigations from the area of the Beskid Żywiecki range (Obidowicz 2003), it can be stated that since 4800 BP a rapid expansion of this tree began in this part of the Western Carpathians, and since 4500 BP it started to spread in lower parts of the Tatra Mountains (Obidowicz 1996), whereas in the northern forelands of these mountains fir began to appear only sporadically.

4500 – 4000 BP

In the Sudetes and in the lower central area of the Carpathians between the Western and Eastern Carpathians (Beskid Niski range and Jasło-Sanok Depression) the amount of *Abies* pollen slightly increased, which might suggest the beginning of its expansion there.

The 4000 BP map shows an increase in its percentage values (3–5%) in the area of the Moravian Gate.

3500 BP

Since 3500 BP a significant centre of fir distribution has occurred in the western part of the Western Carpathians. In pollen diagrams from this area pollen percentage values are close to their maximum (Puścizna Rękowiańska – more than 20%, Obidowicz 1996). The second centre in western Poland, indicated on this map around the site of Kunice, is due to the statistical effects (no nearby sites to exert an influence on it).

3000 BP

The centre in the Sudetes becomes more pronounced, and a further expansion of the range of fir, both eastwards and northwards, takes place as far as the Małopolska Upland.

2500 BP

The 2500 BP map illustrates the maximum range of *Abies alba* in Poland, exceeding the present northern limit of its contiguous distribution. A new centre of expansion appears in the Beskid Niski range.

2000 BP

This map shows a reduction of the range of fir from its maximum, with areas of abundance of fir distinctly restricted to the Sudetes, the Carpathians, and the Małopolska Upland.

1500 – 100 BP

The 1500 BP map records a continuing slow retreat of the range of fir, particularly in central Poland and in the Małopolska. In the Carpathians and the Sudetes there are no significant changes.

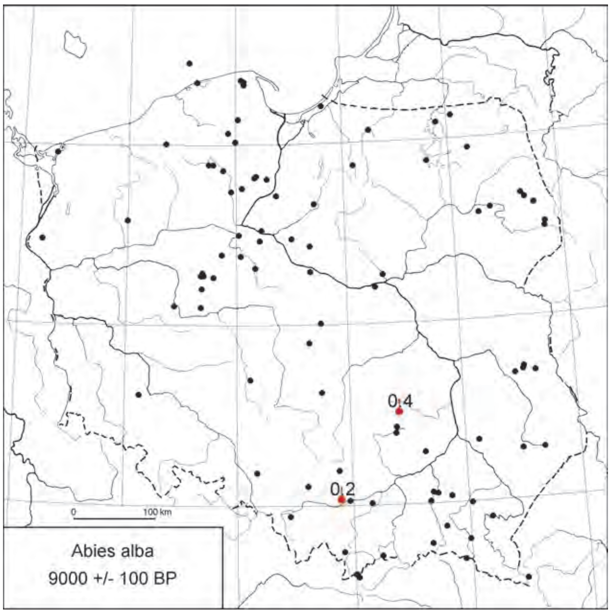
On the 1000 and 500 BP maps the highest pollen values of fir are recorded from the central part of the Sudetes and from the Polish part of the Eastern Carpathians.

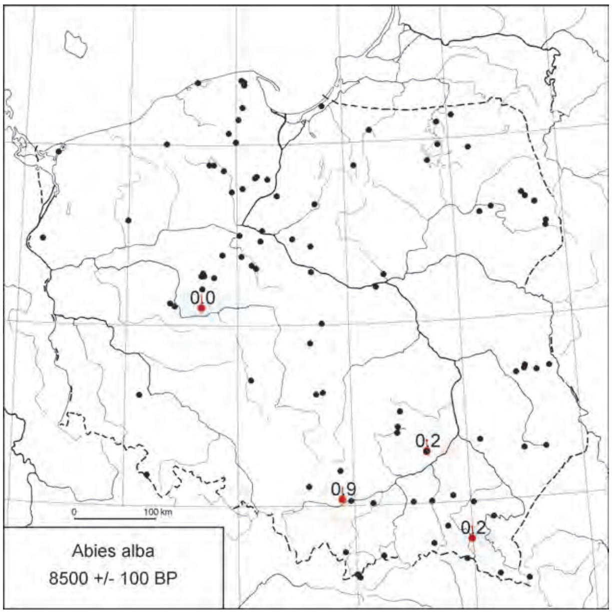
The picture on 100 BP map of this tree shows its highest abundance in the central part of the Sudetes, in the western part of the Western Carpathians and in their foreland. However, this does not reflect the distribution of *Abies alba* in Poland at the present time.

CONCLUSIONS

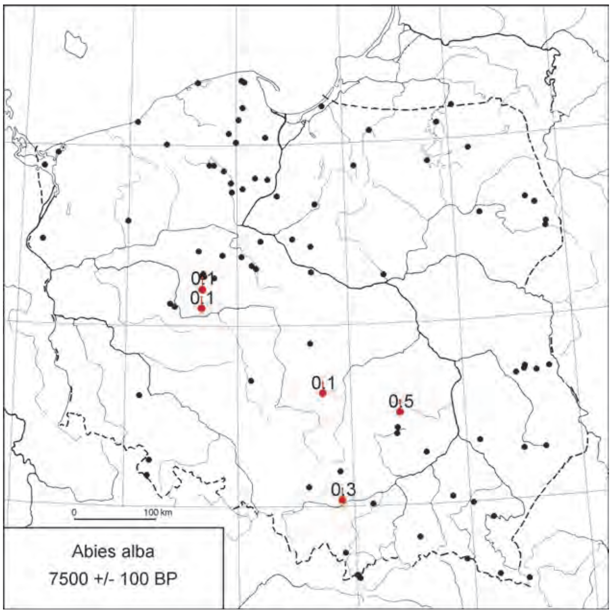
Fir migrated to Poland from its refugia in the Balkan and the Apennine Peninsulas. However, it is not quite clear when this took place. Since about 5000 BP fir has already been present in the Carpathian forests and maybe also in the forests of the Sudetes. Between 2500 and 2000 BP this tree occupied its widest area in Poland during the Holocene. The subsequent reduction of the areas of fir distribution did not take place in the mountains but affected mainly the adjacent regions. The presence of charcoal in sites from the Roman Period (Lityńska-Zając 1997) indicates that this process could have had mainly anthropogenic reasons.

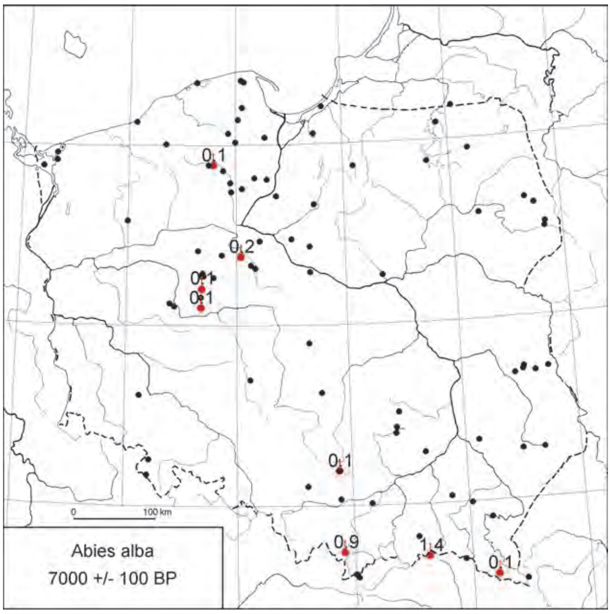
Fig. 27. *Abies alba*: dot and isopollen maps for 9000–100 ^{14}C yr BP

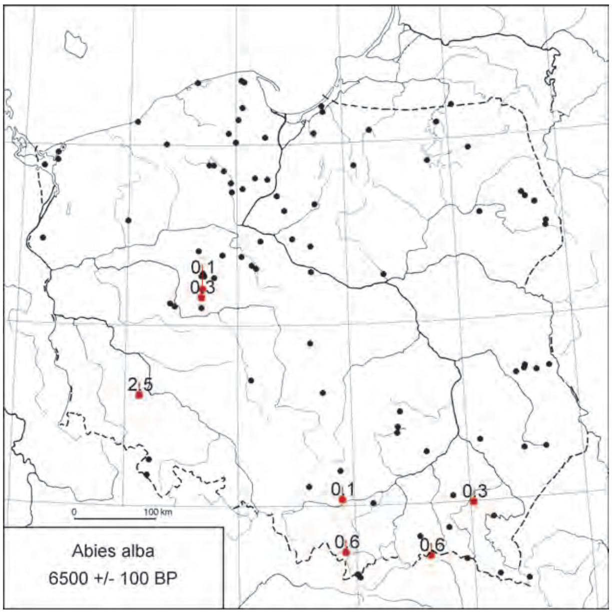

0.4
0.2
0 100 km
Abies alba
9000 +/- 100 BP

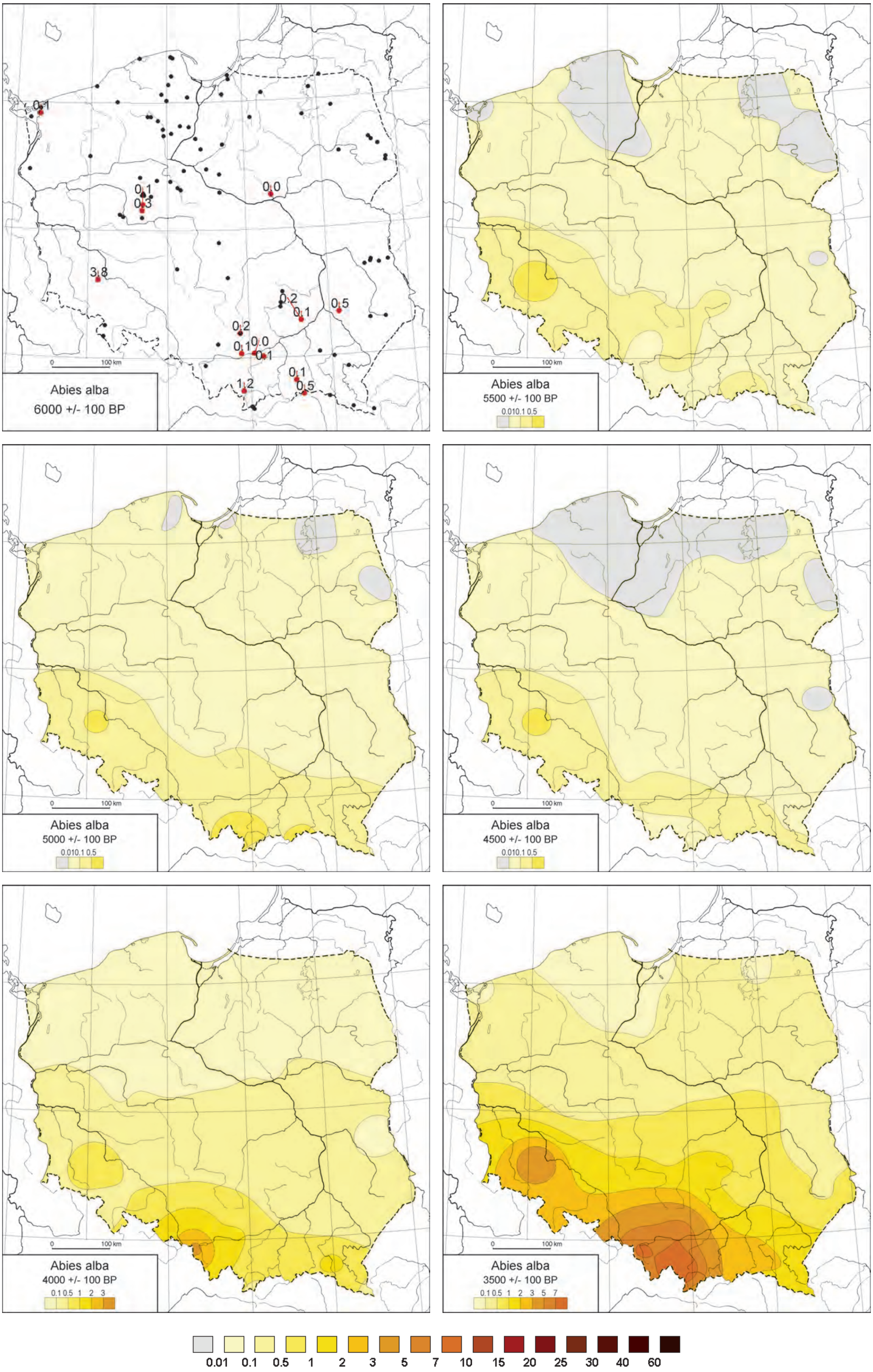

0.0
0.2
0.9
0.2
0 100 km
Abies alba
8500 +/- 100 BP

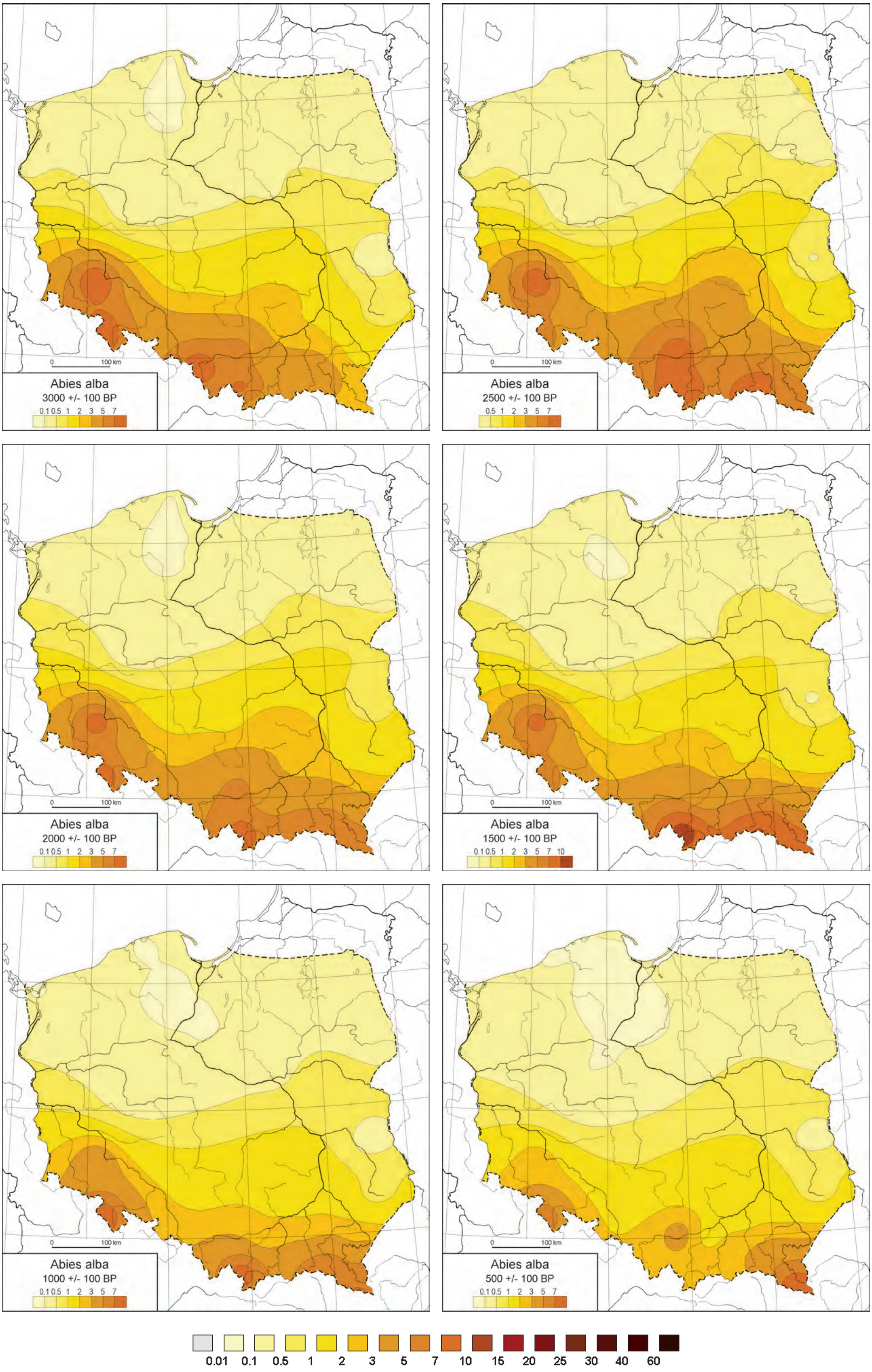

0.0
0.1
0.1
0.2
0 100 km
Abies alba
8000 +/- 100 BP

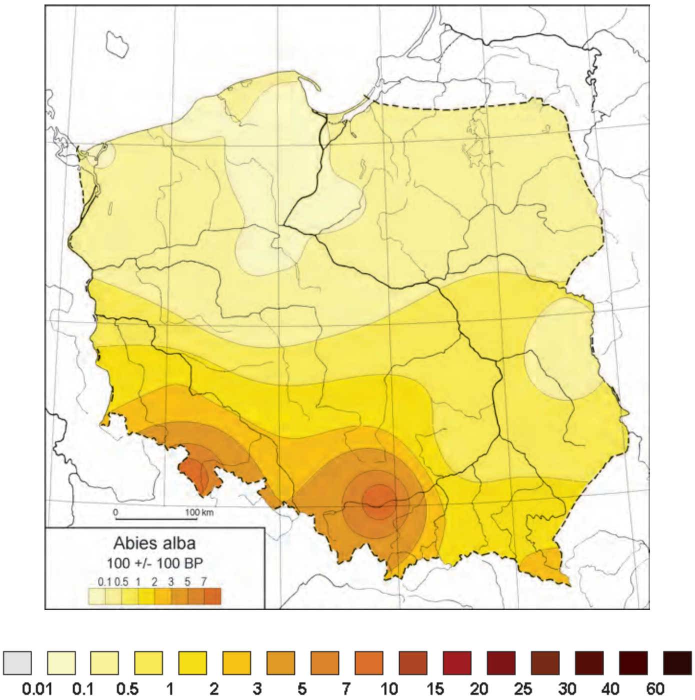

0.1
0.1
0.1
0.5
0.3
0 100 km
Abies alba
7500 +/- 100 BP


0.1
0.2
0.1
0.1
0.1
0.9
1.4
0.1
0 100 km
Abies alba
7000 +/- 100 BP


0.1
0.3
2.5
0.1
0.3
0.6
0.6
0 100 km
Abies alba
6500 +/- 100 BP


0.1
0.1
0.3
0.0
3.8
0.2
0.1
0.5
0.2
0.1
0.0
0.1
1.2
0.1
0.5
0 100 km
Abies alba
6000 +/- 100 BP
Abies alba
5500 +/- 100 BP
0.01 0.1 0.5
Abies alba
5000 +/- 100 BP
0.01 0.1 0.5
Abies alba
4500 +/- 100 BP
0.01 0.1 0.5
Abies alba
4000 +/- 100 BP
0.1 0.5 1 2 3
Abies alba
3500 +/- 100 BP
0.1 0.5 1 2 3 5 7
0.01 0.1 0.5 1 2 3 5 7 10 15 20 25 30 40 60


0 100 km
Abies alba
3000 +/- 100 BP
0.1 0.5 1 2 3 5 7
0 100 km
Abies alba
2500 +/- 100 BP
0.5 1 2 3 5 7
0 100 km
Abies alba
2000 +/- 100 BP
0.1 0.5 1 2 3 5 7
0 100 km
Abies alba
1500 +/- 100 BP
0.1 0.5 1 2 3 5 7 10
0 100 km
Abies alba
1000 +/- 100 BP
0.1 0.5 1 2 3 5 7
0 100 km
Abies alba
500 +/- 100 BP
0.1 0.5 1 2 3 5 7
0.01 0.1 0.5 1 2 3 5 7 10 15 20 25 30 40 60


0
100 km
Abies alba
100 +/- 100 BP
0.1 0.5 1 2 3 5 7
0.01
0.1
0.5
1
2
3
5
7
10
15
20
25
30
40
60

Acer L. – **Maple**

AGNIESZKA M. NORYŚKIEWICZ, ANNA FILBRANDT-CZAJA, BOŻENA NORYŚKIEWICZ,
AND DOROTA NALEPKA

PRESENT DISTRIBUTION IN EUROPE

Acer is a diverse genus, rich in species. From among 190 species and subspecies (Boratyński 1999) only thirteen occur in Europe (Huntley & Birks 1983), with *Acer campestre* L., *Acer pseudoplatanus* L., and *Acer platanoides* L. being the most widespread.

Acer campestre, field maple, occurs mainly in central and southern Europe, from Spain to the Ukraine and in the north it reaches central England, Denmark and southern Sweden (Browicz & Gostyńska 1963).

Acer pseudoplatanus, sycamore, has expanded mainly in central Europe. It is absent from the northern part of the continent (Scandinavia) and from the western part of the Mediterranean region (Huntley & Birks 1983).

Acer platanoides, Norway maple, is the most widespread maple species in Europe. As a holarctic species it is common throughout central Europe. It occurs from central France and the Pyrenees in the west as far as the central part of the Ural Mountains in the east (Boratyński & Browicz 1976). In the north, in Scandinavia, it extends up to 63°N (Hultén 1950), and in the south the boundary of its distribution runs through central Italy, central Greece, south-eastern Bulgaria and central Ukraine.

PRESENT DISTRIBUTION IN POLAND

Polish flora contains three species of *Acer*: *A. platanoides*, *A. pseudoplatanus* and *A. campestre* (Fig. 28). The first is a transgressive species occurring almost throughout the country apart from the mountain areas (Boratyński & Browicz 1976). The other two reach the north-eastern limit of their distribution in Poland (Boratyński 1999). *Acer pseudoplatanus* is native to the mountains, in the south Polish uplands, in the western part of the Wielkopolska-Kujawy Lowland, and in Pomerania (Zając A. & Zając M. 2001). However, a lot of its sites within this range are of anthropogenic origin (Zając M. 1996). The occurrence of *Acer campestre* is scattered but it occurs more often in the Kujawy and Wielkopolska areas, in the east-Carpathian foothills as well as in south-western Poland (Zając A. & Zając M. 2001).

ECOLOGY

All *Acer* species mentioned are not sensitive to climatic continentality and grow well in the temperature conditions found across the whole of Poland. Only occasionally they may be damaged by frost. *Acer pseudoplatanus* displays the greatest tolerance, whilst *Acer campestre* is the least resistant particularly to freezing. *Acer* species are shade-tolerant trees with moderate moisture requirements (Zarzycki et al. 2002). *Acer pseudoplatanus* is the only species that has a higher demand for soil and air humidity (Puchalski & Prusinkiewicz 1990). *Acer* species vary in their soil preferences; in Poland, however, all native species occur on eutrophic or at least mesotrophic soils (Zarzycki et al. 2002). The least demanding is *Acer campestre*, most commonly occurs on slightly moist, mesotrophic, on mineral-humic and on moderately acid soils, whilst *Acer pseudoplatanus* is the most demanding with respect to a sufficient abundance of nutrients and occurs on damp, medium acid to weakly alkaline eutrophic soils (Boratyński & Filipiak 1999, Zarzycki et al. 2002). Because of their relatively high resistance to pollution, as well as their widely appreciated decorative qualities, *Acer* species are often planted in urban areas (Karolewski 1999).

Flowers of the native species are bisexual, assembled in hanging panicles or corymbs. *Acer platanoides* blooms earliest, even before its leaves open, whilst the other two Polish species bloom in May, following the appearance of the leaves (Sokołowska 1980). The characteristic double winged fruits of *Acer* species ripen between the middle of August and the middle of October. Maple and sycamore are trees that regenerate freely under natural conditions (Tylkowski 1999). These tree species reach 12 m (*A. campestre*) to 30 m in height (*A. pseudoplatanus*, *A. platanoides*).

Maples occur mainly in mesotrophic, multi-species deciduous forests. Particular *Acer* species occur in different woodland communities. *Acer pseudoplatanus* is a characteristic species of the *Tilio platyphyllis-Acerion pseudoplatani* sub-alliance and regionally is an indicator

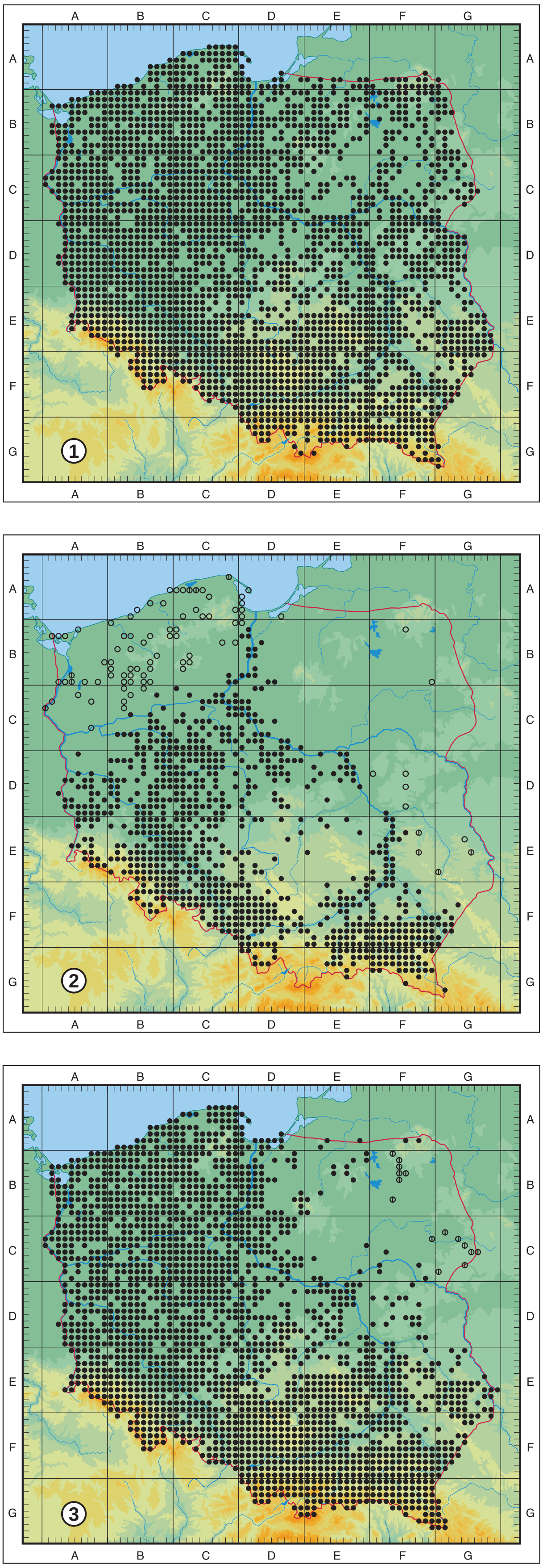


Fig. 28. Present-day distribution of 1 – *Acer platanoides* L., 2 – *A. campestre* L., and 3 – *A. pseudoplatanus* L. in Poland: ○ – synanthropic sites, ⦶ – status of site unknown or uncertain (after Zając A. & Zając M. 2001)

species of the *Aceri-Tilietum* association (Matuszkiewicz W. 2001). *Acer platanoides* is one of the characteristic species of the *Querco-Fagetea* class and is regarded as an indicator species only in the *Aceri-Tilietum* slope association (Jutrzenka-Trzebiatowski 1999b). *Acer campestre* is in Poland a characteristic species of some thermophilous brushwood communities of the *Rhamno-Prunetea* class, as well as of deciduous forests associations from the *Querco-Fagetea* class, particularly in the central-European *Galio-Carpinetum* (Matuszkiewicz W. 2001, Matuszkiewicz W. & Matuszkiewicz A. 1985).

POLLEN PRODUCTION AND DISPERSAL

Morphological features of the pollen grains of the Polish species of *Acer* fall within a similar range of variation and consequently are all recorded under the single category *Acer campestre*-type (Clarke & Jones 1980, Moore et al. 1991). As the species of *Acer* under discussion are insect-pollinated, they produce relatively small amount of pollen, thus the frequency of this taxon in the pollen assemblages is usually that of its actual occurrence in plant communities (Delcourt et al. 1984). However, the number of pollen grains produced by the different species varies. For example, one flower of *Acer pseudoplatanus* produces more than 23 thousand grains whilst one flower of *Acer platanoides* generates only about eight thousand (Dyakowska 1959). Research on the recent pollen rain, carried out in the Natural Reserve at Wierzchlas has indicated just a small number of maple pollen grains in the surface assemblages in spite of the presence of maple trees in the surrounding forest (Noryśkiewicz A.M. 1997). Several years' research on annual pollen deposition has revealed that *Acer* pollen is poorly represented in the pollen rain in deciduous forests, which contain maple. The mean annual percentage value over a four year period reached just 0.4% of the total pollen sum (Noryśkiewicz A.M. 2001).

EXPANSION IN EUROPE DURING THE LATE GLACIAL AND HOLOCENE

Acer survived the Vistulian glaciation in refugia located in the southern Alps and along their margins, as well as in southern Europe and in the Black Sea area (Lang 1994). According to Huntley and Birks (1983) by 10,000 BP *Acer* had consolidated its range in south-eastern Europe. Rapid expansion towards the north, with migration rates 500–1000 m yr^{-1} (between 10,000 and 9000 BP) resulted in a wide spread of *Acer* in the European mountains. This was followed by its retreat from south-east Europe since 8000 BP and by a northwards expansion as far as southern Poland. Further expansion resulted in the maximum distribution of *Acer* in the European part of Russia and around the Baltic Sea, with a continuous range from Bulgaria to

Poland. A distinct contraction of the range of *Acer*, as well as a decrease in percentage pollen values, is visible in later times.

MIGRATION PATTERN IN POLAND (Fig. 29)

9500 – 9000 BP

Low percentage pollen values (0.01–0.03%), recorded in south-eastern Poland, indicate the earliest appearance of *Acer* in Poland, presumably migrating from this direction. Its appearance in north-west Poland, not confirmed on following maps, may suggest redeposition or long-distance transport rather than a separate migration pathway.

8500 – 8000 BP

During that time there was a distinct northward expansion of *Acer*. Its range covered the whole southern part of the country. In the east it crossed the valley of the Bug river and in the west it approached the line of the Warta river. The percentage pollen values are still small (0.1%) except for the south-east outskirts of Poland and the Kłodzko Depression where these values increased to 0.5%. Due to its relatively low pollen production, even a low *Acer* representation in pollen assemblages is a good indicator of its local presence.

7500 BP

About 7500 BP the expansion of *Acer* further northward was recorded. In the western part of Poland its range went beyond the Noteć river and beyond the northern state boundary east of Vistula river. Disappearance of *Acer* pollen from the south-east area (i.e. the Sandomierz Depression, the Roztocze and Lublin Upland) seems to be susceptible to various interpretations. In the pollen diagrams *Acer* occurs as a discontinuous curve, thus its absence in that area could be the result of the method of selecting time horizons.

7000 – 5000 BP

At that time *Acer* spread presumably throughout Poland. Its percentage pollen values exceed 0.1%. Higher pollen values (up to 0.5%) are recorded in south-western Poland. This picture may confirm the main direction of *Acer* migration from the southern European glacial refugia.

4500 – 4000 BP

After 4500 BP *Acer* expansion progressed. On the 4000 BP map *Acer* pollen values from 0.1 to 0.5% are characteristic of the whole country. It was the period of maximum distribution and abundance of *Acer* in the forests for the whole Holocene. Such a picture resulted probably from an overlap of populations of different *Acer* species migrating into the area of Poland from both the south and the south-east.

3500 – 3000 BP

The first signs of *Acer* decline appeared ca. 3500 BP and were particularly visible in north-eastern and central Poland. At this time the *Acer* decline may be explained as a result of anthropogenic deforestation (Huntley & Birks 1983, Delcourt et al. 1984). On the other hand, according to Tobolski (1976, 1999), the natural tendency for *Acer*, as a mesocratic species, to begin to disappear from forests during the oligocratic stage of the interglacial cycle cannot be excluded.

2500 – 500 BP

The next maps show a continuing trend of decrease of *Acer* abundance. Almost throughout Poland the pollen percentage values are low (0.01–0.1%). Only in some regions of southern Poland are these values higher but never exceed 0.5%. These may be attributed to the occurrence of *A. pseudoplatanus* in the mountainous areas.

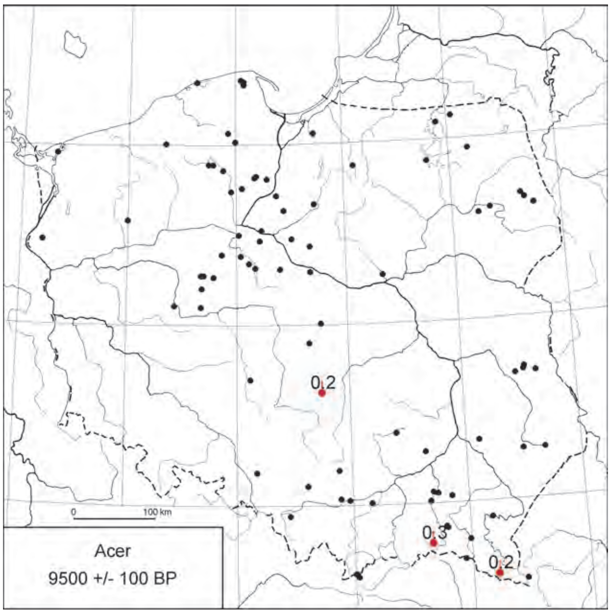
100 BP

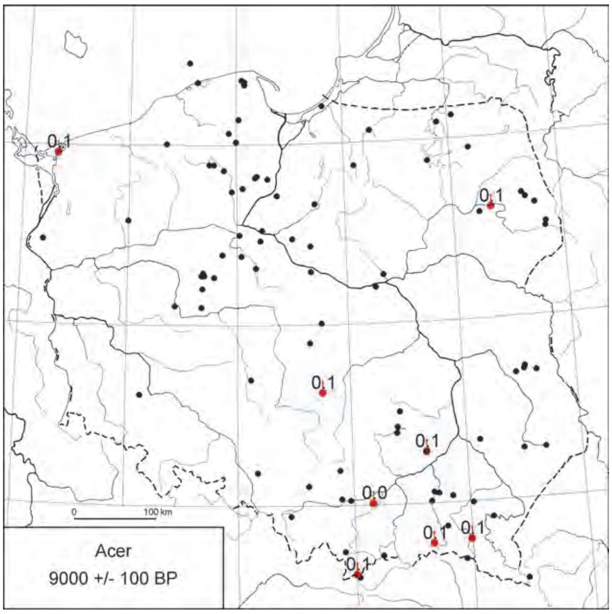
The present-day distribution of *Acer* covers the whole territory of Poland. Its pollen values are less than 0.1%. This has resulted presumably from intensive deforestation and the subsequent reduction of mixed deciduous forest areas and from the generally very low pollen productivity of *Acer*. This low but even frequency of *Acer* pollen values can be associated rather with the common and widespread introduction of this taxon into varied anthropogenic tree-stands than with its natural occurrence in forest communities (Tumiłowicz 1999).

CONCLUSIONS

On the isopollen maps constructed for the area of Poland the *Acer* species (*A. platanoides*, *A. pseudoplatanus* and *A. campestre*) are represented by low pollen values, never exceeding 1% of the total sum of AP + NAP. These low values of *Acer* pollen in Holocene sediments may be explained by the following reasons: low pollen production due to insect pollination of *Acer* flowers; poor dispersal of pollen grains released from anthers, as well as the grains being relatively heavy. Despite its low pollen percentage values the genus *Acer* is regarded as an important constituent of deciduous forests in the Holocene (Huntley & Birks 1983, Tobolski 1999). In Poland, the maximum expansion of *Acer* occurred between 4500 and 4000 BP. It is difficult to define the migration routes of particular *Acer* species. Nevertheless, the isopollen maps show clearly that the *Acer* immigration into Poland came generally from the south (including south-eastern and south-western directions).

Fig. 29. *Acer*: dot and isopollen maps for 9500–100 ^{14}C yr BP


0.2
0.3
0.2
0
100 km
Acer
9500 +/- 100 BP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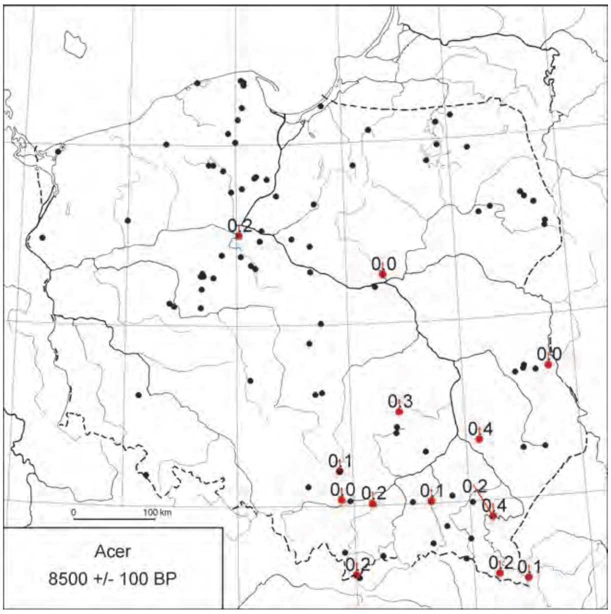
0.1
0.1
0.1
0.0
0.1
0.1
0.1
0
100 km
Acer
9000 +/- 100 BP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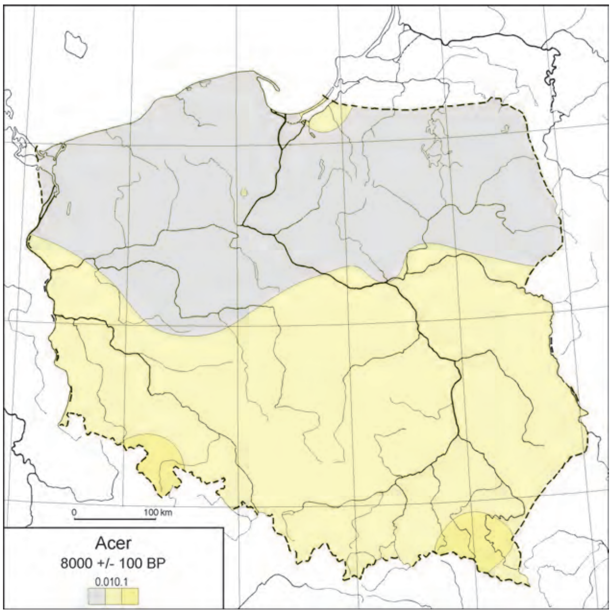
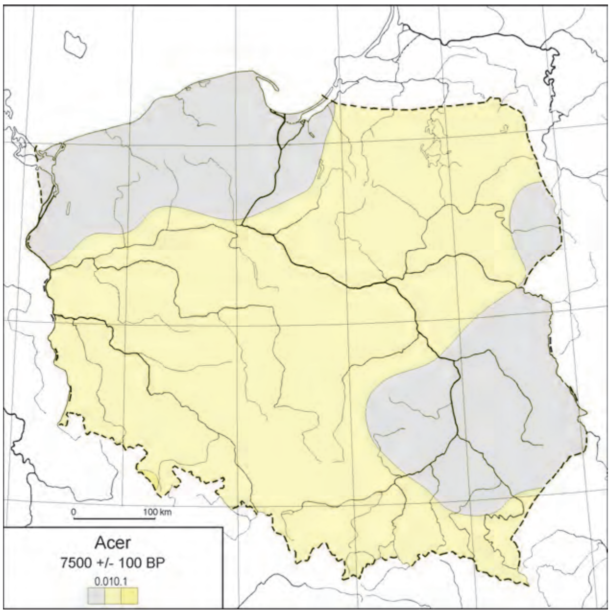
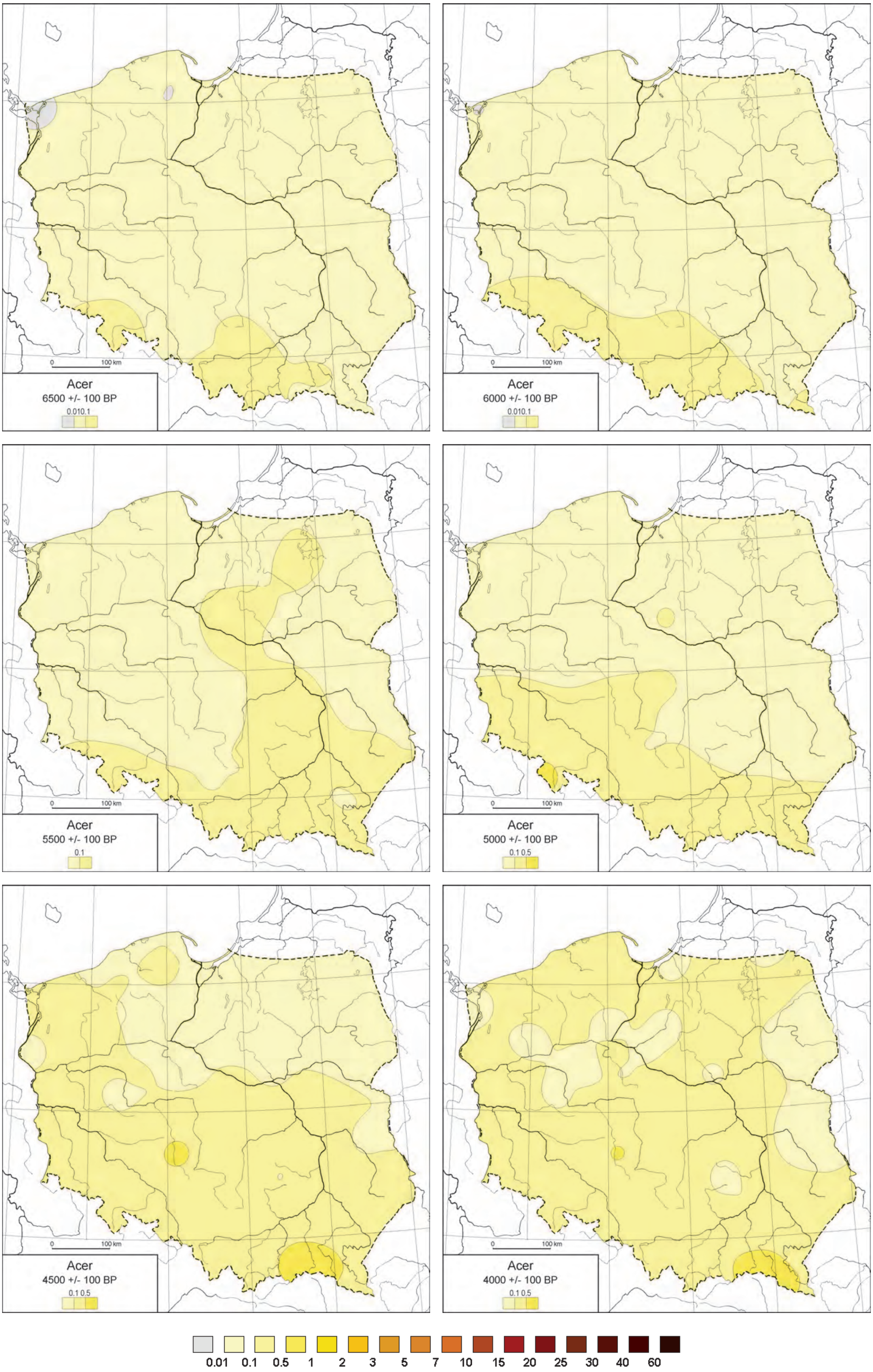
0.0
0.0
0.3
0.4
0.1
0.0
0.2
0.1
0.2
0.4
0.2
0.2
0.1
0
100 km
Acer
8500 +/- 100 BP

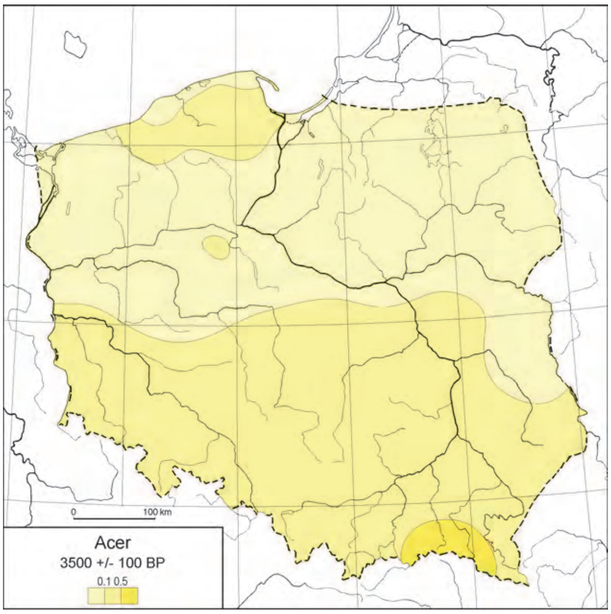

0
100 km
Acer
8000 +/- 100 BP
0.01
0.1


0
100 km
Acer
7500 +/- 100 BP
0.01
0.1


0
100 km
Acer
7000 +/- 100 BP
0.01
0.1


0.01
0.1
0.5
1
2
3
5
7
10
15
20
25
30
40
60


0 100 km
Acer
6500 +/- 100 BP
0.01 0.1
0 100 km
Acer
6000 +/- 100 BP
0.01 0.1
0 100 km
Acer
5500 +/- 100 BP
0.1
0 100 km
Acer
5000 +/- 100 BP
0.1 0.5
0 100 km
Acer
4500 +/- 100 BP
0.1 0.5
0 100 km
Acer
4000 +/- 100 BP
0.1 0.5
0.01 0.1 0.5 1 2 3 5 7 10 15 20 25 30 40 60


0
100 km
Acer
3500 +/- 100 BP
0.1 0.5


0
100 km
Acer
3000 +/- 100 BP
0.1 0.5


0
100 km
Acer
2500 +/- 100 BP
0.1


0
100 km
Acer
2000 +/- 100 BP
0.1


0
100 km
Acer
1500 +/- 100 BP
0.1


0
100 km
Acer
1000 +/- 100 BP
0.01 0.1


0.01
0.1
0.5
1
2
3
5
7
10
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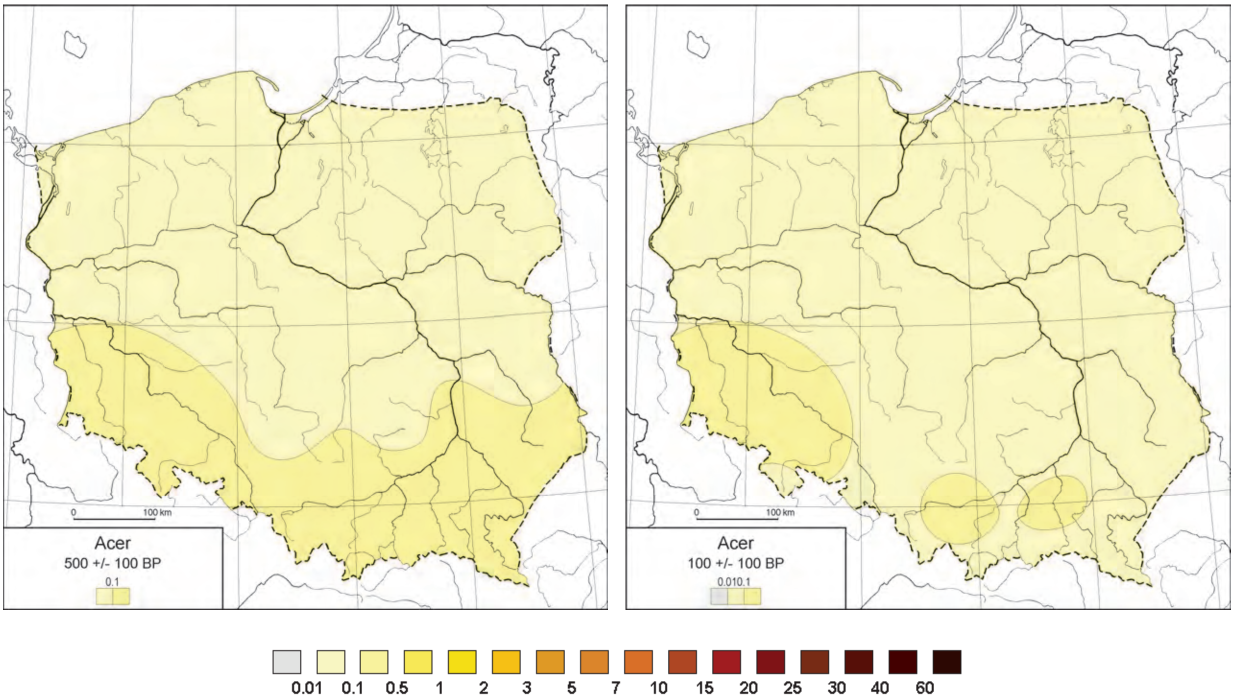
25
30
40
60


0
100 km
Acer
500 +/- 100 BP
0.1
0
100 km
Acer
100 +/- 100 BP
0.01
0.1
0.01
0.1
0.5
1
2
3
5
7
10
15
20
25
30
40
60

Alnus Mill. – **Alder**

Kazimierz Szczepanek, Kazimierz Tobolski and Dorota Nalepka

Four species of alder occur in Europe: *Alnus glutinosa* (L.) Gaertner, *A. incana* (L.) Moench, *A. viridis* (Chaix) DC. in Lam. & DC., and *A. cordata* (Loisel.) Loisel., the latter occurring only in Corsica and in south-western Italy (Huntley & Birks 1983).

In Poland, the genus *Alnus* Mill. is represented by three species. Two of them are trees: *A. glutinosa* and *A. incana*, the third one *A. viridis* is a small shrub confined in its occurrence to the Bieszczady Mountains (Zając A. & Zając M. 2001). The isopollen maps record the history of both of these tree species of alders, as their pollen grains are not distinguished in pollen analyses (their fossil fruits are easy to distinguish). On the other hand it is possible to identify pollen and fruits of *A. viridis* in subfossil material (Ralska-Jasiewiczowa 1980, Burga & Perret 1998).

Present distribution in Europe and in Poland

The ranges of each of the tree species of alder growing in Poland are different (Fig. 30). Apart from quite important geographic differences there are also some ecological differences. *Alnus glutinosa* is an Euro-Siberian-Atlantic-Sub-Mediterranean species (Boratyńska & Boratyński 1977), whilst *A. incana* displays a European-west-Siberian-boreal-mountainous distribution (Gostyńska-Jakuszewska & Hantz 1978). *A. glutinosa* is common throughout the country. However, it avoids higher altitudes in the mountains (Zając A. & Zając M. 2001) and usually does not exceed the foothill zone (Boratyńska & Boratyński 1977). *A. incana* is not so common; its sites are mainly situated in southern Poland and along the whole course of the Vistula river (Zając A. & Zając M. 2001). Additionally, this species also has a northern centre extending from the Suwałki Lake District to the Tuchola Forest (Gostyńska-Jakuszewska & Hantz 1978). *A. incana* has been included by Pawłowska (1972) in the mountain plants of the Sudetian-Carpathian group. Zając M. (1996) has also placed it within the group of mountain plants of the Amphi-Arctic-Alpine range. *A. incana* in the Tatra Mountains reaches a maximum altitude of 1350 m and, in the Beskidy Mountains, 1080 m a.s.l. (Pawłowski 1972).

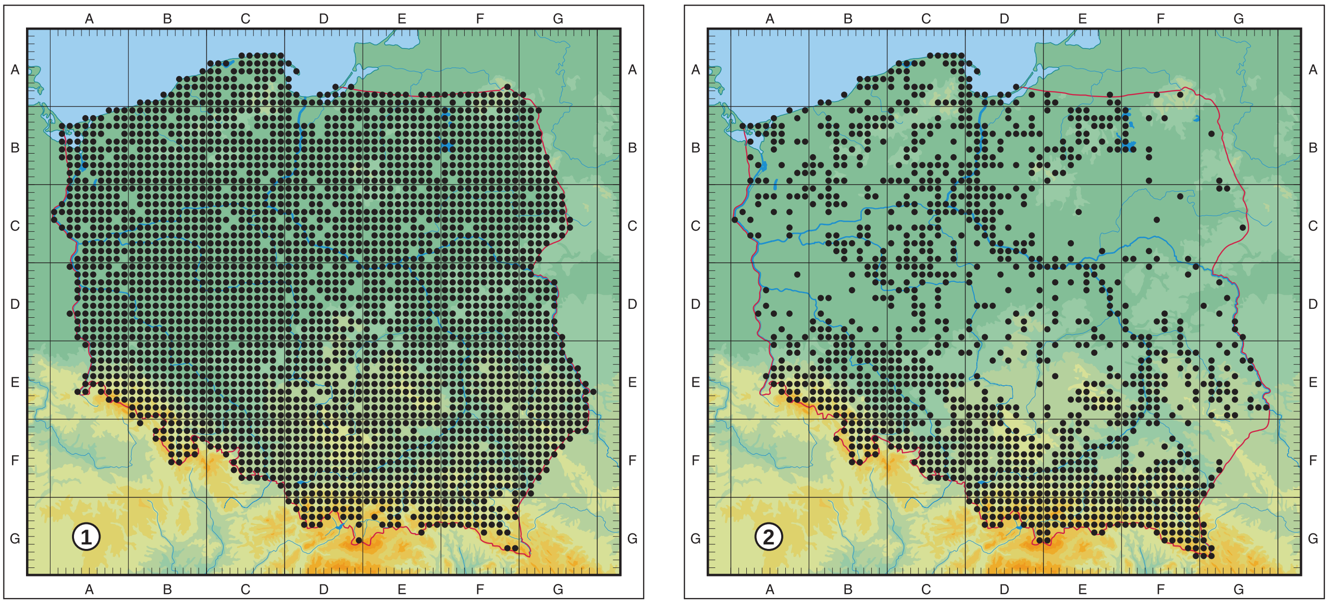


Fig. 30. Present-day distribution of 1 – *Alnus glutinosa* (L.) Gaertn. and 2 – *A. incana* (L.) Moench in Poland (after Zając A. & Zając M. 2001)

ECOLOGY

The ecological requirements of the both species under discussion are complementary according to Pancer-Kotejowa and Zarzycki (1980). This enables *Alnus incana* to exist in the wider area of the boreal zone and to occupy the higher sites in the mountains. Both species occur on mineral and organic soils, but the natural and semi-natural tree-stands of *A. glutinosa* grow on the peaty soils, whereas *A. incana* demands mainly young alluvial soils. They display a similar range of soil requirements in regard to acidity and moisture, although *A. incana* is able to tolerate lower moisture conditions (Pancer-Kotejowa & Zarzycki 1980). Their restricted distribution within natural forest communities is due to their low competitive abilities (Ellenberg 1996). Both species are characterised by tolerance of considerable fluctuations of water level but *A. incana* unlike *A. glutinosa* does not cope with long-lasting flooding (Pancer-Kotejowa & Zarzycki 1980), whereas *A. glutinosa* displays lower tolerance to any length of drought. Marek (1965) has demonstrated convincingly one specific feature of *A. glutinosa*, its ability to form peat. The majority of the communities belonging to the *Alnetea glutinosae* class are able to accumulate peat deposits of a few meters thickness. This feature may be helpful in interpretation of the isopollen maps, as peat sites with alder pollen primarily indicate the presence of *A. glutinosa* rather than *A. incana*.

Syntaxonomy of the communities with alder (Matuszkiewicz W. 2001, Zarzycki et al. 2002) reflects their ecological differentiation. *A. glutinosa* occurs in a few associations (mainly peat-forming) of a separate phytosociologic class *Alnetea glutinosae*, as well as in the communities of the *Alno-Ulmion* (=*Alno-Padion*) order. *A. incana* is present in associations combined exclusively into the *Alno-Ulmion* order included in the *Querco-Fagetea* class.

Both *A. glutinosa* and *A. incana* can be regarded as pioneer plants (Lang 1994) easily occupying new or previously disturbed habitats (Pancer-Kotejowa & Zarzycki 1980). The ability to assimilate free nitrogen (up to 130 kg/ha^{-1} per year^{-1}) through the symbiosis with Actinomycetales situated in root nodules, is an advantageous feature, enabling colonisation of infertile habitats which become more fertile in a short time.

POLLEN PRODUCTION AND DISPERSAL

Significant representation of both tree alders in the pollen flora results from their abundant pollen production. The male catkins flower in March and April before leaf development. If they grow in the same habitats *A. incana* flowers several days to three weeks prior to *A. glutinosa* (Pancer-Kotejowa & Zarzycki 1980).

EXPANSION IN EUROPE DURING THE LATE GLACIAL AND HOLOCENE

Huntley and Birks (1983) basing on palynological evidence have accepted the existence of glacial refugia of alder in Corsica, the Carpathians, south-western Russia and in the region of the Bay of Biscay. Bennett et al. (1991) have mentioned about others from southern Italy and Greece, and van Zeist et al. (1975) have recorded the presence of alder pollen in south-western Turkey and northern Iran during the Late Glacial. Studies of DNA of *A. glutinosa* chloroplasts (King & Ferris 1998) indicate that the majority of the northern and central European areas were occupied by *A. glutinosa* deriving from the Carpathian refugia.

According to Środoń (1981) *A. incana* may have survived in the Northern Carpathians over the period of the maximum extent of the Vistulian glaciation. Interpretation of the early post-glacial isopollen maps should not ignore the evidence for the Late Glacial age of sites with *A. incana* macrofossils (Środoń 1981).

MIGRATION PATTERN IN POLAND (Fig. 31)

13,000 – 12,000 BP

The 13,000–12,000 BP maps provide information about sparse sites for alder with very low pollen values. In the south-eastern part of the Carpathians and their forelands several sites are significant: Podbukowina (Mamakowa 1962) where *Alnus* pollen values reach 4.8%, 8.2% (with *Corylus* at 12,000 BP=1.5%) and Jasło (Harmata 1995a, b) with values of 1.5% and 1.4%, and some others.

Contamination of sediments with pollen of thermophilous (Tertiary) taxa makes it difficult to prove that alder occurred in the region at that time, although the presence of *A. incana* might be possible.

11,500 – 10,500 BP

On the 11,500–10,500 BP maps the number of sites with trace values of *Alnus* pollen increases. In numerous pollen diagrams from Late Glacial sediments the genus *Alnus* is represented by low-percentage curves (rarely >0.5%, sporadically >1%). These values themselves do not prove the presence of alder in the area of Poland (*Corylus* maps of the same age contain similar values of its pollen!), but wood of alder has also been recorded (Witów – Wasylikowa 1964, Besko – Koperowa 1970, Kraków – Mamakowa 1970, Czajków – Szczepanek 1971a, Wolbrom – Latałowa 1976). According to Środoń (1981), it can be assumed that even both alder species may have occurred in Poland already during the Late Glacial.

10,000 – 9500 BP

The number of the sites with low values of *Alnus* pollen grows significantly at the 10,000 and 9500 BP levels. The centres of increased concentration of pollen (max. >2%) are situated in central-southern Poland; however, they are located in different areas on each of the maps.

9000 BP

Three centres with higher values of *Alnus* pollen (3–5%) developed along the axis of the Vistula river located at the Moravian Gate, then in the Sandomierz Depression, together with Świętokrzyskie Mountains, and finally in the region where the rivers Vistula, Bug and Narew join. It is possible that this may indicate a migration route of *Alnus* from the south-west through the Moravian Gate and then along the Vistula valley towards the north.

8500 BP

The whole eastern part of Poland together with the Carpathians, and as far as the Warta river valley to the west, is represented by alder pollen values of >3%. These values suggest that alder was present at the sites investigated or in their close vicinity. A centre of higher values (up to 15%) suggests a migration route across the lower area the central Carpathians towards the uplands of central Poland. A wide belt with higher pollen values of alder (up to 10%) is shown on this map, indicating the presence of alder species in plant communities, along the valley of the Vistula river from the Carpathians towards the Baltic Sea and the Mazurian Lake District. Only the central and northern part of western Poland displays lower values of alder pollen (2–5%).

8000 – 6500 BP

The 8000 to 6500 BP maps illustrate *Alnus* expansion over the whole area of Poland, particularly in the northern and central parts of the country. In the south, in the Sudetes, the Carpathians and in their forelands expansion of this tree was slower and less intensive. This was probably an area where *A. incana* was more common, usually restricted to the valleys of the mountain rivers and streams, and amounts of *A. glutinosa* were small. The 8000 BP map seems to be distinguished by the abundant occurrence of alder (>15%) in the Polish Eastern Carpathians. The following maps 7500 and 7000 BP are characterised by more abundant occurrence of alder in the region of the Moravian Gate (10–15%), and by the reduction in its presence in the Beskid Niski range, the Jasło-Sanok Depression (<7%), and in adjacent areas in the south-east. On the 6500 BP map only the area of the Carpathians is conspicuous by the lower occurrence of *Alnus* there.

6000 – 2500 BP

The 6000 to 2500 BP maps are characterised by an almost uniform cover of values of alder pollen (15–20%) across the territory of Poland. The 6000 and 5500 BP maps show still more areas with pollen values <15% in southern Poland and in the Odra and Vistula valleys. Locally occurring values >25% are characteristic of the 5000–3500 BP maps. On the majority of maps from the time interval 6000–2500 BP, the mountainous areas, such as the Sudetes and the Carpathians with their adjacent forelands, are characterised by slightly decreased abundance of alder. This may be associated with the restricted occurrence of *A. glutinosa*. Locally higher concentrations of alder pollen are mostly found in the area between the Pilica and Vistula rivers.

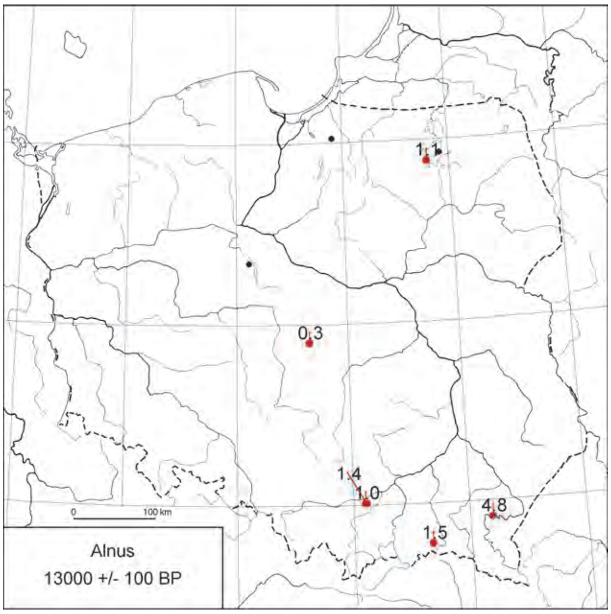
2000 – 100 BP

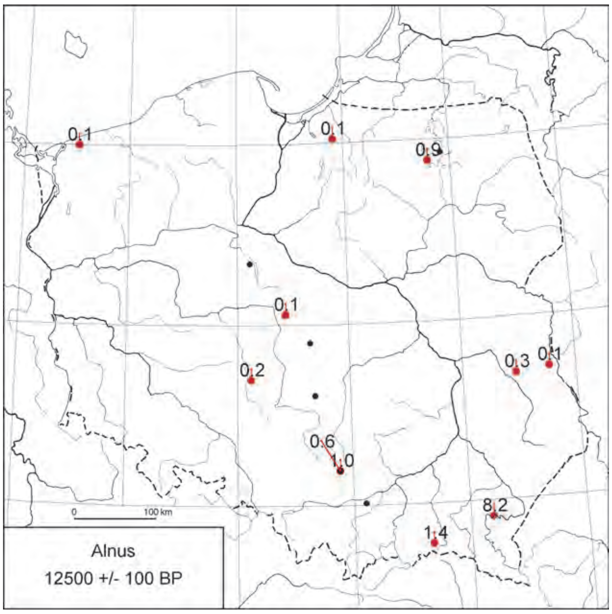
The 2000 and 1500 BP maps record a decrease in the frequency of alder in plant communities, particularly in the areas east of the Vistula river, in the Sudetes, and partly in the Western Carpathians. The further decline in the frequency of alder on the 1000, 500 and 100 BP maps results apparently from transformation of the vegetation cover by human management.

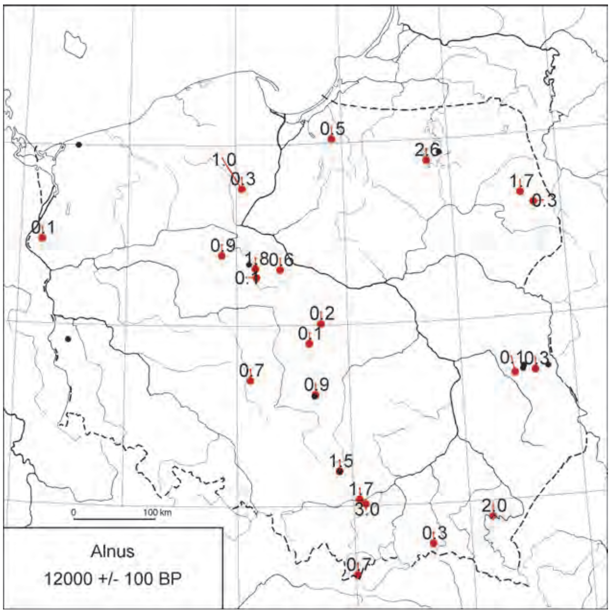
Conclusions

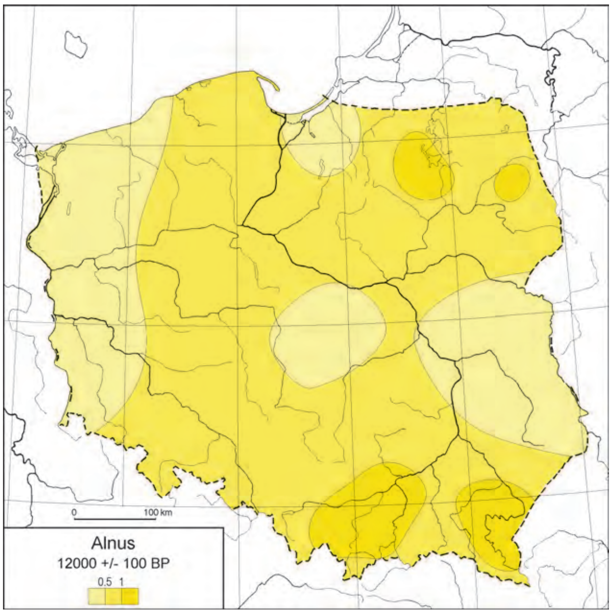
The 8500 BP map, recording an *Alnus* migration route along the Vistula river basin, may relate to a considerable frequency of *A. incana*. A wave of expansion on the subsequent map 8000 BP is most likely associated with *A. glutinosa*. The maps for 8000 to 6500 BP are characterised by local areas of higher values of *Alnus* pollen (15–20%), which extend gradually, giving a rather uniform pattern of occurrence of this tree in Poland. On the 6500 BP map three areas can be recognised in the patterns of alder pollen distribution: 1. almost the whole of the northern and central Polish lowlands with the central uplands as far as the Świętokrzyskie Mountains, with the highest pollen values (15–20%); 2. the western uplands, together with the Odra river valley, the Sudetes, and the eastern uplands together with Wołyń and Polesie Lubelskie, showing moderate values (10–15%); 3. the Carpathians and part of the adjacent forelands with the lowest values (5–10%). Spread of alder in the mountains has always been limited by habitat factors relating to altitude above sea level. *A. incana* has probably been the main alder species occurring there throughout the Holocene.

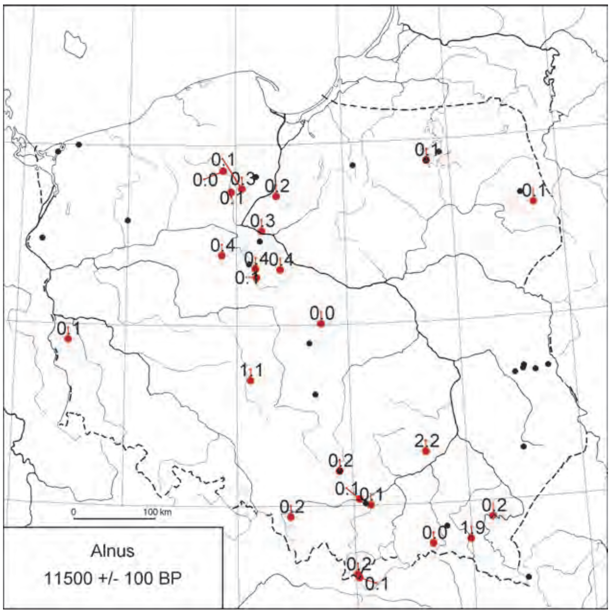
Fig. 31. *Alnus*: dot and isopollen maps for 13,000–100 ^{14}C yr BP

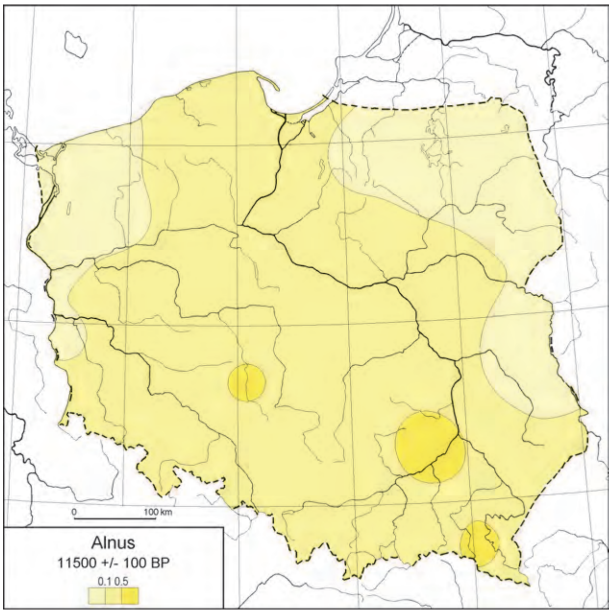






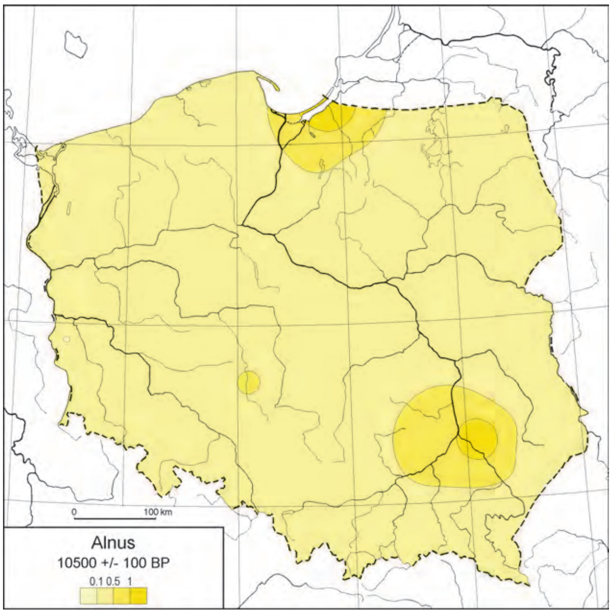


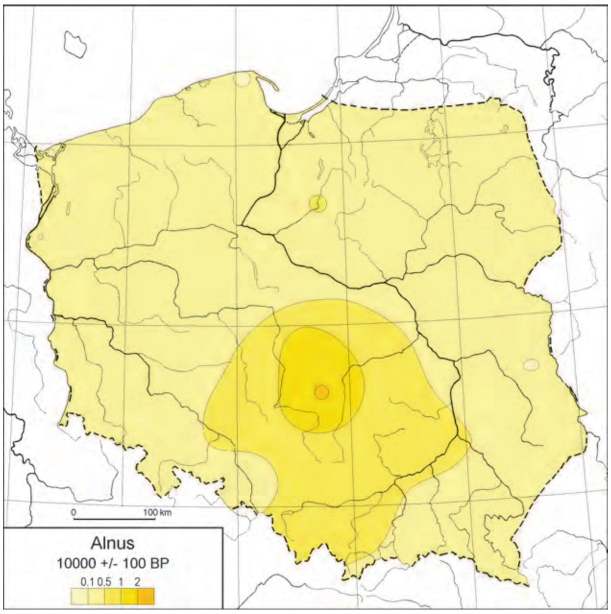


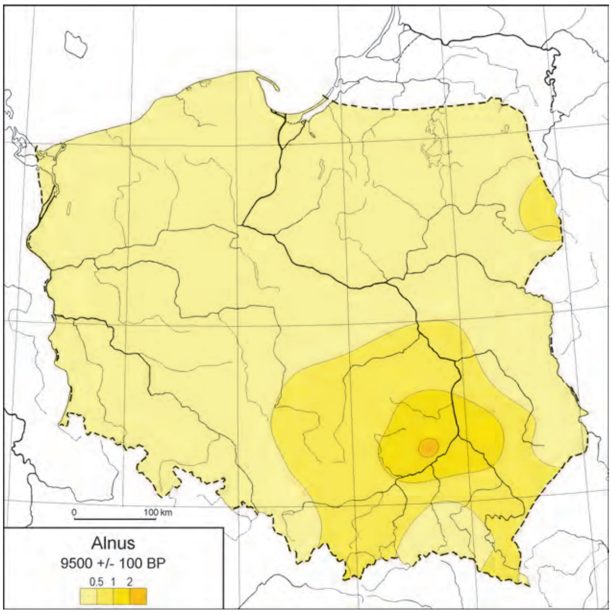


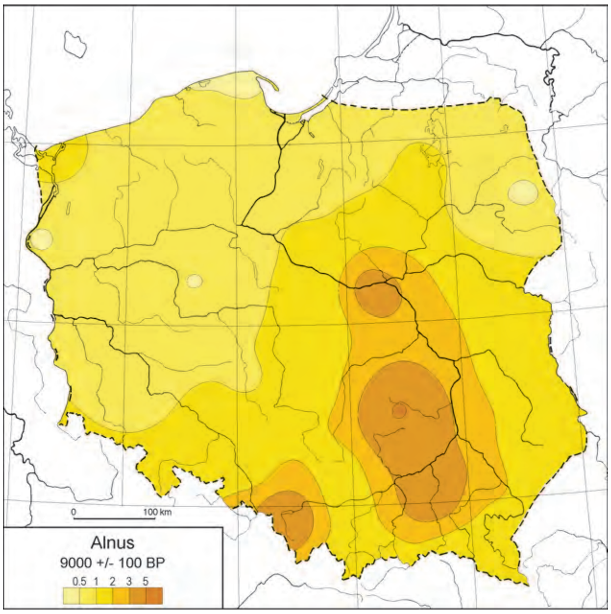
0.01 0.1 0.5 1 2 3 5 7 10 15 20 25 30 40 60

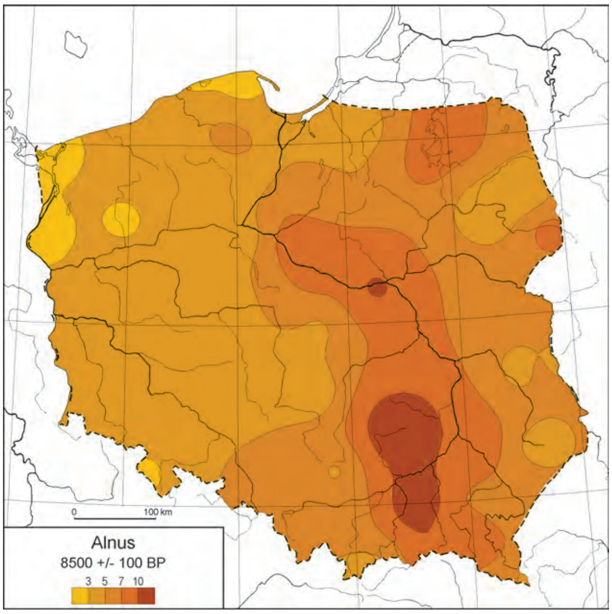

0
100 km
Alnus
11000 +/- 100 BP
0.1


0
100 km
Alnus
10500 +/- 100 BP
0.1 0.5 1

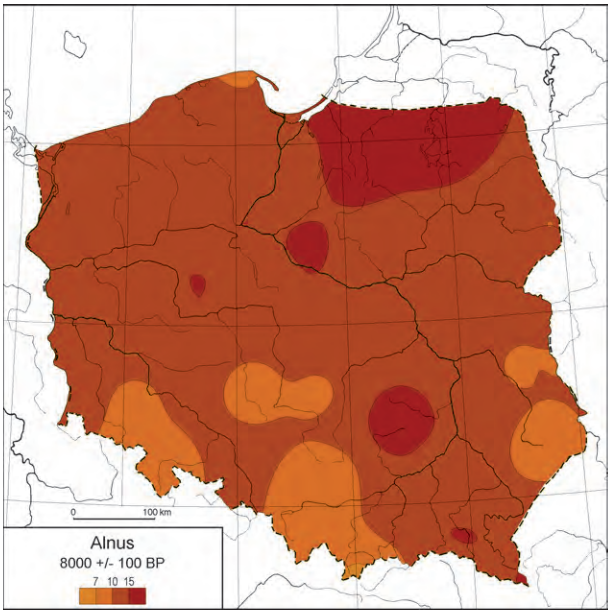

0
100 km
Alnus
10000 +/- 100 BP
0.1 0.5 1 2

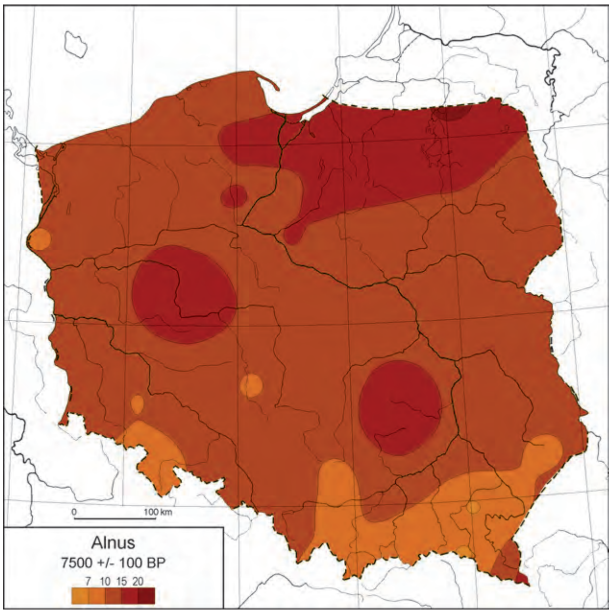

0
100 km
Alnus
9500 +/- 100 BP
0.5 1 2

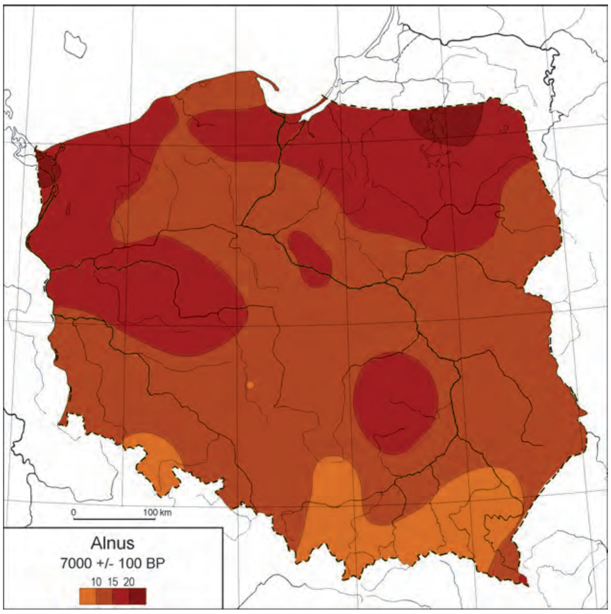

0
100 km
Alnus
9000 +/- 100 BP
0.5 1 2 3 5

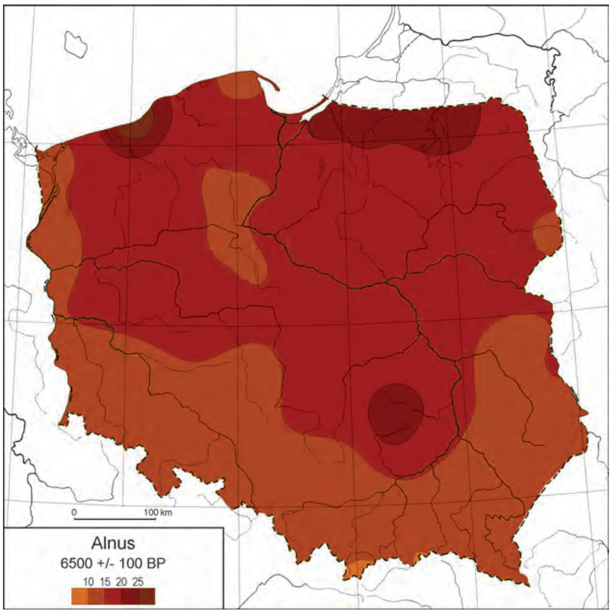

0
100 km
Alnus
8500 +/- 100 BP
3 5 7 10

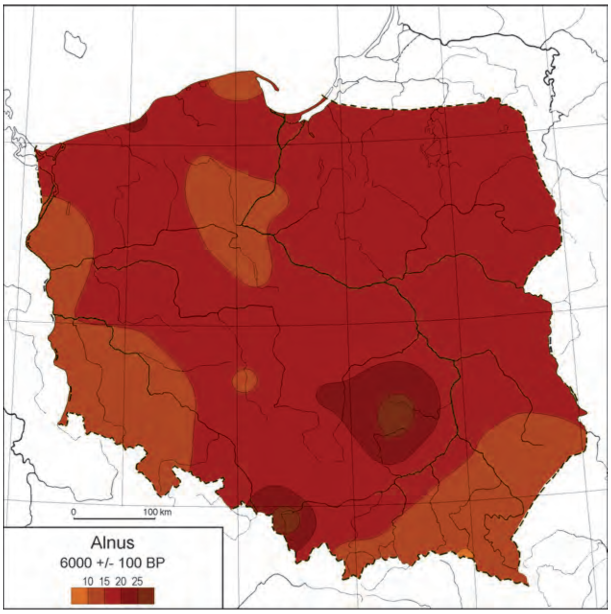

0.01 0.1 0.5 1 2 3 5 7 10 15 20 25 30 40 60

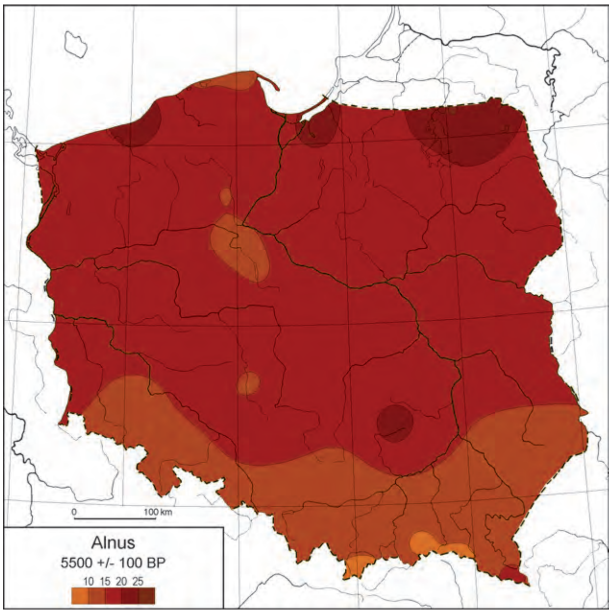

0
100 km
Alnus
8000 +/- 100 BP
7 10 15


0
100 km
Alnus
7500 +/- 100 BP
7 10 15 20


0
100 km
Alnus
7000 +/- 100 BP
10 15 20


0
100 km
Alnus
6500 +/- 100 BP
10 15 20 25


0
100 km
Alnus
6000 +/- 100 BP
10 15 20 25


0
100 km
Alnus
5500 +/- 100 BP
10 15 20 25


0.01
0.1
0.5
1
2
3
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7
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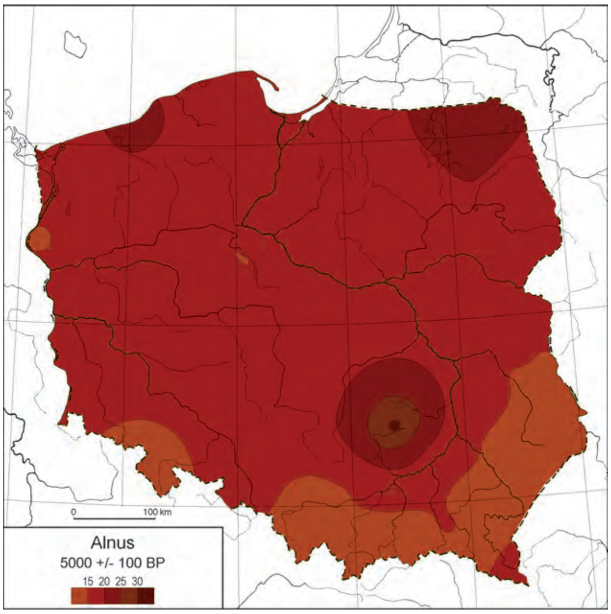
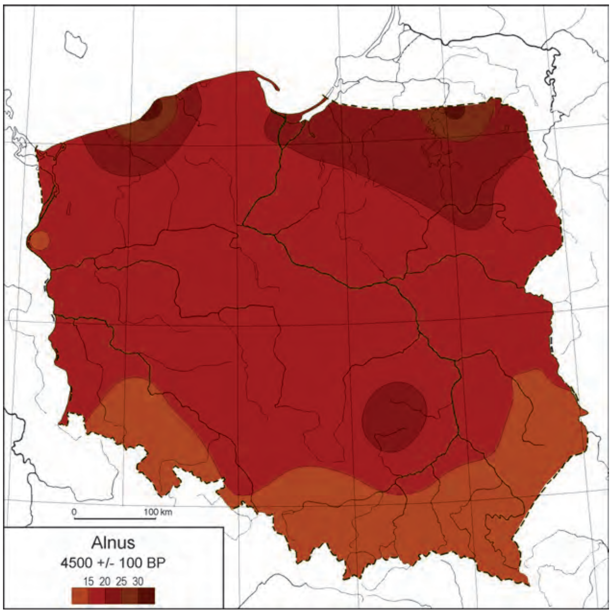
30
40
60


0
100 km
Alnus
5000 +/- 100 BP
15 20 25 30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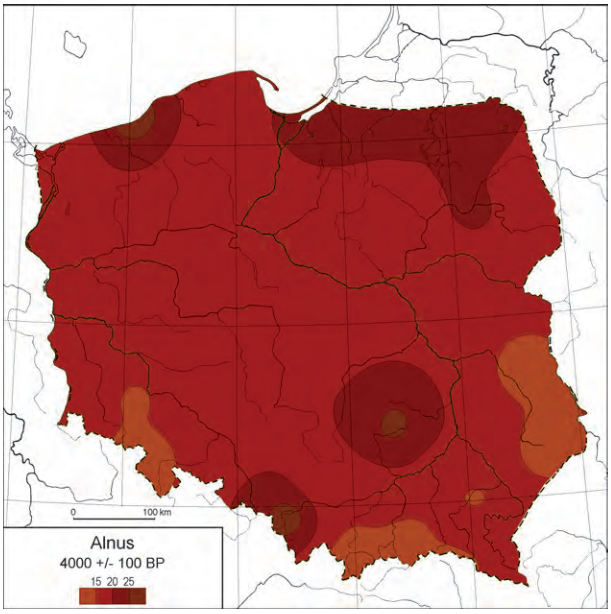
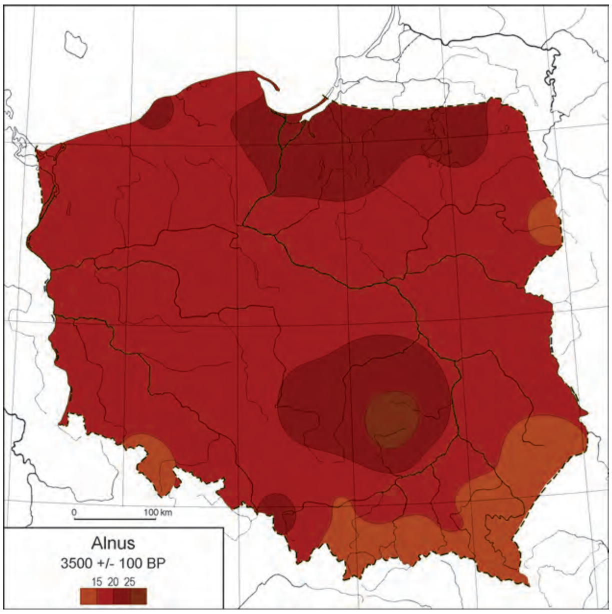
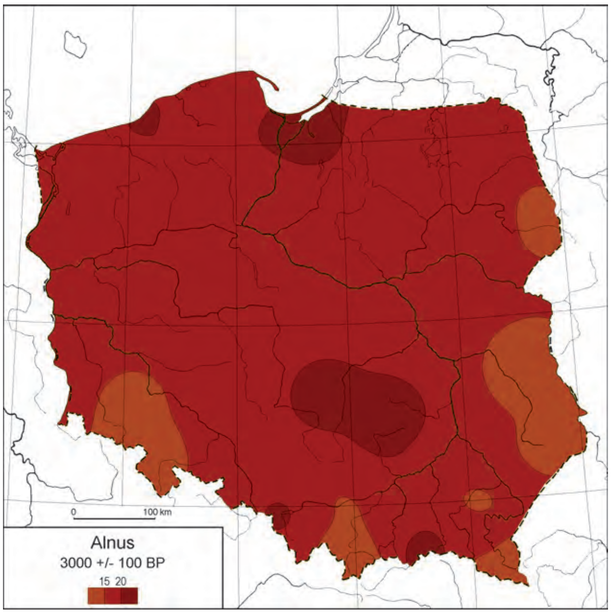
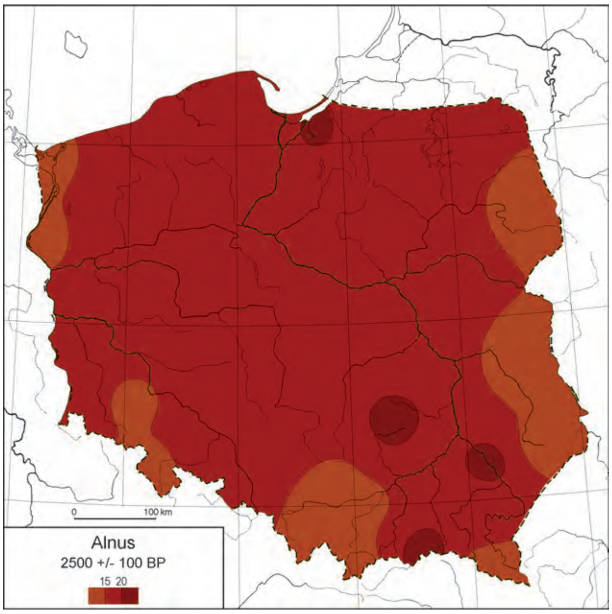
100 km
Alnus
4500 +/- 100 BP
15 20 25 30


0
100 km
Alnus
4000 +/- 100 BP
15 20 25


0
100 km
Alnus
3500 +/- 100 BP
15 20 25


0
100 km
Alnus
3000 +/- 100 BP
15 20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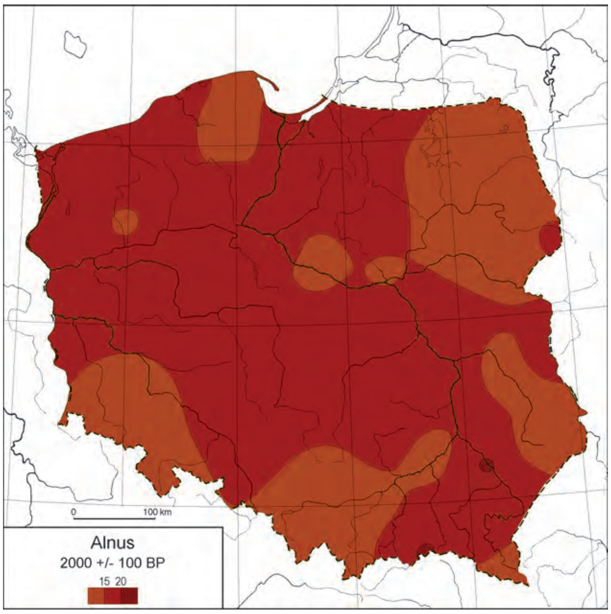
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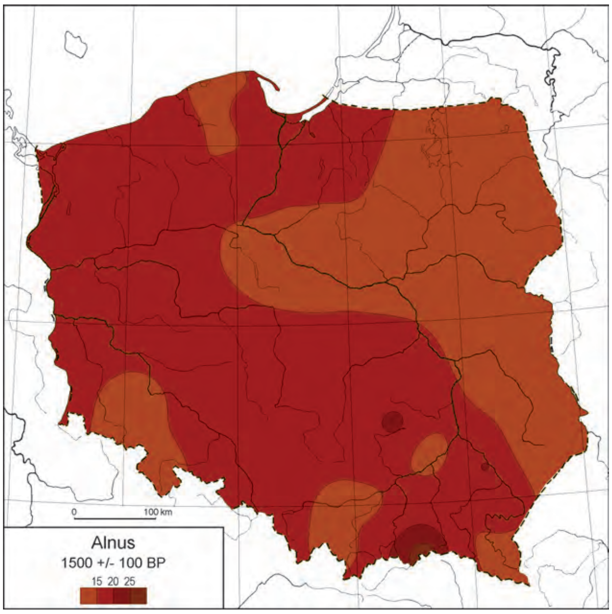
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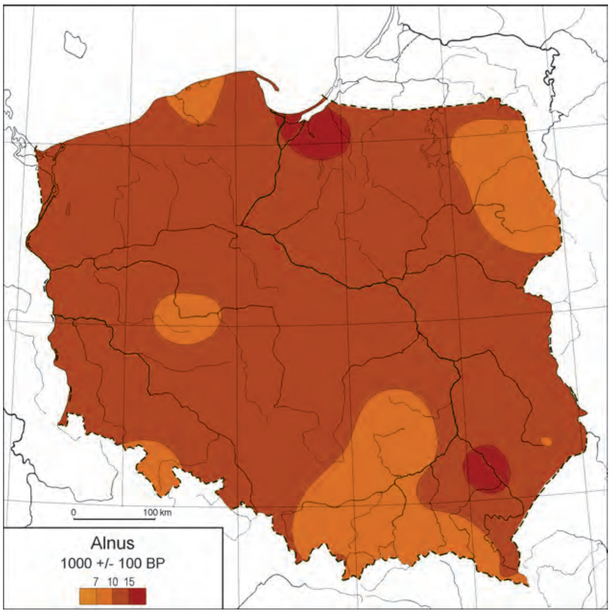
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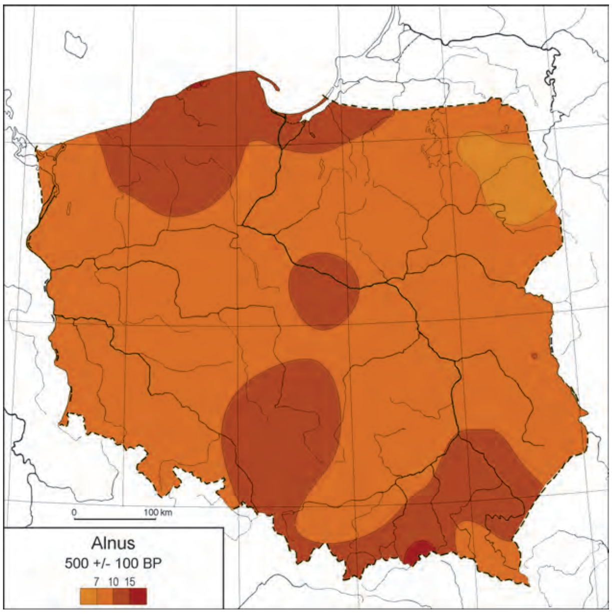
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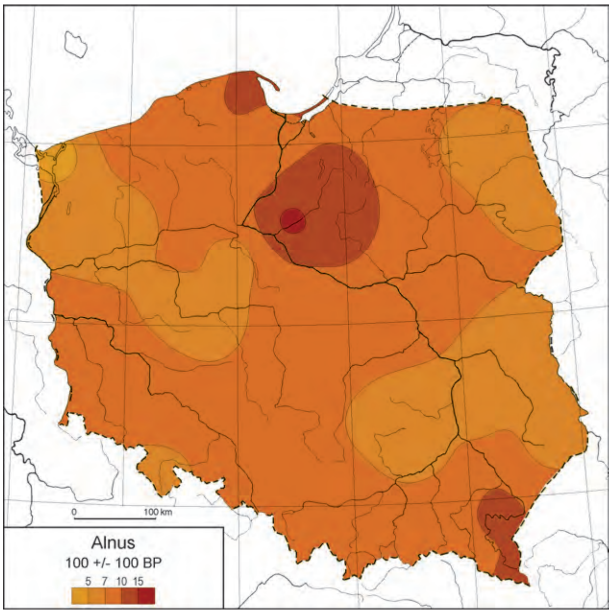
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Betula L. – **Birch**

MAGDALENA RALSKA-JASIEWICZOWA, AGNIESZKA WACNIK, KAZIMIERA MAMAKOWA,
AND DOROTA NALEPKA

The taxonomic account of the genus *Betula* in Flora Europaea (Tutin et al. 1964) recognises the presence of four species of birch in Europe: *B. pendula* Roth, *B. pubescens* Ehrh., *B. humilis* Schrank, and *B. nana* L. Jentys-Szaferowa (1979) identifies two species of tree birches within the region of Poland – *B. pendula* and *B. pubescens*, and three other taxa whose systematic rank is not explicitly defined. They are *B. obscura* A. Kotula, *B. oycoviensis* Besser included in the complex '*verrucosae*', and *B. carpatica* Waldst. & Kit. ex Willd. belonging to the complex '*pubescentes*'. The Polish flora also contains the two species of shrub birches: *B. humilis* and *B. nana*.

PRESENT DISTRIBUTION IN EUROPE

The genus *Betula* is restricted in its appearance to the Northern Hemisphere, especially to the cool and temperate zones. The northern limit of the range of *Betula* is formed by birches from the section *Nanae*, which extend furthest north in the west of Greenland to 79°N and in arctic Asia to north of 70°N. In the south the range of *Betula* only extends below latitude 20°N in a few areas in southern Spain and Sicily (Jalas & Suominen 1976, 1988b).

B. pendula occurs throughout Europe except for Iberia, the Mediterranean lowlands, northern Fennoscandia and the Arctic. *B. pubescens* avoids only the Mediterranean basin (Huntley & Birks 1983). Birches from the section *Nanae* found furthest to the north are a group of closely associated and interbreeding taxa whose main species is *B. nana*. Studies from northern Finland have proved the phenomena of hybridisation and introgression between *B. pubescens* and *B. nana*, from which have originated a lot of montane birch varieties (trees and shrubs). Such a genetic inheritance brings with it great plasticity, which in turn makes adaptation to different growing conditions and flowering in northern latitudes easier (Mäkelä & Hyvärinen 2000). The tree birches form the natural northern forest limit in the sub-arctic zone north of the coniferous boreal forests.

PRESENT DISTRIBUTION IN POLAND

The genus *Betula* is represented in Poland, apart from the species mentioned above, by a number of hybrids and subspecies. In Poland *B. nana*, *B. humilis*, *B. oycoviensis*, and *B. pubescens* subsp. *carpatica* are all at the present-day limits of their distribution areas, or even grow at single localities, whereas *B. pendula* and *B. pubescens* subsp. *pubescens* are widespread (Zając A. & Zając M. 2001) and of great importance both ecologically and also economically.

B. pendula occurs throughout Poland, but in the mountains its presence is more prominent in the lower rather than the upper montane forest zone (Fig. 32). The upper limit of its range (Polica range 1300 m, the Gorce range 1270 m, the Bieszczady Mountains 1160 m a.s.l.) is similar to that of *B. pubescens* subsp. *pubescens*. *B. pubescens* is also found throughout Poland, but in particular *B. pubescens* subsp. *carpatica* generally occupies higher altitudes, as in the Tatra Mountains (up to ca. 1740 m a.s.l.), and in the Sudetes (up to ca. 1500 m a.s.l.). The lower altitudinal limit of this subspecies occurs at about 900–1000 m a.s.l. (Browicz 1979).

ECOLOGY

The genus *Betula* is essentially a pioneer taxon, light-demanding in all phases of its development, with a high tolerance of climatic and soil conditions. It fruits abundantly every year and intensively every 2–3 years; the fruits, light winged, flattened nutlets, are rapidly dispersed far and wide by wind action (Jaworski 1994, Faliński 1997).

Betula pendula is well adapted to continental conditions, tolerates summer high temperatures and very cold winters. Like *B. pubescens* it is resistant to frost, developing buds that can tolerate temperatures down to –4°C. It has a considerable requirement for soil warmth. It is particularly light-demanding and develops and grows well in full light. Despite the fact that it is a species with a high transpiration rate, it does not tolerate a high level of ground water. It grows best on moderately humid soils.

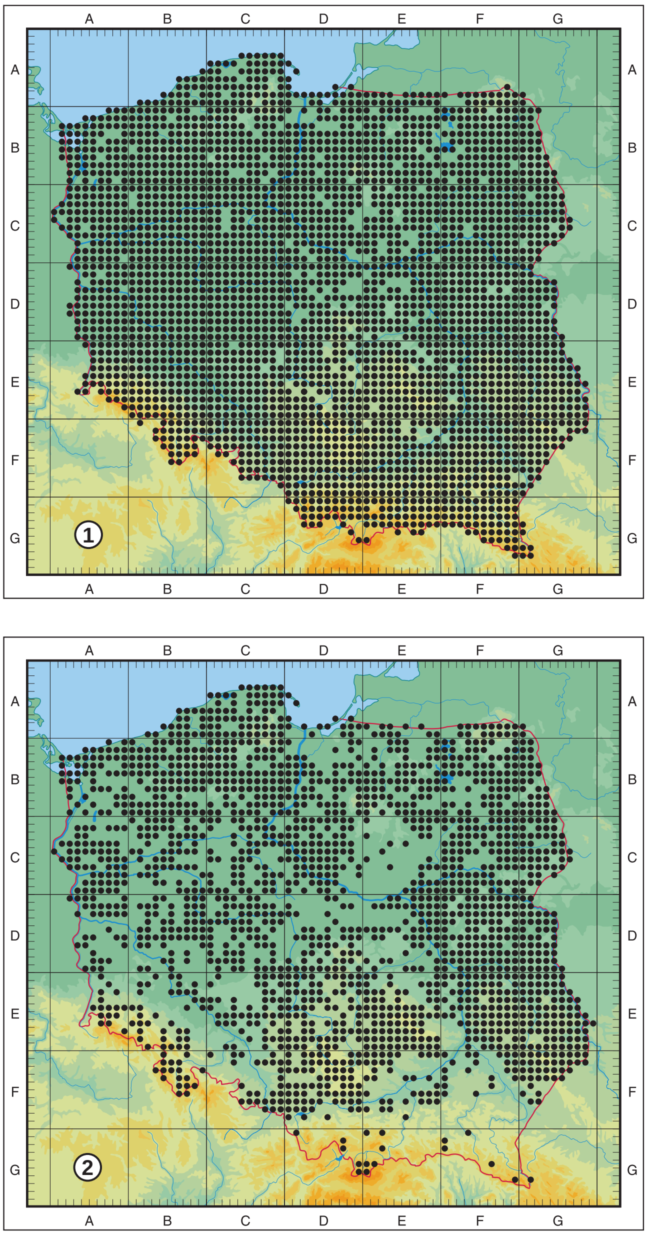

Fig. 32. Present-day distribution of 1 – *Betula pendula* Roth and 2 – *B. pubescens* Ehrh. subsp. *pubescens* in Poland (after Zając A. & Zając M. 2001)

It prefers light textured soils, in particular loamy sands and it can also colonise minerogenic and peaty soils, but avoids rendzinas (Zarzycki 1979). In waterlogged or moderately poor habitats it gives way to *B. pubescens*.

B. pendula grows slowly in the first year, but later its growth is rapid. On good soils it can become fully grown in 10–15 years. It can reach 20–30(35) m in height and 50–60 cm in diameter. Trees may live up to 90–100 years. Due to its broad habitat requirements (rather similar to those of *Pinus sylvestris*) it is typically a pioneer species, growing frequently on deforested areas (Zarzycki 1979, Faliński 1997).

Betula pubescens is a still less demanding species with regard to climatic conditions. It is even more resistant to frost; partly developed buds can tolerate a temperature of –4 (–5)°C. It can tolerate shaded sites better than *B. pendula*. However, it demands a higher level of humidity. It usually grows on peat soils and mineral-peat soils. It tolerates flooding quite well and avoids dry habitats (Zarzycki 1979).

Birches, due to their wide ecological amplitude are components of almost all woodland communities. In most of them they occur in company with other tree species. However, on waterlogged ground in northern and north-eastern parts of Poland, considerable areas are covered with stands of the damp-ground association *Betuletum pubescentis*, in which *Betula pubescens* is the dominant species.

Betula is a component of very varied plant communities from very dry dune pine forests to mires, from poor to fertile ash-elm carrs. It is a component, among others, of pine-birch swamp woods *Dryopteridi thelypteridis-Betuletum pubescentis*, the Pomeranian swamp birch-pine forest *Vaccinio uliginosi-Betuletum pubescentis*, spruce forests *Betulo pubescentis-Piceetum*, spruce forests on peats *Sphagno girgensohnii-Piceetum*, the Pomeranian birch-oak woodland *Betulo-Quercetum roboris*, central-European acidophilous humid woodland *Molinio caeruleae-Quercetum* (Wojterski 1979, Jutrzenka-Trzebiatowski 1999a, Matuszkiewicz J.M. 2002).

In studies of vegetation history, birches serve the function of indicators of climate and of the successional stage of vegetation. Shrub birches found in fossil material are useful climate indicators. The presence of *B. nana* allows the temperature of the coldest month to be determined as below 0°C (Kolstrup 1980, Tobolski 1991a, Granoszewski 1998a). The tree birches because of their behaviour as pioneer species yield information about the character and activation of successional processes. The occurrence of *B. pubescens* defines the July mean temperature as being not lower than 10°C (Paus 1992).

POLLEN PRODUCTION AND DISPERSAL

All birches are wind-pollinated and produce large amounts of light pollen, which enables its wide dispersal. The production of a single inflorescence (catkin) may amount to 5,452,500±415,383 grains, and its average weight is 6.09±0.16 g $^{-10}$ (Szafer & Wojtusiakowa 1969).

In Poland *Betula* flowers from the second half of April almost to the end of May (Szczepanek 1994a, b, 1997). Production of pollen in birches is said to follow a two-year cycle (Atkinson & Larsson 1990, Jäger et al. 1991). The beginning of pollination is closely related to the air temperature within the period of 40 days prior to the occurrence of pollen in the air (Spieksma et al. 1995).

It has been assumed that a value of 10% of *Betula* pollen in pollen assemblages is the minimum, which may indicate its local presence. Pollen values >25% can indicate local birch-dominated woodlands, and >50% reflect a situation where birch-dominated woodlands cover the landscape (Huntley & Birks 1983).

EXPANSION IN EUROPE DURING THE LATE GLACIAL AND HOLOCENE

From the onset of the Late Glacial the presence of birch pollen values >25% in assemblages from different regions of Europe has been recorded. According to Paus (1988) tree birches were present in southern Norway about 12,700 BP. A distinct increase in *Betula* pollen values is shown on isopollen maps from the Allerød period about 12,000–11,000 BP (Berglund et al. 1994, Lotter 1999, Stebich 1999). After the extent of birch woodlands had been temporarily reduced during the Younger Dryas there was an increase in their importance at the opening of the Holocene, with birch again a key taxon (Veski 1998, Poska & Saarse 1999, Bos 2001). A continuous zone of birch woodlands extended at that time from the British Isles to Russia. By 9000 BP the birch zone became fragmented in western and central Europe by the expansion of thermophilous trees, but in Greenland, Iceland and northern Fennoscandia it remained continuous. The areas covered by birch woodlands gradually became more restricted until about 5000 BP. After this period *Betula* increased in importance once again, but both as a result of anthropogenic transformations of habitats and the activation of secondary successional processes (Huntley & Birks 1983), and, in the north of Fennoscandia and the Arctic, as a result of climatic changes (Hyvärinen 1976).

In northern Finland *B. pubescens* was present throughout the whole Holocene. In the territory of Finnish Karelia its macrofossils were found at about 9400 BP. *B. pubescens* is at present the most common tree north of the pine zone. It is only absent from the tops of high mountains and from waterlogged, marshy regions (Mäkelä & Hyvärinen 2000).

MIGRATION PATTERN IN POLAND (Fig. 33)

Isopollen maps present the combined pollen values of the genus *Betula* because in the majority of pollen diagrams *B. nana*-type has not been differentiated. The morphological pollen type '*Betula*' comprises mainly *B. pendula* and *B. pubescens*. Nevertheless, *B. nana* pollen can constitute a small part of the *Betula* values presented on isopollen maps that relate to the Late Glacial.

It is certain that dwarf birches (*Betula* sectio *Nanae*) and probably also tree birches (*Betula* sectio *Albae*) survived the Vistulian Pleniglacial period in the refugia of the Northern Carpathians and their foreland. There is ample evidence for this from the macrofossils recovered from Pleni-Vistulian interstadials (presumably equivalent to the Hengelo/Denekamp group) from Dobra n. Limanowa dated at 32,550±450 BP (Środoń 1968), from Nowa Huta at 27,745±300–18,400±250 BP (Mamakowa & Środoń 1977), from Brzeźnica at 27,805±330 BP (Mamakowa & Starkel 1974), from Łążek at 25,580±2420 BP (Mamakowa 1968), and from other undated sites. In the deposits of an interstadial episode, lacking any precise stratigraphic position but dated at 16,925±325 BP, from Smerek in the Bieszczady Mountains (Ralska-Jasiewiczowa 1980), as well as pollen grains, macrofossils of *Betula nana*, *B. pubescens* subsp. *carpatica* and *B.* sectio *Albae* were found.

Macrofossils show that since the Oldest Dryas *B. nana* has been present in central Poland (Wasylikowa 1964), also in the Małopolska Upland (Latałowa & Nalepka 1987) and in the Nowy Targ Basin of the Tatra Mountains foreland (Koperowa 1962). A fruit scale of *B. nana* was found in the Bølling interstadial sediments of Lake Miłkowskie at the Mazurian Lake District (Wacnik 2003). Since the Bølling interstadial *B.* sect. *Albae* has occurred in central Poland (Wasylikowa 1964), and since the Oldest Dryas, in the region of the Mazurian Lake District, the presence of *B. pubescens* subsp. *pubescens* and *B. pubescens* subsp. *tortuosa* has been determined (Ralska-Jasiewiczowa 1966). From the same time interval *B. pubescens* and *B. pendula* have also been found at Białystok Upland (Kupryjanowicz 2000).

14,000 – 13,500 BP

Isopollen maps older than 13,000 BP record the occurrence of *Betula* from sporadic sites in the eastern lake districts with pollen values about 20–43% (14,000 BP) and about 30–40% (13,500 BP), which suggest its presence in that region. However, with so few assemblages from this period, it is difficult to maintain that it was abundant. It might have been *Betula pubescens* subsp. *tortuosa*, which grows at present in the Arctic. A single site from Warmia contains about 15% of *Betula* pollen.

13,000 BP

The map presents scattered sites – again from the Mazurian Lake District and central Poland (30%, 20%), from the Baltic Coastal Zone (about 15%) and also from the south of Poland (10%, 5%) as well. This suggests that birch may have been present in the lake districts and in central-north Poland.

12,500 – 12,000 BP

During the Bølling climatic warming the tree birches, which may then have been *Betula pubescens* subsp. *tortuosa*, subsp. *pubescens*, and *B. pendula* (cf. Wasylikowa 1964), gradually extended into central-northern and eastern Poland, with pollen values increasing up to 30–40% and even to a maximum of 50% in the Land of the Great Mazurian Lakes and in Polesie Lubelskie. This was the maximal Late Glacial expansion of birch in Poland. Lower values (10–20%) are present in montane areas, their forelands and in western upland regions.

11,500 BP

In the mid-Allerød the presence of birch was considerably restricted by a dynamic expansion of pine, and in montane regions also by larch. Southern regions showed *Betula* pollen values of 10–25%. A contribution of 30–40% persisted only in the north-eastern lake districts, in the river basins of the Biebrza and the Narew and on the western coast of the Baltic Sea.

11,000 BP

At the boundary of the Allerød and Younger Dryas when the maximal expansion of pine during the Late Glacial took place, a further restriction of birch distribution has been mapped. In the north-western part of Poland the concentration of birch pollen is higher than in other lowland regions, which may indicate its successful competition with pine under more oceanic climatic conditions. Yet birches retreat from montane regions and from the western highlands where they lose out in competition with larch, as a result of more severe climate.

10,500 BP

In the middle part of the Younger Dryas, birches again expand spreading in a mosaic way in the regions of the western lake districts, in eastern Poland and in the eastern mountain foothills. This may have happened because of a lack of stronger competition from other trees, mainly on the part of pine. However, in the southern highlands and mountains they still were in competition with larch. They were less abundant in the river basins of the upper Vistula and the Dunajec (up to 15% pollen values).

10,000 BP

A rapid expansion of birches in response to the Holocene amelioration of the climate began very quickly and spread throughout central and northern Poland. Pollen values up to 40%, and locally even higher, extend from the northern Sudetian foothills in the west up to Wołyń in the east. The southwards expansion of birch gradually grew less significant in the mountains and their forelands, where pine became dominant.

9500 BP

This map shows a progressive expansion of birch woodland. High *Betula* pollen values still indicate its spread southwards. Over the whole of the eastern lake districts, together with Mazovian Lowland up to the line of the rivers Vistula and the Bug with the Narew they are represented by 40–50%. It was the time of the maximal expansion of birches throughout the territory of Poland during the Holocene. Pollen values below 15% occur only in the Eastern Carpathians, where spruce was then expanding.

9000 BP

The participation of birches in woodland communities significantly declined. Pollen values reaching 30–40% persist only in north-eastern Poland and in Wielkopolska. These changes can partly be related to the expansion of hazel migrating from the north-west and west. Isopolls for pollen values of 10–25%, which indicate a decline in birch, or its restriction within scattered forest communities, retreat northwards, and the pollen values decline. In the low region of the middle Carpathians and its foreland *Betula* values fall below 10%. At this time the Carpathians and nearby foothills were invaded by elm from the south-east, and a further expansion of spruce took place there.

8500–6000 BP

The expansion of hazel and elm resulted in a considerable decline of birch, whilst alder replaced *Betula pubescens* in humid and wet habitats. The 8500 BP map shows rather even *Betula* values (20–25%) throughout lowland regions of northern Poland, which on the 8000 BP map continue to fall still lower, though with higher values locally in Polesie. The occurrence of birch in the south of Poland showed no significant change.

The pattern of the birch pollen values on the maps from the Atlantic optimum is still similar. It is very likely that birches were absent from the Carpathians and the Sudetes and the presence of *Betula* pollen there may be explained by long distance transport.

5500–5000 BP

The area showing *Betula* pollen values of 15–20% shrinks. Birch is still found in the western lake districts (sandy outwash areas) and to the south-east along the river basins of the Vistula, Bug, and Wieprz, with higher values in marshy regions of Polesie Lubelskie. In the Carpathians and the Sudetes the presence of birch pollen is still sparse.

4500–3500 BP

Although this was the period of the full development and then decline of the Neolithic settlements, whose economy favoured the expansion of pioneer birch woodlands, the maps show a fixed picture of a more reduced representation of birch. The whole country except for the southern belt of mountains where birch pollen is sparse (below 10%), shows birch pollen values of 10–15%, which is close to the limit accepted by Huntley and Birks (1983) as the minimum for the local presence of birch. Enclaves with a more abundant occurrence are still present in the region of sandy soils of the Tuchola Forest and the marshes of Polesie Lubelskie.

3000–1500 BP

The process of colonising abandoned agricultural land by pioneer birch woodlands is reflected on isopollen maps only from the beginning of Lusatian cultural settlements in Poland and the vast deforestation caused by their activities. First, at about 3000 BP, an increase in *Betula* values up to 20% took place in north-eastern Poland reaching the Warta river, and, from 2500 BP, pollen values below 10% indicating absence of birch, are limited only to the Carpathians. With the decline of the Lusatian culture, evidence for a high birch presence increases south-westwards and it is most abundant in the eastern lake districts (up to 25%). The processes of birch expansion are also recorded during the Roman Period (2000 BP). However, the process of regeneration of mixed deciduous forests connected with the economic regression during the Migration Period did not significantly affect the 1500 BP map, apart from the fact that the zone of restricted birch contribution in the south of Poland was widened.

1000 – 100 BP

Maps for the time of the establishment and development of the Polish State register a progressive process of complete deforestation and the development of an agricultural landscape. Therefore, the 1000 BP map shows a significant decline in birch throughout western Poland. The 500 BP map presents *Betula* with pollen values of 10–15% evenly throughout the country, but locally still lower. On the modern map (100 BP), only north-eastern Poland shows birch pollen values indicating a locally significant presence (10–15% or more).

Isopollen maps calculated with the Cyperaceae included into pollen sum

In the Late Glacial part of *Betula* set of maps, several maps (12,000–10,000 BP) based on the pollen sum with Cyperaceae included have been added, because they showed the pattern of isopolls substantially different from those calculated with Cyperaceae excluded. The whole rest of both sets of maps did not show any essential differences.

The map representing the decline of Bølling (12,000 BP) reflects a distinct decrease in *Betula* contribution in the south Poland – in the mountain and foreland areas. Some reduction of the values in *Betula* isopolls occurring also in the western part of the country and on the uplands is to be seen on the maps from Allerød (11,500 BP), spreading in the whole Poland at the Allerød/Younger Dryas transition (11,000 BP), and diminishing gradually its scale in the advanced Younger Dryas (10,500 BP), and at the beginning of the Holocene (10,000 BP).

It seems that the Late Glacial oscillations of climate stimulated the development of herb vegetation rich in Cyperaceae taxa, but the spread of forests initiated by the amelioration of climate at the beginning of the Holocene limited those processes.

The presentation of both types of maps gives a useful example showing how far the right choice of the pollen sum influences the isopollen pattern obtained.

Conclusions

Both dwarf and probably tree birches survived the Pleniglacial of the last glaciation in the Polish Carpathians and their foreland, according to the evidence of numerous macrofossils finds. The presence of the tree birches in the Polish lowland before the Bølling has not been confirmed, yet their expansion after 12,500 BP in central and north-eastern Poland is unquestionable. The succeeding expansion of birch in the Allerød period was restricted in its later part as a result of the expansion of pine, and larch in the mountains, and thereafter by the climatic changes during the Younger Dryas.

The maximal Holocene expansion of birches took place at about 9500 BP. In later parts of the Holocene their role declined significantly under the pressure from other trees forming mixed deciduous forests. A serious decline of birches took place in high mountainous areas.

The secondary succession of pioneer birch woodlands related to the Neolithic settlement shows little impact upon the pollen maps, however this phenomenon was recorded following the development of the Lusatian culture, and then the Roman Period. The declines in birch contributions caused by a process of complete deforestation are registered by maps dating from 1000 BP.

Fig. 33. *Betula*: dot and isopollen maps for 14,000–100 ^{14}C yr BP. Maps showing *Betula* isopolls calculated with *Cyperaceae* included into pollen sum are added for the Late Glacial time horizons and distinguished by green background of map legend


21.5
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Betula
14000 +/- 100 BP


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29.7
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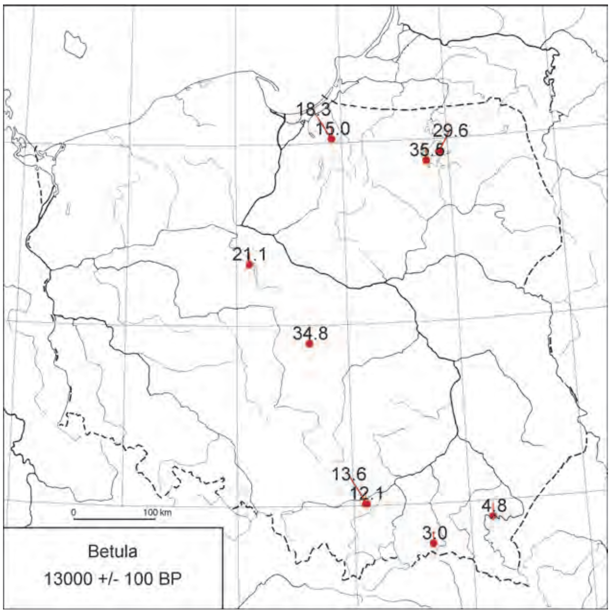
100 km
Betula
13500 +/- 100 BP


18.3
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35.6
21.1
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13.6
12.1
4.8
3.0
0
100 km
Betula
13000 +/- 100 BP


32.1
32.7
28.7
37.0
36.8
20.7
43.2
35.6
60.1
55.7
37.6
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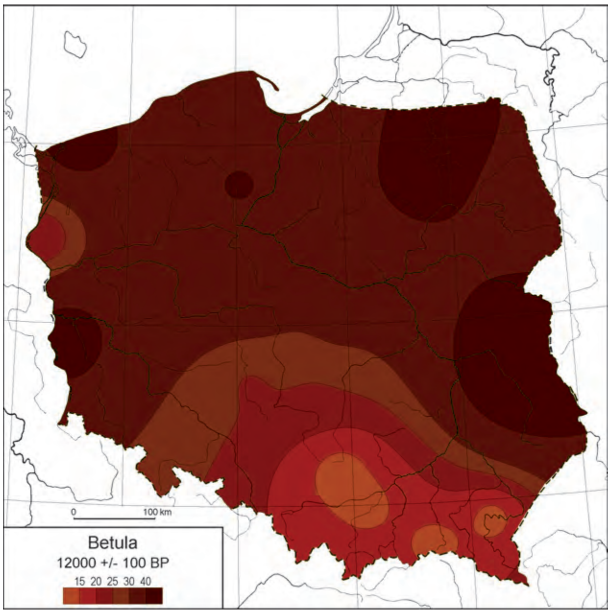
100 km
Betula
12500 +/- 100 BP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Betula
12000 +/- 100 BP
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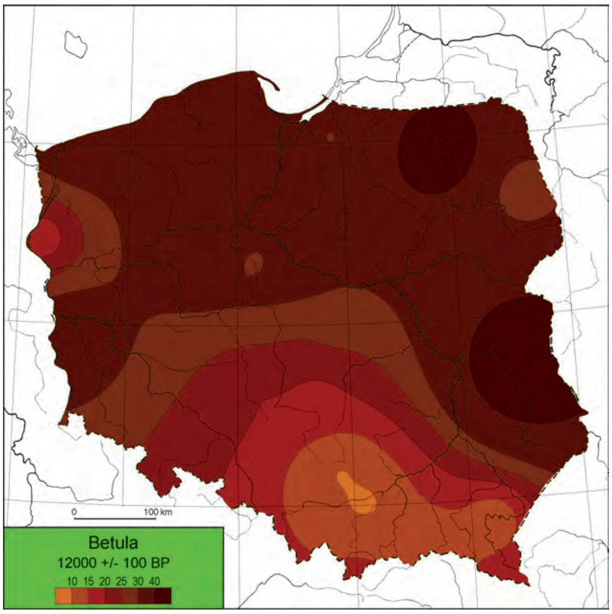
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100 km
Betula
12000 +/- 100 BP
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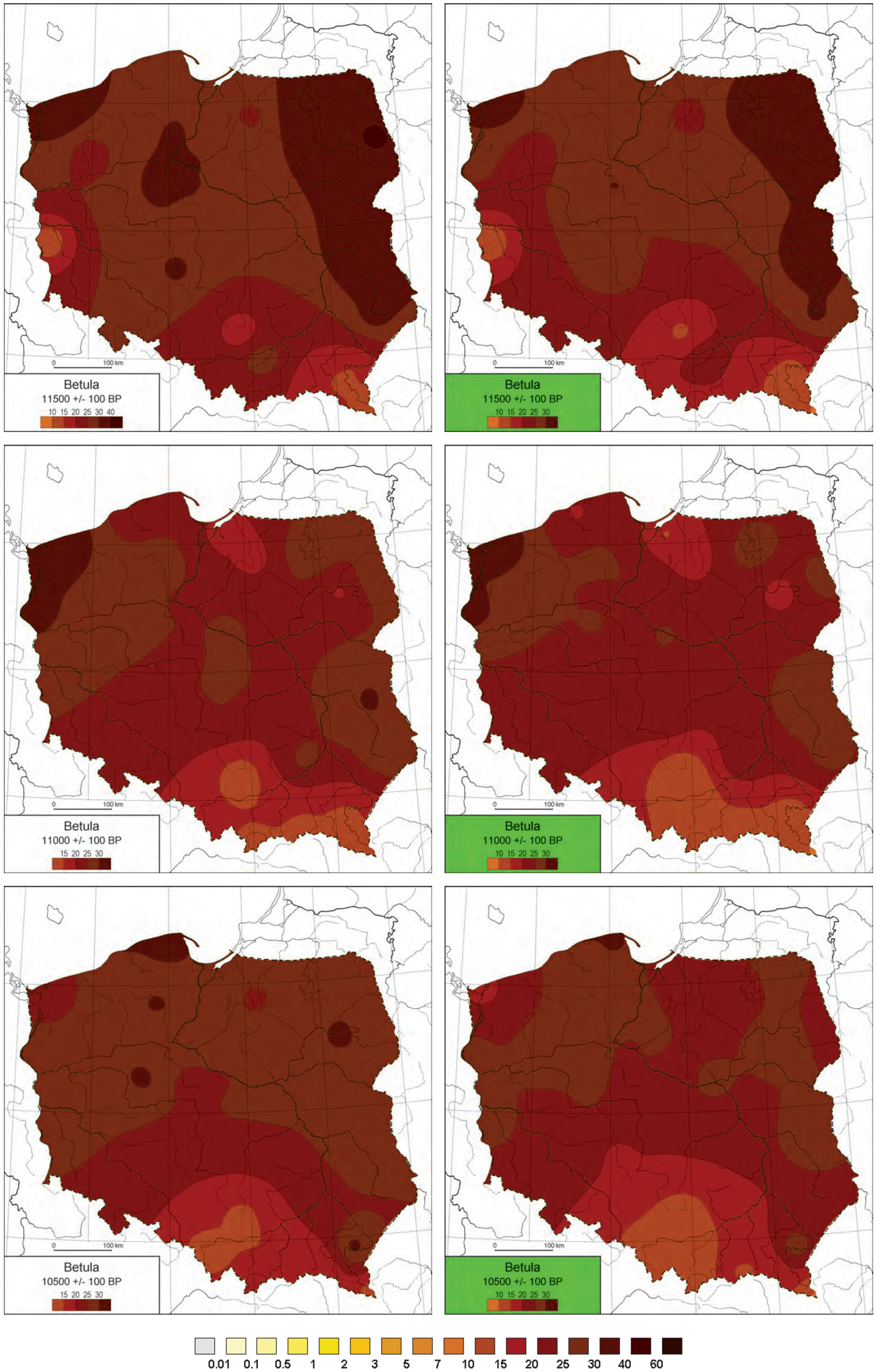
0 100 km
Betula
11500 +/- 100 BP
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Betula
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Betula
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11000 +/- 100 BP
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Betula
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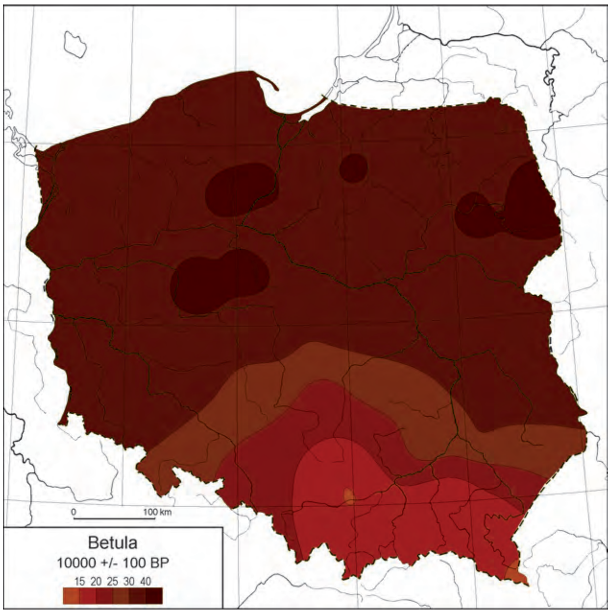
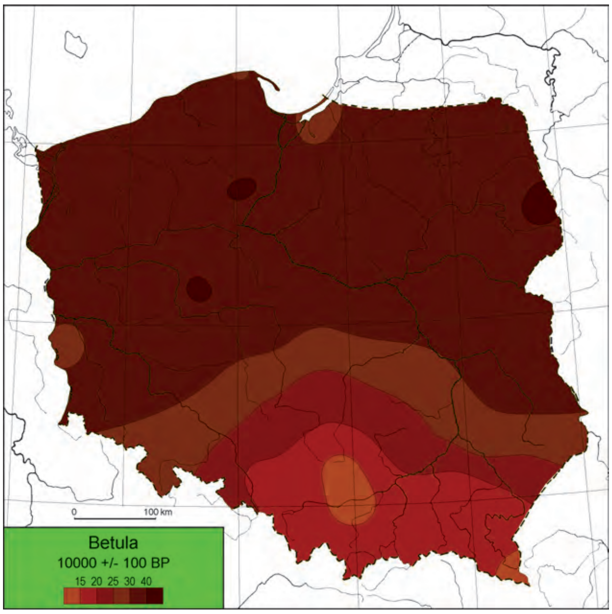

0
100 km
Betula
10000 +/- 100 BP
15 20 25 30 40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100 km
Betula
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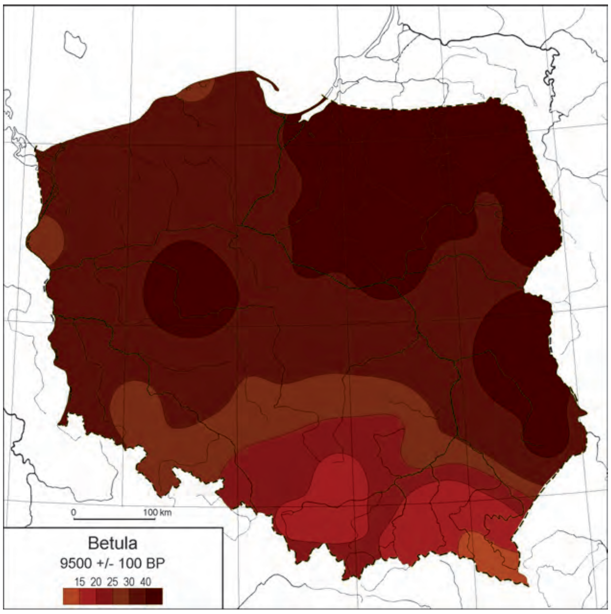
15 20 25 30 40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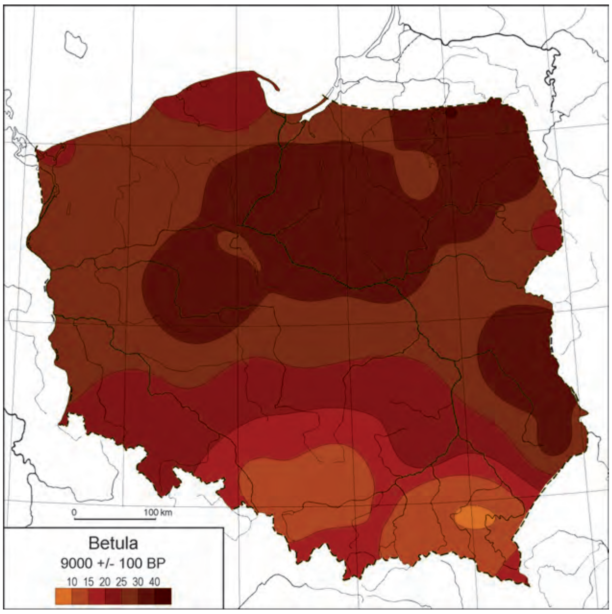
100 km
Betula
9500 +/- 100 BP
15 20 25 30 40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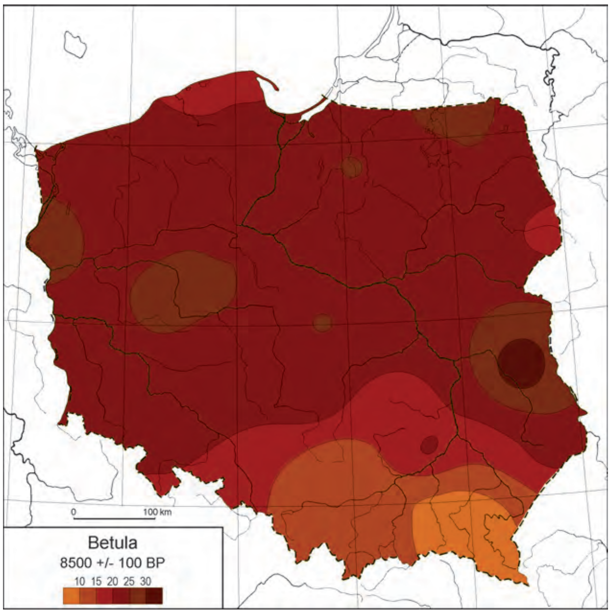
100 km
Betula
9000 +/- 100 BP
10 15 20 25 30 40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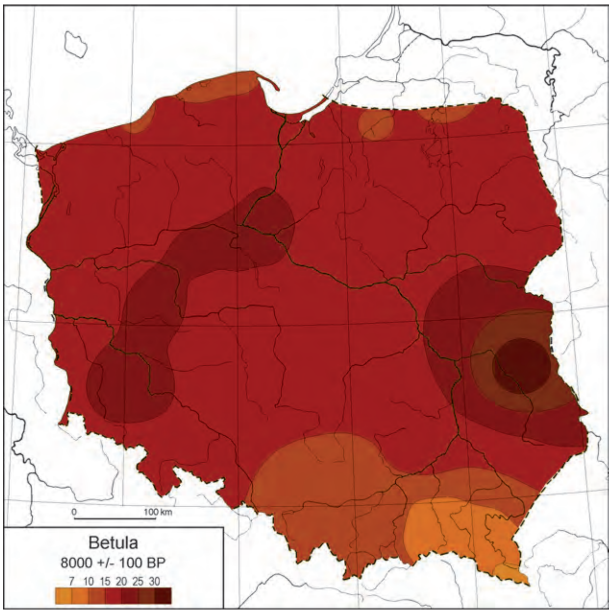
10 15 20 25 30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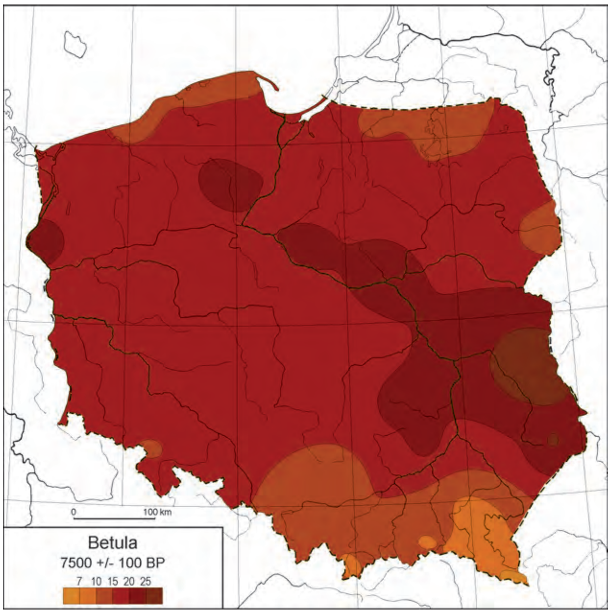
8000 +/- 100 BP
7 10 15 20 25 30


0.01 0.1 0.5 1 2 3 5 7 10 15 20 25 30 40 60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7500 +/- 100 BP
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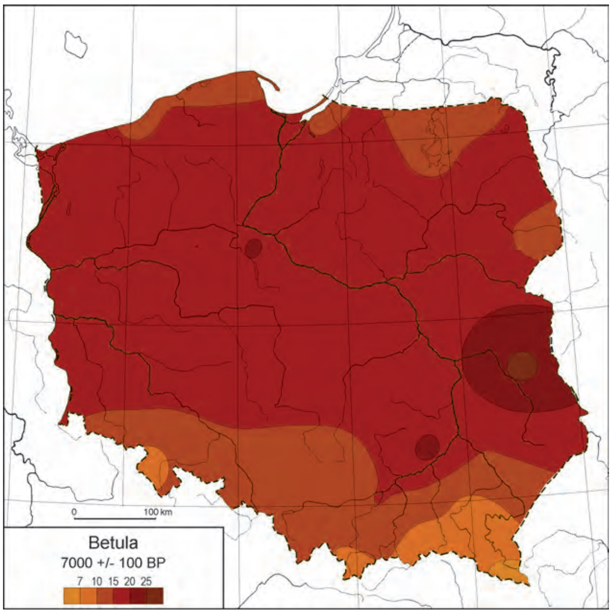
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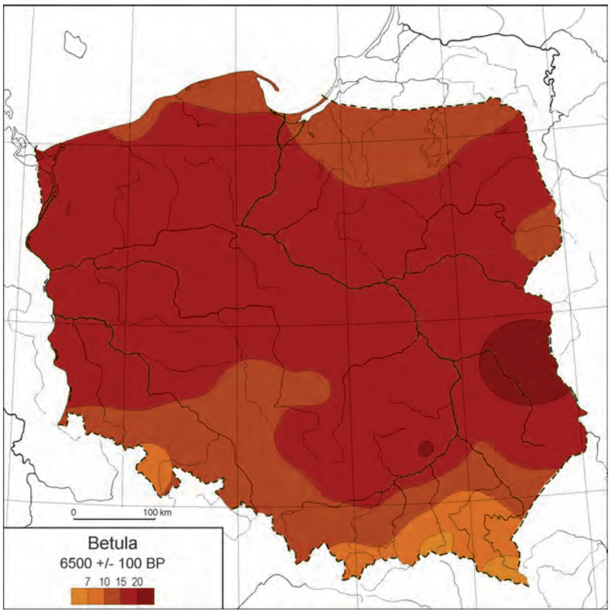
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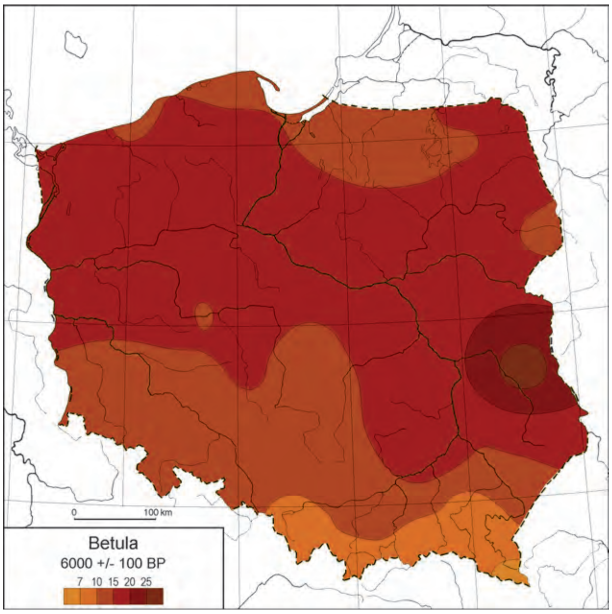
100 km
Betula
6500 +/- 100 BP
7 10 15 20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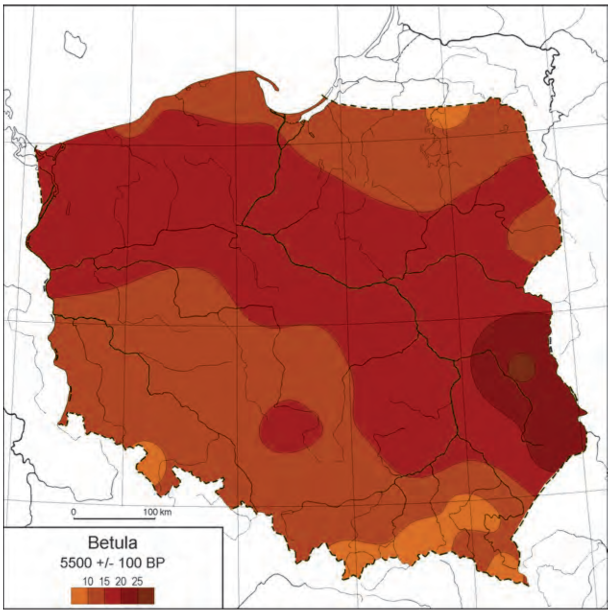
100 km
Betula
6000 +/- 100 BP
7 10 15 20 25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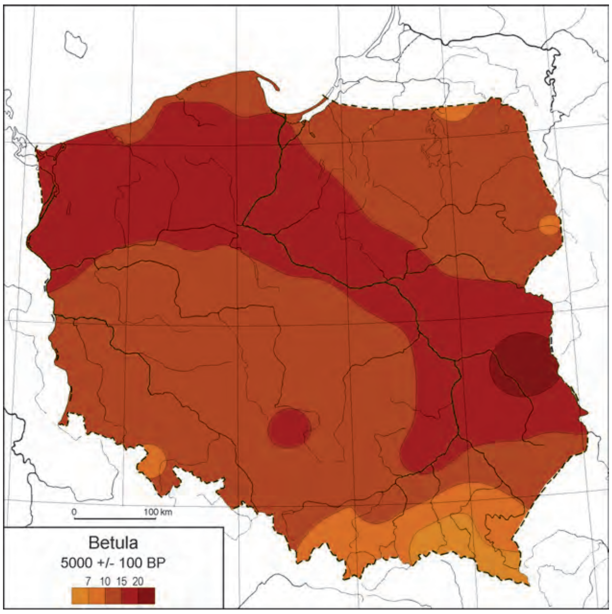
Betula
5500 +/- 100 BP
10 15 20 25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Betula
5000 +/- 100 BP
7 10 15 20


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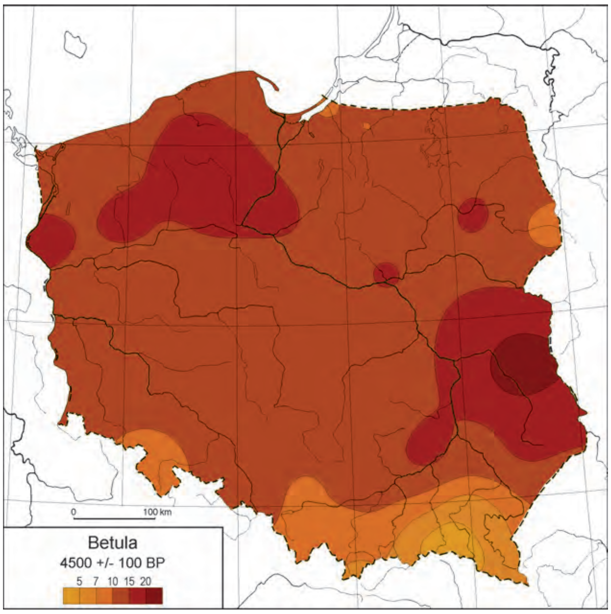
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100 km
Betula
4500 +/- 100 BP
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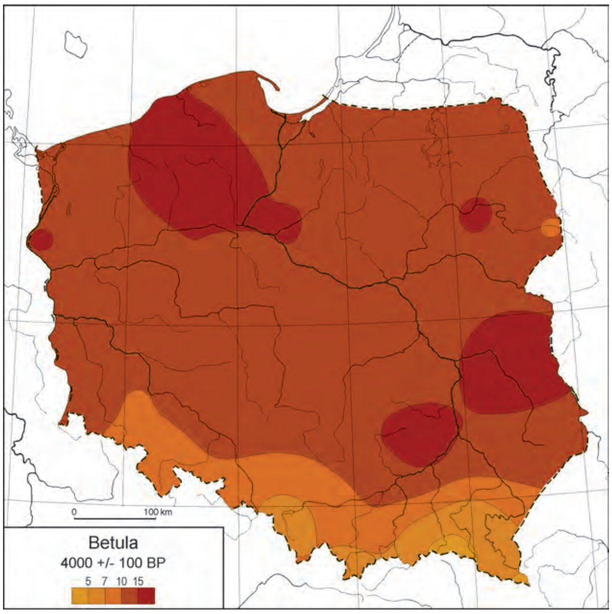
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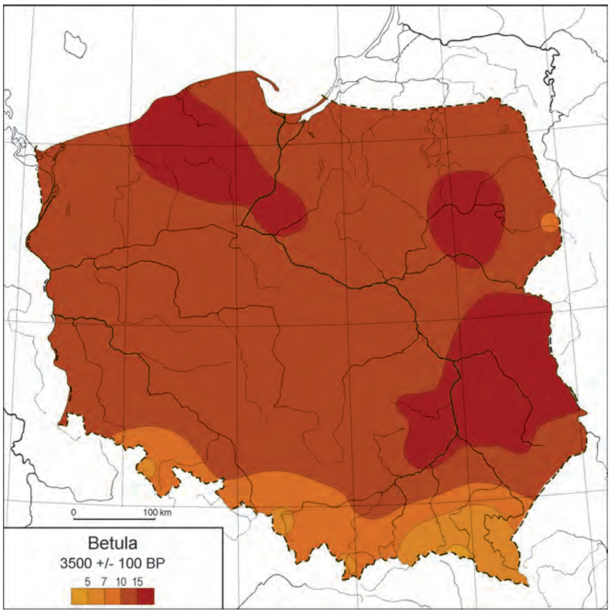
100 km
Betula
4000 +/- 100 BP
5 7 10 15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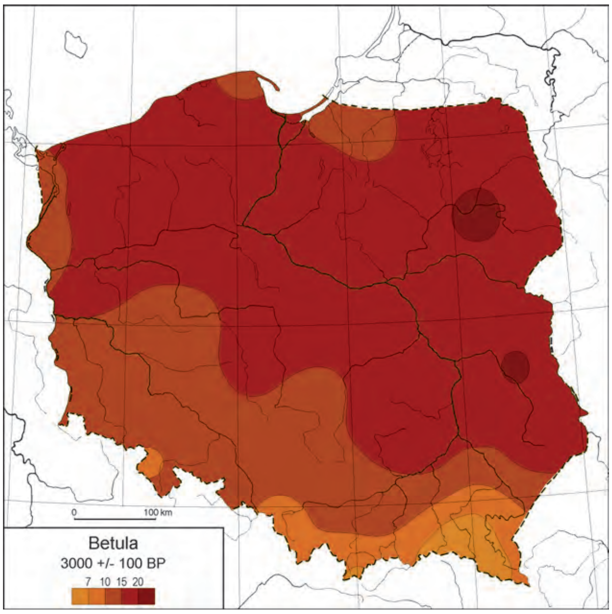
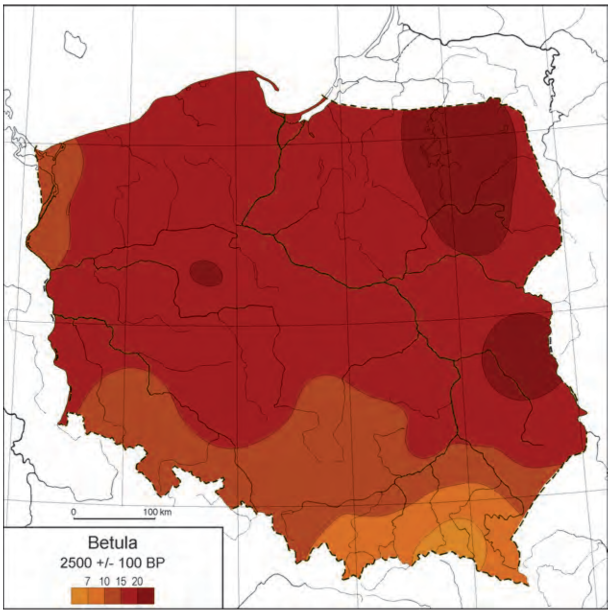
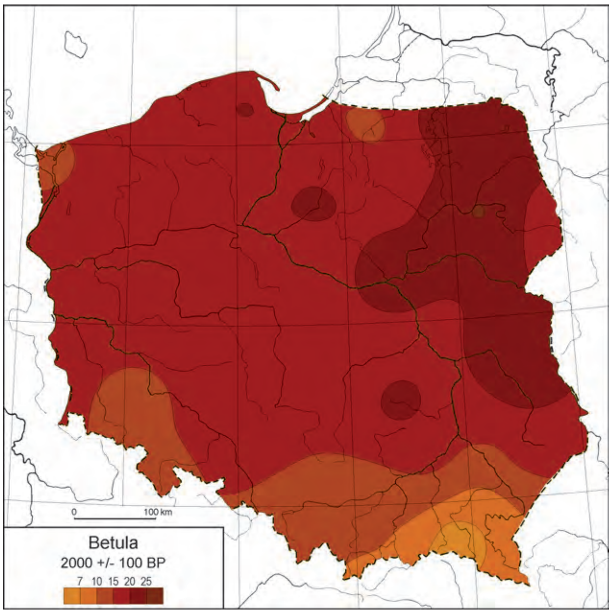
3500 +/- 100 BP
5 7 10 15


0
100 km
Betula
3000 +/- 100 BP
7 10 15 20


0
100 km
Betula
2500 +/- 100 BP
7 10 15 20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100 km
Betula
2000 +/- 100 BP
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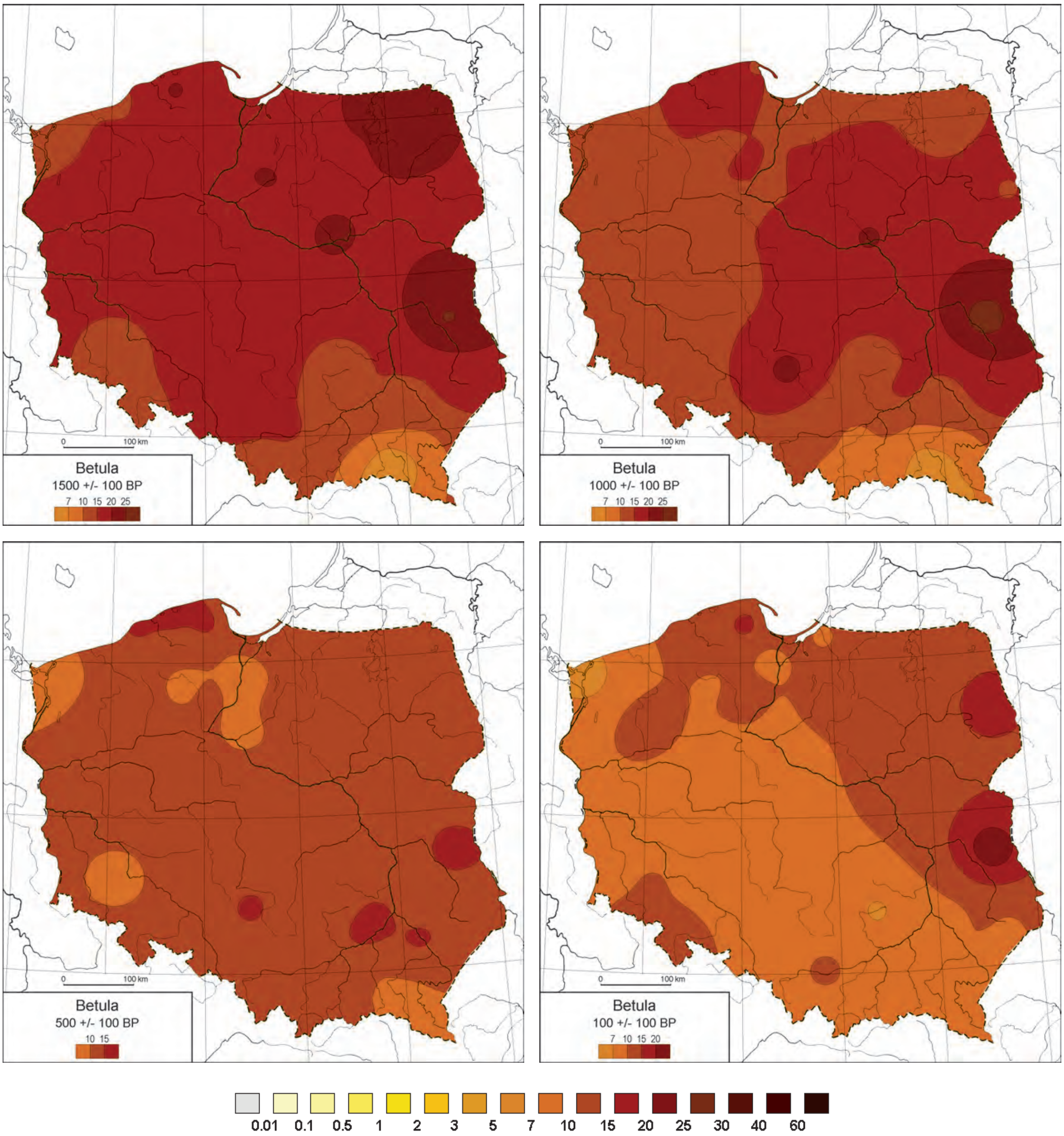
0.01 0.1 0.5 1 2 3 5 7 10 15 20 25 30 40 60


0
100 km
Betula
1500 +/- 100 BP
7 10 15 20 25
0
100 km
Betula
1000 +/- 100 BP
7 10 15 20 25
0
100 km
Betula
500 +/- 100 BP
10 15
0
100 km
Betula
100 +/- 100 BP
7 10 15 20
0.01
0.1
0.5
1
2
3
5
7
10
15
20
25
30
40
60

Carpinus betulus L. – **Hornbeam**

Magdalena Ralska-Jasiewiczowa, Grażyna Miotk-Szpiganowicz, Joanna Zachowicz,
Małgorzata Latałowa, and Dorota Nalepka

Present distribution in Europe

Only two species of hornbeam occur in Europe: *Carpinus betulus* L. and *C. orientalis* Mill. The range of *C. orientalis* comprises south-eastern Europe, and to the west it extends as far as Sicily. *C. betulus* is a species common over the greater part of central southern and western Europe (Fig. 34). In the west it reaches the coasts of the North Atlantic Ocean. In the north its boundary runs across southern England and Jutland, and in southern Sweden it extends to beyond latitude 57°N (its most northern site). Its southern boundary runs along the margin of the Pyrenees, across parts of the Apennine and Balkan Peninsulas and along the southern coast of the Black Sea, to the southern Caucasus as far as Iran. In the east its distribution boundary runs south-east from the Baltic coast of Lithuania to the regions of Vilnius, and Minsk in Belarus, down to the valley of the middle Dniestr river and the mouth of the Danube. However, it excludes the Black Sea lowland (Boratyńska 1993).

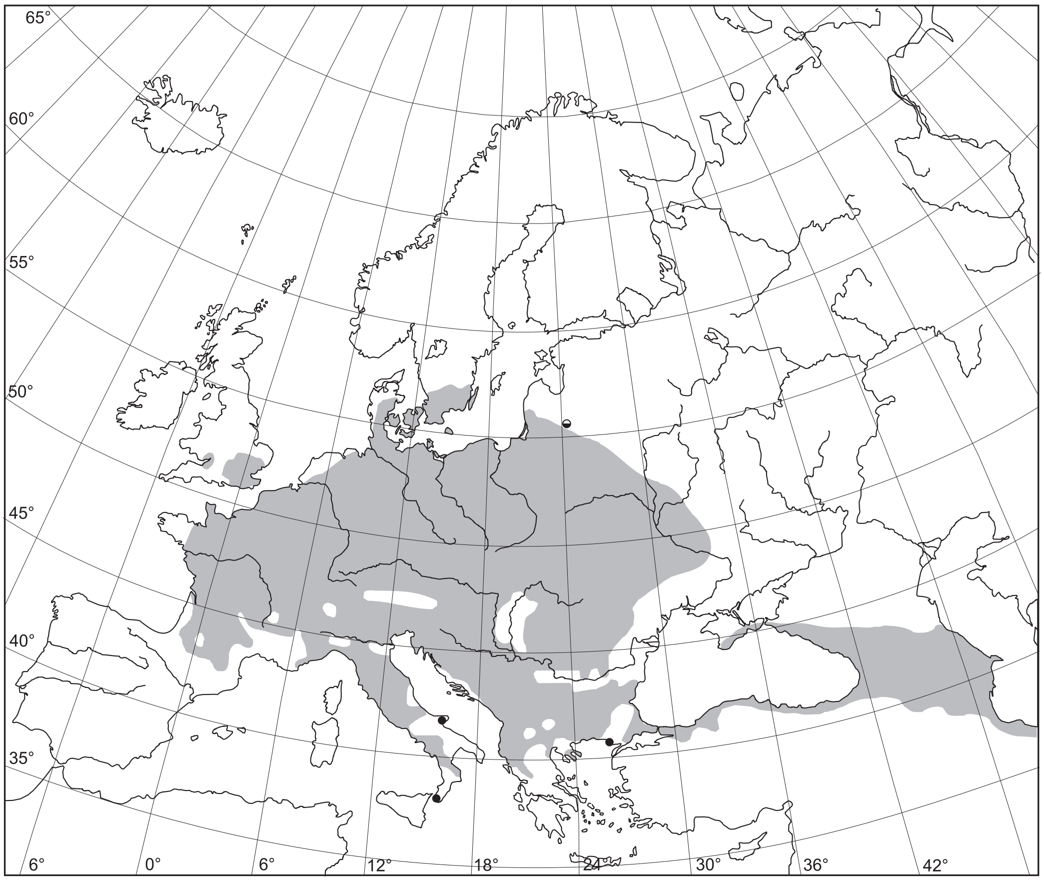


Fig. 34. *Carpinus betulus* – map of present-day distribution in Europe: ● – native isolated occurrence, ◒ – status of site unknown or uncertain (after Jalas & Suominen 1976 and Boratyńska 1993)

Carpinus betulus is a lowland species and in the mountains generally does not exceed an altitude of 700–1000 m a.s.l. Only in very high mountain ranges does it reach 1200 to 1300 m a.s.l. (Boratyńska 1993).

Present distribution in Poland

In Poland hornbeam is a transgressive species, that is to say that Poland lies entirely within the wider distribution limits of this species (Fig. 35). *Carpinus betulus* occurs throughout the country mainly in the lowlands and on the uplands, where its contiguous range generally does not exceed an altitude of 500 m a.s.l. However, the highest individual sites occur in the Bieszczady Mountains at 900 m a.s.l., whilst in the Beskidy Mountains and Gorce range its sites reach locally up to 600–700 m a.s.l. It does not grow in the Tatra Mountains, but in the Sudetes it extends up to 790 m a.s.l. (Boratyńska 1993).

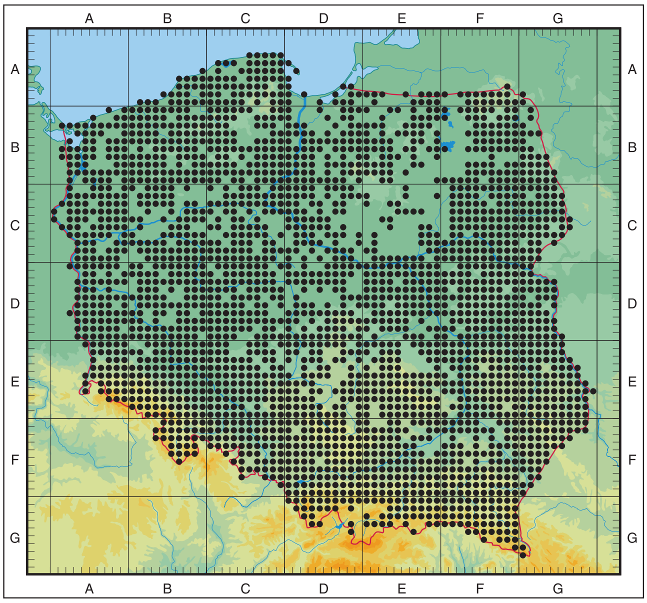


Fig. 35. Present-day distribution of *Carpinus betulus* L. in Poland (after Zając A. & Zając M. 2001)

Ecology

Hornbeam is a component of species-rich, fertile deciduous forests, in company with oak, lime and maple, in which it forms the second stratum of trees forming a dense layer within the interior of the forest.

In Poland it grows under moderately warm conditions, even in the warmest regions and microhabitats (Zarzycki et al. 2002). Lack of sufficient warmth for the development of seeds during the late spring frosts may be a factor limiting its range in the east (Faliński & Pawlaczyk 1993). In Atlantic Europe lack of very warm and long-lasting summer seasons, necessary for regular fruiting of hornbeam, may also be a factor unfavourable to its reproductive success (Huntley & Birks 1983). Considering the distribution of oak-hornbeam forests with lime, in which hornbeam is the most important tree, it is suggested that limiting factors include a mean May temperature above 11°C, a mean July temperature above 16–17°C, and with the monthly means of maximum daily temperatures from April till August also significant (Matuszkiewicz J.M. 2002).

In the regions where forests assigned to the *Carpinion betuli* alliance occur, the total yearly precipitation fluctuates between a minimum of 518 mm and a maximum of 894 mm with a mean value of 609 mm. Hornbeam occurs also in other forest communities, particularly in beechwoods, in areas where the parameters mentioned above are exceeded.

Hornbeam is tolerant of a wide range of soil moisture conditions, preferring slightly moist and moist soils but not tolerating the driest and shallowest soils (Faliński & Pawlaczyk 1993). It can tolerate a wide range of soils: it prefers fertile mesotrophic and meso-eutrophic soils, generally brown and lessivé on a loamy, sandy-loamy or loamy-rocky substratum, as well as rendzinas, loess and also brown alluvial soils with a gley horizon (Faliński & Pawlaczyk 1993).

Hornbeam, often considered as a shade-tolerant species, is actually rather heliophilous, and it requires much more light than the majority of forest trees to grow to maturity from a juvenile stage. Its seedlings die in great numbers due to lack of light and under such circumstances the juvenile stage lasts longer (Faliński & Pawlaczyk 1993).

Hornbeam is a tree favoured by a continental climate. In the western, more Atlantic part of its range it loses out in competition with the more oceanic beech, and, by contrast, in the east where beech disappears, it becomes an important component of forests. However, it favours moderate continentality displaying intolerance of late frosts and drought (Faliński & Pawlaczyk 1993).

Hornbeam occurring in a dense forest starts fruiting at the age of 30 years, while specimens growing in the open places achieve this at the age of 20 years. Successful fruiting occurs every 2–3 years. Hornbeam develops its seeds from May to October. Its fruit is a winged nutlet and its fruiting structures form racemes (Suszka 1993). Some fruits fall in the autumn and sprout in the spring and others stay on the trees and fall during the winter, inducing a deeper state of dormancy (Falińska 1971). This prolongs the potential germination period to several years and provides a chance of forming a seed bank in the soil, which compensates for the high mortality of seedlings (Faliński & Pawlaczyk 1993).

When reproducing sexually, in favourable habitats hornbeam nutlets are scattered and germinate in an abundance which hampers the establishment of other species (Suszka 1993). However, on abandoned farmlands, overgrown with turf, its seedlings die in great quantities. That is why, in the case of secondary succession, this tree appears relatively late, after the light-seeded pioneer trees.

When reproducing vegetatively, hornbeam shows a considerable ability to form offshoots growing from stumps. This is a very important feature in the case of repeated clearing and coppicing. In nature hornbeam is also able to reproduce by layering, when adventitious roots are formed on branches that have collapsed onto the ground. These processes favour its persistence in forests (Faliński & Pawlaczyk 1993).

Hornbeam is very resistant to browsing by animals. Moderate cattle grazing in the forests may in the past have favoured this tree by opening up the forest, giving hornbeam a competitive advantage since its regrowth is faster than that of other deciduous trees. Under the pressure of browsing, hornbeam can develop into a broad, squat shrub, typical of pastureland, sometimes forming persistent scrub that develops into forest-edge communities of *Prunetalia spinosae*. However, too intensive and long lasting grazing may lead to decimation of young trees. After termination of grazing, regeneration of hornbeam occurs very quickly (Faliński & Pawlaczyk 1993).

Hornbeam is one of the most important components of species-rich, fertile deciduous forests of the *Carpinion betuli* alliance. These are the basic lowland forest communities of central Europe. A characteristic feature of these forests is a layered structure. In north-eastern Poland the highest layer is formed by spruce, the next by oak, lime and maple and then, the third one by hornbeam what forms together a very dense canopy. In western Poland there is no spruce layer and the top of canopy is formed mainly by oaks however, hornbeam always fills the interior part of the forest (Faliński & Pawlaczyk 1993).

Hornbeam grows also in various types of riverine forest together with elm, ash and alder, in thermophilous and acidophilous oak forests, and within nearly all the beech communities, where it displays a tendency to expand (Boratyńska 1993). It also spreads into anthropogenic scrub communities on banks, forest edges or in gorges. Today it forms pure woods only very occasionally, for example at a few sites in eastern Poland and in the Sudetian foreland. Such communities are often a result of anthropogenic degradation (Faliński & Pawlaczyk 1993).

The successful and efficient life strategy of hornbeam in *Carpinion betuli* forests combines features found in many other types of trees, for example those of pioneer tree (high reproductive capacity, rapid colonisation, light-demanding, tolerance of mechanical damage), of oak (longevity, extended seed dormancy), of lime (vegetative regeneration by offshoots and layering), of birch (persistent seed bank), and even of fir (persistent cohorts of juvenile specimens). Combining these various features, hornbeam is a tree that spreads freely and is very often regarded as a weed (Faliński & Pawlaczyk 1993).

POLLEN PRODUCTION AND DISPERSAL

In Poland hornbeam usually flowers at the end of April. It is a wind-pollinated tree. Its pollen season is short, usually lasting a few, rarely a dozen or so days. In successive years the amount of pollen released to the atmosphere is very variable. In years of abundant pollen production it may exceed 3 times the average value and 20 times the amount of poor years. Production of hornbeam pollen displays a biennial rhythm (Aerobiologic Database, Gdańsk 1994–2002). Hornbeam pollen production also depends on a habitat, community and density of tree stands. Compared to other forest trees it is relatively poor pollen producer. It produces two times less pollen than beech and almost three times less than oak (Sugita et al. 1999). *Carpinus* pollen possesses relatively weak aerodynamic features, resulting in it remaining airborne a relatively short time, which limits its capacity for distant distribution. High air temperatures during its flowering period may favour better pollen dispersal by lifting pollen higher into the atmosphere. Analyses of present-day samples from the Wielkopolska (Tobolski 1991b) have allowed estimation of how representative hornbeam values in pollen diagrams are of actual vegetation. In surface pollen assemblages from the interior of an oak-hornbeam forest, this author found only about 10% of hornbeam pollen. In surface samples from the sediments of lakes surrounded by forests with abundant hornbeam the maximum pollen values were 3.2%, and in a lake situated within a deforested area they reached only 1.5%. In surface assemblages from the sediments of a few lakes in Pomerania situated within a zone of forests with hornbeam, *Carpinus* pollen occurred only in small quantity (0.5–2%) (Latałowa & Święta 2002). Although it is not possible to make direct correlation between the analytical results from these samples and those from samples reflecting the past (Tobolski 1991b), these data indicate a considerable underrepresentation of hornbeam in pollen assemblages. Consequently it seems that even values of <1% in some cases may indicate local presence of *Carpinus*, certainly less than the figure proposed by Huntley and Birks (1983). They considered that values >5% indicated a considerable presence of hornbeam in a region, and >10% as indicative of its dominance in local forest communities.

EXPANSION IN EUROPE DURING THE LATE GLACIAL AND HOLOCENE

Over twenty years ago Huntley & Birks (1983) were able to trace in outline the history of the expansion of *Carpinus* in Europe during the Holocene, although, of course, many more recent publications, especially in southern Europe, have added more detail to the story. They surveyed the occurrence of low but scattered values of hornbeam pollen at sites in Italy and eastern and south-eastern Europe in the Late Glacial and at the beginning of the Holocene, prior to 9000 BP. Beginning with signs of a weak expansion at about 8500 BP in Italy, the former Jugoslavia and Romania, they envisaged a front of expansion by 7000 BP, running from north Italy to the north-east extending to south-eastern Poland. The *Carpinus* pollen values recorded at that time in Romania exceeded 10% but had declined by 5500 BP. The data presented in the Huntley & Birks atlas (1983) for 4000 BP and 3000 BP are obviously outdated. *Carpinus* expansion in central Europe, also at lower altitudes in the mountains, started generally at about 4000 BP. Its irregularity probably resulted from two factors: competition with beech and strong associations with the development of prehistoric settlements.

Migration pattern in Poland (Fig. 36)

9000 – 7000 BP

The dispersed and very low *Carpinus* pollen values, showing lack of continuity on subsequent maps evidence long distance transport or rebedding.

6500 – 5000 BP

On the 6500, 6000 and 5500 BP maps *Carpinus* pollen values up to 0.5%, gradually spread from the south, south-west, and the east towards the centre of the country. This may indicate intensification of long-distance pollen transport from the directions mentioned, probably from approaching outposts of migrating hornbeam populations. The subsequent increase of hornbeam pollen values between 5500 and 5000 BP, up to 1–2% in the western part of the Beskid Wysoki range and in the Bieszczady Mountains, probably documents the appearance of the first scattered trees of hornbeam, coming just from these directions and already established at these sites.

Reliable data documenting dominance of hornbeam in forests within the age interval discussed are known from the Retezat Mountains in the southern Carpathians of Romania. The first maximum (>15%) of *Carpinus* pollen has been recorded there between 6645 and 5730 BP (Farcas et al. 1999).

4500 BP

Hornbeam apparently reached the area of the Bieszczady Mountains from the south-east, as evidenced by pollen values of 3–5%. The abundant occurrence of hornbeam in the north-western part of the Romanian Eastern Carpathians as shown by pollen values of 5–15% (even to 20%), is dated to 4200 BP (Farcas et al. 1999, Björkman et al. 2002, 2003). An increase in pollen values up to 2% is recorded in the foothills of the Carpathian Mountains in Poland, and in the Sandomierz Depression as well as along the margins of the Świętokrzyskie Mountains. At the same time values of up to 1% can be found over the whole of south and south-eastern Poland and, in the north-east, in the Suwałki Lake District and in some parts of the Mazurian Lake District.

4000 BP

A strong expansion of hornbeam from the south-east started at that time. In the Bieszczady Mountains, the Beskid Niski range and in the Jasło-Sanok Depression *Carpinus* reached values of 10% and more, and in the eastern foothills together with the Sandomierz Depression up to 5%. In the mountains hornbeam appeared, in general, synchronously with beech, but its expansion advanced much faster. The expansion from the south-west did not develop at that time.

Carpinus pollen values up to 3% are found over most of south-eastern Poland including also the Małopolska Upland. Hornbeam became a substantial element in the deciduous forests there, however in the Lublin Upland, in the Roztocze and Wołyń it occurred in lesser amounts, although at the present day these areas display the most favourable climatic conditions for hornbeam (Matuszkiewicz J.M. 2002). The reasons are unclear.

The lowest pollen values (up to 1%) occur in north-western Poland including the Noteć and the Vistula river basins as far as the middle lake districts. This is a slightly more extensive area in comparison with that where hornbeam finds not very favourable conditions today. There, it has now become ousted by beech (Matuszkiewicz J.M. 2002). The eastern lake districts recorded values up to 2%.

3500 – 3000 BP

At 3500 BP *Carpinus* occupied the lower slopes of the Bieszczady Mountains (pollen values up to 15%) growing mainly in company of *Ulmus* and *Corylus*. It contributed together with *Ulmus* and *Corylus* to the formation of deciduous forests on the mountain foothills and in the Sandomierz Depression. Everywhere in the mountains, locally prior to 3500 BP, the expansion of *Fagus* started to force *Carpinus* down from higher altitudes. Lower representation of hornbeam pollen (up to 5%) is observed in the lower parts of the Western Beskidy Mountains. In the uplands of south-western Poland and in the Sudetes its values are slightly higher (up to 7%).

A distinct expansion of hornbeam proceeded through lowland Poland, from the south to the north west, apart from the Baltic Coastal Zone, part of eastern Poland and the north-eastern lake districts. It is documented by high pollen values (about 20%) particularly in central Poland, and in some pollen diagrams from the Wielkopolska area its values reach 40%.

The high values of hornbeam pollen in those sections of pollen diagrams illustrating the regression of human settlements at the Gniezno Height led Tobolski (1991b) to assume that at about 3400 BP a particular type of pure hornbeam forest occurred in Wielkopolska. This author explained such an intensive development of hornbeam forests in this area as resulting from a stronger continentality of climate than found in other lowland regions of Poland. However, considering this assumption, it seems inexplicable why in the whole area of the most continental part of eastern Poland the amount of hornbeam does not exceed 5% at that period.

On the 3000 BP map the amounts of *Carpinus* fall (3–5%) in the Bieszczady Mountains, in the Beskid Niski range and in their forelands. This is an obvious result of pressure from the strong expansion of beech. In the uplands of south Poland the higher and lower values of hornbeam, are most likely connected with the effects of human settlements. This was the initial period of the development of the Lusatian culture. In the western part of central Poland the strong expansion of hornbeam still advanced, increasing even its previous maximum in the Wielkopolska area. The higher pollen values reach in the east the Bug river valley, Roztocze and Wołyń. *Carpinus* pollen values up to 5% may be found across the whole of northern Poland.

2500 BP

The amounts of hornbeam in the forest communities of Poland fall in comparison with the previous period. The pattern of hornbeam occurrence forms a mosaic, due to the spatial differentiation of economic management. In the areas displaying the higher values on the 3000 BP, map there is a fall in *Carpinus* pollen values at 2500 BP, for example in parts of the Silesian Upland, in the adjacent Kraków-Częstochowa Upland and in the Świętokrzyskie Mountains. Of the western centre of hornbeam occurrence there are only traces left, and the 5% isopoll line shifts southwards, generally to the Kujawy and Mazovian Lowland. This indicates the destruction of forest communities by the long-lasting activities of the Lusatian culture, which was then in its decline stage.

2000 BP

At this time falls of *Carpinus* pollen values below 5% in the southern Poland indicate considerable deforestation. In this area settlements of the Early Roman Period started to appear (Godłowski & Kozłowski 1979) with still moderately developed agriculture (Lityńska-Zając 1997). In the lake districts hornbeam pollen occurs more abundantly than on the 2500 BP map. This may be the consequence of economic recession following the collapse of the Lusatian culture in the earlier part of the Subatlantic period (2400–2200 BP). This phenomenon is recorded in a number of pollen diagrams from the lowlands as small culminations first of birch and then subsequently of hornbeam pollen, which may be observed on the additional 2200 BP map (Ralska-Jasiewiczowa et al. 2003b, Fig. 36, this volume), intermediate between the time horizons used in this atlas.

1500 BP

The 1500 BP map shows the widest and fullest distribution that the hornbeam forests reached during the Holocene. In the western Poland values above 10% run as a broad belt from the northern margins of the Małopolska Upland northwards as far as the Baltic Coastal Zone and central lake districts. Values above 40% appear locally in Wielkopolska and in the maritime region. The majority of the country records pollen values of 7–10% pollen, except for the south, where the *Carpinus* pollen values are lower (the mountains and the uplands occupied by beech) and a belt along the eastern boundary of Poland (many marshy areas). This is a time of general forest regeneration connected with the Migration Period.

1000 – 100 BP

These maps show the gradual regression of hornbeam due to growing human pressures. Slightly higher values persist for a somewhat longer time in the Sandomierz Depression, in the Roztocze area and in the river basin of the middle Vistula. The contraction of hornbeam populations is connected with the different rates of human population growth in Early Medieval and later times.

Conclusions

During the initial period of its expansion, in the eastern part of the Carpathians hornbeam extended its range at the same time as beech but at much faster rate. In the lower montane zone it may have replaced *Ulmus glabra*, which was then in a regression. At that time hornbeam may have formed forests at lower altitudes together with hazel. When beech reached the maximum of its distribution, hornbeam was restricted to habitats in the forelands and its occurrence in the mountains was considerably reduced.

In the lowlands the maximum pollen values of hornbeam occurred in the areas where *Corylus* was abundant earlier in the Holocene (for example in the Wielkopolska area), and hornbeam expansion followed the recession of hazel. As it proceeded from between 4000 and 3500 BP, it is difficult to assume that it was related to climatic conditions. It seems rather that the unstable forest communities, with hazel and oak dominating then in many areas of Poland, were susceptible to penetration by a new species.

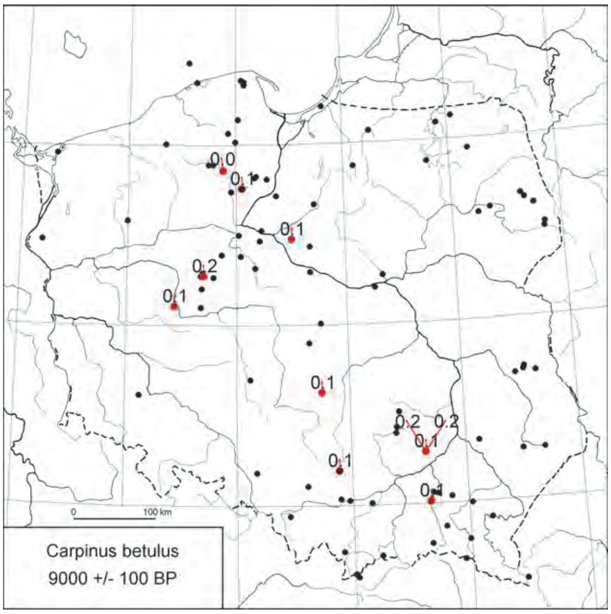
In the period of 3500–1000 BP the maps do not record all the rises and depressions of hornbeam pollen values. It concerns, for example, the second hornbeam rise after the fall of the Lusatian culture (ca. 2400 BP). These phenomena are not synchronous, and do not always fit the time levels used for maps in this paper.

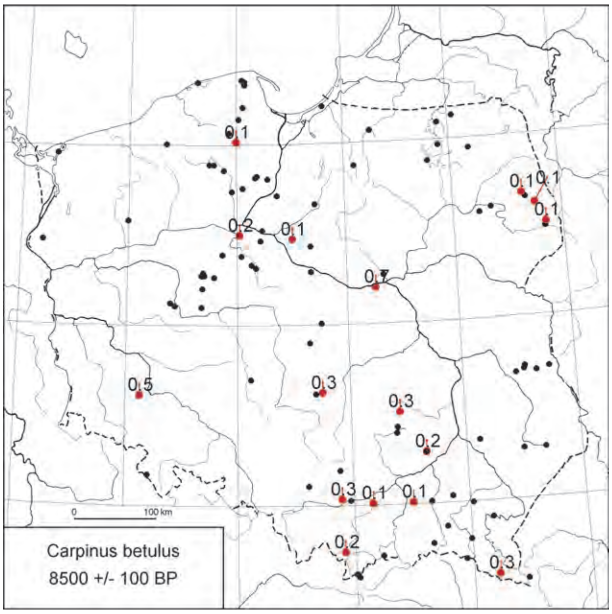
An analysis of the *Carpinus* maps for 3500–1500 BP suggests the following considerations: *Carpinus* is today a species of moderately continental climates (see Ecology, this chapter) and its eastern distribution limit runs not very far from the eastern frontier of Poland.

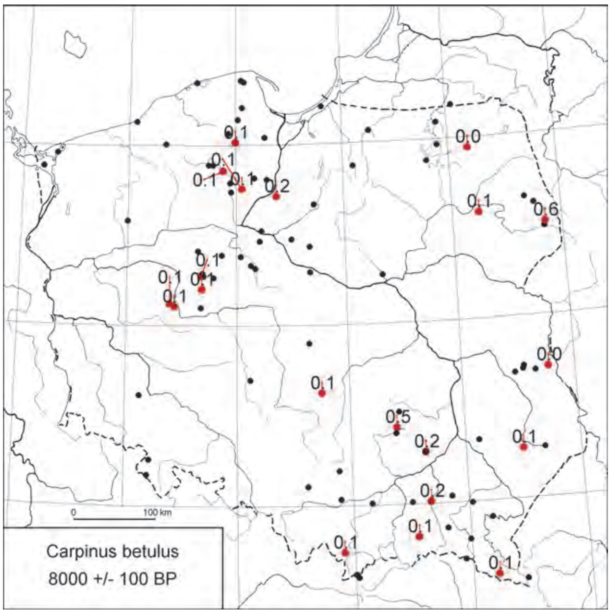
During the period 3500–1500 BP a centre of hornbeam-dominated forests shifted distinctly westwards, where today only impoverished associations of hornbeam forests still grow (Matuszkiewicz J.M. 2002). In eastern Poland hornbeam was then only represented by lower pollen values. Could this have been the result of a more continental climate than today? In the middle of this period (after 2500 BP) a change of climate to cooler and wetter conditions took place. At that time (2500 and 2000 BP maps) *Carpinus* showed a mosaic pattern of distribution with small, dispersed local centres. Around 1500 BP its highest values were concentrated again in the west and north of Poland. Thus, it is quite difficult to explain high values of *Carpinus* in the Wielkopolska by a particular continentality of climate (Tobolski 1991b). It seems rather to be a combination of anthropogenic, edaphic and possibly also some kind of climatic factors. Lower values of hornbeam in the east might be explained by habitat conditions and, possibly, by the proximity of the distribution range limit of the species to the east in Lithuania and Belarus, where the climate is, of course, more continental.

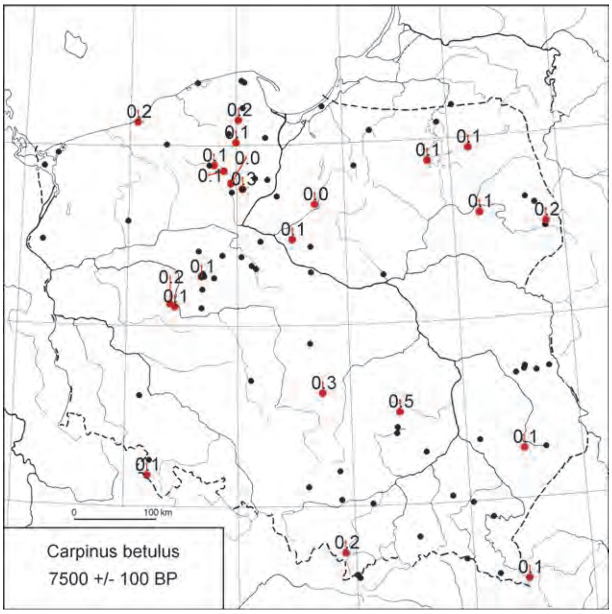
In the majority of pollen diagrams from lowland Poland three expansion periods of hornbeam between 3500 BP to 1500 BP, separated by two periods of its regression have been recorded. In many diagrams these expansions are preceded by rises in birch pollen or are synchronous with them. This pioneer tree is able to colonise, shade, and so destroy the turf formed after abandonment of arable cultivation. At that point, and not before, hornbeam seedlings can become established and form new woodland communities.

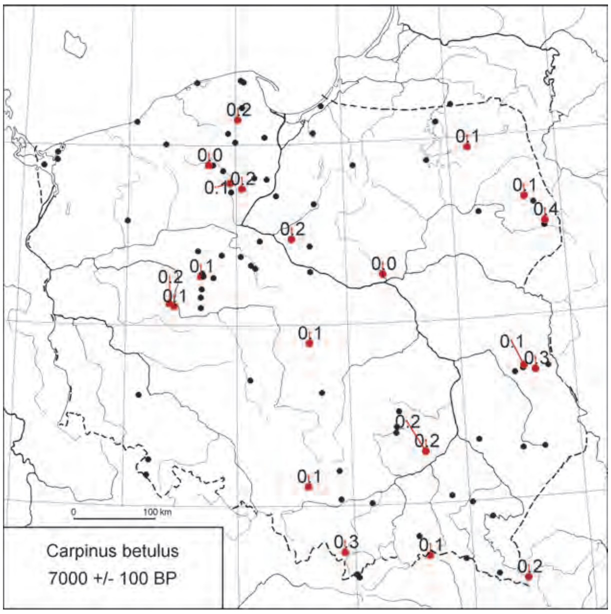
Fig. 36. *Carpinus betulus*: dot and isopollen maps for 9000–100 ^{14}C yr BP. The map for time-horizon 2200 BP is added











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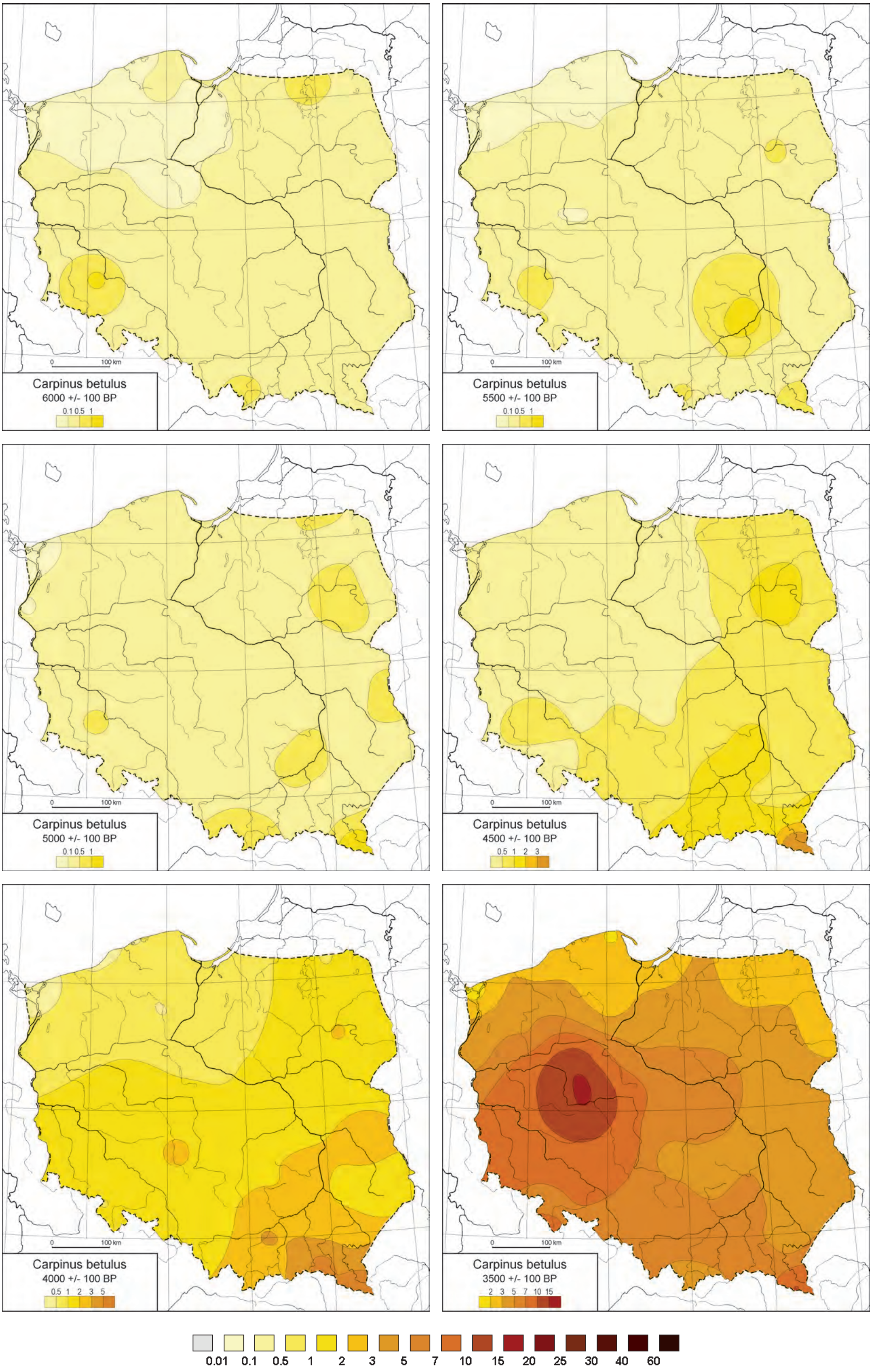
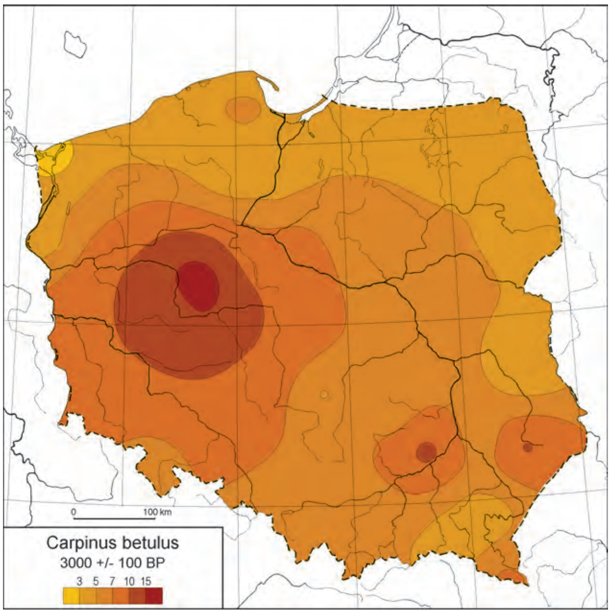
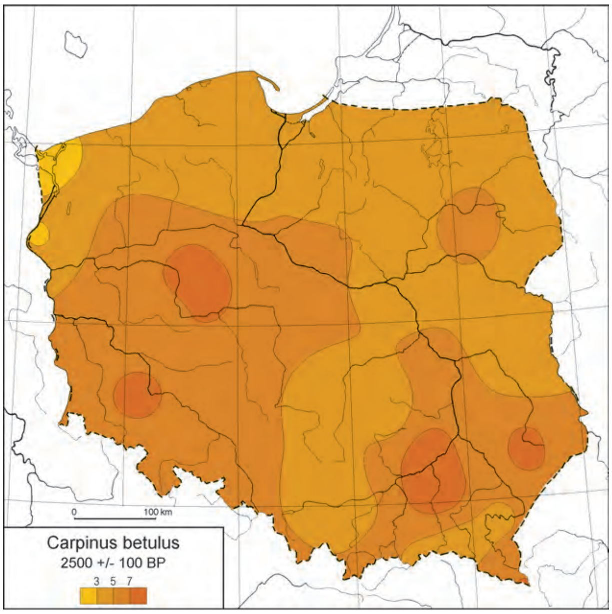
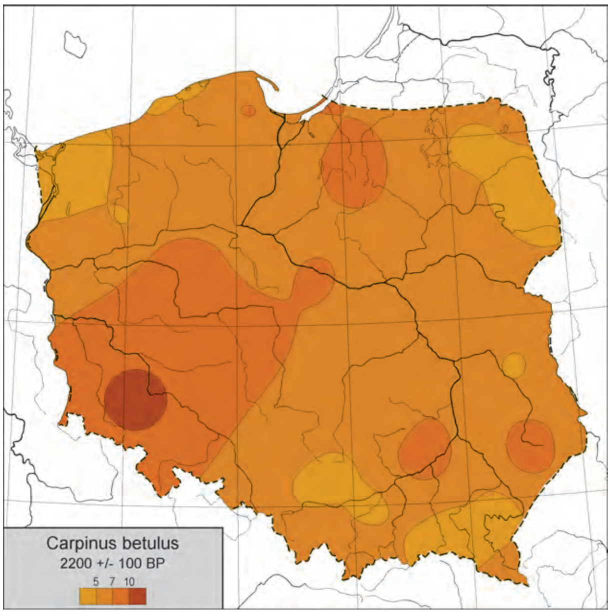
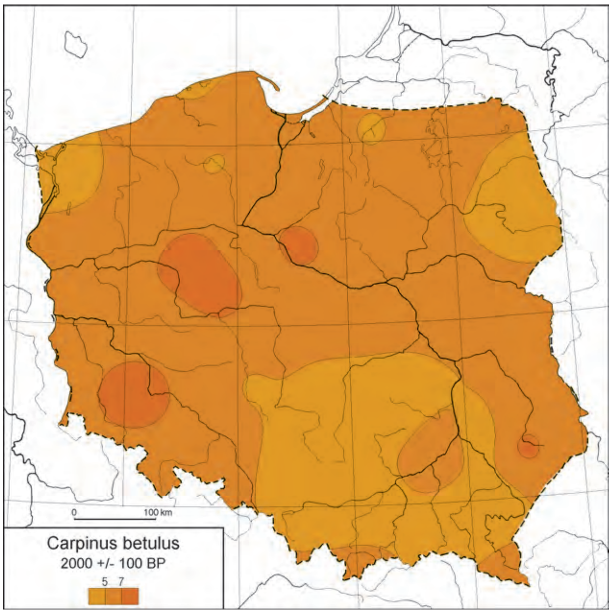
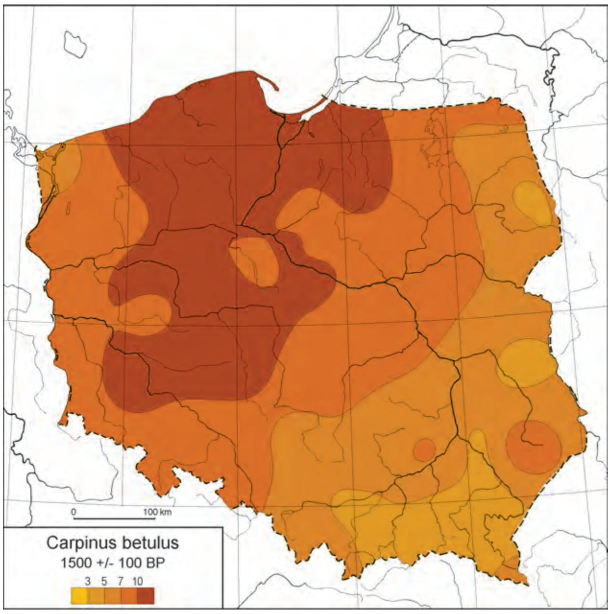

0
100 km
Carpinus betulus
6000 +/- 100 BP
0.1 0.5 1
0
100 km
Carpinus betulus
5500 +/- 100 BP
0.1 0.5 1
0
100 km
Carpinus betulus
5000 +/- 100 BP
0.1 0.5 1
0
100 km
Carpinus betulus
4500 +/- 100 BP
0.5 1 2 3
0
100 km
Carpinus betulus
4000 +/- 100 BP
0.5 1 2 3 5
0
100 km
Carpinus betulus
3500 +/- 100 BP
2 3 5 7 10 15
0.01 0.1 0.5 1 2 3 5 7 10 15 20 25 30 40 60

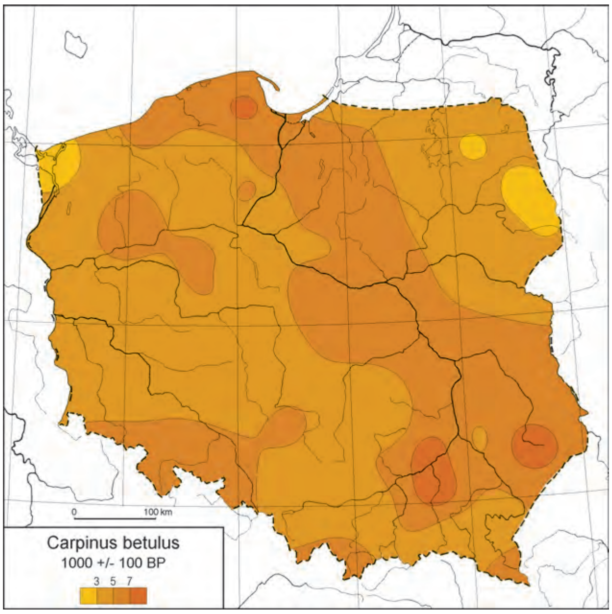












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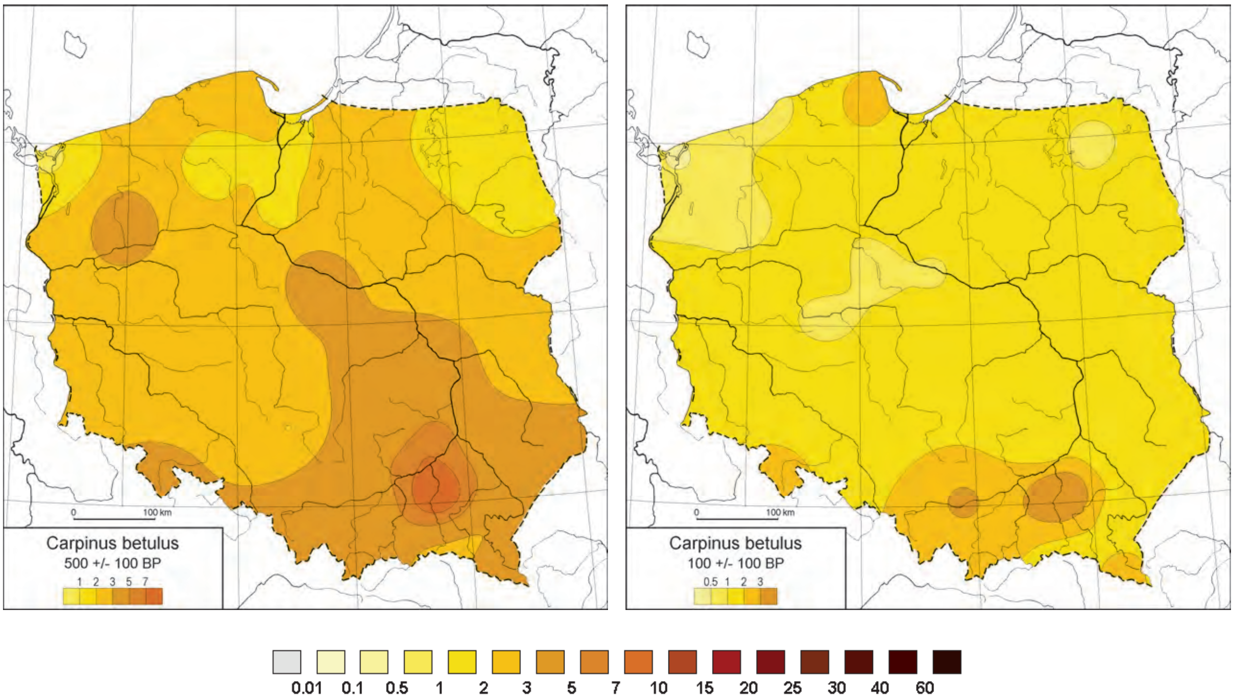
0
100 km
Carpinus betulus
500 +/- 100 BP
1 2 3 5 7
0
100 km
Carpinus betulus
100 +/- 100 BP
0.5 1 2 3
0.01
0.1
0.5
1
2
3
5
7
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15
20
25
30
40
60

Corylus avellana L. – Hazel

GRAŻYNA MIOTK-SZPIGANOWICZ, JOANNA ZACHOWICZ, MAGDALENA RALSKA-JASIEWICZOWA, AND DOROTA NALEPKA

PRESENT DISTRIBUTION IN EUROPE AND IN POLAND

Morphologically *Corylus*-type pollen includes three species of hazel occurring in Europe (*C. avellana* L., *C. colurna* L. and *C. maxima* Miller) and occasionally has included *Myrica* pollen. Of those *Corylus avellana* is the most widespread species. It occurs across almost the whole of Europe as far as the Caucasus Mountains and the Crimean Peninsula. The northern limit of its range runs from the Orkneys in the west up to 68ºN in Norway, 64ºN in Sweden, and 63ºN in Finland. In northern Russia it reaches Lake Ladoga. Hazel is absent from the northernmost parts of Europe and from some coastal regions of southern Europe, particularly in Iberia and the Balkan Peninsula, (Jalas & Suominen 1976, 1988b). The occurrence of *Corylus colurna* and *Corylus maxima* is restricted to certain areas of south-eastern Europe (Jalas & Suominen 1976, 1988b). *Corylus avellana* is the only hazel species occurring in Poland (Fig. 37). It is common in forests and clearings in the whole area including the lower montane forest zone (Szafer et al. 1969, Zając A. & Zając M. 2001).

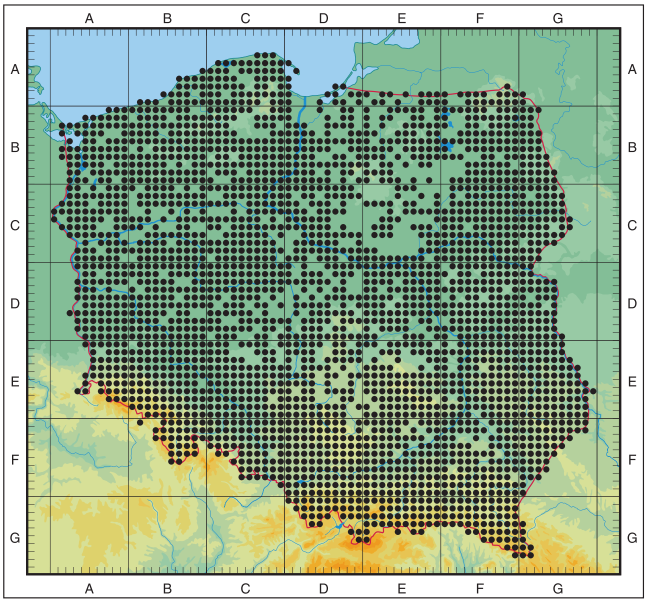


Fig. 37. Present-day distribution of *Corylus avellana* L. in Poland (after Zając A. & Zając M. 2001)

ECOLOGY

Corylus avellana is a large shrub or tree up to 2 to 6 m high. It is a nanophanerophyte (Zarzycki et al. 2002) primarily found in understorey of deciduous, mixed, and coniferous forests (Mowszowicz 1983) as well as in xerothermic brushwoods (Seneta 1991). However, near the northern limit of its range, where the habitat and climatic conditions are unfavourable for mixed deciduous forests, hazel may become one of the dominant species in forest communities (Huntley & Birks 1983). *Corylus avellana* prefers sunny sites, temporarily or periodically shaded, both in the regions with mean yearly temperature ca. 9ºC and in those, such as the lower montane forest zone or the north lowland division, characterised by cool climates (Zarzycki et al. 2002). It dislikes excessively dry climatic conditions (Hegi 1981).

Hazel grows on a wide variety of soils from dry to moist and fertile, acid (pH 4.5–5.5) to neutral, on humic-mineral to sandy clay soils, or on stony clay with a considerable skeletal fraction (Zarzycki et al. 2002). It has been observed to grow best on slightly moist, fertile soils. It is a very tolerant species with regard to light conditions and can grow well even in shaded sites, though then it sets fruit more sparsely. It avoids infertile, dry and wet soils. It plays an important role in biocoenoses – it provides shaded conditions for soil formation, to which it contributes easily-decomposing litter; it also supplies nuts for rodents and birds to consume (Seneta 1991).

Corylus avellana occurs mainly in associations of the *Querco-Fagetea* class. It is often accompanied by *Poa nemoralis* and *Viola reichenbachiana* in the communities of this class. *Acer platanoides*, *Fraxinus excelsior*, *Anemone nemorosa*, *Carex sylvatica*, *Galium odoratum*, and *Hepatica nobilis* occur also frequently together with hazel, though not in all associations (Matuszkiewicz J.M. 2002).

POLLEN PRODUCTION AND DISPERSAL

The pollination period of hazel generally occurs during February and March but it can be postponed until April in the case of cold springs (Aerobiologic Database, Gdańsk 1994–2002). It is quite difficult to interpret the role of *Corylus* in plant communities on the basis of its pollen percentage values. Investigations of surface pollen deposition have proved that hazel can still occur locally even when its pollen values are lower than 2%. Values between 2% and 25% suggest that hazel is present in mixed, deciduous forests, mainly in the shrub layer, whereas pollen values higher than 25% indicate its presence in woodland communities where hazel is either one of the main species or even dominant (Huntley & Birks 1883).

Andersen (1970) proposed a pollen productivity factor of 1.0 for *Corylus*, where it occurs as an understorey shrub, but 4.0 when it is present as a canopy tree, with reference to *Fagus sylvatica* as the standard species, whose pollen productivity is 1.0. The rate of *Corylus* pollen fall in air is 0.025 m/sec and its productivity factor in relation to grasses (Gramineae=1) is 1.4 (Sugita et al. 1999). As *Corylus* produces its pollen before the appearance of leaves when the wind speed between trees is relatively high, pollen can be transported quite long distances (Birks & Birks 1980).

EXPANSION IN EUROPE DURING THE LATE GLACIAL AND HOLOCENE

Corylus pollen can be found in Quaternary deposits of different ages (Huntley & Birks 1983). In the Late Glacial interstadials, low values (below 2%) of *Corylus*-type pollen occur in many scattered sites in the areas exposed on retreat of the continental ice-sheet. In southern Europe low but continuous presence of *Corylus* is recorded at this time from Lago Grande di Monticchio in Italy (Huntley et al. 1999) and other evidence may suggest the existence of a local centre there around 11,500 BP (Huntley & Birks 1983). Furthermore, Huntley and Birks refer to two or three other local centres – around the Bay of Biscay, in south-east Europe, and possibly in the north east, the latter indicated by the early expansion of hazel in Lithuania.

The rapid and intensive *Corylus* expansion between 10,000 and 9000 BP, connected with the climate improvement, may have also been caused by its migration from small local centres existing in the south and west of Europe. This seems to be more probable than migration from a few distant refugia. The fragments of fossil leaves and nuts of *Corylus*, dated between 8500 and 8000 BP, found in Sweden in the Scandes Mountains, indicate that the rate of *Corylus* immigration after deglaciation was maybe too quick to proceed from distant refugia (Stewart & Lister 2001). In any case, the migration trend from south-west to north-east is strongly marked.

The rapid early Holocene expansion of *Corylus* was probably related to various factors, such as favourable climatic conditions (right amount of heat during the vegetative season, not very severe winters), the presence of fertile and not leached morainic soils (Danielsen 1970), limited competition (there was still no great expansion of deciduous trees), as well as the location of a number of *Corylus* refugia in different parts of Europe.

Between 9000 and 6000 BP there was further northward expansion of *Corylus* but at the same time its significance in central and eastern Europe decreased. In consequence, high pollen values are limited to the area of Western Europe. Around 5000 BP a southward shift of its northern limit has been detected, caused probably by deterioration of climate. Progressive continentality of climate, as well as the anthropogenic factor, has also influenced the distribution of *Corylus* since 5000 BP (Huntley & Birks 1983).

MIGRATION PATTERN IN POLAND (Fig. 38)

12,000 – 10,500 BP

In the Late Glacial *Corylus* pollen occurred in small quantity (0.1–0.8%) in many sites in Poland, mainly in the central lowlands and south Poland. Its pollen values never exceed 1%. At 10,500 BP slightly higher values appear in the Tatra and Świętokrzyskie Mountains. The fact that they are accompanied everywhere by pollen of thermophilous trees suggests that their occurrence is the result of redeposition.

10,000 BP

At the beginning of the Holocene *Corylus* pollen values are relatively low (<1%). Pollen values of 2% appear to the north of the Sandomierz Depression. Exceptional values of hazel pollen of >10% recorded only from the Łódź Upland on this isopollen map probably suggest contamination of sediments by younger material rather than the presence of a *Corylus* refugium.

9500 BP

An increase in the importance of *Corylus* in plant communities is observed across the whole area of Poland. Generally, its pollen values reach up to 2%. Higher values are recorded from Western Pomerania, the Mazurian Lake District, and the Bieszczady Mountains, perhaps reflecting scattered stands in those regions.

9000 BP

This map clearly shows that the main *Corylus* expansion into the Polish territories came from the north-west. The area of the highest hazel pollen values (to 10%) covers north-western Poland as far as the north-west part of the Mazurian Lake District (>10% at Wolin Island and Warmia). Still higher percentages of this species (15 to 40%) are found in the adjacent regions of north-eastern Germany (Jahns 1999, 2000, 2001). The high values found in the area of the Moravian Gate suggest the existence of yet another southern *Corylus* migration route into Poland. Areas of south-eastern Poland were still beyond the range of the *Corylus* expansion.

8500 BP

Further *Corylus* expansion proceeded over the whole area of Poland. The highest pollen values (up to 20%) seen in western parts confirm the direction of *Corylus* migration from western Europe. On the wet soils of the Biebrza river catchment and of Polesie Lubelskie, but also in the Małopolska Upland, *Corylus* frequencies were still lower.

8000 BP

The highest *Corylus* values are concentrated in central-western Poland, and in the north-eastern part of the country, with the centres (>20%) recorded in Wielkopolska and at Warmia.

The similar values also occurred in the Carpathian Mountains and their foreland. In other regions of Poland *Corylus* pollen reaches up to 15%.

7500–5000 BP

A gradual slow retreat of hazel is observed. The majority of Polish territories show values of >15%. Regions recording higher values shrink. This phenomenon was certainly connected with the expansion and development of mixed deciduous forests where hazel occurred in the shrub layer; thus its flowering abilities were limited. The lowest hazel pollen values (<10%) remain in the Polesie Lubelskie marshes.

From 6000 BP 15% values of *Corylus* are still dominant across the country. The higher values in Wielkopolska are probably connected with the intensification of Neolithic deforestation in this area. The more important role of hazel is indicated in the mountainous areas, where before the appearance of tree species forming the present-day lower montane forest zone, hazel may have been an important component of this zone together with elm and some other species. The marshy regions of eastern Poland are the areas where hazel contribution remained the lowest.

4500–4000 BP

The beginning of *Carpinus* and *Fagus* expansion from the south-east caused the gradual contraction of the East Carpathian and then Wielkopolska centres of *Corylus* distribution. The whole country records 10–15% *Corylus* values. At that time, following the reduction of elm due to Dutch elm disease and widespread Neolithic deforestation, hazel formed, together with oak, open scrub-forest communities resembling those of modern *Quercion petraeae* alliance.

At 4000 BP *Corylus* pollen values begin to decrease strongly from the east, along the Vistula and Bug river valleys as far as the Sandomierz Depression. In central and western Poland *Corylus* representation remains almost constant, and along the Baltic coastal areas its pollen values increase up to 20%. It may be assumed that the majority of Polish territory was still covered by open oak communities with abundant hazel since *Quercus* pollen values remain constant too.

3500 BP

Between 4000 and 3500 BP a progressive rapid reduction in *Corylus* pollen is observed in the greater part of Poland except for its northern part. In the Vistula and Wieprz river valleys its values decrease to below 7%. In the Carpathians and in their forelands there are only local patches with higher values. The process of *Corylus* regression in the Polish lowlands advanced from the east and was connected with the expansion of *Carpinus*, which proceeded from the south-east up towards Wielkopolska.

3000 BP

A further intensive decrease in *Corylus* pollen percentages is observed on the following map. Values below 5%, which, in the case of a shrub producing pollen so abundantly, must imply only its scattered occurrence, are present over the whole of central Poland. Slightly higher pollen values (5–7% or more) are recorded in the south-east, in the Carpathians and in western Poland. Only in the Baltic Coastal Zone and in part of Pomerania did hazel remain more abundant. Such a considerable reduction of *Corylus* occurrence in Poland may have been connected with the initial development of settlements of the Lusatian culture, with the expansion of *Carpinus betulus*, which had its maximum values in Wielkopolska, and with the expansion of beech, particularly in southern Poland.

2500–1500 BP

Between 3000 and 2500 BP the development of Lusatian settlement progressed over the whole country. This may have contributed considerably to a further decrease in the abundance of *Corylus*. It showed pollen values of 3–5%, consistently distributed throughout Poland, with local patches yielding lower values in the eastern marsh areas. This suggests that increasing humidity of climate could have caused a progressive reduction in the distribution of *Corylus* in areas of naturally high ground-water level. Those regions also revealed lower *Corylus* values on the previous maps.

The 2000 and 1500 BP maps do not present many differences in *Corylus* distribution in comparison with the 2500 BP map. At 1500 BP the areas of low values appear in the central and eastern lake districts. This can be connected with the considerable development of shady deciduous forests during the Migration Period. A local development of *Corylus* scrub is recorded in the Nida Basin.

1000–500 BP

The economic development connected with the origin of the Polish State is marked by an overall fall in *Corylus* pollen values. On the 500 BP map *Corylus* pollen values of 3–5% again appear in the marshy areas of the Biebrza and Narew catchments as well as in the eastern part of the Carpathians and their foreland.

100 BP

The increased values *Corylus* in the Carpathians expand a little into the area of the Tatra and Western Beskidy Mountains where they reach up to 7%. The rest of the country shows *Corylus* pollen values of 1–2% or less. Clearly this is an effect of the recent devastation of natural plant communities.

CONCLUSIONS

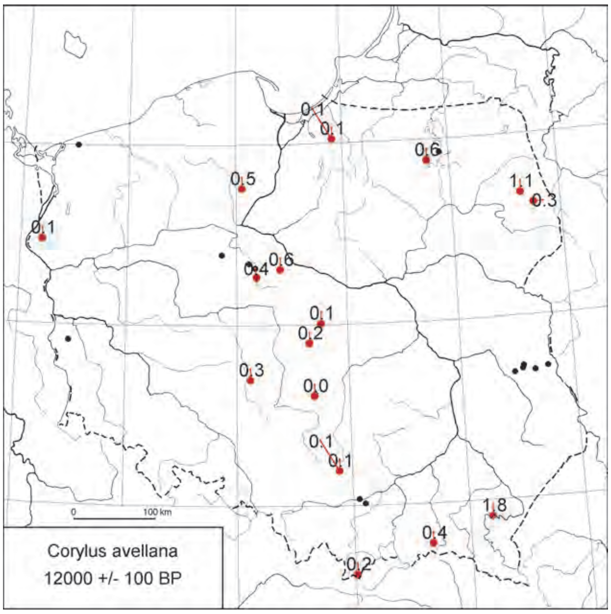
Corylus migration from the north-west direction may have originated from a refugium or migration centre situated around the Bay of Biscay. A migration route via the Moravian Gate is also indicated. Migration from the north-east, from a centre in Lithuania, might also be possible, though the existence of this centre needs to be better dated. However, finds of *Corylus* macrofossils from before 8000 BP in Scandes Mountains suggest indirectly the probability of its arrival from refugia situated much closer than refugia in southern Europe.

The early Holocene *Corylus* expansion into the area of Poland began between 9500 and 9000 BP in the northern regions and lasted up to 8500 BP when hazel also colonised the south-eastern areas. In the mountains hazel was probably an important component of the lower montane forest zone before the appearance of *Fagus* and *Abies*. It may have formed the upper forest limit at a comparatively low altitude on shallow skeletal soils instead of spruce (Bieszczady Mountains). Between 5500 (5000) and 4000 (3500) BP, in lowland Poland hazel, together with oak, commonly formed open scrub-forest communities, ecologically unstable, being the consequence of Neolithic deforestation.

Around 3500–3400 BP the apparent decline in the importance of *Corylus* was the result of the following factors: development of new cultures (pre-Lusatian and Lusatian) with their new types of agriculture, changes in soils connected with the maturity and leaching, the rapid expansion of hornbeam which was eliminating hazel, and similarly in some areas the spread of beech.

→

Fig. 38. *Corylus avellana*: dot and isopollen maps for 12,000–100 ^{14}C yr BP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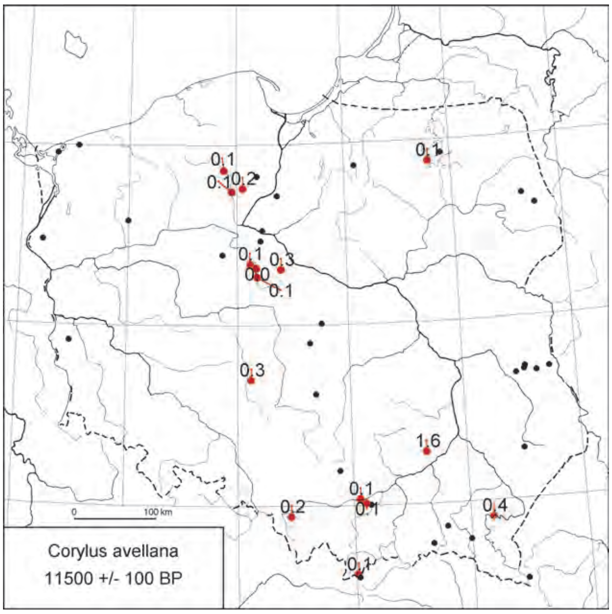
12000 +/- 100 BP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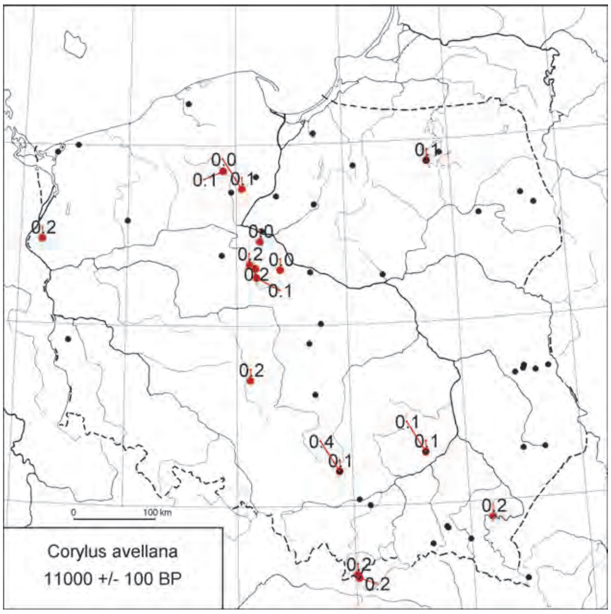
Corylus avellana
11500 +/- 100 BP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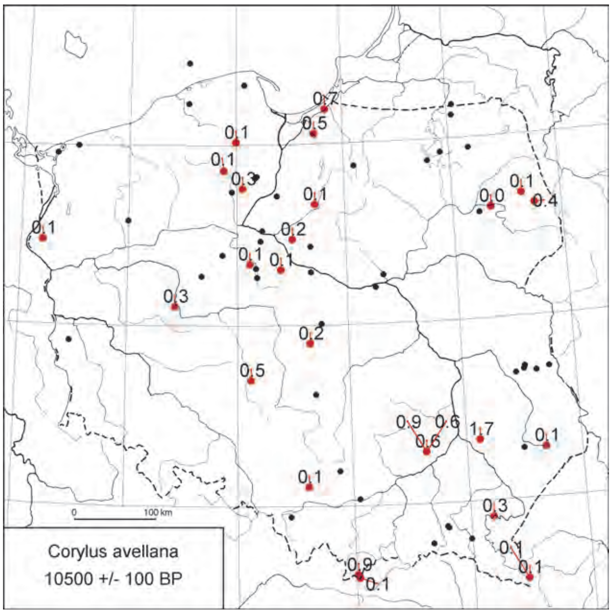
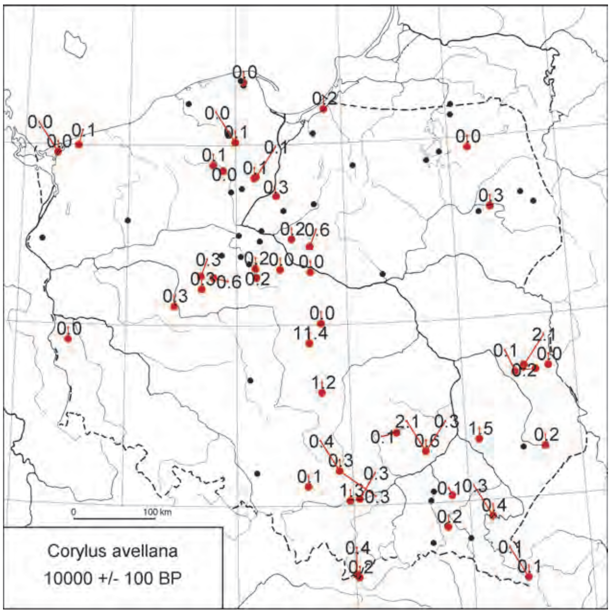
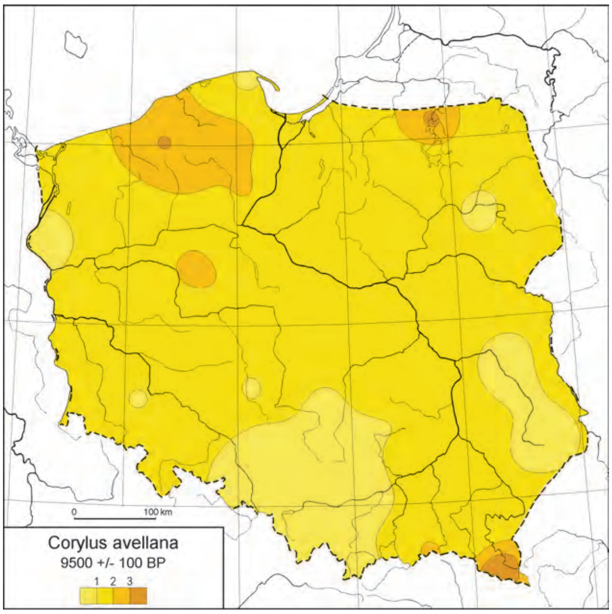
Corylus avellana
11000 +/- 100 BP


0 100 km
Corylus avellana
10500 +/- 100 BP


0 100 km
Corylus avellana
10000 +/- 100 BP


0 100 km
Corylus avellana
9500 +/- 100 BP
1 2 3


0.01
0.1
0.5
1
2
3
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7
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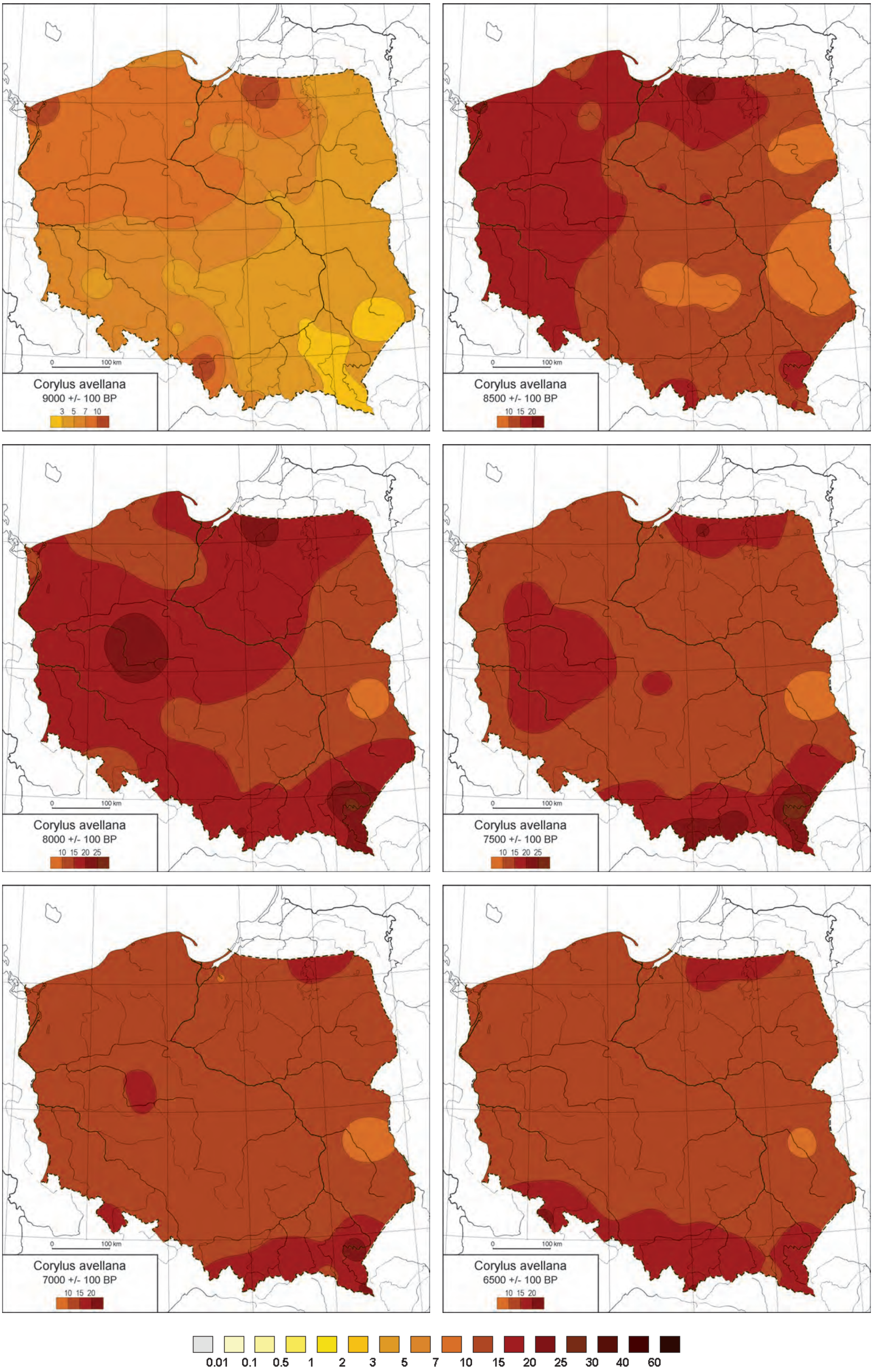
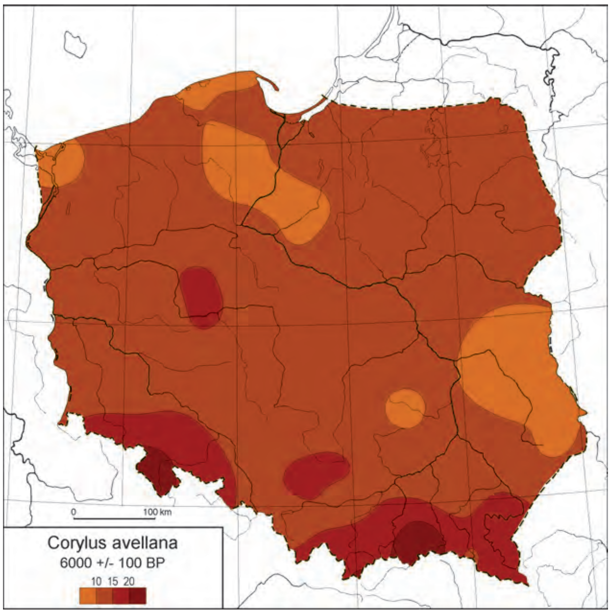
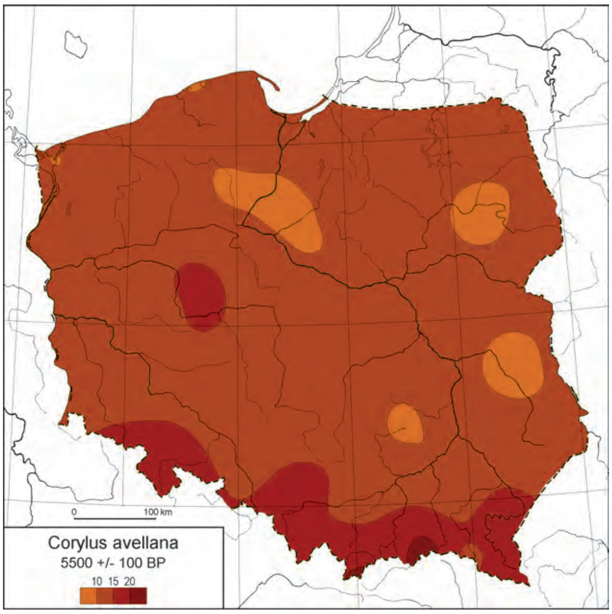
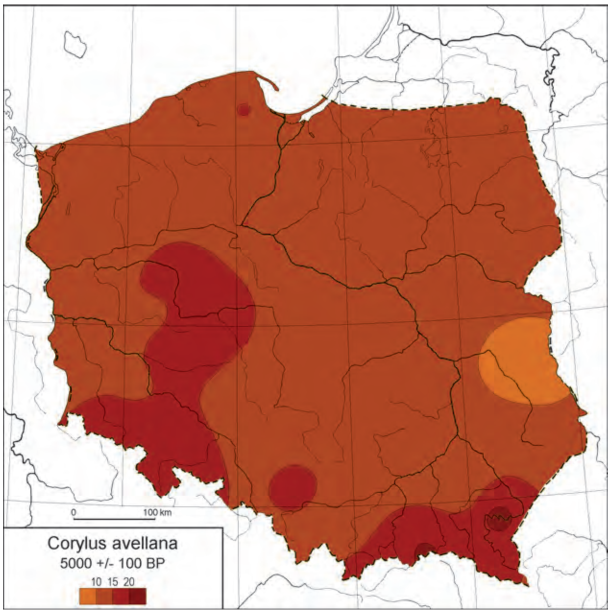
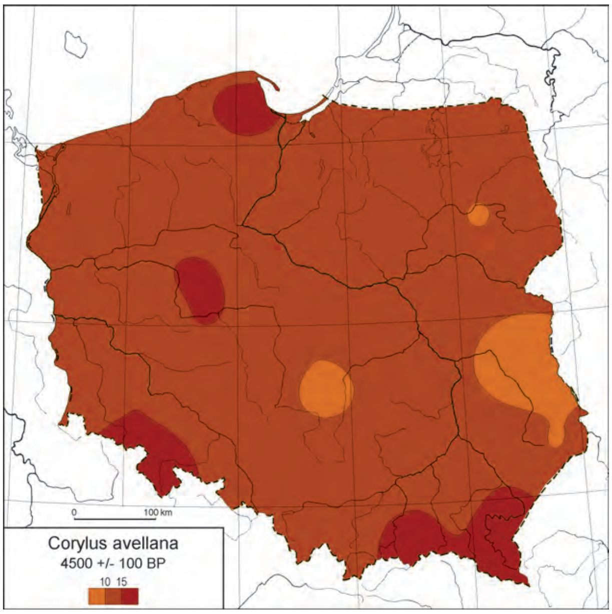
25
30
40
60

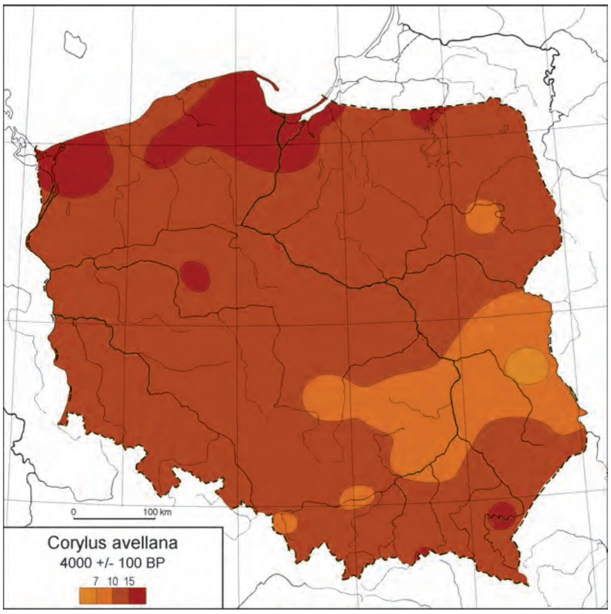

0
100 km
Corylus avellana
9000 +/- 100 BP
3 5 7 10
0
100 km
Corylus avellana
8500 +/- 100 BP
10 15 20
0
100 km
Corylus avellana
8000 +/- 100 BP
10 15 20 25
0
100 km
Corylus avellana
7500 +/- 100 BP
10 15 20 25
0
100 km
Corylus avellana
7000 +/- 100 BP
10 15 20
0
100 km
Corylus avellana
6500 +/- 100 BP
10 15 20
0.01 0.1 0.5 1 2 3 5 7 10 15 20 25 30 40 60

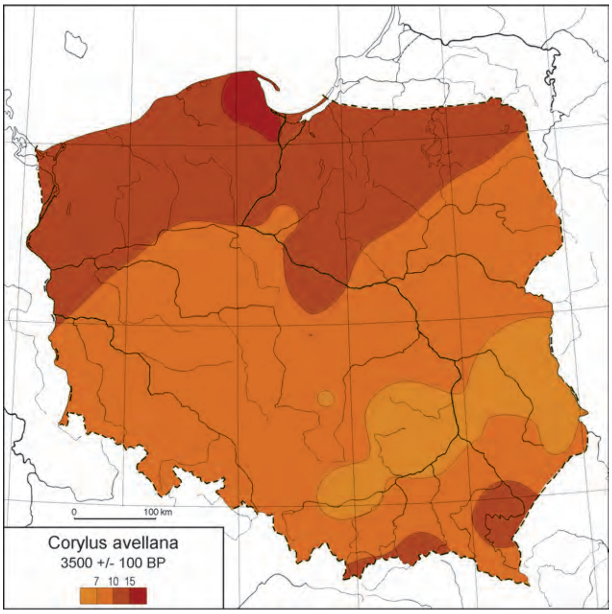












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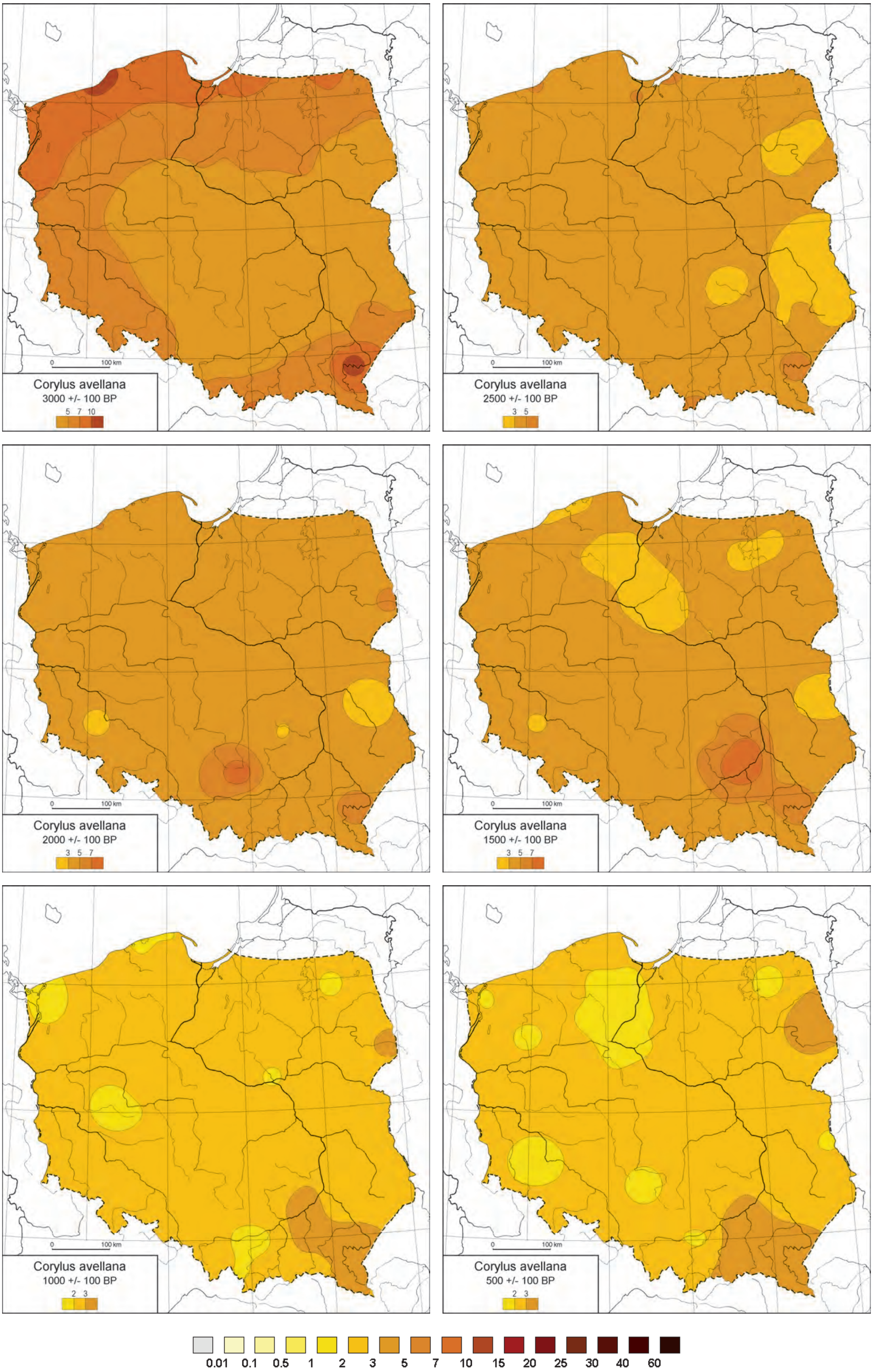
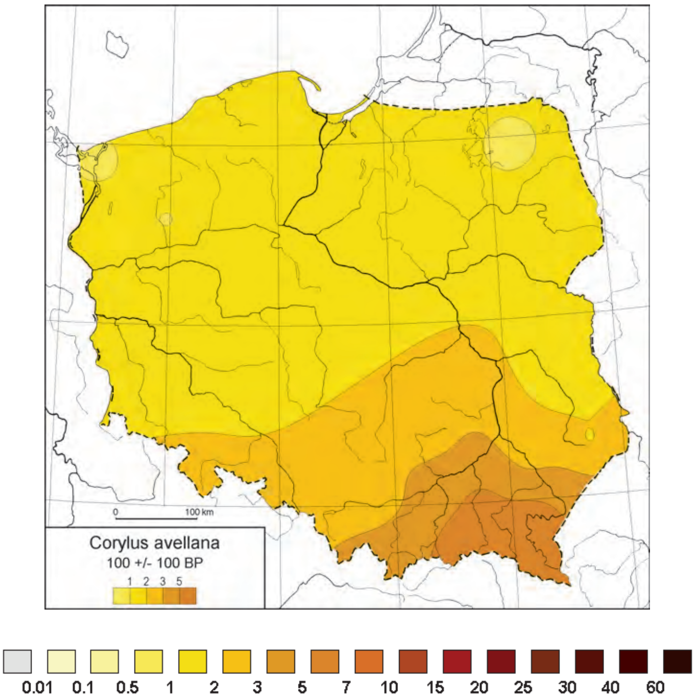

0
100 km
Corylus avellana
3000 +/- 100 BP
5 7 10
Corylus avellana
2500 +/- 100 BP
3 5
Corylus avellana
2000 +/- 100 BP
3 5 7
Corylus avellana
1500 +/- 100 BP
3 5 7
Corylus avellana
1000 +/- 100 BP
2 3
Corylus avellana
500 +/- 100 BP
2 3
0.01 0.1 0.5 1 2 3 5 7 10 15 20 25 30 40 60


0
100 km
Corylus avellana
100 +/- 100 BP
1 2 3 5
0.01 0.1 0.5 1 2 3 5 7 10 15 20 25 30 40 60

Ephedra L. – **Joint-fir**

WOJCIECH GRANOSZEWSKI AND DOROTA NALEPKA

The genus *Ephedra* L., which includes more than 40 species (Mussayev 1978), belongs to the order Ephedrales of the class Gnetopsida. Three *Ephedra* species occur in Europe: *Ephedra fragilis* Desf. with subsp. *fragilis*, and subsp. *campylopoda* (C.A. Meyer) Ascherson & Graebner, *E. distachya* L. with subsp. *distachya* and subsp. *helvetica* (C.A. Meyer) Ascherson & Graebner and *E. major* Host, also with two subspecies: subsp. *major* and subsp. *procera* (Fischer & C.A. Meyer) Markgraf (Markgraf 1964).

PRESENT DISTRIBUTION IN EUROPE

This genus occurs in southern Europe, in the Mediterranean region, in the mountains of Greece, and in the Alps (Markgraf 1964). *E. distachya* is the species with the widest distribution, whose range includes also western Siberia (Mussayev 1978). At present it is absent from the territory of Poland. The nearest site of *E. distachya* occurs in western Podole, on the Dniestr river (Szafer et al. 1924). It grows also in southern Slovakia (Lhotská et al. 1987).

ECOLOGY

The species of *Ephedra* are adapted to warm and dry climate (Szweykowska & Szweykowski 1997). The overall range of *E. distachya* indicates its considerable tolerance of conditions of continental climate (Mussayev 1978). Species of *Ephedra* are members of different communities of Mediterranean brushwoods and of steppe communities. They grow on poor, sandy soils, and on rocky sites in the mountainous areas. *E. distachya* flowers from May to June, and bears fruit from July (Takhtajan 1981). Its fruits are eaten by animals and so dispersed, whereas the remaining species have wind-dispersed fruits (Lhotská et al. 1987).

POLLEN PRODUCTION AND DISPERSAL

The species of *Ephedra* are dioecious, wind-pollinated plants but sporadically visited by insects (Szweykowska & Szweykowski 1997). The genus *Ephedra* is comparatively a moderate pollen producer (Welten 1957). Its pollen can be transported very long distances (Maher 1964, Birks 1973). *Ephedra* pollen in fossil assemblages does not exceed 1%. Values higher or equal to 3%, are thought to indicate local and abundant occurrence of *Ephedra* scrub (Welten 1957).

EXPANSION IN EUROPE DURING THE LATE GLACIAL AND HOLOCENE

Pollen of *Ephedra* is permanently present in the Late Glacial deposits (since 13,000 BP) in southern Europe and in the Alps. At that time its pollen values reach 3% in the south of France, whereas in the other parts of Europe its values in assemblages do not exceed 1% (Huntley & Birks 1983). About 11,000 BP the maximum values are recorded from sediments in south-eastern Europe. At this time, in the Balkan Peninsula, *Ephedra* pollen may amount to even 10% of the basic pollen sum (Huntley & Birks 1983). At the same time in north and central Europe its values do not exceed 1%.

Since the beginning of the Holocene a decrease in *Ephedra* pollen values has been observed. Only in the southern parts of the Iberian and Apennine Peninsulas and in the south-eastern part of the Balkan Peninsula, does *Ephedra* pollen reach 3% of the pollen sum of trees and shrubs (Huntley & Birks 1983). By 9000 BP *Ephedra* pollen appears regularly only in the Mediterranean region and in the Alps, and sporadically in north and central Europe (from long-distance transport).

MIGRATION PATTERN IN POLAND (Fig. 39)

From 14,000 to 11,500 BP *Ephedra* pollen was recorded at only a very few sites in north-eastern, central and south-eastern Poland. In the period of 11,500 to 10,000 BP the number of sites, where the presence of *Ephedra* pollen has been recorded, increases. These are distributed mainly in eastern and central Poland but also in the lake districts (Ralska-Jasiewiczowa 1966). Since the beginning of the Holocene the number of sites with *Ephedra* pollen has declined drastically, and their distribution has been quite irregular, particularly in the east of the country and in central Poland. The latest record of *Ephedra* pollen is seen on the 1500 BP map. All the Holocene finds of *Ephedra* pollen, with the exception of the early Holocene ones, are most likely due to long-distance transport. The actual presence of *Ephedra* in the territory of Poland, either in the Late Glacial or in the Holocene has not yet been confirmed by the presence of macrofossils. The occurrence of *Ephedra* within the present flora of Ukraine and Slovakia may suggest that this species could have been a component of our flora in a period when the climatic conditions enabled development of steppe communities in Poland, that is in the Late Glacial and at the beginning of the Holocene.

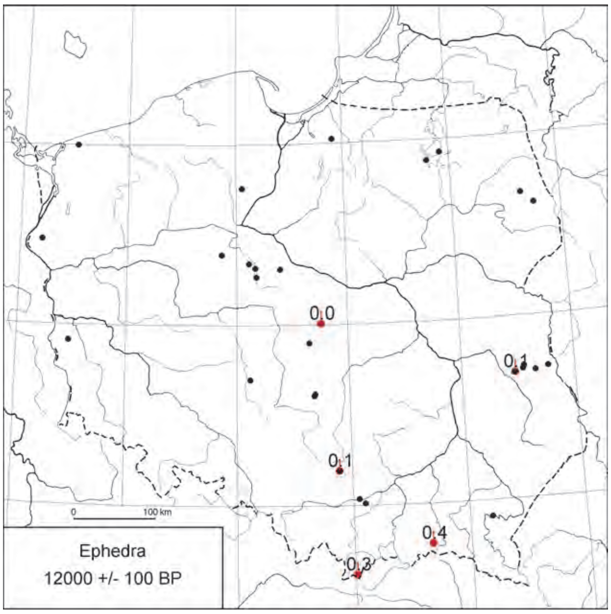
Fig. 39. *Ephedra*: dot maps for 14,000–1500 ^{14}C yr BP (the maps of time horizons without *Ephedra* pollen finds recorded, have been omitted)

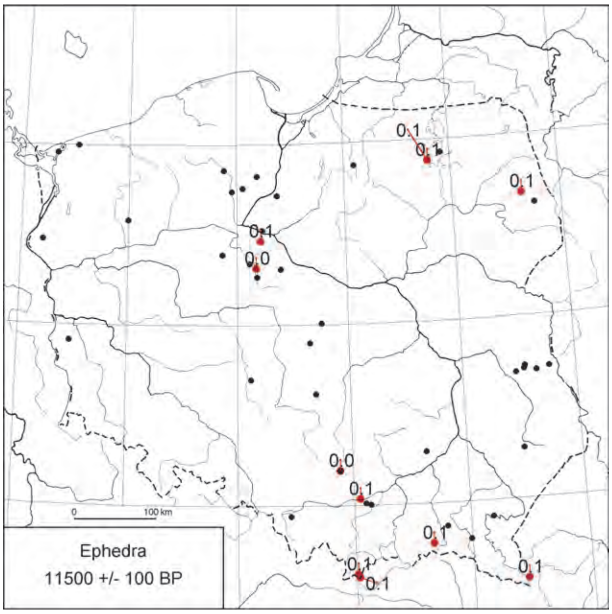

0.0
0.1
0 100 km
Ephedra
14000 +/- 100 BP

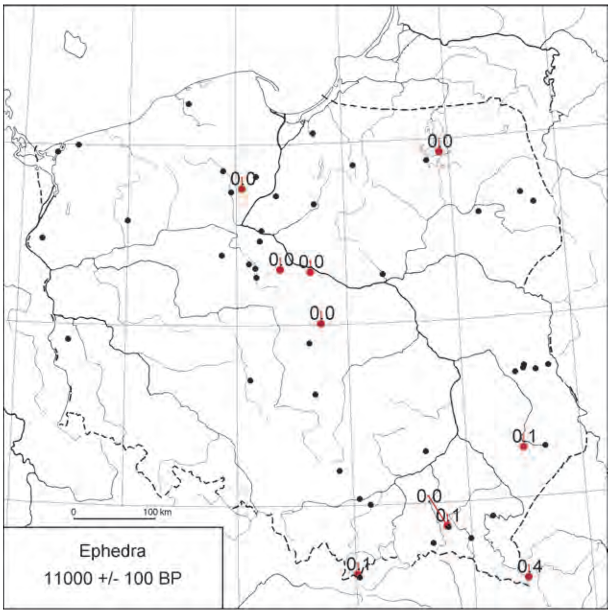

0.2
0 100 km
Ephedra
13500 +/- 100 BP

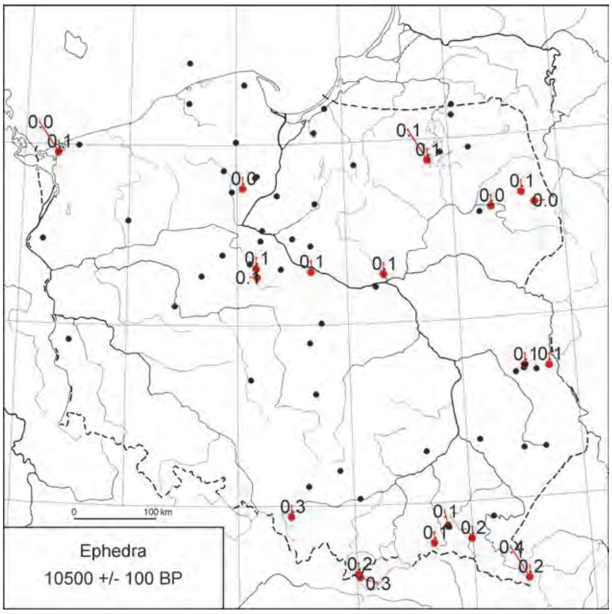

0.1
0 100 km
Ephedra
13000 +/- 100 BP

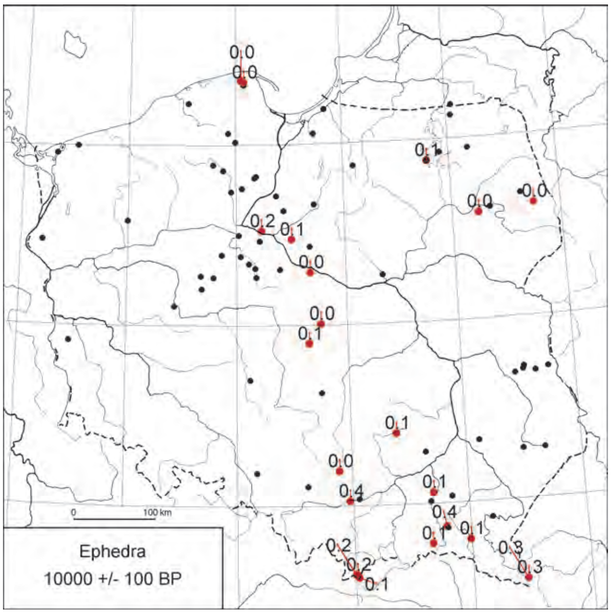

0.3
0.0
0.3
0 100 km
Ephedra
12500 +/- 100 BP

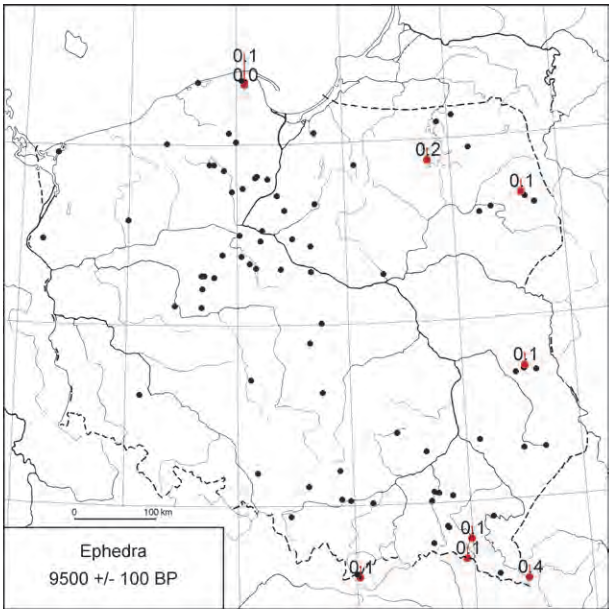

0.0
0.1
0.1
0.4
0.3
0 100 km
Ephedra
12000 +/- 100 BP

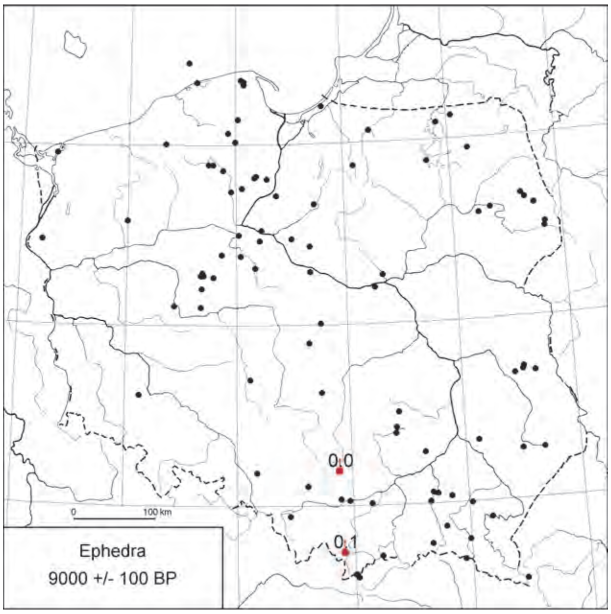

0.1
0.1
0.1
0.1
0.0
0.0
0.1
0.1
0.1
0.1
0.1
0.1
0 100 km
Ephedra
11500 +/- 100 BP

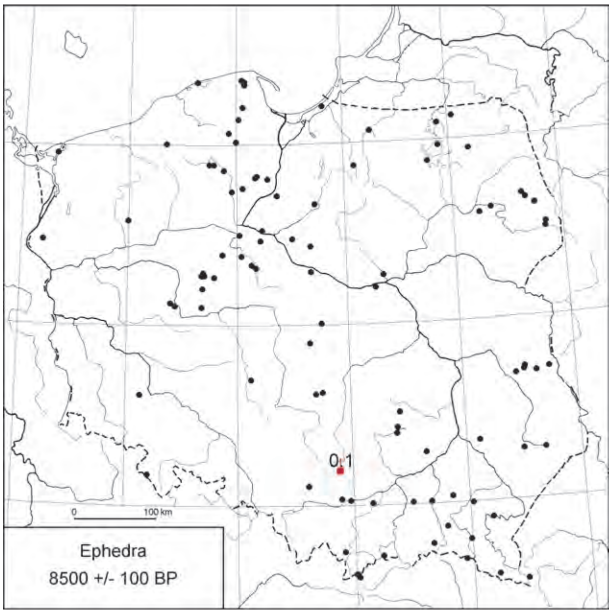

0.0
0.0
0.0
0.0
0.0
0.1
0.0
0.1
0.1
0.4
0
100 km
Ephedra
11000 +/- 100 BP


0.0
0.1
0.1
0.1
0.0
0.0
0.1
0.0
0.1
0.1
0.1
0.1
0.1
0.1
0.3
0.1
0.1
0.2
0.4
0.2
0.2
0.3
0
100 km
Ephedra
10500 +/- 100 BP

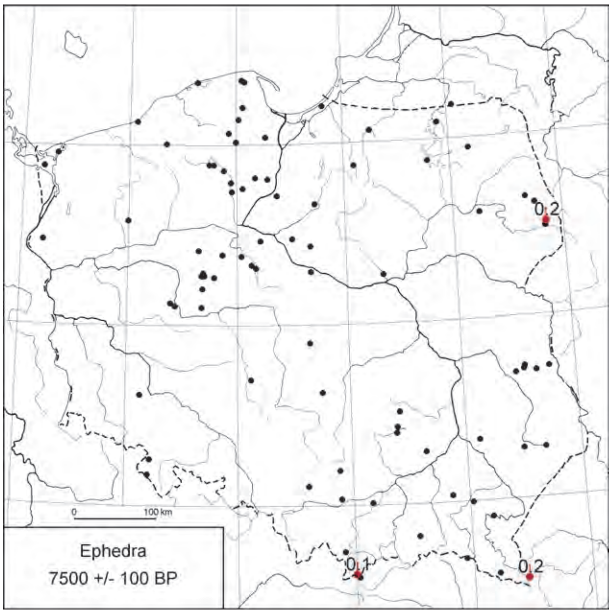

0.0
0.0
0.1
0.0
0.0
0.2
0.1
0.0
0.0
0.1
0.1
0.0
0.4
0.1
0.4
0.1
0.1
0.2
0.2
0.1
0.3
0.3
0
100 km
Ephedra
10000 +/- 100 BP

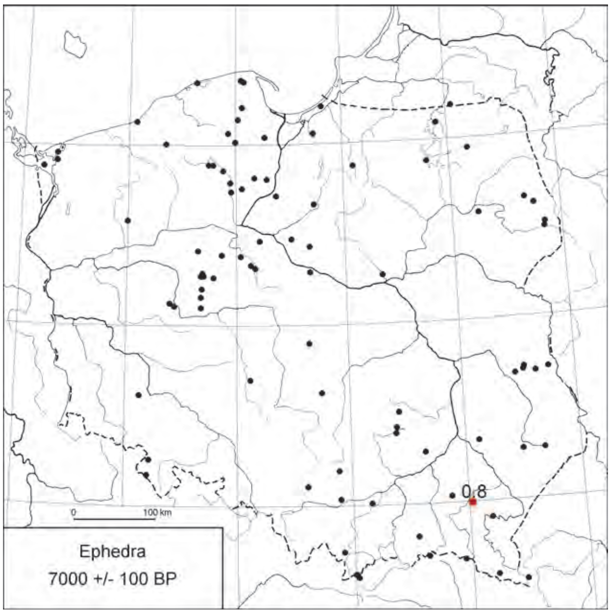

0.1
0.0
0.2
0.1
0.1
0.1
0.1
0.1
0.4
0
100 km
Ephedra
9500 +/- 100 BP

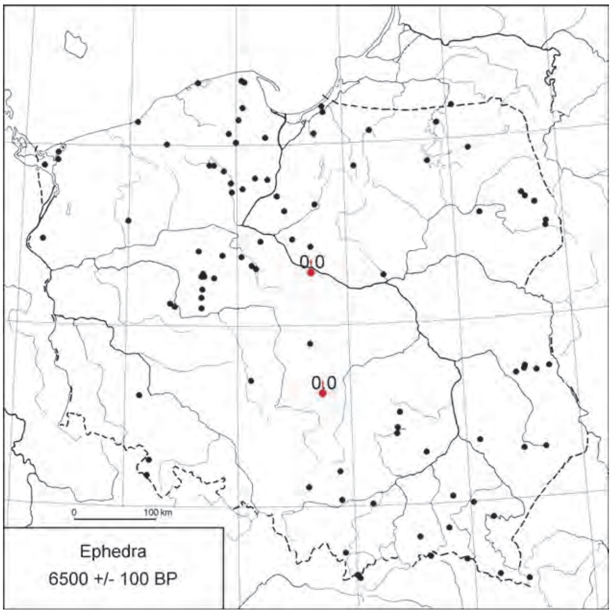

0.0
0.1
0
100 km
Ephedra
9000 +/- 100 BP

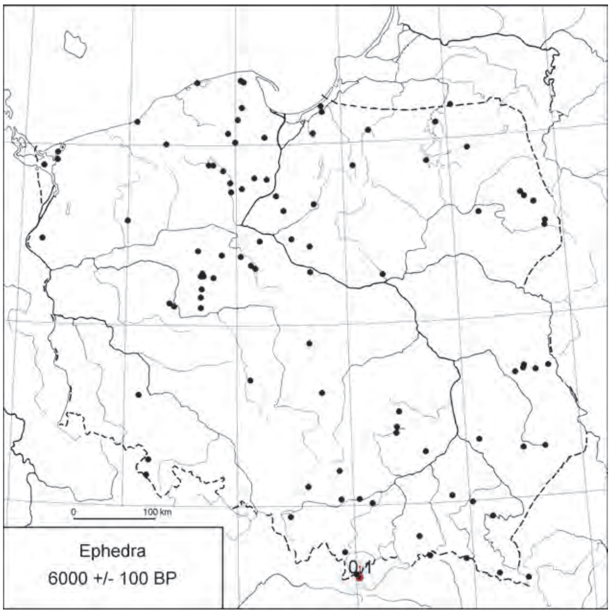

0.1
0
100 km
Ephedra
8500 +/- 100 BP

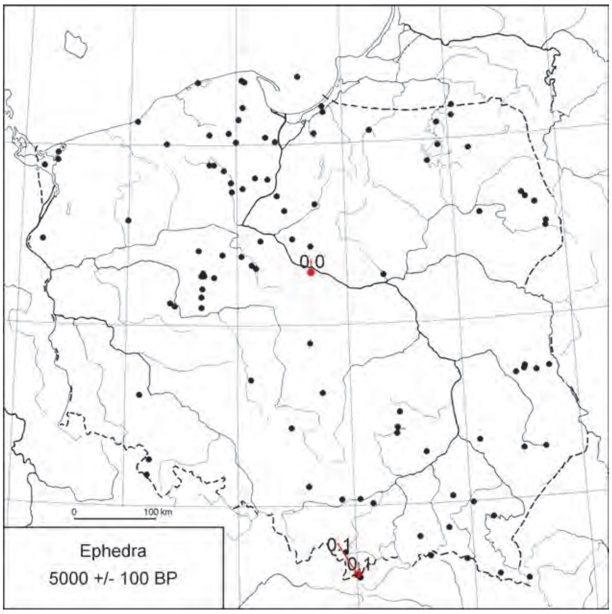

0.1
0
100 km
Ephedra
8000 +/- 100 BP
0.1
0.1

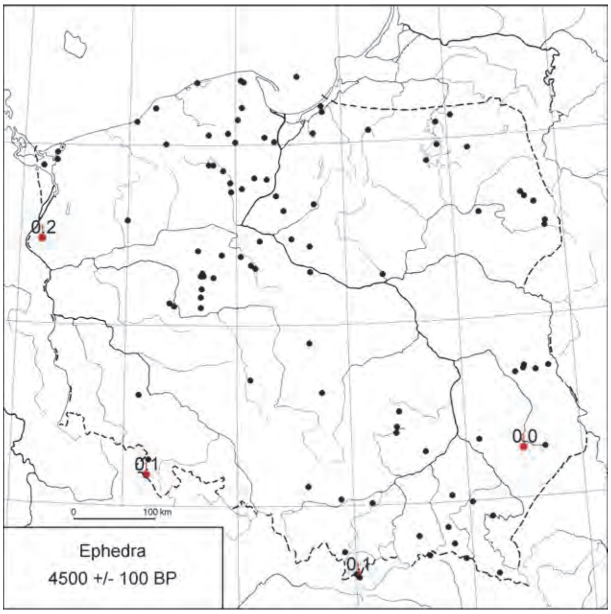

0.2
0
100 km
Ephedra
7500 +/- 100 BP
0.1
0.2

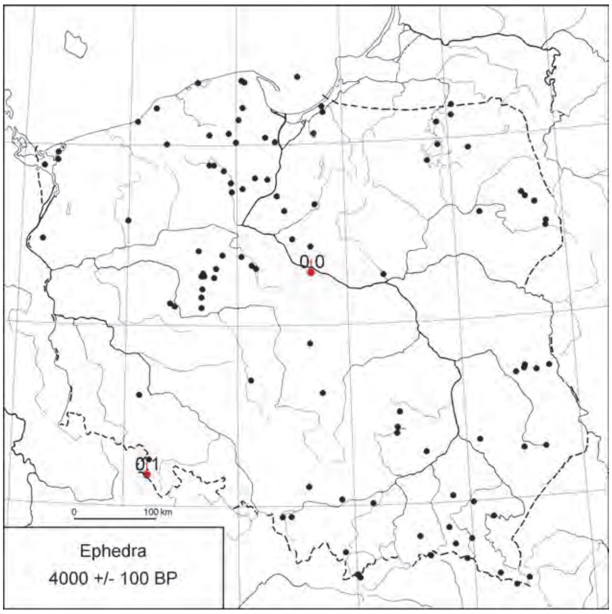

0.8
0
100 km
Ephedra
7000 +/- 100 BP

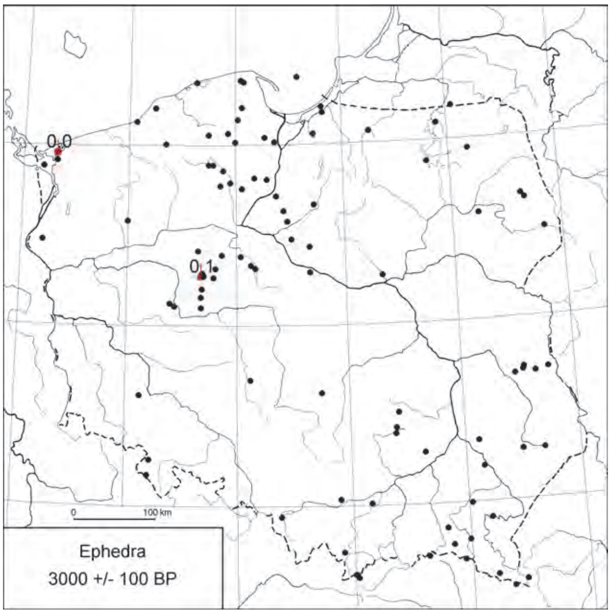

0.0
0.0
0
100 km
Ephedra
6500 +/- 100 BP

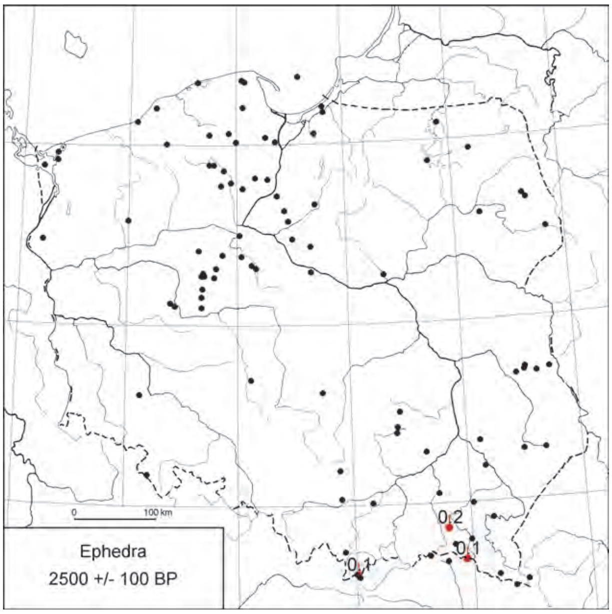

0
100 km
Ephedra
6000 +/- 100 BP
0.1

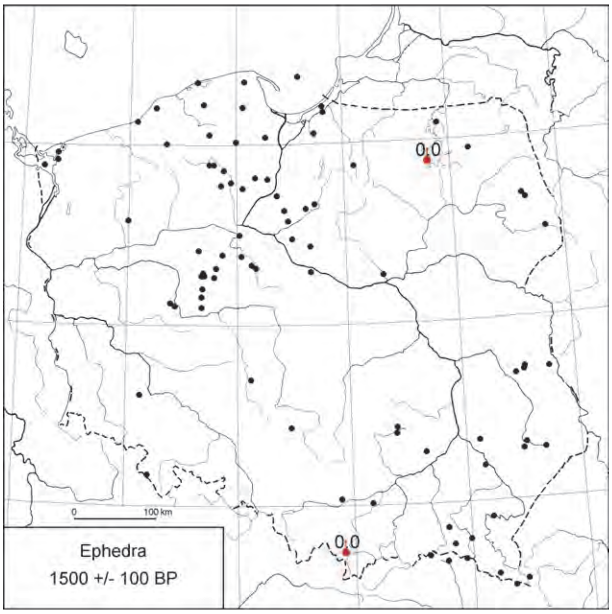

0.0
0
100 km
Ephedra
5000 +/- 100 BP
0.1
0.1


0.2
0.1
0.0
0.1
0 100 km
Ephedra
4500 +/- 100 BP


0.0
0.1
0 100 km
Ephedra
4000 +/- 100 BP


0.0
0.1
0 100 km
Ephedra
3000 +/- 100 BP


0.2
0.1
0.1
0 100 km
Ephedra
2500 +/- 100 BP


0.0
0.0
0 100 km
Ephedra
1500 +/- 100 BP

Fagus sylvatica L. – **Beech**

Małgorzata Latałowa, Magdalena Ralska-Jasiewiczowa, Grażyna Miotk-Szpiganowicz,
Joanna Zachowicz, and Dorota Nalepka

There are two well defined species of genus *Fagus* occurring recently in Europe: *Fagus sylvatica* L. and *F. orientalis* Lipsky, the latter growing only in south-eastern part of Europe. The third species *F. taurica* Popl. is regarded as a variant of *F. sylvatica* and occurs sporadically in the areas when the two species meet (Tutin et al. 1964).

Present distribution in Europe

The only representative of the genus *Fagus* in Poland is *F. sylvatica* L. Beech is a Subatlantic species, avoiding areas of continental climate. Its range covers southern, central and western Europe, reaching the southern part of the British Islands, and southern Scandinavia (Fig. 40). In the south it is found in the northern and some central areas of the Iberian Peninsula, almost throughout Italy, including Sicily, and the Balkan Peninsula, except for the Peloponnese. To the east, it barely occurs beyond Poland, and in the south-east just extends to the Ukraine, with an outlying population in the Crimean Peninsula. Within its main area of distribution, it is, however, absent from the more continental areas of the Great Hungarian Plain and also the lower Danube valley (Meusel et al. 1965).

Fig. 40. *Fagus sylvatica* – map of present-day distribution in Europe: ● – native isolated occurrence, ◒ – status of site unknown or uncertain (after Jalas & Suominen 1976, Boratyńska & Boratyński 1990, and Podbielkowski 1991)

PRESENT DISTRIBUTION IN POLAND

In Poland beech reaches the north-eastern limit of its range (Fig. 41). It runs from the northern margin of the Mazurian Lake District towards the south-west through Kujawy, and the Wielkopolska Lake Districts towards the Warta and Prosna river valleys, and next eastwards across the Łódź Upland to reach as far as the Lublin Upland. Beyond the limit of its contiguous distribution it also occurs at some scattered sites. In Poland there are clearly two distinct centres of this species, one in Pomerania and the second in the mountains and uplands. In the Pomerania the best-preserved beech woods occur in the morainic areas of the last glaciation and around their margins. In the mountains beech is a very important component of lower montane zone forests reaching 1200 m a.s.l. (the Tatra Mountains). It is abundant and widespread in the Western Bieszczady Mountains, where it is the main component of the forests, comprising about 50% of their composition and occupying the areas from an altitude of 550 m a.s.l., sometimes 400 m a.s.l., up to the upper forest limit (ca. 1200 m a.s.l.). In the Sudetes the lower montane forest zone which would naturally be dominated by beech forests (but where spruce has recently been much planted) occurs from an altitude of 450–500 m a.s.l. up to 1000 m a.s.l. (Boratyńska & Boratyński 1990).

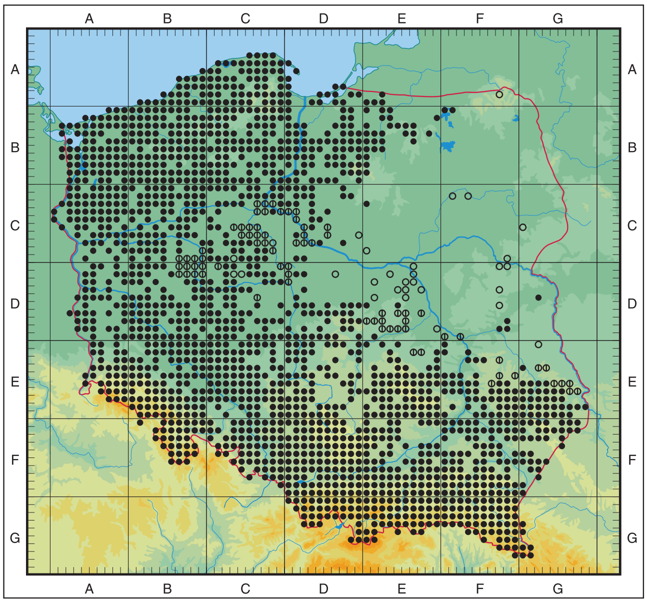


Fig. 41. Present-day distribution of *Fagus sylvatica* L. in Poland: ○ – synanthropic sites, ⦶ – status of site unknown or uncertain (after Zając A. & Zając M. 2001)

ECOLOGY

The principal beech forest communities in Poland form two groups: there are fertile and acid beechwoods, which in the lowland areas and in the mountains are represented by vicariant associations. The lowland association of acidophilous beechwood *Luzulo pilosae-Fagetum* is replaced in the mountains by *Luzulo luzuloidis-Fagetum*, whereas the lowland association *Galio odorati-Fagetum* is replaced by two piedmont-montane associations *Dentario enneaphyllidis-Fagetum* and *Dentario glandulosae-Fagetum* (Matuszkiewicz J.M. 2002).

The range of *F. sylvatica* in the north and east of Europe is restricted by temperature conditions whereas its southern limit is determined by moisture deficiency. This species is particularly sensitive to spring frosts, which are unfavourable for its regeneration. This is also apparent in Poland where beech distinctly avoids areas of dry and continental climate (Boratyńska & Boratyński 1990). However, factors controlling its distribution limit in north-east Poland are not quite clear, as the amount of precipitation is sufficient for the development of beechwoods, and also the temperature conditions probably do not exceed values adverse for this species there (Matuszkiewicz J.M. 2002).

Beech grows on a variety of soil types – from rendzinas through brown soils to podzols. Depending on local biotic and soil conditions, humus of mull- or moder- or even mor-type accumulates beneath beech forests. This species has a very strong influence on the development of the habitats in which it grows. This is positive on richer soils with relatively fast decomposition of litter, but on acid soils, where decomposition of litter is slow and followed by soil leaching, that limits considerably both tree growth and the development of a herb layer (Dzwonko 1990). Rackham (1980) and Aaby (1983) consider that beech has only a limited potential for expansion within communities that exist under stable ecological conditions, whereas it is a strong competitor where the ecological stability is disturbed. Growing to considerable height, its branching crowns restrict the access of light to the interior of the forest, which hampers the development of more light-demanding species, including some trees. On poor soils beech causes further acidification of habitats, and the surface net of roots developed by beech is an additional negative factor that prevents establishment of seedlings (Andersen 1984). Under certain conditions this results in the development of pure stands of beech woodland.

POLLEN PRODUCTION AND DISPERSAL

Beech flowers plentifully every few years. Its pollen season usually lasts about two weeks, and in Poland it occurs at the end of April and the beginning of May (Szczepanek 1994a, b, Aerobiologic Database, Gdańsk 1994–2002). This species is one of the more copious pollen producers (the ratio of its pollen production as compared to that of grasses is estimated at 6.7:1.0); however, its poor dispersal ability results in beech being under-represented in pollen assemblages (Sugita et al. 1999). Huntley and Birks (1983) have based their interpretation of their isopollen maps on the assumption that 2% beech pollen values indicate its local, scattered presence in vegetation communities, whereas values >5% indicate the occurrence of beech-dominated forests on a regional scale. Björkman (1996), however, uses much lower *Fagus* pollen values to interpret beech distribution, following field observations by Woods and Davis (1989). These authors accept a probable presence of the first beech stands at values of 0.5% in regional pollen diagrams, and a certain presence of beech stands on a local scale when pollen values are 0.5–1%, whereas a regional expansion would be indicated by values of 2–5%.

Expansion in Europe during the Late Glacial and Holocene

Available data concerning the location of beech refugia during the last glaciation and the subsequent expansion of this tree in Europe during the Holocene are ambiguous. Additionally, the lack of convincing evidence for the presence of *Fagus* in western and central Europe during the Eemian interglacial complicates attempted explanations of its history (Lang 1994, Pott 2000). In southern Europe during that interglacial it was an important component of the forests in the Black Sea basin (Bozilova & Djankova 1976) and was also present on the Apennine Peninsula (Magri 1998), whereas in other regions of the south it expanded not earlier than during the interstadials of the Early Vistulian (de Beaulieu & Reille 1984, Tzedakis 1994). The scarce grains of *Fagus* pollen found at numerous Eemian sites further north are interpreted as a result of long-distance transport or as pollen reworked from older deposits (Środoń 1985, 1990a, Mamakowa 1989). The location of refugia of mesophilous species of deciduous trees during the last glaciation, and their migration pathways during the Holocene, have been the subject of active discussion (Bennett et al. 1991, Tzedakis et al. 2002, Stewart 2003).

Both widely accepted traditional opinions (Huntley & Birks 1983, Lang 1994) and recent genetic investigations (Taberlet et al. 1998, Pott 2000) have concluded that the refugia situated in the Balkans or in Italy were the source of the central-European beech populations. However, other papers have appeared recently (Willis et al. 2000, Stewart & Lister 2001) putting forward the hypothesis, on the basis of sites with a conjunction of radiocarbon-dated charcoal fragments and (very low) traces of temperate pollen types from glacial-stage sediments, that small refuge areas existed with specific milder local climatic conditions, scattered throughout Europe, where the temperate elements of forest flora and fauna, beech among them, could have persisted. Western Slovakia and north-eastern Hungary have been cited as potential 'cryptorefuge' areas (Stewart & Lister 2001). It should be emphasised that one of the earliest palynological records of the Holocene beech expansion in Europe derives from sites located relatively close to the southern Polish state border, in the valley of the upper Wełtawa. The first distinct expansion of beech has been dated there at 7500 BP (Svobodová et al. 2001). Some years earlier Rybničková and Rybniček (1996) pointed out a very early presence of scattered *Fagus* sites (ca. 9000 BP) and the expansion of this tree in the area of southern Moravia around 8200 BP.

Migration pattern in Poland (Fig. 42)

9000 – 7500 BP

The maps show dispersed sites with low *Fagus* pollen values located mostly in southern and central-northern Poland, their numbers increasing on the subsequent maps. They may originate from the long distance transport and/or from the contamination of pollen samples with the younger sediment.

7000 – 5500 BP

On the maps for this period one can trace the *Fagus* isopollen lines extending progressively northwards with values of 0.1 to 0.5% (sporadically slightly higher), which may indicate the slow migration of beech from areas of occurrence situated south of Poland, primarily from southern areas of the Czech and Moravia into the Sudetes and then into the Western Carpathians. Less clear is the direction of beech expansion into the Bieszczady Mountains. It could have reached this area via the valleys along the southern side of the Western Carpathians or along the arc of the Eastern Carpathians. On the 7000 BP map scattered low values occur in the Carpathians and Sudetes, together with their forelands, and around the Moravian Gate basin. Around 6500 BP they expand into the Sandomierz Depression and Małopolska Upland with the Świętokrzyskie Mountains. The 6000 BP map illustrates the shift of isopolls to the north-east up to the Lublin Upland. At this time values of 1% appear in the Orawa area. The 5500 BP map indicates a small and local increase of beech pollen values (up to 0.5–1.0%) in the Sudety and Bieszczady Mountains, suggesting the earliest occurrences of *Fagus sylvatica* in these mountain ranges.

5000 – 4500 BP

Further movement of isopolls reflects the beginning of efficient expansion of beech in the Polish parts of the Carpathians and Sudetes; the 1% isopollen line includes the whole area of the Carpathians with up to 2% values in Orawa, and in the Sudetes, together with their foreland.

The pattern on the 4500 BP map confirms, the already marked progress of *Fagus* expansion into the Polish mountains from three directions: south-east, south-west and west. In the Sudetes and the Bieszczady Mountains the pollen values reach up to 2–3%. In the Bieszczady Mountains the first rise of the *Fagus* curve up to 5% occurs already at about 4400–4300 BP (Ralska-Jasiewiczowa 1980), together with the appearance of *Carpinus*. Hornbeam peaks much quicker, but later declines under the pressure of the rising dominance of beech. Beech and hornbeam also appear synchronously in other areas, e.g. in the north-western part of the Romanian Eastern Carpathians (Björkman et al. 2002, 2003).

4000 BP

Increased isopollen values reflect the further expansion of beech. In the Sudetes the percentage pollen values reach 5% indicating substantial amounts of this species in the local forests. In the Bieszczady Mountains the representation of beech pollen rises to over 10%. At the same time the beech pollen values in the Western Carpathians do not exceed 2%. Not earlier than about 3800 BP a distinct expansion of beech began on the Czech side of the Orava Basin, as recorded by pollen values above 5% (Rybniček & Rybničková 2002). The 1% boundary isopoll moves northward to the Wielkopolska area and the Bug-Narew river valleys.

3500 BP

Two distinct centres of high *Fagus* pollen values have developed in the Polish mountains. In the Sudetes they exceed 15%. In the Bieszczady Mountains the representation of beech pollen rises rapidly up to 30% (Ralska-Jasiewiczowa 1980), indicating the regional occurrence of beech-dominated forests. Macrofossils of *Fagus* have been found at the site of Cergowa in the vicinity of the Dukla Pass at a horizon dated at 3600 BP (Szczepanek 2001). Values of up to 10% connect all the mountainous areas together with their foothills and foreland basins such as Moravian Gate, Sandomierz Depression, and Silesian Lowland. They indicate the regional occurrence of beech-dominated forests. At this time beech undoubtedly formed the forests in the Małopolska Upland, the Świętokrzyskie Mountains, Roztocze and the Lublin Upland. Northward movement of the 1–2% isopolls suggests that beech stands may have also appeared in areas of central Poland.

3000 BP

During this time a steady expansion of beech is recorded; values of up to 7% cover the whole of the Carpathians and probably also the Sudetes. Between 3500 and 3000 BP the lower forest zone presumably formed in the mountains. At this time, in pollen diagrams from the mountains, the amounts of *Corylus* and *Ulmus* pollen decrease considerably (see the isopollen maps of *Corylus* and *Ulmus*, this volume). Decrease of spruce pollen representation in the Eastern Carpathians and Sudetes is also marked at this period. These phenomena illustrate presumably the occupation by beech of the habitats in the lower montane forest zone, occupied up to this time by forests with elm (*Ulmus glabra*), hazel and spruce. In the Bieszczady Mountains spruce, which had persisted at the lower altitudes until this time, failed to migrate upwards and occupy the upper montane forest zone, as happened in the Western Carpathians under similar pressure from beech; thus it was gradually eliminated. Beech became more frequent (2–5%) in the Małopolska Upland, the Świętokrzyskie Mountains and Roztocze. Probably at this time scattered stands of beech appeared in the western part of the Baltic coastal area (Western Pomerania).

2500 BP

A very well documented change to a more oceanic, wetter and colder climate (Ralska-Jasiewiczowa & Starkel 1988), resulted in a gradual but constant northward expansion of the range of beech and its clear expansion from the north-west into the Baltic Coastal Zone and Pomerania. Those phenomena proceeded, in spite of the fact that contemporaneous human settlement and management activities effectively hampered the growth of forests. An increase in the role of beech and an extension of its range are, therefore, nevertheless, marked throughout the whole area of its occurrence both in the southern mountains and uplands and in the north-western lowlands.

Apart from the mountainous regions, beech-dominated forests (5–7% of pollen) occupied the south-western part of Małopolska Upland, and they played an important role (3–5% pollen values) in its north-eastern part with the Świętokrzyskie Mountains and also in the Roztocze. Beech forests appeared also in the western part of the Baltic coastal area. Their dynamic expansion in that region was further encouraged by the huge scale of disturbance and destruction inflicted on the existing oak forests as a result of the management activities of the Lusatian culture.

2000 BP

In the Eastern Carpathians *Fagus* pollen values reach or even exceed 30%. An area with slightly lower values covers the less elevated Beskid Niski range, the adjacent Jasło-Sanok Depression and the eastern foothills, extending as far as the eastern regions of the Western Carpathians. In their ranges further to the west and in the Tatra Mountains *Fagus* pollen values reach up to 10%, and on the Czech side of the Orava they can exceed 15% (Rybniček & Rybničková 2002). Similarly high amounts of beech pollen occur in the Sudetes. This all emphasises what a significant role *Fagus* was playing in the forests of the Polish mountains at this period. The most important change in comparison with the previous period is the consolidation and territorial expansion of beech in the north-western part of the country.

1500 BP

The economic collapse recorded in many areas of Poland, and associated with the Migration Period, is marked on pollen diagrams as a regeneration phase of forest communities. For beech it was the period of maximum development, and probably at that time this species reached in Poland the present limit of its range. The greatest changes in beech dynamics occurred in north-western Poland, where it occupied mainly the morainic hills of Pomerania. In pollen diagrams from Wolin Island its abundance reaches up to 40% at this time (Latałowa 1992). The cooler and wetter climate developing at this time (Blackford & Chambers 1991) and the weakening of economic pressure on disturbed areas exploited previously by the tribes of the Lusatian and Early Iron-Age cultures were both factors advantageous for beech expansion.

1000 – 500 BP

Growth of both settlements and of economic activity during the Early Middle Ages and Middle Ages resulted in the reduction of areas occupied by forests, and in consequence the amount of beech in the forest communities declined. This is reflected in the reduction of *Fagus* pollen values in comparison with the previous period. In southern Poland the range of *Fagus* in the Carpathians did not undergo any substantial changes beyond the reduction of the higher values in the westernmost ranges of the Western Beskidy Mountains. In the upper Vistula river basin pollen values decreased to 3–5%. More radical changes occurred in the north-western part of the beech range, where its pollen frequencies decreased by several percent. This probably resulted from more intensive deforestation there than in the mountainous areas; in this case the isopolls illustrate rather the scale of deforestation than any decrease of the contribution of beech within the forest communities. In the north-eastern part of the Baltic Coastal Zone the role of beech as a major forest dominant started to increase not earlier than during the Middle Ages (Latałowa 1982).

100 BP

The modern map gives a very restricted picture, compared with the actual occurrence of beech in present natural communities (Zając A. & Zając M. 2001). The high values, reaching 20%, occur only in the Bieszczady Mountains, where dominant beech has formed a dense lower montane forest zone represented mainly by the *Dentario glandulosae-Fagetum* association (Matuszkiewicz J.M. 2002). There it has the broadest altitudinal range (450–1150 m a.s.l.) of all Polish mountain areas, covering all the slopes.

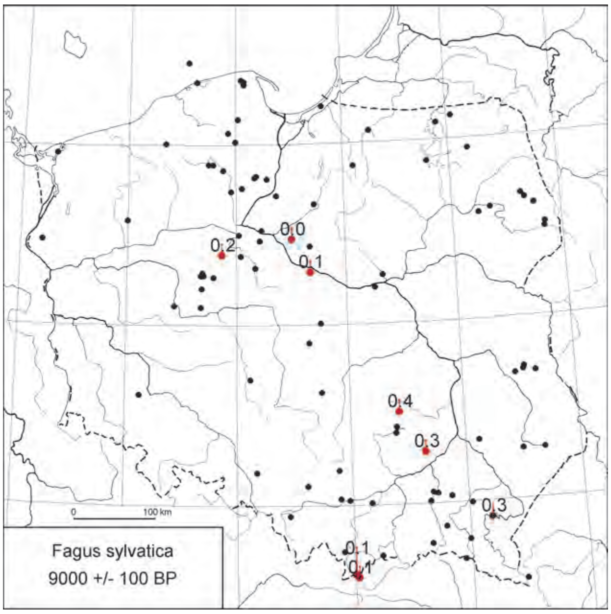
Rather high pollen values (up to 7%) reach westwards to the Wisłok river, including also the Beskid Niski range and Pieniny Mountains. In the Western Beskidy Mountains the fertile Carpathian beechwoods also occur, but in those regions devastated by human interference they are supplanted by spruce. Similar pollen values of beech have been found in the Sudetes, representing there the Sudetic association *Dentario enneaphyllidis-Fagetum*. Isopolls with values of 3–5% run along the Odra river valley up to the upper Vistula river valley, and across the Sandomierz Depression as far as Western Wołyń. Such values also appear in northern Poland, in the Kaszuby Upland. In the remaining part of the country the isopolls show lower values with minima in Wielkopolska and adjacent western parts of Mazovian Lowland and the lake districts. Comparison of the modern isopollen map with the present distribution of beech in Poland shows that the isopolls do not distinguish the areas lying within the limit of the beech range from those situated beyond this limit. This may be an effect of the generally low amount of deciduous tree pollen, beech among them, produced under the conditions of advanced deforestation of these areas.

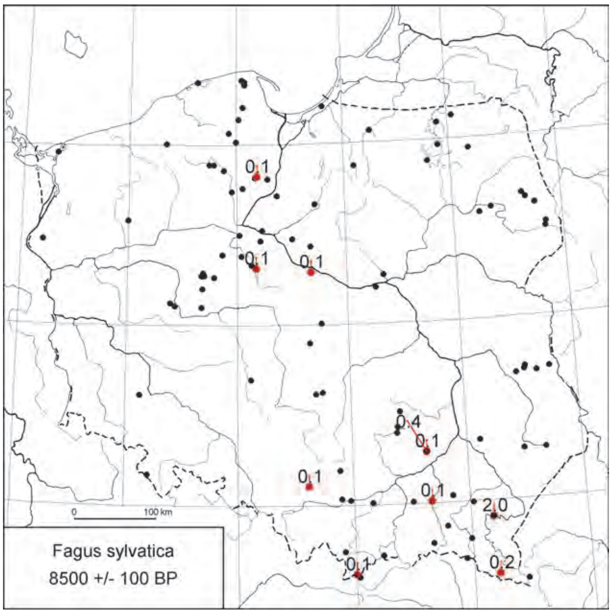
CONCLUSIONS

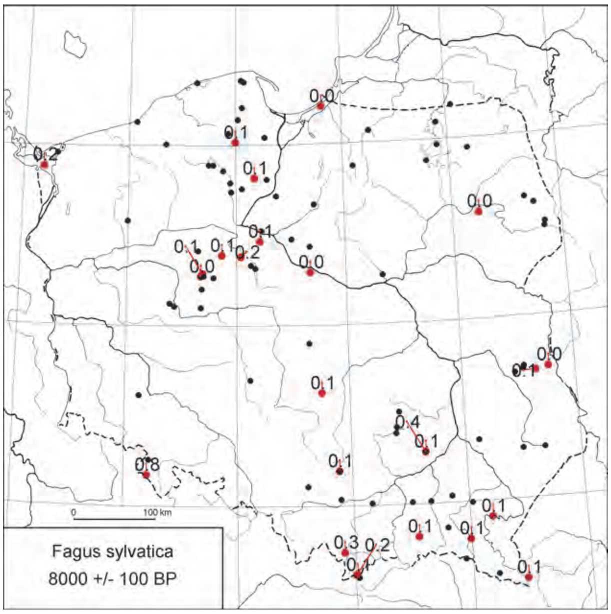
Fagus sylvatica appeared in Poland between 5500 and 5000 BP along the mountain ranges of the Bieszczady and Sudetes, and less intensively from the direction of the Western Beskidy Mountains. At about 3000 BP it began also to expand dynamically in the north-western part of the country. It entered the Sudetes and Western Beskidy Mountains coming from the Czech and Moravian territories, whereas in the Bieszczady Mountains it rather appeared to be migrating along the southern slopes of the Carpathians (or possibly from the north-western outskirts of the Hungarian Plain). At first beech expanded in the mountains, descending next onto their forelands, and reaching, with scattered sites, the Lublin Upland and southern Wielkopolska. It arrived in north-western Poland from Mecklenburg, extending its range along the Baltic Coastal Zone. It reached its widest distribution between 2000 and 1000 BP, however, even during that period it played an insignificant role in central Poland, where the hornbeam-dominated forests were most widespread (Tobolski 1990). Also its eastward advance along the Baltic Coastal Zone was probably slowed down as a result of the simultaneous, dynamic expansion of *Carpinus* in the central and eastern parts of this region (Latałowa 1995, 1997).

The following stages of the extension of the range of beech were stimulated by climatic changes, particularly towards greater precipitation (Ralska-Jasiewiczowa 1983, Huntley 1988). Its rate of migration across Poland was stimulated mainly by the cooler and wetter conditions at the onset of the Subatlantic period, generating vegetational changes, particularly in the north-western part of the country. A regional geographical analysis of the dates for the beginning of beech expansion (rapid increase of pollen amount) revealed differences of often several hundred years. It may be suggested that in many areas human activity was an additional advantageous factor for the spread of this species (Aaby 1986, Latałowa 1992, 1997, Pott 1997). According to the opinion of some authors, beech is still in a phase of expansion and its range is showing further extension (Huntley & Birks 1983). This is confirmed by investigations carried out in southern Sweden (Björkman 1996). Also the north-eastern limit of its present range running across Poland probably shows some advance. Analyses of climatic data suggest that present conditions in north-eastern Poland should not be a limiting factor for the natural spread of beech into these areas (Matuszkiewicz J.M. 2002).

Fig. 42. *Fagus sylvatica*: dot and isopollen maps for 9000–100 ^{14}C yr BP


0.0
0.2
0.1
0.4
0.3
0.3
0.1
0.1
0
100 km
Fagus sylvatica
9000 +/- 100 BP


0.1
0.1
0.1
0.4
0.1
0.1
0.1
2.0
0.1
0.2
0
100 km
Fagus sylvatica
8500 +/- 100 BP

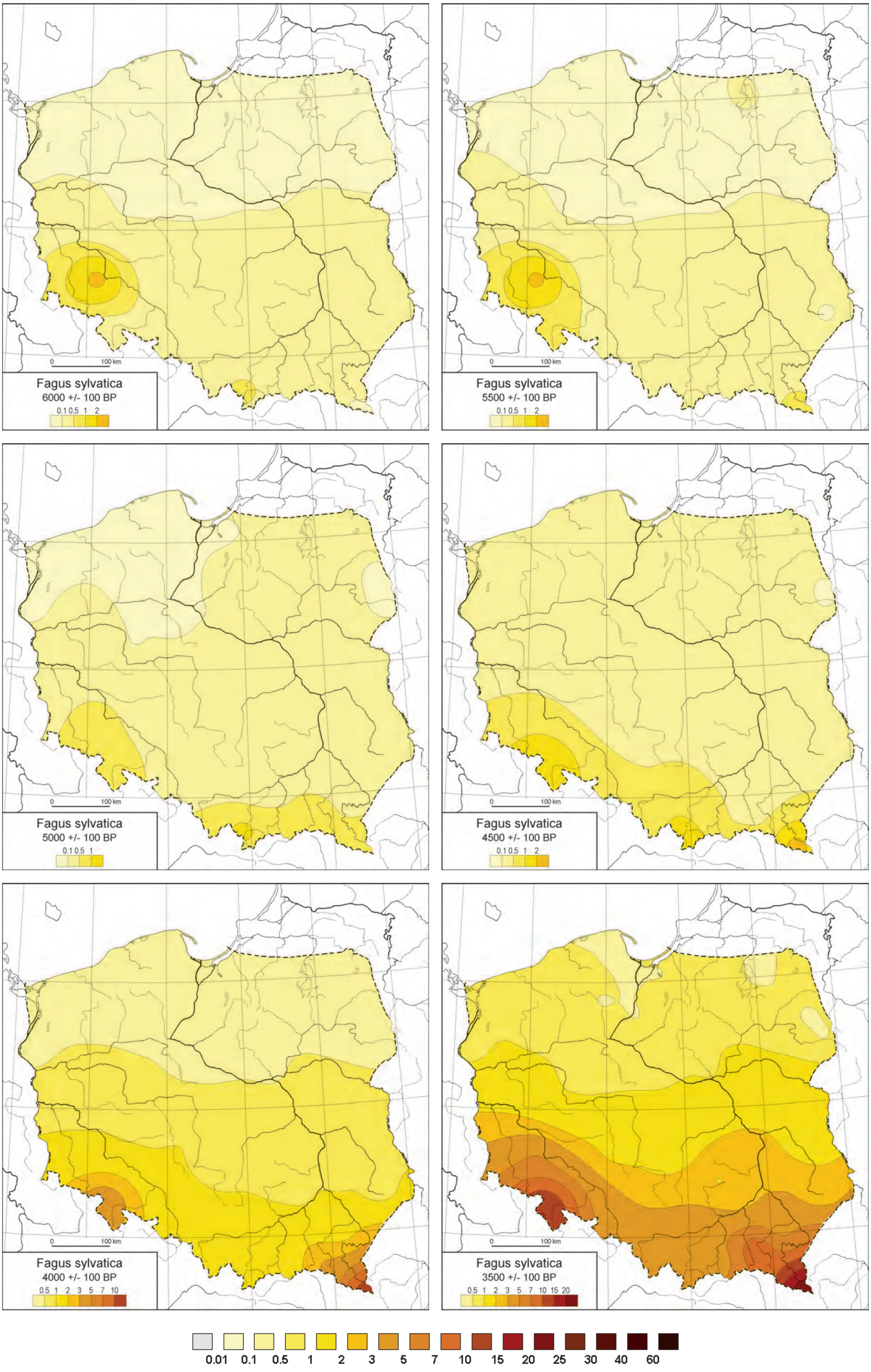

0.0
0.2
0.1
0.1
0.0
0.1
0.1
0.1
0.2
0.0
0.0
0.0
0.0
0.1
0.1
0.4
0.1
0.8
0.1
0.1
0.1
0.1
0.3
0.2
0.1
0.1
0
100 km
Fagus sylvatica
8000 +/- 100 BP

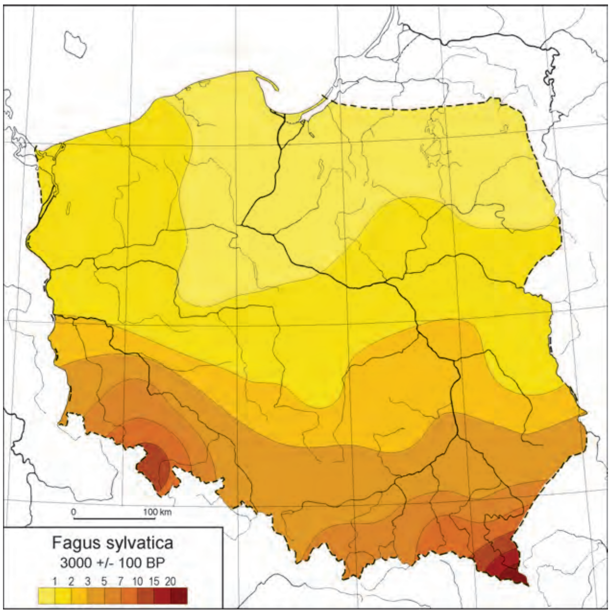

0
100 km
Fagus sylvatica
7500 +/- 100 BP
0.01
0.1

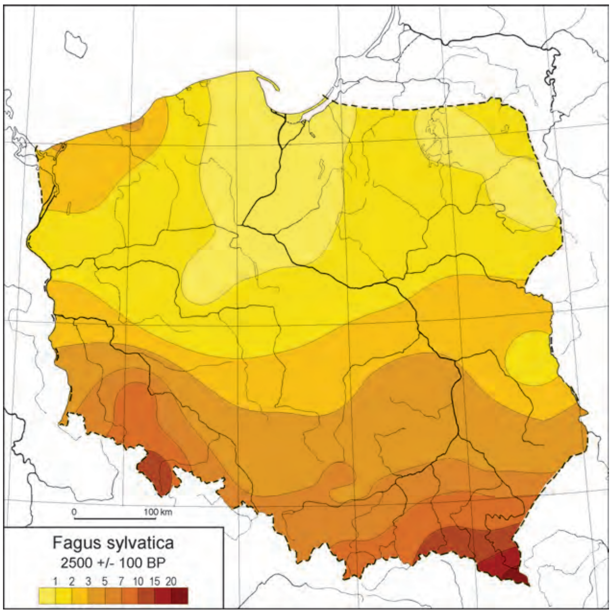

0
100 km
Fagus sylvatica
7000 +/- 100 BP
0.01
0.1

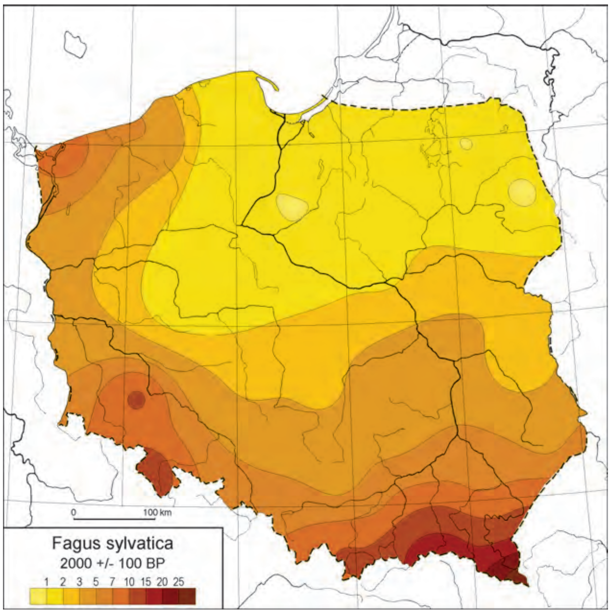

0
100 km
Fagus sylvatica
6500 +/- 100 BP
0.01
0.1
0.5

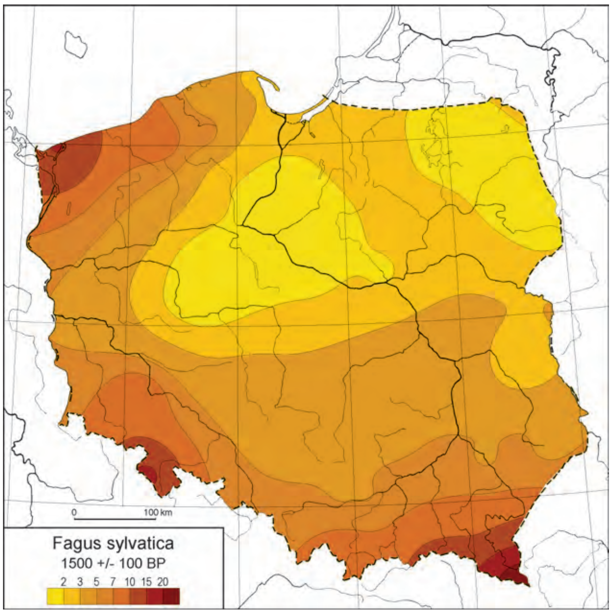

0.01
0.1
0.5
1
2
3
5
7
10
15
20
25
30
40
60

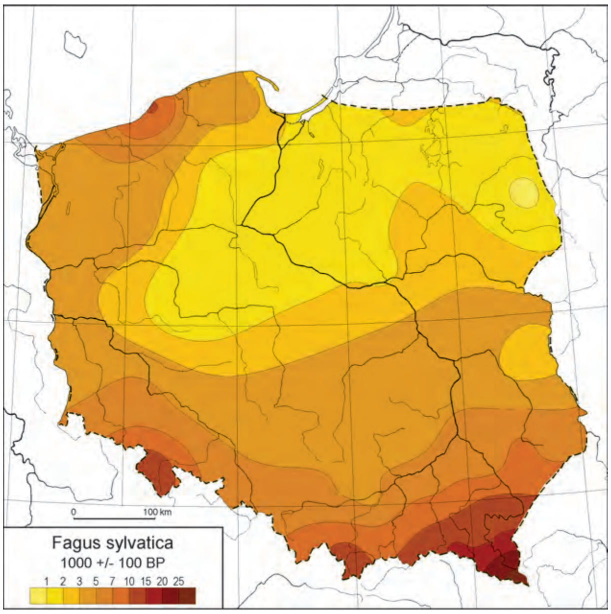

0 100 km
Fagus sylvatica
6000 +/- 100 BP
0.1 0.5 1 2
0 100 km
Fagus sylvatica
5500 +/- 100 BP
0.1 0.5 1 2
0 100 km
Fagus sylvatica
5000 +/- 100 BP
0.1 0.5 1
0 100 km
Fagus sylvatica
4500 +/- 100 BP
0.1 0.5 1 2
0 100 km
Fagus sylvatica
4000 +/- 100 BP
0.5 1 2 3 5 7 10
0 100 km
Fagus sylvatica
3500 +/- 100 BP
0.5 1 2 3 5 7 10 15 20
0.01 0.1 0.5 1 2 3 5 7 10 15 20 25 30 40 60

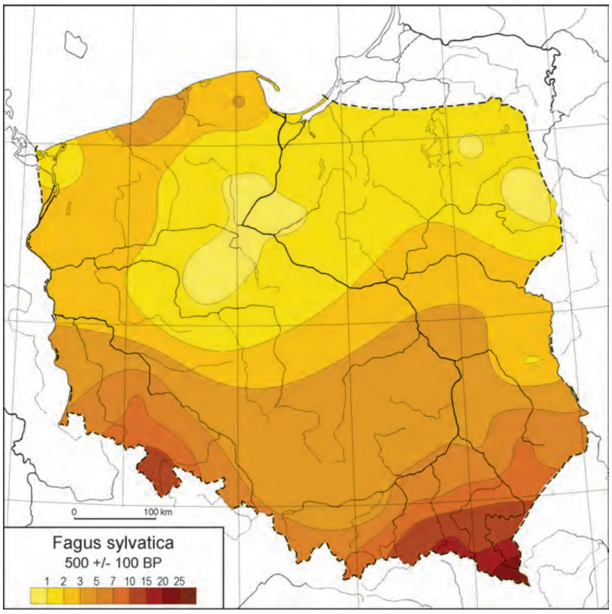

0
100 km
Fagus sylvatica
3000 +/- 100 BP
1 2 3 5 7 10 15 20


0
100 km
Fagus sylvatica
2500 +/- 100 BP
1 2 3 5 7 10 15 20

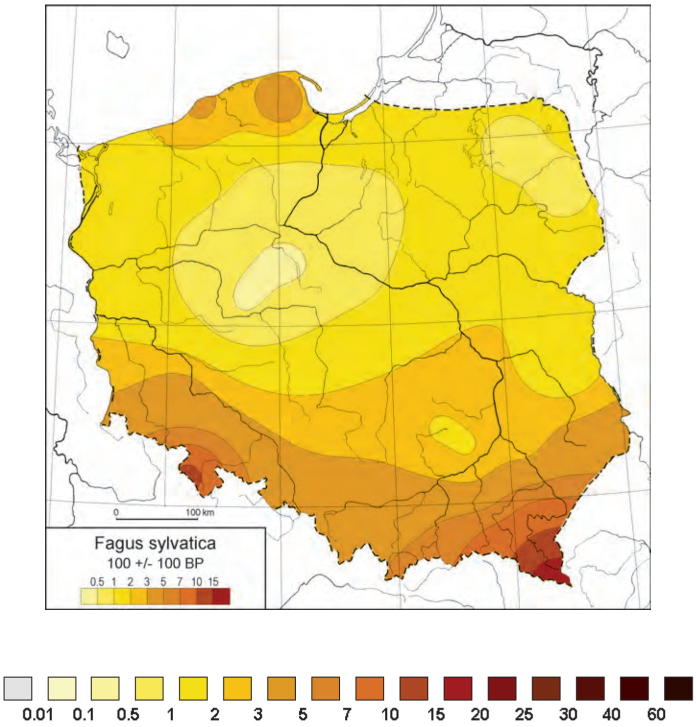

0
100 km
Fagus sylvatica
2000 +/- 100 BP
1 2 3 5 7 10 15 20 25


0
100 km
Fagus sylvatica
1500 +/- 100 BP
2 3 5 7 10 15 20


0
100 km
Fagus sylvatica
1000 +/- 100 BP
1 2 3 5 7 10 15 20 25


0
100 km
Fagus sylvatica
500 +/- 100 BP
1 2 3 5 7 10 15 20 25


0.01 0.1 0.5 1 2 3 5 7 10 15 20 25 30 40 60


0
100 km
Fagus sylvatica
100 +/- 100 BP
0.5 1 2 3 5 7 10 15
0.01 0.1 0.5 1 2 3 5 7 10 15 20 25 30 40 60

Fraxinus excelsior L. – **Ash**

KAZIMIERZ TOBOLSKI AND DOROTA NALEPKA

PRESENT DISTRIBUTION IN EUROPE

Fraxinus excelsior L. is a species occurring in Europe and also in Asia Minor (Boratyńska & Boratyński 1976). In the north it reaches central Sweden and northern Finland, in the east the upper and central valley of the Volga river, and in the south it reaches just the northern edge of the Iberian Peninsula, but occurs over much of the Apennine Peninsula and the Balkans. It has been pointed out by Meusel et al. (1978) that at the sites located in the European sub-Mediterranean regions *Fraxinus excelsior* is found only in the cool and moist montane zones. In Asia this species grows in northern Turkey and Iran, and around the Caspian Sea.

PRESENT DISTRIBUTION IN POLAND

In Poland (Fig. 43) ash is a transgressive species (Boratyńska & Boratyński 1976) and is quite regularly distributed throughout Poland (Zając A. & Zając M. 2001). In the mountains it rarely occurs over 800 m; its highest location was recorded at Kuźnice in the Tatra Mountains at about 1000 m a.s.l. (Boratyńska 1995). It is rather rare in forests and is restricted mainly to floodplain communities. For a long time it has been cultivated in parks, along roads and around houses.

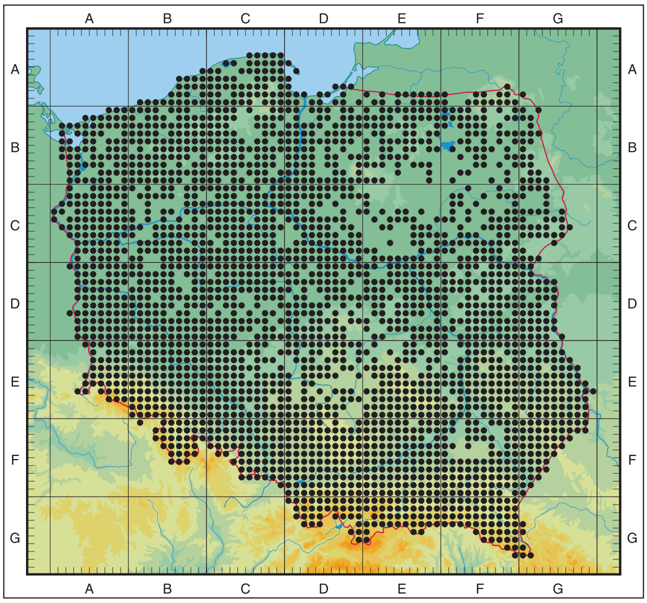


Fig. 43. Present-day distribution of *Fraxinus excelsior* L. in Poland (after Zając A. & Zając M. 2001)

In the present-day boundaries of Poland only *Fraxinus excelsior* is found, but during the Holocene *Fraxinus angustifolia* may have been present too. The slight differences in morphological structure of the pollen grains of the two species are undetectable during routine palynological analyses (Tobolski 1995), therefore some palynologists prefer to use the term '*Fraxinus excelsior*-type' (Punt et al. 1991). Present-day sites of *Fraxinus angustifolia* are found just beyond the southern border of Poland, in the Czech Republic and Slovakia (Meusel et al. 1978).

ECOLOGY

Fraxinus excelsior is a high forest tree and belongs to a small group of the tallest trees of the European continent. In the Białowieża Forest, in rather unfavourable subcontinental and sub-boreal conditions for ash, and only a 180-day growing season, it reaches a height up to 42 m and its trunk reaches up to 160 cm in diameter (Faliński & Pawlaczyk 1995). It prefers the warm temperate climate of the European sub-oceanic area (Ellenberg et al. 1991, Zarzycki et al. 2002). It has a varied and quite wide tolerance of hydrological conditions, soil type and light conditions. According to Faliński and Pawlaczyk (1995) it can grow well under high surface moisture and groundwater conditions; it is tolerant of seasonal inundation and floods. In forest communities it prefers a well-established humus accumulation layer, slightly acid to slightly alkaline, with a relatively fast decomposition of biomass and a favourable proportion of carbon to nitrogen (Faliński & Pawlaczyk 1995). It belongs to plants of low competitive ability, but this is moderated by production of large quantities of seedlings, capable of rapid growth (Ellenberg 1996). In Poland, with a few exceptions, ash does not form pure forest stands but is quite a significant component of a few mesotrophic and eutrophic forest communities of the *Alno-Padion* alliance as well as other damp forest communities of the *Querco-Fagetea* class.

Observations of the dynamics of present-day *Fraxinus excelsior* stands place this species among post-pioneer plants (Faliński & Pawlaczyk 1995). Such behaviour of ash is confirmed by its history during the Quaternary. As in the interglacial periods and also in the Holocene, it penetrated into existing forest communities which, mostly, had already managed to establish stable meso-trophic or eutrophic conditions.

POLLEN PRODUCTION AND DISPERSAL

Fraxinus excelsior is wind-pollinated and begins to flower in April before coming into leaf. It can develop male, female or hermaphrodite flowers (‘gender diphasy’) (Faliński & Pawlaczyk 1995). Free-standing trees start flowering at the age of 25, whereas trees growing within forest flower after 40 years. Ash maintains its ability to flower for up to 250 years (Lang 1994). Its pollen production is rather low, up to 160,000 pollen grains in an inflorescence, less than other trees species, for example, almost an order of magnitude less than pine (Pohl 1937). Ash is characterised by years of high seed production separated by barren periods lasting for several years. Dispersal of its winged fruits (samaras) is achieved by both wind and animal dispersal (Faliński & Pawlaczyk 1995).

Percentage pollen values of ash approximately represent, or maybe slightly underrepresent, its percentage presence in the vegetation. Little is known about the flowering behaviour and pollen production of ash in different habitats.

MIGRATION PATTERN IN POLAND (Fig. 44)

10,000 – 8000 BP

For *Fraxinus excelsior* Lang (1994) lists four refugial areas including the eastern Alps and the Carpathians. Postglacial expansion and migration of ash to Poland must have been related to these centres. At the time levels of 9500 and 9000 BP, the isopoll for 0.5% first covers the south-eastern part of Poland and later expands, signalling advancing migration of ash from a south-eastern direction by distant pollen transport from places still far away from Poland. The expansion of ash in Poland may have taken place about 8500 years ago because the isopoll indicating values 0.5–1% covers a fairly large part of south-eastern Poland. On the next map the range of this isopoll covers almost two-thirds of Poland, and at the same time the south of Poland in the region of the Carpathians and the Kłodzko Basin shows values 1.0–2.0%. Despite little information available about the significance of pollen deposition at these values, the isopoll value of 0.5% seems to confirm the occurrence of ash in Poland, expanding there during the early Holocene. This assumption is supported by data collected by Bremówna and Sobolewska in the Białowieża Forest (after Tobolski 1995).

7500 – 4000 BP

Continuing expansion led to the development of the distribution cover of ash, visible on the 7500 and 7000 BP maps. In the period between 6500 and 6000 BP two areas developed where ash gained a more significant role in the structure of forests. One such area was established in southern Poland and the other started to form in Wielkopolska. The 5500 BP map shows Wielkopolska with maximum values of *Fraxinus* pollen. The most marked concentration is found in the region of Gniezno Lake District. The following 5000 BP map shows a decrease in the area lying within the ash pollen isopolls 3.0 and 5.0%, and in the next millennium the isopoll for 3.0% encompassed much the same area of the Wielkopolska.

3500 – 100 BP

A clear decline of ash in the region of Wielkopolska is seen from 3500 years ago, against a background of major forest changes across Poland. The last three millennia illustrate successive phases of fairly continuous decline of the importance of ash in the Polish forests. The last map covering almost the whole territory of Poland within the range of isopoll 0.1%, shows values very similar to those on the 8500 BP map, when *Fraxinus* was deemed to be expanding. However, it must be remembered that at that earlier time there was a well-established woodland cover filtering the pollen rain, in contrast to the present-day picture which relates largely to an open agricultural landscape. It seems that the last map shows the sparse forest cover favouring the long distance transport of native wind-pollinated trees.

CONCLUSIONS

To sum up, the following facts should be emphasized:

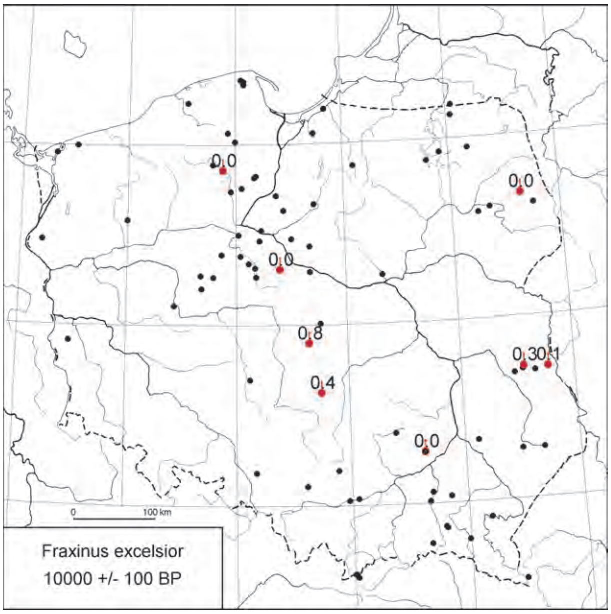
– postglacial expansion of *Fraxinus excelsior* was typical of that of mesocratic trees;

– ash played a significant role in the forest cover from 6500 to 4000 years ago;

– after this period the role of this tree in forest communities steadily decreased;

– the main reason for postglacial differences in the occurrence of ash related to changing climatic conditions.

Fig. 44. *Fraxinus excelsior*: dot and isopollen maps for 10,000–100 ^{14}C yr BP



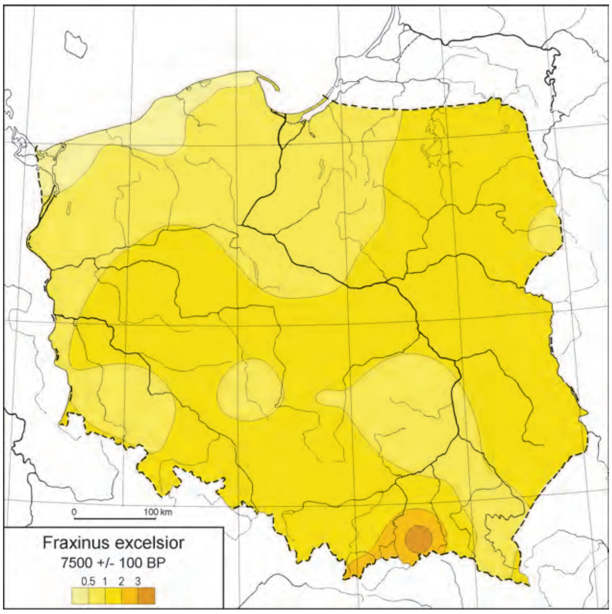
Fraxinus excelsior
10000 +/- 100 BP

Fraxinus excelsior
9500 +/- 100 BP

Fraxinus excelsior
9000 +/- 100 BP

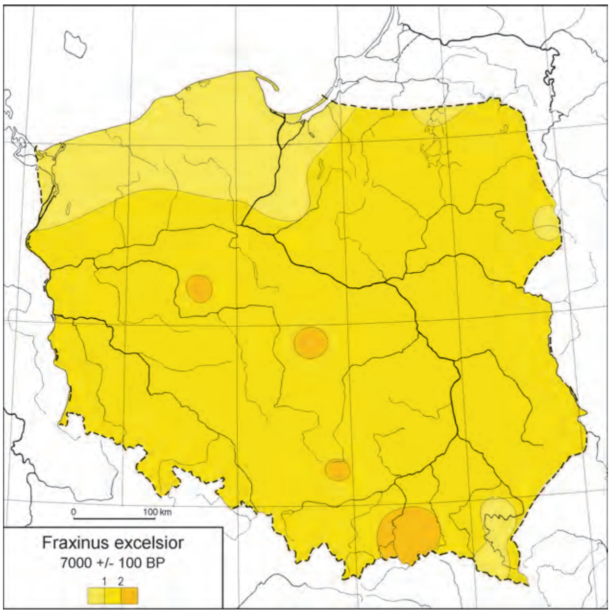
Fraxinus excelsior
8500 +/- 100 BP

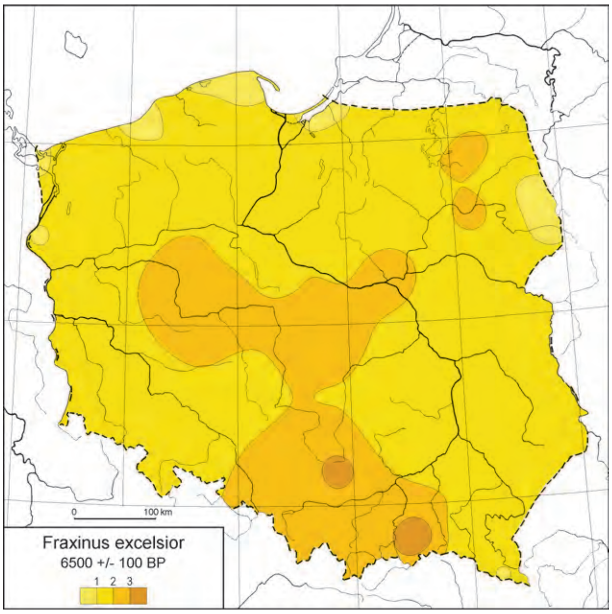
Fraxinus excelsior
8000 +/- 100 BP

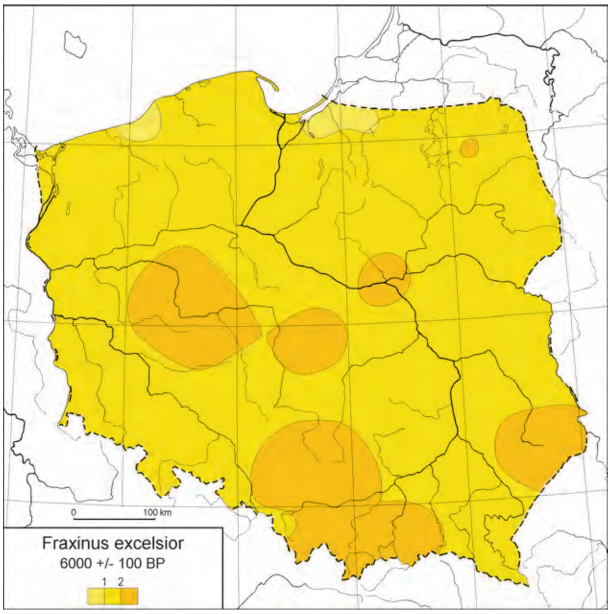


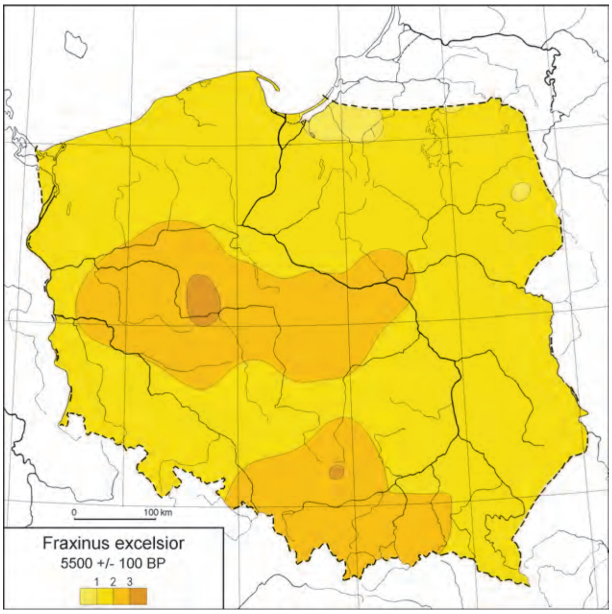
Fraxinus excelsior
7500 +/- 100 BP

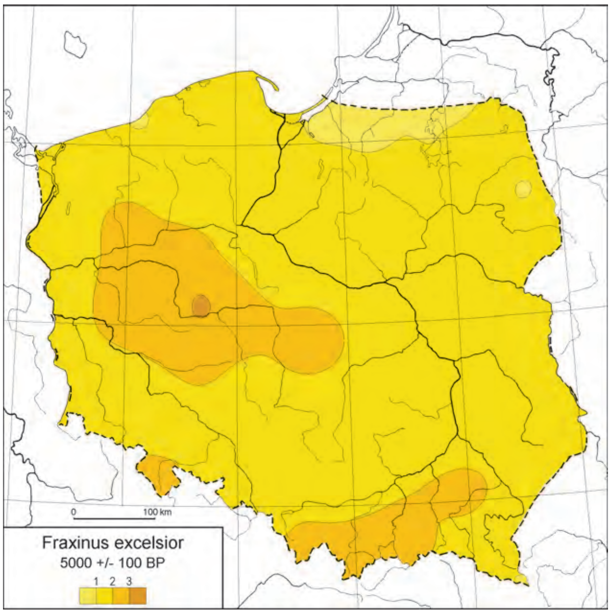
0.01 0.1 0.5 1 2 3 5 7 10 15 20 25 30 40 60

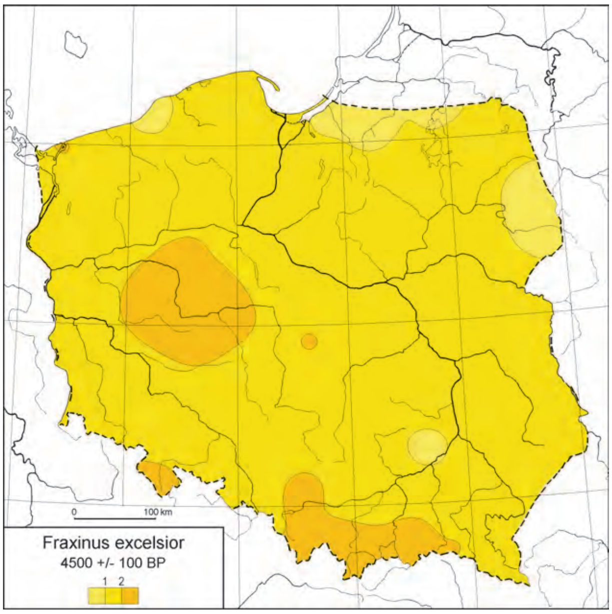

Fraxinus excelsior
7000 +/- 100 BP


Fraxinus excelsior
6500 +/- 100 BP

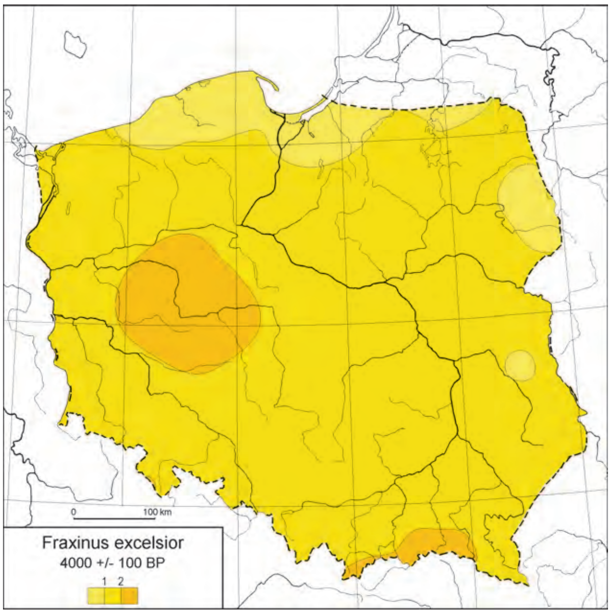

Fraxinus excelsior
6000 +/- 100 BP

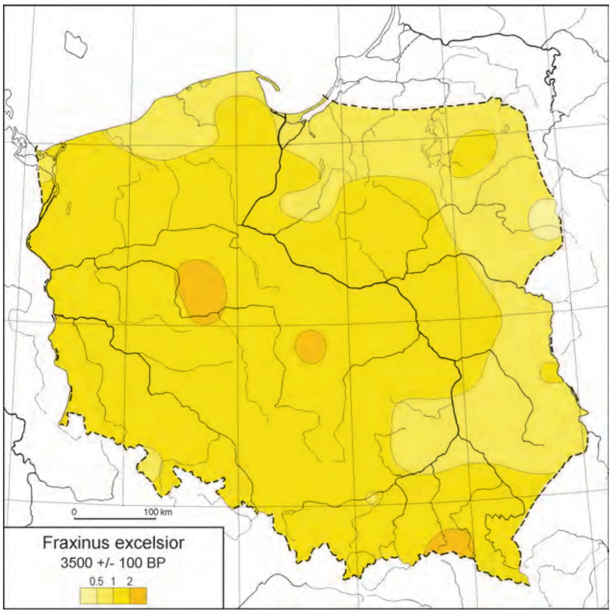

Fraxinus excelsior
5500 +/- 100 BP

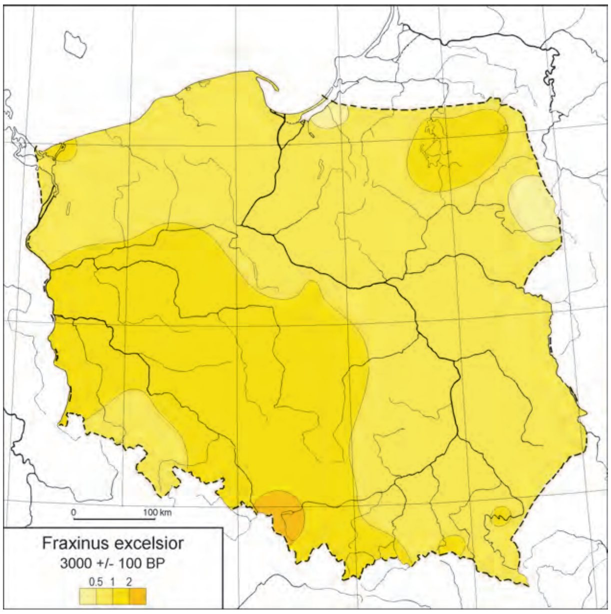

Fraxinus excelsior
5000 +/- 100 BP

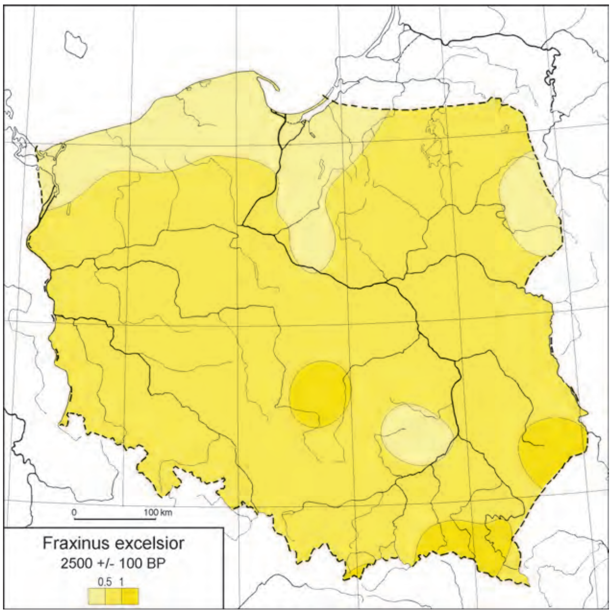

Fraxinus excelsior
4500 +/- 100 BP

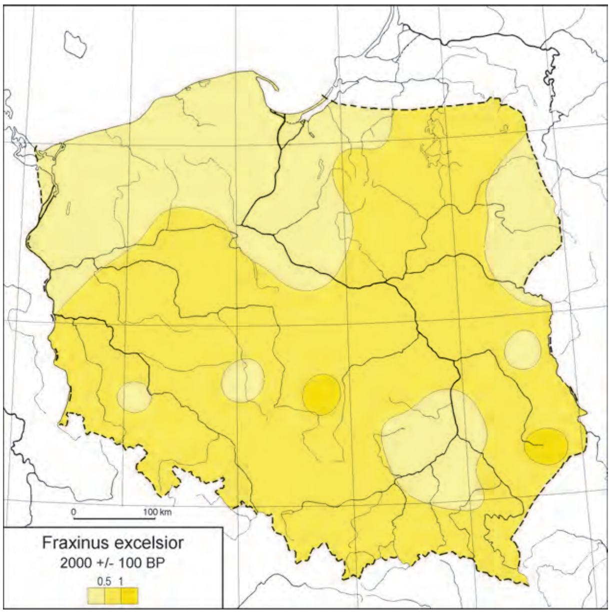
0.01 0.1 0.5 1 2 3 5 7 10 15 20 25 30 40 60


0
100 km
Fraxinus excelsior
4000 +/- 100 BP
1 2


0
100 km
Fraxinus excelsior
3500 +/- 100 BP
0.5 1 2


0
100 km
Fraxinus excelsior
3000 +/- 100 BP
0.5 1 2


0
100 km
Fraxinus excelsior
2500 +/- 100 BP
0.5 1


0
100 km
Fraxinus excelsior
2000 +/- 100 BP
0.5 1


0
100 km
Fraxinus excelsior
1500 +/- 100 BP
0.5


0.01
0.1
0.5
1
2
3
5
7
10
15
20
25
30
40
60


0
100 km
Fraxinus excelsior
1000 +/- 100 BP
0.5


0
100 km
Fraxinus excelsior
500 +/- 100 BP
0.1 0.5 1


0
100 km
Fraxinus excelsior
100 +/- 100 BP
0.1 0.5


0.01
0.1
0.5
1
2
3
5
7
10
15
20
25
30
40
60

Hedera helix L. – **Ivy**

WOJCIECH GRANOSZEWSKI, KRZYSZTOF M. KRUPIŃSKI, MAŁGORZATA NITA, AND DOROTA NALEPKA

PRESENT DISTRIBUTION IN EUROPE

Hedera helix L. is a Mediterranean-Atlantic species (Fig. 45). The eastern limit of its range runs along the north-eastern coast of the Black Sea in the south, to the Gulf of Riga on the Baltic coast in the north. It occurs in the southern part of the Scandinavian Peninsula (Hultén & Fries 1986).

PRESENT DISTRIBUTION IN POLAND

Hedera helix grows throughout the country, and, close to the north-eastern boundary of Poland, it reaches the eastern limit of its occurrence (Fig. 46).

ECOLOGY

Ivy is a liana. In Poland it occurs under moderately warm climatic conditions in half-shaded to fully-exposed sites. It requires full sunlight (20–100%) to flower and bear fruit, whereas for vegetative development 2% light is sufficient (Pałczyński et al. 1995). In terms of continentality of climate, ivy prefers the conditions of temperate to slightly oceanic climates (Zarzycki et al. 2002). It avoids a distinctly continental climate (Seneta 1981a, 1996). During severe winters, when habitat and climatic conditions become less favourable, ivy freezes above the snow cover. Ivy growing in the Białowieża

Fig. 45. *Hedera helix* – map of present-day distribution in Europe: ● – native isolated occurrence (after Meusel et al. 1978)

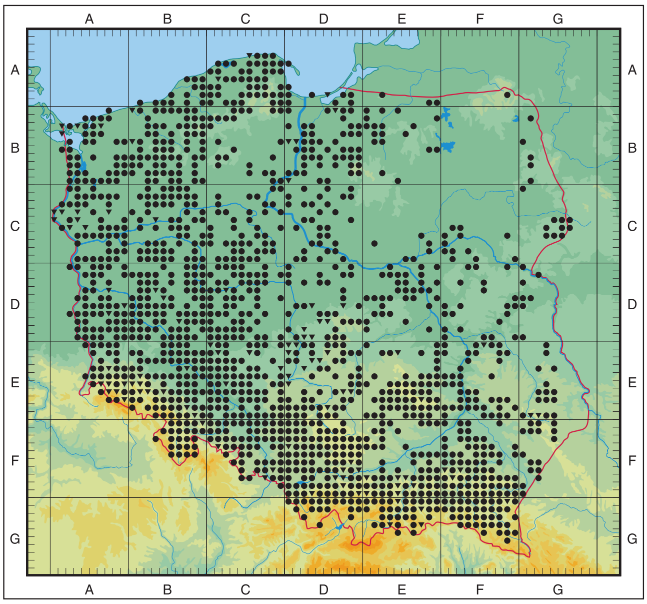


Fig. 46. Present-day distribution of *Hedera helix* L. in Poland: ▼ – sites with flowering specimens (after Zając A. & Zając M. 2001)

Forest just creeps around the lowest parts of tree-trunks and does not bear fruit, while ivy plants occurring in western Poland climb high, reaching the crowns of trees, where they flower and bear fruit (Czarnowski 1978). The present sites of ivy in the Pieniny Mountains are characterised by a mean temperature of –3.3°C in January and +16.4°C in July (Jasiewicz 1951). Ivy can also be found flowering at sites in the lower course of the Vistula river and in southern Poland (Fig. 46, and Mamakowa 1962). In Denmark, under conditions of oceanic climate, it cannot grow and flower beyond the –2°C isotherm for the coldest month (Iversen 1944). In general, it grows on slightly moist soils in forest communities of the *Fagetalia sylvaticae* order (Matuszkiewicz W. 2001).

Ivy flowers from September to October (Szafer et al. 1953). Its fruits (berries) ripen in spring.

POLLEN PRODUCTION AND DISPERSAL

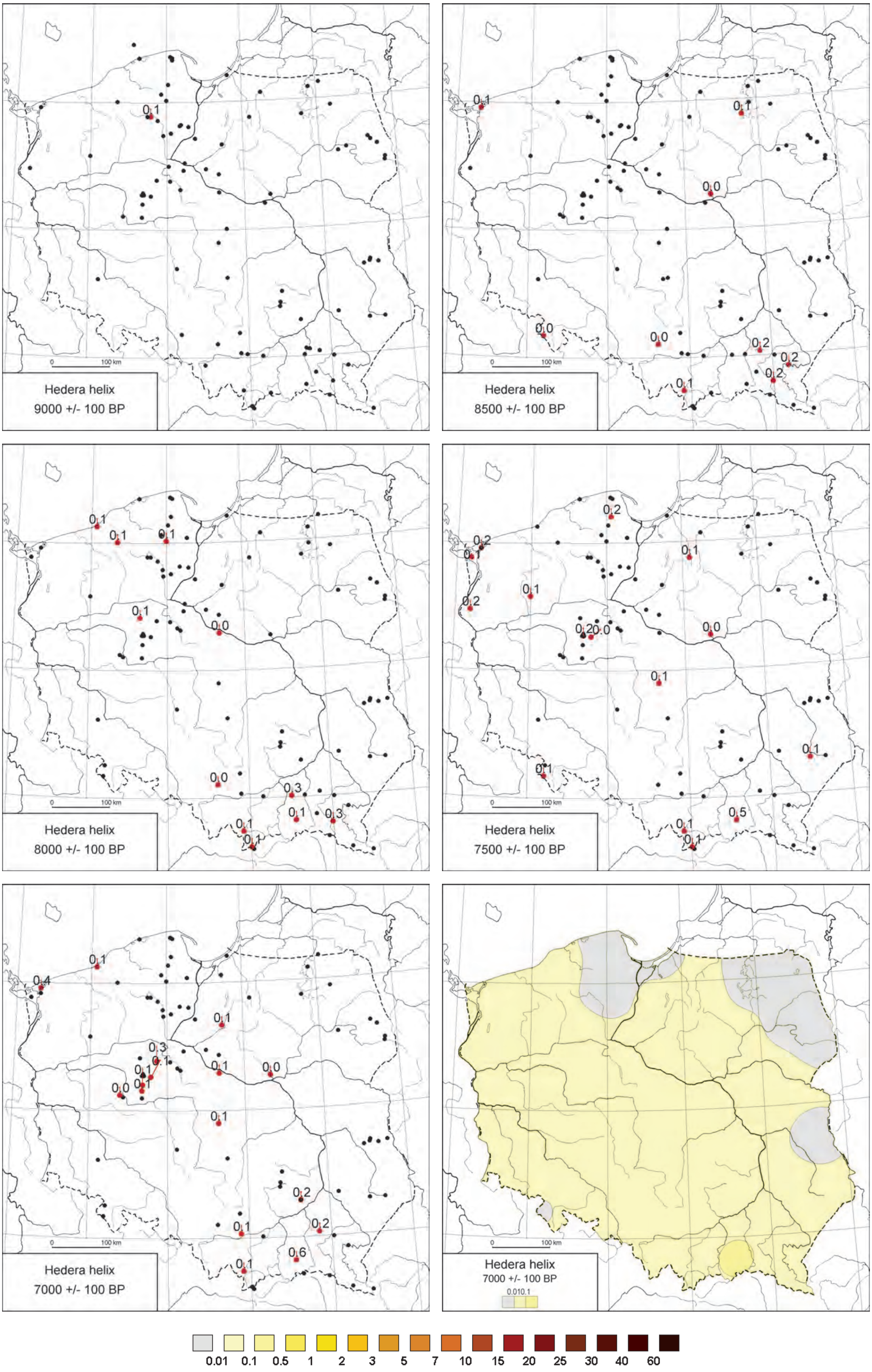
Ivy is an insect pollinated (flies) and honey-yielding plant (Seneta 1996). Its pollen values in pollen assemblages are low, most often 0.1% to 0.2%, exceptionally up to 0.7%. In assemblages derived from the warmest phases of Pleistocene interglacial periods *Hedera* pollen is also often recorded, though not regularly, in amounts similar to those of the Holocene.

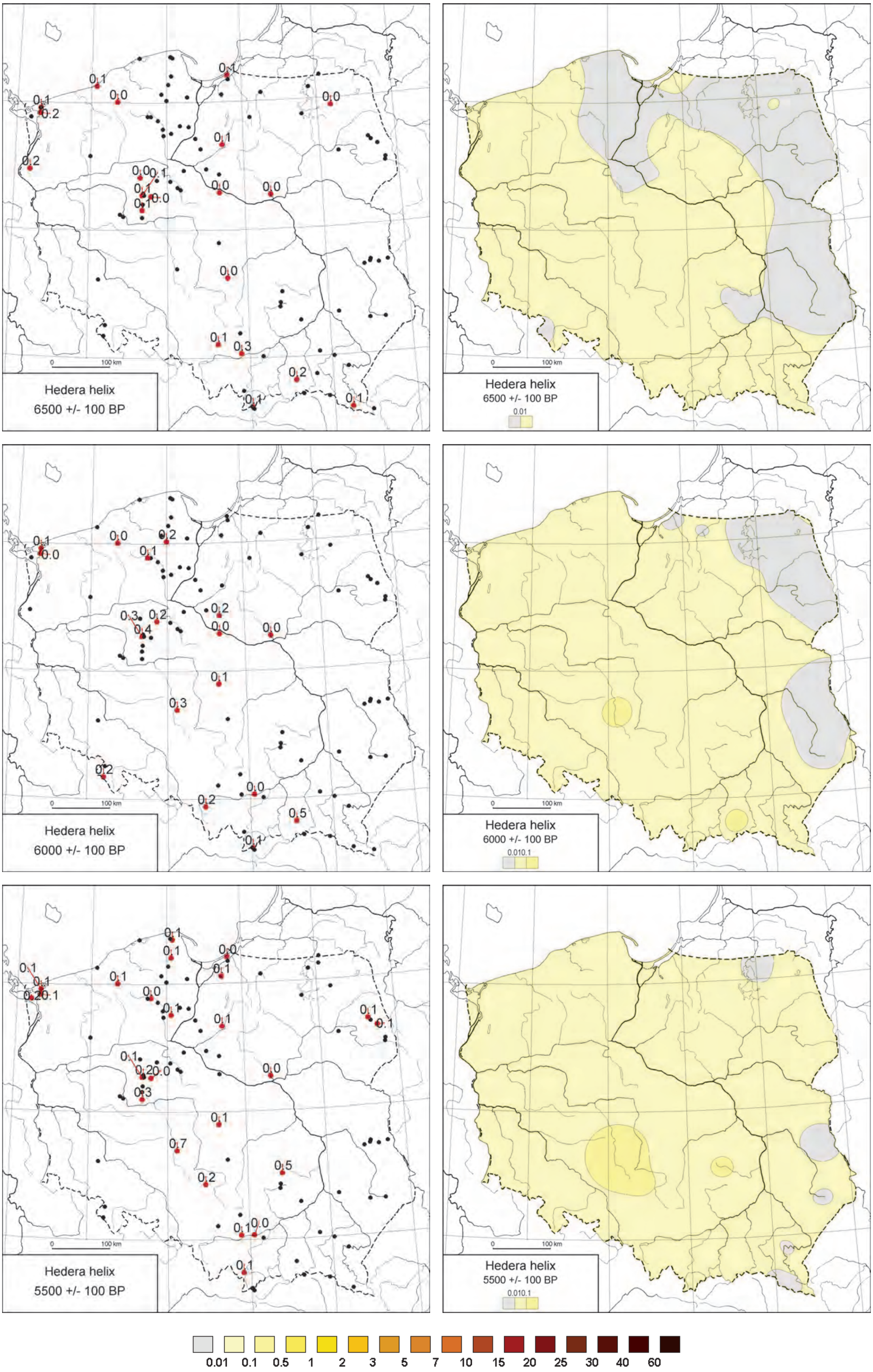
EXPANSION IN EUROPE AND IN POLAND DURING THE LATE GLACIAL AND HOLOCENE

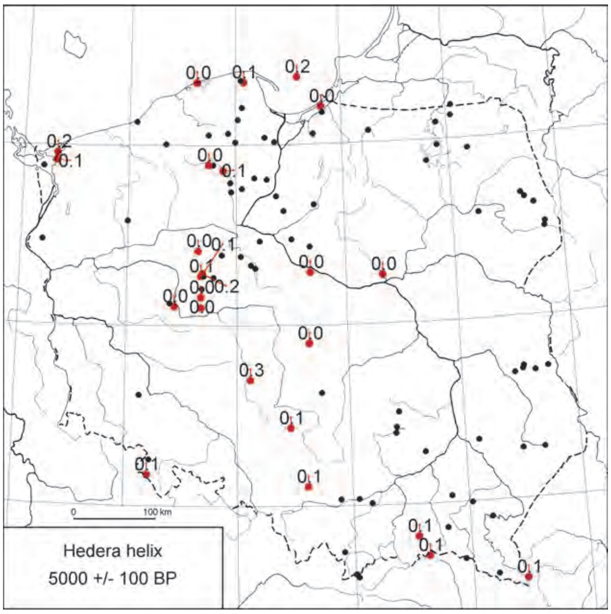
According to Huntley and Birks (1983) in the middle Holocene the range of *Hedera helix* was more restricted to the north than at present.

In Poland (Fig. 47), the first single occurrence of its pollen was recorded during the oldest part of the mesocratic stage (at about 9000 BP) in the Pomeranian Lake District. About 500 years later (8500 BP) this taxon appeared sporadically in the area of north-eastern Poland, and slightly more often and more abundantly, though still in low quantity, in the uplands of southern Poland, mainly in the south-eastern part of the country. In the period from 8000 BP to 3000 BP its range included the whole country, except for eastern Poland. The map for 4000 BP shows a distinct retreat of *Hedera* towards the west, what may signal a temporary change of climate, including a rise of its continentality, coming from the east. Between 3000 and 2500 BP the number of sites, from which ivy pollen was recorded, declined drastically. This trend has persisted up to the most recent time intervals.

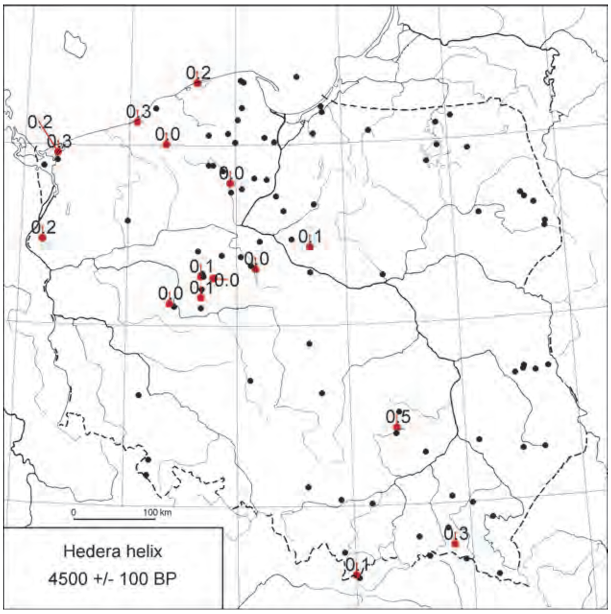
Fig. 47. *Hedera helix*: dot and isopollen maps for 9000–100 ^{14}C yr BP


0
100 km
Hedera helix
9000 +/- 100 BP
0.1
Hedera helix
8500 +/- 100 BP
0.1
0.1
0.0
0.0
0.0
0.2
0.2
0.2
0.1
Hedera helix
8000 +/- 100 BP
0.1
0.1
0.1
0.1
0.0
0.0
0.3
0.1
0.3
0.1
0.1
Hedera helix
7500 +/- 100 BP
0.2
0.2
0.1
0.1
0.2
0.1
0.2
0.0
0.0
0.1
0.1
0.1
0.5
0.1
0.1
Hedera helix
7000 +/- 100 BP
0.1
0.4
0.1
0.3
0.1
0.1
0.1
0.0
0.1
0.0
0.1
0.2
0.1
0.2
0.6
0.1
Hedera helix
7000 +/- 100 BP
0.01
0.1
0.01
0.1
0.5
1
2
3
5
7
10
15
20
25
30
40
60

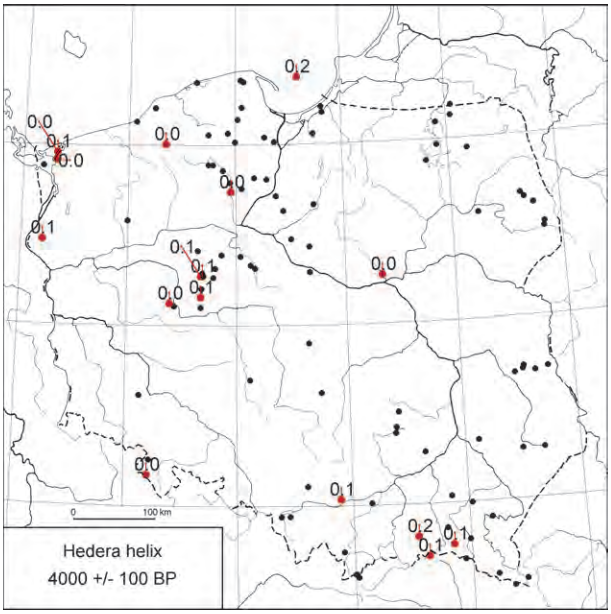

Hedera helix
6500 +/- 100 BP
0.01
Hedera helix
6000 +/- 100 BP
0.01 0.1
Hedera helix
5500 +/- 100 BP
0.01 0.1
0
100 km
0.01
0.1
0.5
1
2
3
5
7
10
15
20
25
30
40
60

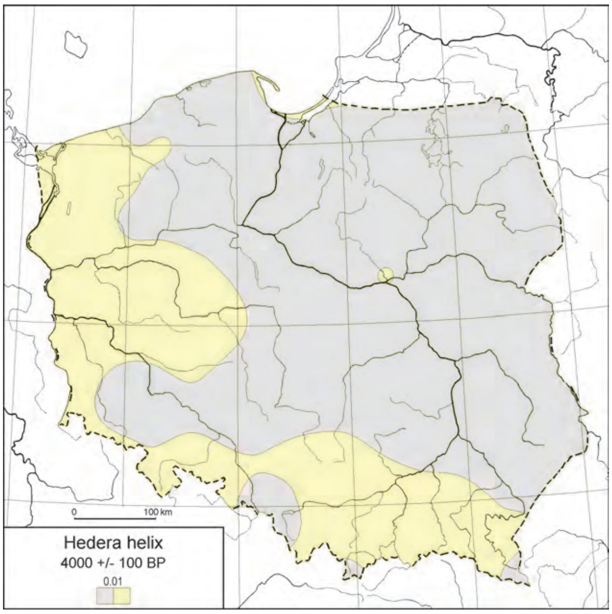

0.0
0.1
0.2
0.0
0.2
0.1
0.0
0.1
0.0
0.1
0.1
0.0
0.0
0.0
0.0.2
0.0
0.0
0.0
0.3
0.1
0.1
0.1
0.1
0.1
0.1
0
100 km
Hedera helix
5000 +/- 100 BP


0
100 km
Hedera helix
5000 +/- 100 BP
0.01
0.1

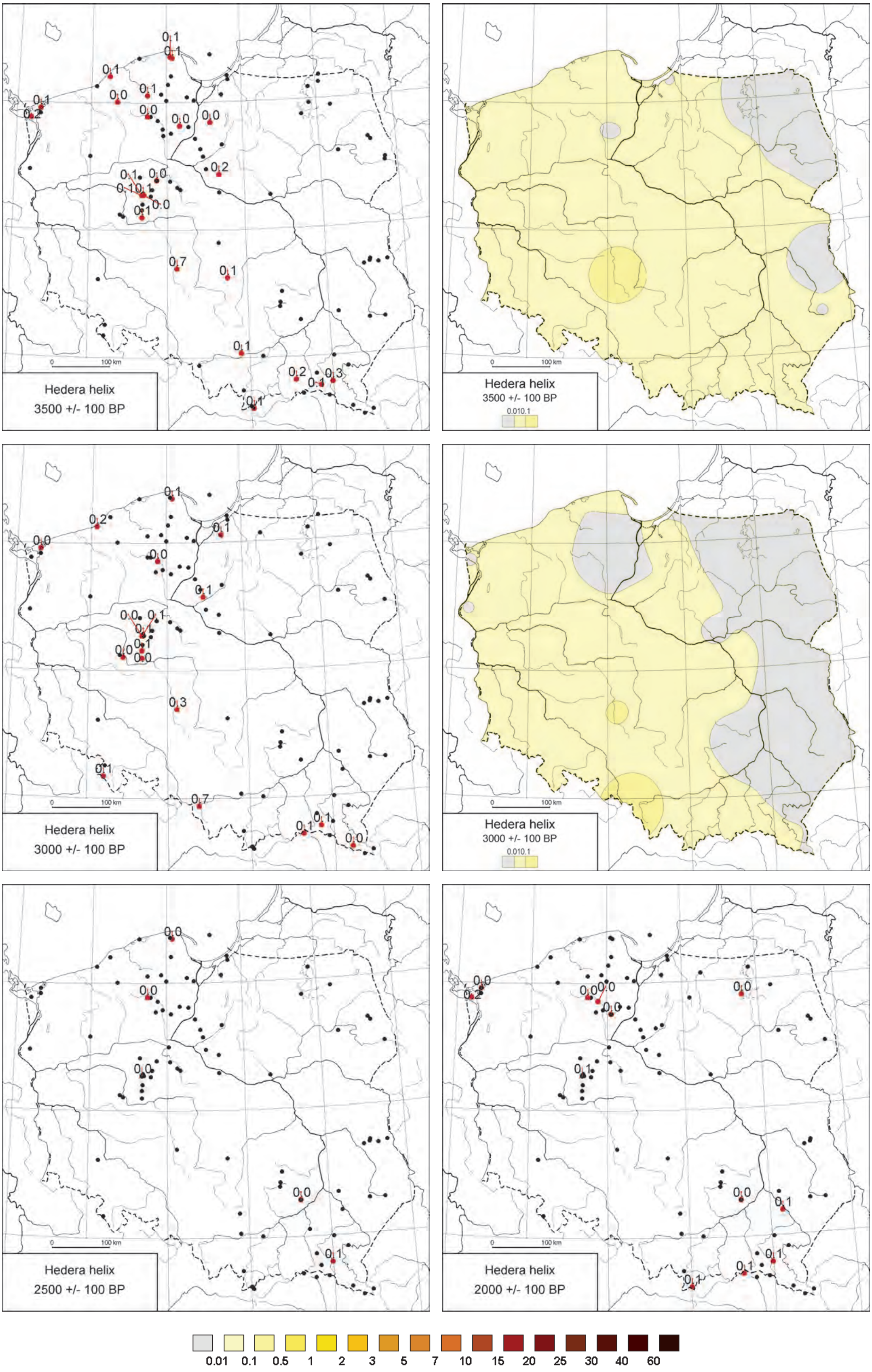

0.2
0.3
0.2
0.3
0.0
0.0
0.2
0.1
0.1
0.0
0.0
0.1
0.0
0.0
0.5
0.3
0.1
0
100 km
Hedera helix
4500 +/- 100 BP

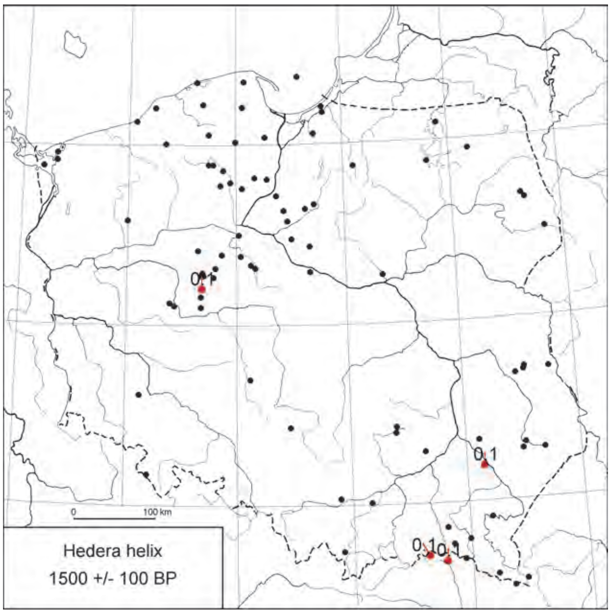

0
100 km
Hedera helix
4500 +/- 100 BP
0.01
0.1

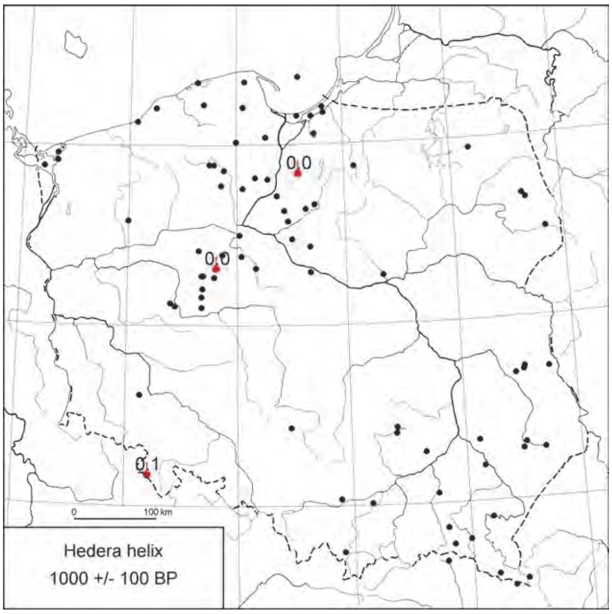

0.2
0.0
0.1
0.0
0.0
0.0
0.1
0.1
0.1
0.0
0.1
0.0
0.0
0.1
0.2
0.1
0.1
0
100 km
Hedera helix
4000 +/- 100 BP

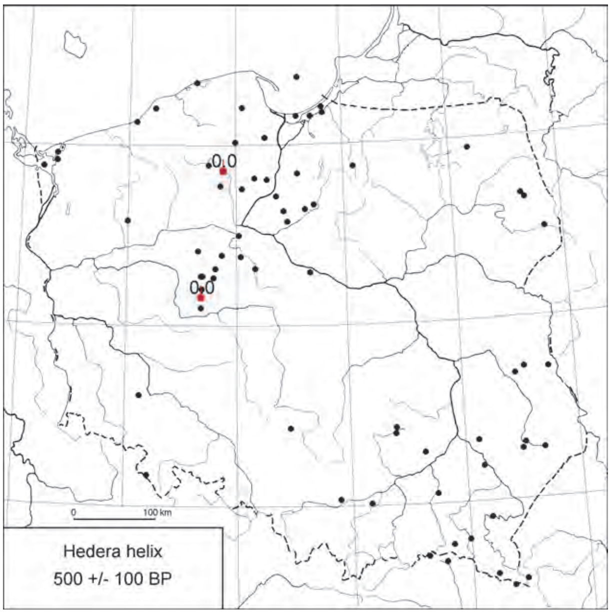

0
100 km
Hedera helix
4000 +/- 100 BP
0.01

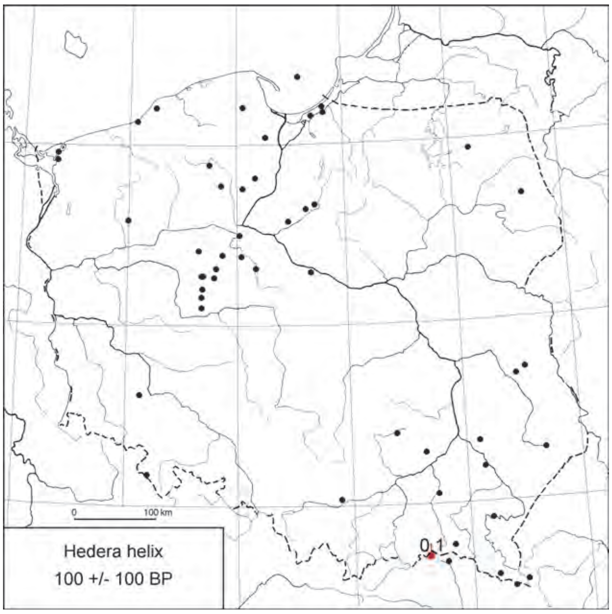

0.01
0.1
0.5
1
2
3
5
7
10
15
20
25
30
40
60


Hedera helix
3500 +/- 100 BP
Hedera helix
3500 +/- 100 BP
0.01 0.1
Hedera helix
3000 +/- 100 BP
Hedera helix
3000 +/- 100 BP
0.01 0.1
Hedera helix
2500 +/- 100 BP
Hedera helix
2000 +/- 100 BP
0 100 km
0.01
0.1
0.5
1
2
3
5
7
10
15
20
25
30
40
60


Hedera helix
1500 +/- 100 BP


Hedera helix
1000 +/- 100 BP


Hedera helix
500 +/- 100 BP


Hedera helix
100 +/- 100 BP

Hippophaë rhamnoides L. – Sea-buckthorn

KRZYSZTOF M. KRUPIŃSKI, KAZIMIERZ TOBOLSKI, MAGDALENA RALSKA-JASIEWICZOWA,
AND DOROTA NALEPKA

PRESENT DISTRIBUTION IN EUROPE AND IN POLAND

Hippophaë rhamnoides L. is an Euro-Asiatic species with a discontinuous range, stretching from Spain as far as central China (Browicz et al. 1977). In Europe it occurs mainly along the sea coasts (the North Sea, along some parts of the Baltic Sea coast, the Black Sea and the Mediterranean) and locally is quite abundant in the mountains, particularly in the Alps. In the eastern part of the continent its distribution area covers the Caucasus and north-eastern Turkey, while in Scandinavia it goes slightly beyond the Arctic Circle. Many sites are of anthropogenic origin because, particularly recently, *Hippophaë* has gained importance in the cultural landscape (in land reclamation) (Browicz et al. 1977, Meusel et al. 1978).

In Poland (Fig. 48) its natural sites occur only along the Baltic Sea coast, though it is not evenly distributed there (Browicz et al. 1977). It is not quite certain whether all of these localities are natural, as it can be observed from the map in the Distribution Atlas of Vascular Plants in Poland (Zając A. & Zając M. 2001).

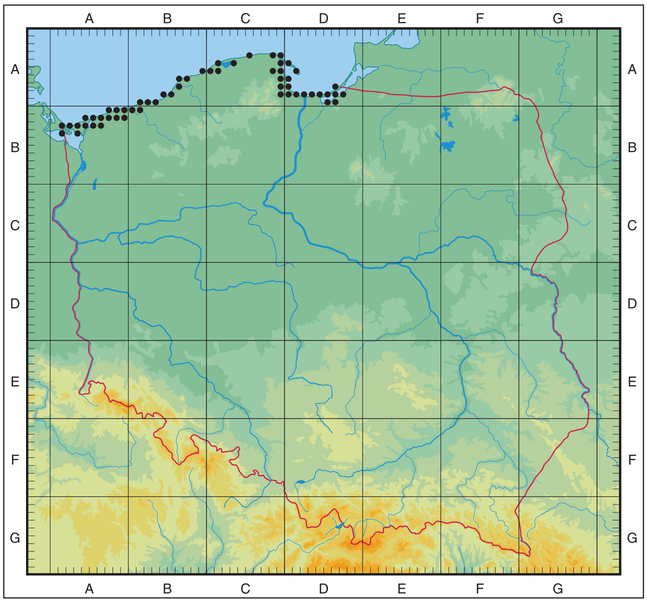


Fig. 48. Present-day distribution of *Hippophaë rhamnoides* L. in Poland (after Zając A. & Zając M. 2001)

ECOLOGY, POLLEN PRODUCTION AND DISPERSAL

Hippophaë is a dioecious shrub reaching up to 10 m in height and able to form dense and extensive scrub. In places exposed to strong winds it forms much smaller shrubs (up to 0.5 m). It flowers in the spring before development of the leaves and is anemophilous. Its juicy berries, rich in vitamin C, ripen in August and September and are distributed by animals, particularly birds. The germination rate of its seeds, excreted by birds through their alimentary canal, is 95–100% (Ellenberg 1996).

Sea-buckthorn always forms the top layer of vegetation and is listed among the absolute heliophytes (Ellenberg et al. 1991, Zarzycki et al. 2002). Only Landolt (1977) gave it a rating of 4 in the 5-grade scale of light requirements. It can grow on different substrata such as poor dune sands, compacted and undisturbed boulder-clay, and on stony riverside alluvium. It prefers slightly calcareous soils (Huntley & Birks 1983). It is a pioneer plant thus it can effectively colonise fresh habitats with raw, mineral soils, both loose and compact, and poor or rich in nutrients. This feature results from the possession of root nodules where symbiosis with nitrogen-fixing bacteria takes place, thus increasing the amount of nitrogen compounds in the soil. Limited persistence of sea-buckthorn bushes is influenced by soil nematodes, which after some time interrupt the fixing of atmospheric nitrogen (Pott 1995).

Sea-buckthorn tolerates a wide-range of temperatures from the boreal zone to the Mediterranean one and also a wide range of continental conditions (Meusel et al. 1978). In central Europe it occurs in a few plant communities: *Salici arenariae-Hippophaëtum rhamnoidis* Br.-Bl. et de Leeuw 1936, limited to maritime dunes, and *Hippophao-Sambucetum nigrae* Boerboo 1960.

Hippophao-Berberietum (Siegrist 1928) R.Tx ex Moor stands occur on gravelly alluvial deposits in the Alpine foreland (Pott 1995). The plant communities mentioned above have been recognised in western Europe, but they are probably absent from Poland (Matuszkiewicz W. 2001).

The history of European sites of sea-buckthorn has interested researchers for some decades (Lang 1994). In Poland the Quaternary history of this species was presented by Środoń (1970). Krupiński (1992) described its occurrence in the interglacials and Czubiński (1956, 1964) emphasized its role as an indicator species in the Late Glacial plant communities of Wielkopolska. A lot of new information about fossil sites of sea-buckthorn has been gathered over the last thirty years. It has been mainly recorded as pollen grains, but further, its peltate hairs have often been found on palynological slides. Sometimes along with very high amounts of pollen grains a lot of peltate hairs can also be found during the analysis of macrofossils. Other macroscopic finds of sea-buckthorn (seeds, wood) have been only sporadically recorded in Poland (Ralska-Jasiewiczowa 1980).

EXPANSION IN EUROPE DURING THE LATE GLACIAL AND HOLOCENE

During the Late Glacial and, particularly at about 13,000 BP, high pollen values of *Hippophaë* (up to 10%) occurred in the Alps and in the continental part of north-eastern Europe (Huntley & Birks 1983). Furthermore it has been recorded in central Europe at many Late Glacial sites, where its sometimes high values generally precede the spread of forests in the Bølling and Allerød. At the beginning of the Holocene in these areas, the amounts of sea-buckthorn decrease, and are represented by only occasional pollen grains. In Scandinavia, *Hippophaë* pollen appears at many sites, not earlier than at the beginning of the Holocene, reaching in the mountains more than 5%. These values decrease by 8000 BP and in the following periods sea-buckthorn occurs only sporadically, mainly in the Alps and along the sea coasts (Huntley & Birks 1983).

MIGRATION PATTERN IN POLAND (Fig. 50, p. 122)

14,000 – 13,500 BP

Hippophaë pollen already appears on the oldest maps and it is unlikely that it is reworked. Thus it should be accepted that sea-buckthorn was already growing *in situ* at this time. It occurs on both maps at two sites in the region of the Great Mazurian Lakes with pollen values of <1%, and on the 13,500 BP map also in Warmia with a value as high as 4.8% (but dating of this site might be questionable). This was anyway an episodic appearance, as on the following map its value is only 0.1% at that site.

13,000 – 12,500 BP

During the Bølling there is an increase in the number of sites with a considerable amount of sea-buckthorn: in the Mazurian Lake District (3.6%, 4.8%) and in central Poland (Łódź Upland 3%). On the 12,500 BP map new sites appear in central Poland – from the Wielkopolska Lowland in the north to the southern part of the Małopolska Upland. In the east it occurs from the Mazurian Lake District to the Polesie Lubelskie area. It is accepted that the appearance of sea-buckthorn precedes the development of forests, mainly birch woods.

12,000 BP

At the end of the Bølling higher occurrences of sea-buckthorn appear in northern and central Poland. In the Tuchola Forest, the Wielkopolska/Kujawy Lowlands, the Łódź Upland, and in the Mazurian Lake District they are marked by values of ca. 3–8%. In the latter region the *Hippophaë* pollen values reach 21% just after 12,000 BP. At the mouth of the Odra river an isolated site with a pollen value of 32.7% appears. It is the time of maximum sea-buckthorn occurrence in Poland. Its range reached then the Carpathian foothills in the south-east.

11,500 BP

In the mid-Allerød the sites of *Hippophaë* are grouped along a north-south belt from the Tuchola Forest through Kujawy, Łódź and the Małopolska Uplands down to the western margins of the Sandomierz Depression. In the east they occur locally in the Mazurian Lake District and at junction of the Biebrza and Narew rivers, and in the west at the mouth of the Odra river. However, in all these places the values are lower than 1% and most often only single pollen grains occur. These are the remnants of a previous abundant occurrence. The only higher value (1.2%) is recorded in the Bieszczady Mountains. The pattern of site distribution suggests the retreat of sea-buckthorn towards the south-east.

11,000 – 10,500 BP

In the Younger Dryas, the distribution range of *Hippophaë* contracts markedly. On the 11,000 BP map a few sites with single pollen grains appear, from the Tuchola Forest up to Łódź Upland, in the north-east of the country, and sporadically in the Roztocze area. The 10,500 BP map is similar, with a group of sites in the Kujawy area and with sporadic occurrences on the Baltic Sea coast, at the mouth of the Odra river and in the Mazurian Lake District. This is the Late Glacial minimum of the range of *Hippophaë* in Poland.

10,000 – 9500 BP

The 10,000 BP map is the last one with a noticeable number of sea-buckthorn pollen records in Poland. The number of sites is higher than on the two previous maps, but everywhere with the values not exceeding 0.1%. These are sites on Wolin Island, on the Baltic Sea coast near Gdańsk, and in the Drawsko Lake District, and, furthermore, in the south-east in the Polesie Lubelskie, and in the Sandomierz Depression. On the 9500 BP map there are only three relict sites of this species.

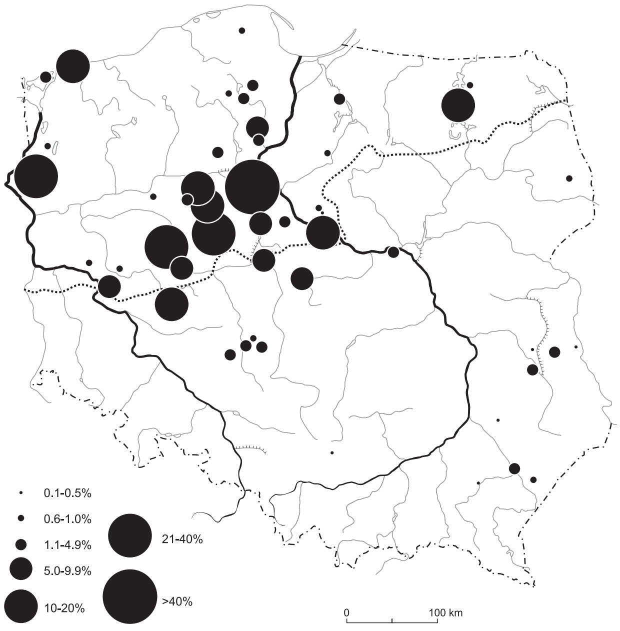


Fig. 49. Maximum percentage values of *Hippophaë rhamnoides* pollen in Poland (Tobolski 2003). According to Tobolski the majority of sites (particularly on Wielkopolska-Kujawy Lowland) may be correlated with the Meiendorf biozone (Tobolski unpubl.). Dotted line – maximum extent of the Vistulian glaciation

DISCUSSION AND CONCLUSIONS

In the Late- and earliest post-Glacial vegetational history of Poland the occurrence of sea-buckthorn has been recorded as short-lived but very significant episode. At a few sites it has been recorded in pollen diagrams in considerable amounts, however, only over short intervals of time and just before the Late Glacial expansion of the forest. The majority of sites are characterised by the minute amounts of its pollen. These sites are scattered in many places through all the Late Glacial and sometimes even the early Holocene stratigraphic units.

The map illustrating the maximum amounts of pollen of this species (Fig. 49) is an alternative to the isopollen maps presenting the history of sea-buckthorn (Tobolski 2003). This map contains also the data from literature for those sites that were not included in the isopollen maps. A considerable contrast in Figure 49 between the symbols illustrating percentage values within the ranges of 1.1–4.9% and 5.0–9.9% is meant to stress the poor pollen production of this species, and its important role within the plant cover, if it exceeds 5% of the total pollen sum (Lang 1994).

According to Tobolski (unpubl.) the majority of sites displaying high percentage values of sea-buckthorn pollen can be correlated using palynostratigraphy. For example, the Wielkopolska sites with the maximum presence of sea-buckthorn pollen, in many cases confirmed by the accumulation of the peltate hairs (Kubiak-Martens 1998, Tobolski 1998) have been ascribed by Tobolski to the Meiendorf biozone. The calendar dates of this unit are given as the years 14,450–13,800 (Litt et al. 1998, Litt et al. 1999). Tobolski puts forward the assumption that the same stratigraphic position should be attributed to sites with a high amount of sea-buckthorn pollen occurring in the western and eastern parts of the lake districts. Similar calendar dates are said to define the early interstadial at Lake Perespilno, Polesie Lubelskie, eastern Poland, correlated with the Bølling sediments at Witów, and the Mikołajki and Łukcze lakes (Ralska-Jasiewiczowa et al. 1999). When the Meiendorf calendar dates proposed above are converted into the conventional ^{14}C age, this gives dates placed roughly between 13,500 and 12,000 BP.

The Polish sites with the maximum values of sea-buckthorn pollen are located either within the area which was covered by the Vistulian ice-sheet or in its immediate vicinity. According to Tobolski such a distribution illustrates the pioneer role of sea-buckthorn in the primary succession that developed shortly after deglaciation of the Vistulian ice-sheet. This interpretation is not in contradiction to the stratigraphic position of the optimum occurrence of sea-buckthorn in Poland. A tendency for this shrub to colonise the areas just abandoned by glacial retreat is supported by two facts:

– a sporadic presence of sea-buckthorn pollen grains during the younger parts of the Late Glacial (for example during the Younger Dryas);

– the location of the early Holocene sites for this species (Preboreal and Boreal periods) in those regions of Scandinavia (Lang 1994, Fig. 6.4-8) that were still within the range of the ice-sheet during the Younger Dryas.

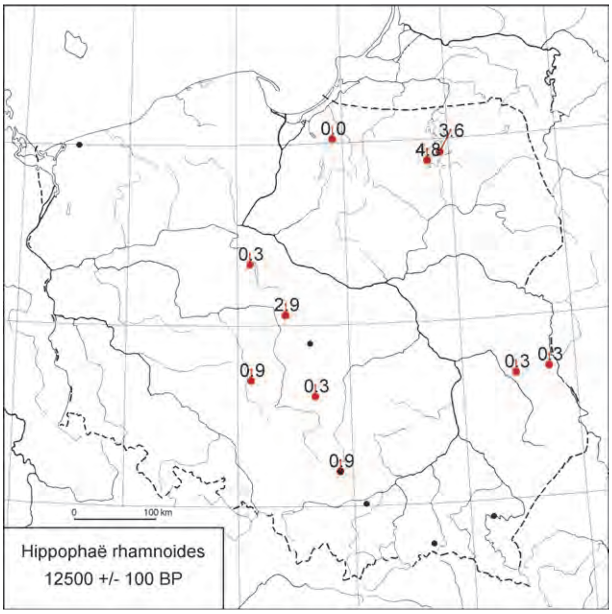
Further investigations (supported by analysis of macrofossils) are required particularly at sites in the Wielkopolska-Kujawy Lowland and in the lake districts, where high values of sea-buckthorn pollen have been recorded.

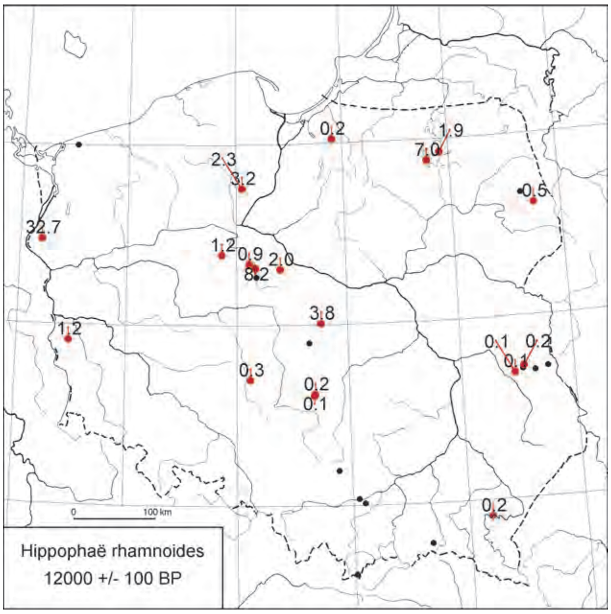
Fig. 50. *Hippophaë rhamnoides*: dot maps for 14,000–9000 ^{14}C yr BP

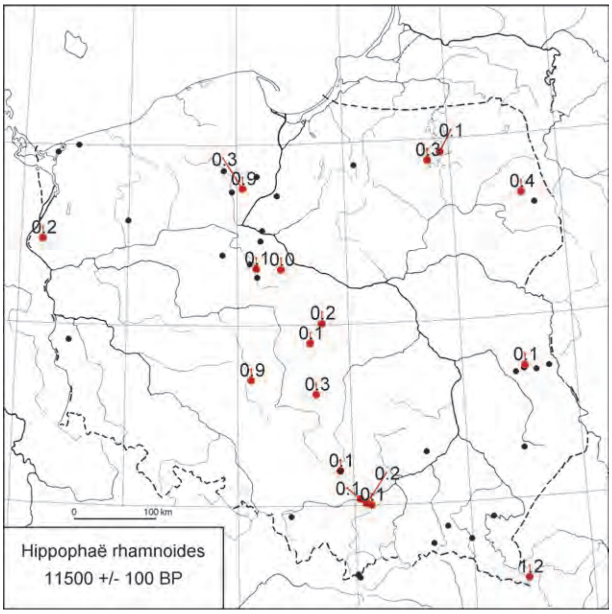

0.1
0.4
0
100 km
Hippophaë rhamnoides
14000 +/- 100 BP

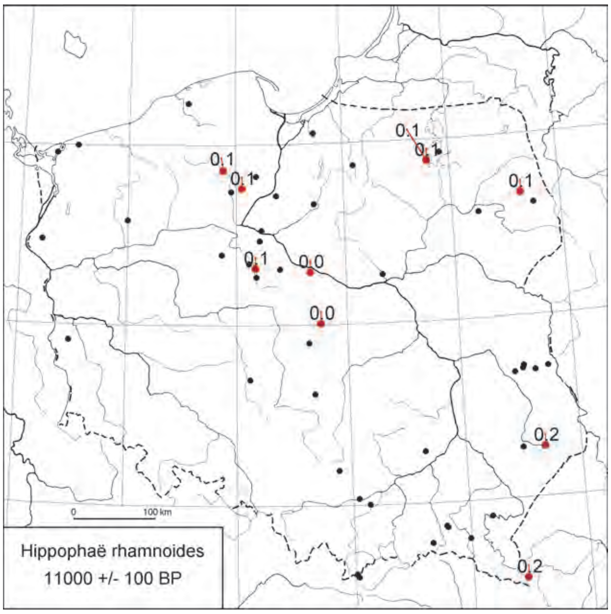

4.8
0.8
0.2
0
100 km
Hippophaë rhamnoides
13500 +/- 100 BP

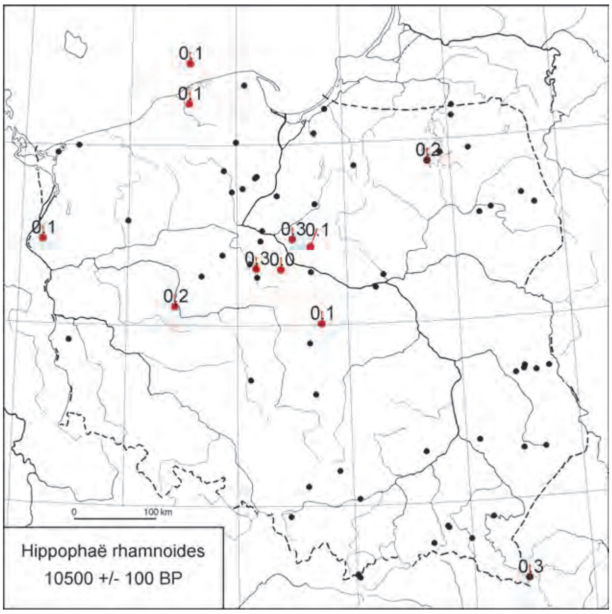

0.1
0.2
0.3
3.0
0.2
0
100 km
Hippophaë rhamnoides
13000 +/- 100 BP

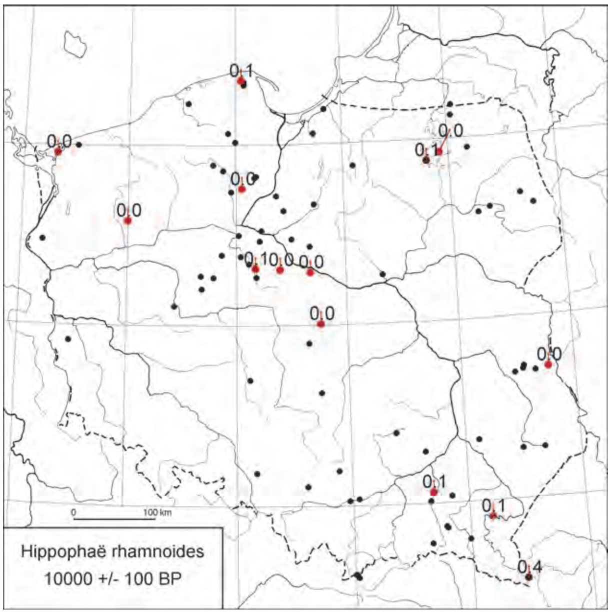

0.0
3.6
4.8
0.3
2.9
0.9
0.3
0.3
0.3
0.9
0
100 km
Hippophaë rhamnoides
12500 +/- 100 BP

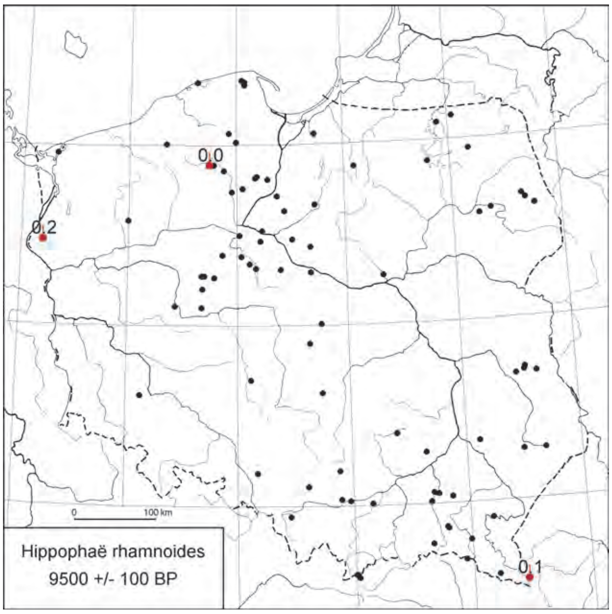

0.2
1.9
7.0
2.3
3.2
0.5
32.7
1.2
0.9
2.0
8.2
3.8
1.2
0.1
0.2
0.1
0.3
0.2
0.1
0.2
0
100 km
Hippophaë rhamnoides
12000 +/- 100 BP

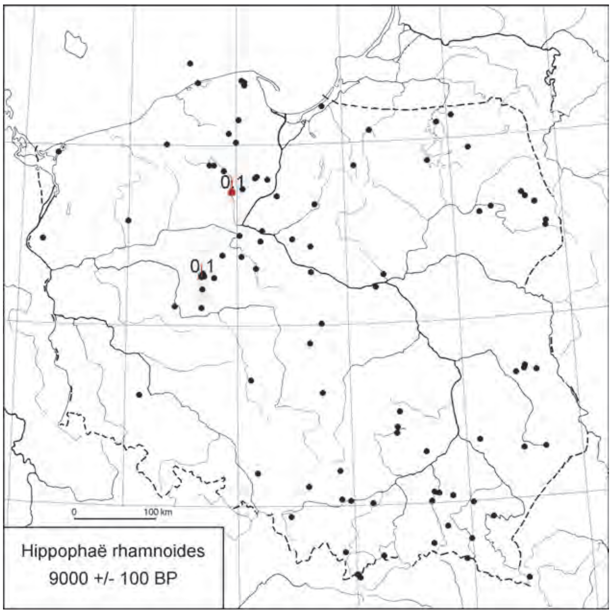

0.1
0.3
0.3
0.9
0.4
0.2
0.1
10.0
0.2
0.1
0.1
0.9
0.3
0.1
0.2
0.1
0.1
1.2
0
100 km
Hippophaë rhamnoides
11500 +/- 100 BP


Hippophaë rhamnoides
11000 +/- 100 BP
0
100 km
0.1
0.1
0.1
0.1
0.1
0.1
0.0
0.0
0.2
0.2


Hippophaë rhamnoides
10500 +/- 100 BP
0
100 km
0.1
0.1
0.2
0.1
0.3
0.1
0.3
0.0
0.2
0.1
0.3


Hippophaë rhamnoides
10000 +/- 100 BP
0
100 km
0.1
0.0
0.0
0.1
0.0
0.0
0.1
0.0
0.0
0.0
0.0
0.1
0.1
0.4


Hippophaë rhamnoides
9500 +/- 100 BP
0
100 km
0.0
0.2
0.1


Hippophaë rhamnoides
9000 +/- 100 BP
0
100 km
0.1
0.1

Juniperus communis L. – Juniper

Iwona Okuniewska-Nowaczyk, Mirosław Makohonienko, Małgorzata Latałowa,
Krystyna Milecka, Krzysztof M. Krupiński, and Dorota Nalepka

Juniperus is the only native genus representing the Cupressaceae family growing in Poland and in the other areas of central Europe (Jalas & Suominen 1973, 1988a). Two juniper species, from among eight European species, occur in Poland: *Juniperus communis* L. (with the subspecies: *J. communis* subsp. *communis* and *J. communis* subsp. *alpina* (Suter) Čelak. = *Juniperus nana* Willd.), and *J. sabina* L.

Present distribution in Europe and in Poland

Juniperus communis subsp. *communis* is widespread in Europe as far as the northern part of Scandinavia, and in Poland it is common in all the lowlands as well as at lower montane altitudes (Fig. 51). The upper limit of its range is difficult to be established since the botanical data do not always report the localities of each subspecies separately (Boratyńska & Boratyński 1978). *J. communis* subsp. *alpina*, associated with the high mountain areas of Europe and the Arctic zone, in Poland grows mainly in the Tatra Mountains up to 2000 m a.s.l., on Babia Góra Mountain and in the Sudetes (Zając A. & Zając M. 2001). *Juniperus sabina* is known only from the Pieniny Mountains, where it forms small populations at three sites, forming the northern limit of its geographic range (Zarzycki & Wróbel 2001). The geographic distribution of the genus *Juniperus* on the isopollen maps for Poland shows that the maps illustrate exclusively pollen of *J. communis*, however, it may be assumed that at the end of the last glaciation *J. communis* subsp. *alpina* could have had much wider distribution than at present.

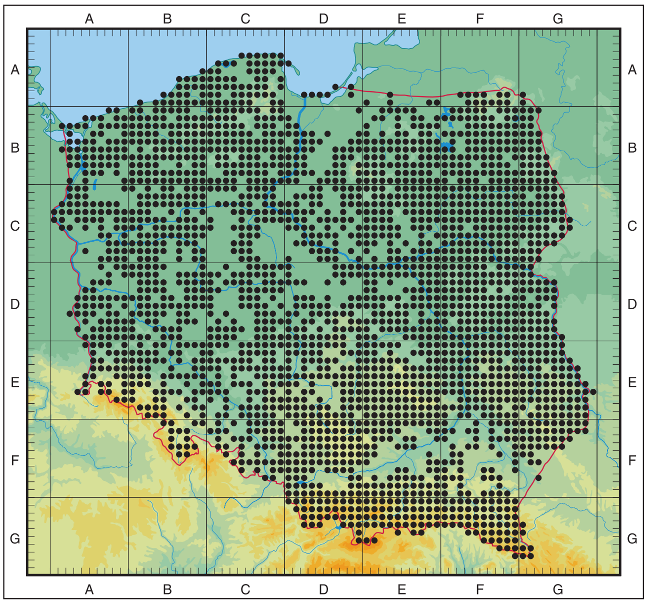


Fig. 51. Present-day distribution of *Juniperus communis* L. subsp. *communis* in Poland (after Zając A. & Zając M. 2001)

Ecology

Juniperus communis finds its most favourable conditions in mesotrophic habitats, on dry and slightly moist, acid or weakly acid soils (pH from 4.5 to 6.5). This species is also able to colonise poor habitats such as sandy wasteland, dunes, and heaths, and less frequently boggy sites. It is a drought-resistant species forming an extensive and shallow root system. Light conditions have greater influence on its growth than the quality of the soil (Bobiński 1974, Tomanek 1994, Zarzycki et al. 2002). *J. communis* is a light-demanding species tolerating only very little shade. In the north and in the mountains, its occurrence is restricted by the extremely low temperatures and precipitation. In the severe sub-arctic and alpine climate *J. communis* has the habit of a dwarf shrub. Its growth under conditions of low temperature depends on snow cover, which protects branches against frost and wind; in this severe climate suitable snow cover guarantees abundant flowering of juniper (Iversen 1954).

J. communis is a pioneer species. It constitutes an important component of Arctic-Alpine plant communities both along the northern forest limit, where it contributes to shrub communities with *Betula nana* and different species of *Salix* (Dahl 1998), and along the upper forest limit in the mountains. Juniper also occurs in open forest communities. It is characteristic of pine forests on mineral soils (Matuszkiewicz W. 2001), but it also appears in mixed forests altered by anthropogenic activity, and even in well-lit oak woodland, where it provides evidence of past grazing. It is found in abandoned fields and pastures, where it plays an essential role in the process of secondary succession (Faliński 1980).

POLLEN PRODUCTION AND DISPERSAL

In Poland, the main season for juniper pollen production is in April (Szczepanek 1994a, b, Aerobiologic Database, Gdańsk 1994–2002). *J. communis* is a dioecious, and wind-pollinated species, and relatively prolific pollen producer. The rate of pollen productivity in relation to grasses (1), estimated on the basis of monitoring the agriculture areas of south Sweden, is 2.1 (Sugita et al. 1999). However, under a tree canopy, in conditions of weak or insufficient light, juniper does not flower or flowers very poorly (Bobiński 1974). According to some authors *Juniperus* pollen is very light – the rate of its fall in air has been estimated at about 0.016 m/s (Eisenhut 1961, after Sugita et al. 1999) which suggests good dispersal. This somewhat contradicts the earlier opinion of Huntley and Birks (1983) who assumed poor dispersal. The latter authors accept the occurrence of single pollen grains of *Juniperus* in an assemblage, as an indicator of its presence in the local vegetation. Values >5% should suggest, according to those authors, its abundant occurrence on a regional scale. According to Iversen (1954) the representation of *Juniperus* pollen in sediments depends, among other things, on the growth-habit of the plant. Thus, in the case of dwarf shrubs the emission of pollen is poorer than that of full-sized shrub morphotypes. Iversen quoted an example from Greenland, where juniper has the shape of a dwarf shrub, and its values in the modern pollen assemblages reaches only about 3%, in spite of being well represented in the plant communities.

The relatively small *Juniperus* pollen grains are, in fossil material, transparent and usually deformed by tearing. Small papillae, that form the only surface elements, are most often lost. Due to difficulties in identification, juniper pollen was usually omitted in older palynological studies. Also even in recent investigations, where fossil material has been strongly damaged, the recorded *Juniperus* pollen values may be low in comparison with its actual occurrence in the sediment. Apart from effects resulting from the methods of preparation of the present isopollen maps (Nalepka & Walanus, this volume), this is an additional reason why these maps probably contain lower values than actual representative ones.

EXPANSION IN EUROPE DURING THE LATE GLACIAL AND HOLOCENE

The isopollen maps illustrating the distribution of juniper in Europe at about 13,000 BP (Huntley & Birks 1983), show in many areas of the south and west part of the continent, *Juniperus* pollen values exceeding 2%, with the highest values (above 50%) in the British Isles and in the Alps. According to these maps, at about 12,000 BP the juniper expansion towards the east is marked, penetrating the area of northern Germany and Poland to south-eastern Europe. A distinct reduction in the role of juniper across the whole of Europe took place at the beginning of the Holocene. In most areas this process proceeded during subsequent periods until the Early Middle Ages. About 1000 BP, an increase in pollen values of this taxon is recorded again, particularly in the Balkans and in south Scandinavia.

MIGRATION PATTERN IN POLAND (Fig. 52)

14,000 – 12,500 BP

The low number of sites for the older part of the Late Vistulian does not allow the drawing of isopolls, and it should be noted particularly that the dot maps show considerable differences in percentage values of *Juniperus* pollen from adjoining sites. As indicated by these data, as early as about 14,000 BP juniper may have been present in Poland, appearing in the initial communities of the Late Pleistocene steppe-tundra, whereas at about 13,500 BP, it could have been locally an important element of treeless plant communities. Between 13,000 and 12,500 BP the role of juniper gradually increased together with an expansion of forest-tundra type communities and then of the first birch forests. During this period higher values of *Juniperus* pollen (3–4%) appear in the southern part of Poland.

12,000 BP

The isopollen map presents the spread of juniper almost over the whole of Poland. The highest pollen values, exceeding 7%, appear locally in the north of the country. A more important role of juniper during this period, corresponding with the Older Dryas, probably illustrates an increase in the role of park tundra resulting from the cooling of climate.

11,500 – 11,000 BP

The maps for this period, corresponding with the warming of the Allerød interstadial, show a decline of *Juniperus* pollen and levelling of its values across the whole of Poland. This phenomenon was connected with the development of birch-pine and pine forests (see isopollen maps for *Betula* and *Pinus*, this volume) and with the simultaneous contraction of habitats for light-demanding juniper. It can be assumed that under the canopy of trees the juniper shrubs considerably restricted their flowering which further decreased the release of pollen of this species into the atmosphere.

10,500 BP

This time horizon represents the middle part of the Younger Dryas, a period of considerable cooling climate. The map illustrates the substantial contribution of juniper to the plant communities, particularly in northern Poland and also its maximum distribution for the last several thousand years. The isopolls exceeding 15% are marked in a belt covering the Pomerania area up to the western part of the Mazurian Lake District. It should be emphasized that, in some pollen diagrams from this area, the maximum *Juniperus* pollen values reach almost 40% in the Younger Dryas (Noryśkiewicz & Ralska-Jasiewiczowa 1989, Latałowa 1999a). Substantial values (3–5%) are also recorded in the Kujawy and northern Wielkopolska and in some regions of central and north-eastern Poland. During the period under discussion, the structure of forests became more open and the forest-tundra communities returned, which meant the reappearance of favourable conditions for the expansion of light-demanding plants, such as juniper. This process was less intensive in southern Poland, where the forest communities were not so strongly transformed by the cooling of climate. As in previous periods, a distinct decline of juniper representation is recorded in the south-eastern part of the country, where at this time the steppe communities with a high amount of *Artemisia* and Chenopodiaceae were gaining in importance (see isopollen maps of these taxa, this volume).

10,000 BP

At the beginning of the Holocene a considerable decline in the role of juniper, at the same time as the development of forest communities, is indicated. As formerly, a gradient in the decline of pollen percentage values from the north-west towards the south-east is distinctly marked. In northern and particularly in north-western Poland juniper is represented by higher amounts (from 2% to >3%), whereas in the south-eastern part its values do not exceed 0.5%.

9500 – 1500 BP

A progressive reduction in the amount of juniper is observed along with the development of pine-birch forests and particularly with the appearance of the components of deciduous forests. On the maps illustrating the amount of *Juniperus* pollen during the major part of the Holocene, isopolls show insignificant values recording a sporadic appearance of single pollen grains in sediments. Detailed analyses of pollen diagrams show that locally juniper was a stable element of the flora during the entire Holocene, and its spread was connected with the agricultural activity of successive prehistoric cultures (Hjelmroos-Ericsson 1981). Nevertheless, until the Early Middle Ages the amount of its pollen did not exceed 1% in value. An increase of *Juniperus* pollen values in the north-east Poland at the site of Miłuki, marked on the 7500 BP isopollen map, is probably caused either by disturbance in sedimentation or by contamination, though it is difficult to be specified (Milecka, unpubl.).

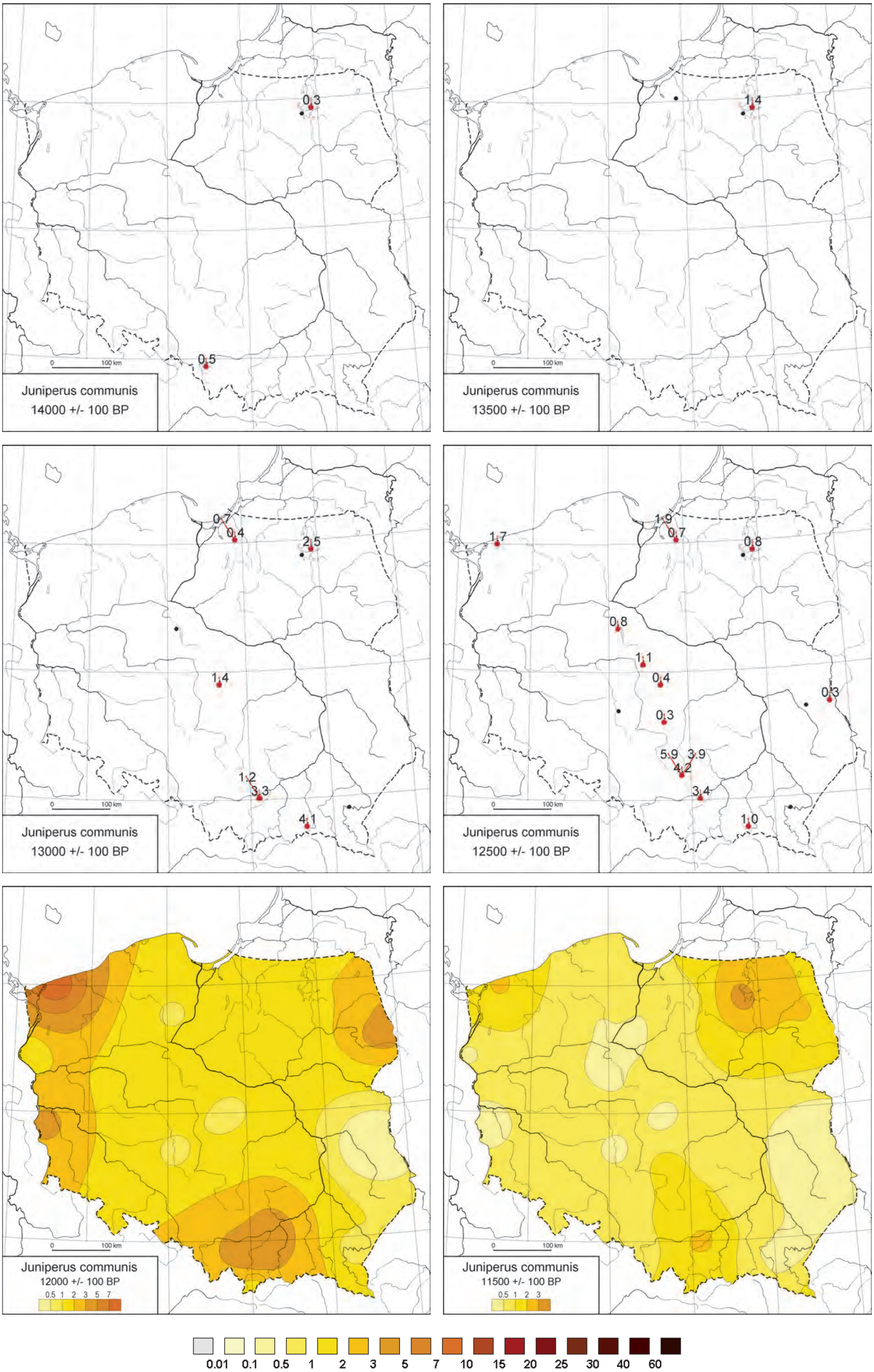
1000 – 100 BP

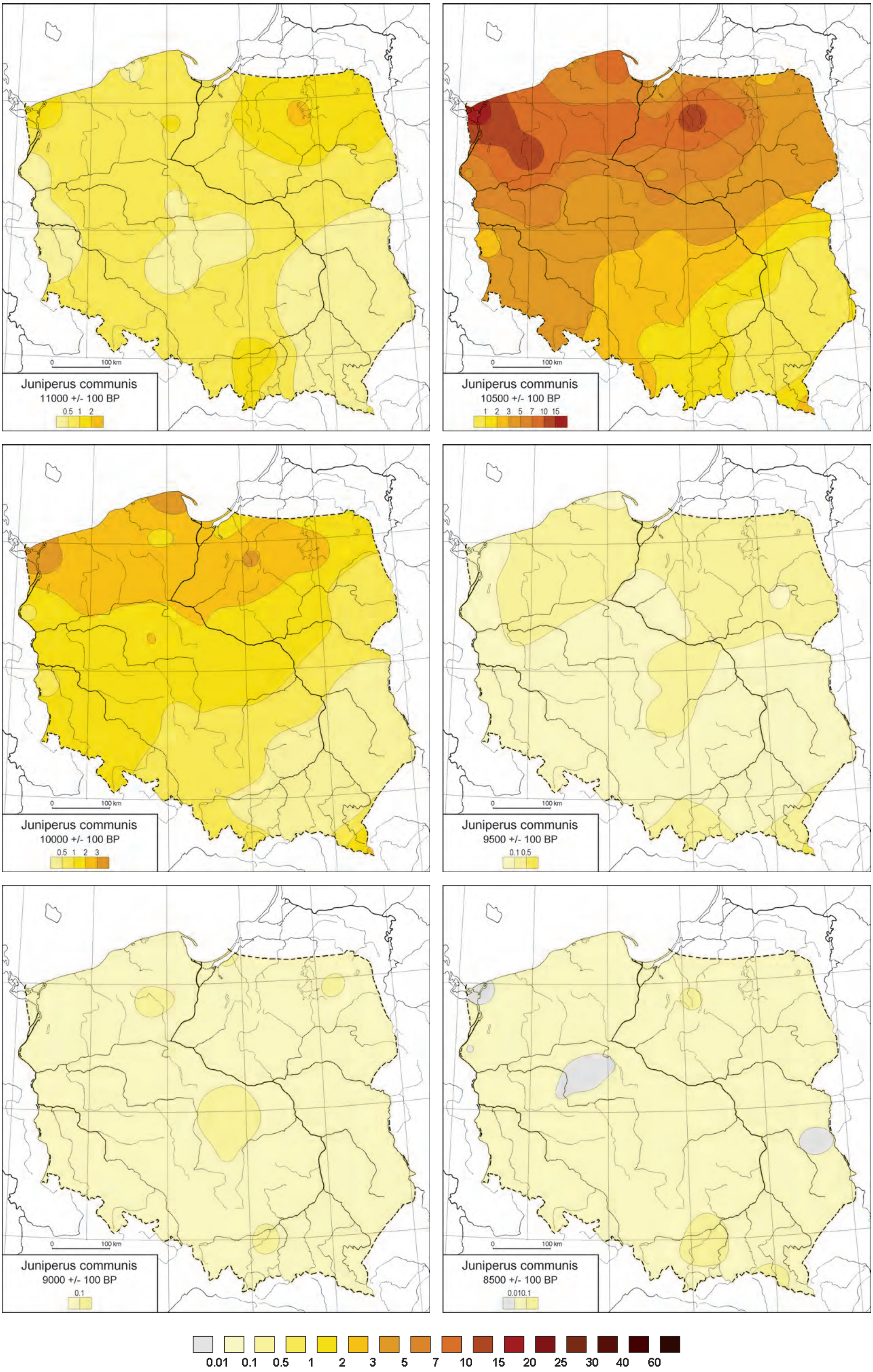
The expansion of juniper, expressed by the reappearance of *Juniperus* pollen at sites throughout the country, is not observed until around 1000 BP, during the period of settlement and economic crisis of Medieval times. In the system of anthropogenic pollen indicators for central Europe, *Juniperus* is regarded, first, as a typical element of dry pastures, and next as an element of grazed forests (Behre 1981). In recent surface assemblages from northern Poland, juniper pollen is mainly associated with forests transformed by anthropogenic activity (Makohonienko et al. 1998). The expansion of juniper initiated during the Early Middle Ages and continued in historic times is a result of intensified human pressures. A synchronous increase of both pine (see isopollen maps for *Pinus*, this volume) and juniper amounts at the cost of deciduous trees is reflected in diagrams from the whole of Poland. The pollen diagrams from Wielkopolska (Makohonienko 2000) and Pomerania indicate that this process occurred both in more fertile habitats within the morainic hills and on poorer sandy soils. In the mountains (500 BP map), an increase of *Juniperus* pollen probably reflects the development of a pastoral economy and the lowering of the upper forest limit resulting from this economy and leading to the widening of the expansion zone of juniper shrubs.

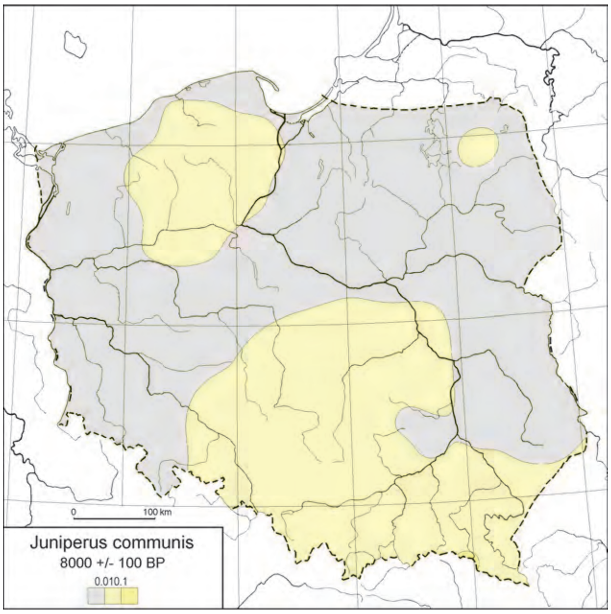
Conclusions

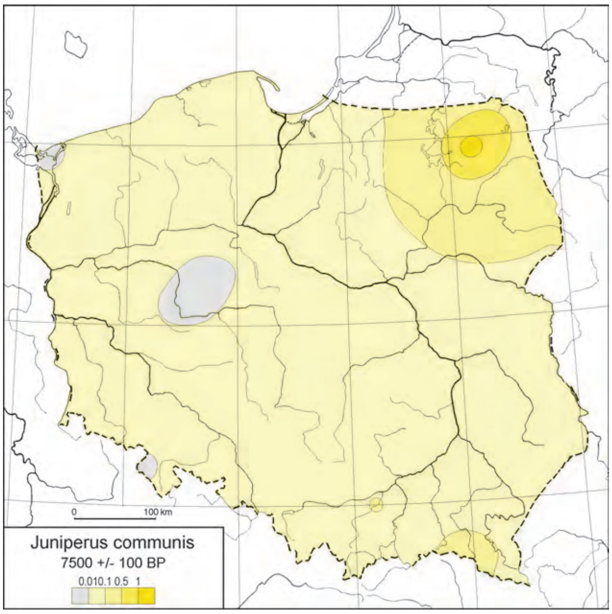
Isopollen maps of *Juniperus* for Poland illustrate the history of the species *Juniperus communis*. This species belonged to the earliest components of the post-glacial vegetation and its importance was considerable in the Younger Dryas, particularly in the northern parts of the country within the limits of the last glaciation. Juniper retreated at the beginning of the Holocene, when the encroachment of forest communities restricted the occurrence of light-demanding species. It persisted sparsely in forest clearings, gaining new possibilities of expansion due to the development of agriculture. However, until the Early Middle Ages it played a minor role in the vegetation of Poland. The isopollen map drawn for modern times reflects, to a small degree, the present contribution of juniper to plant communities. This suggests that *Juniperus* pollen is not sufficiently represented in the pollen assemblages.

Fig. 52. *Juniperus communis*: dot and isopollen maps for 14,000–100 ^{14}C yr BP

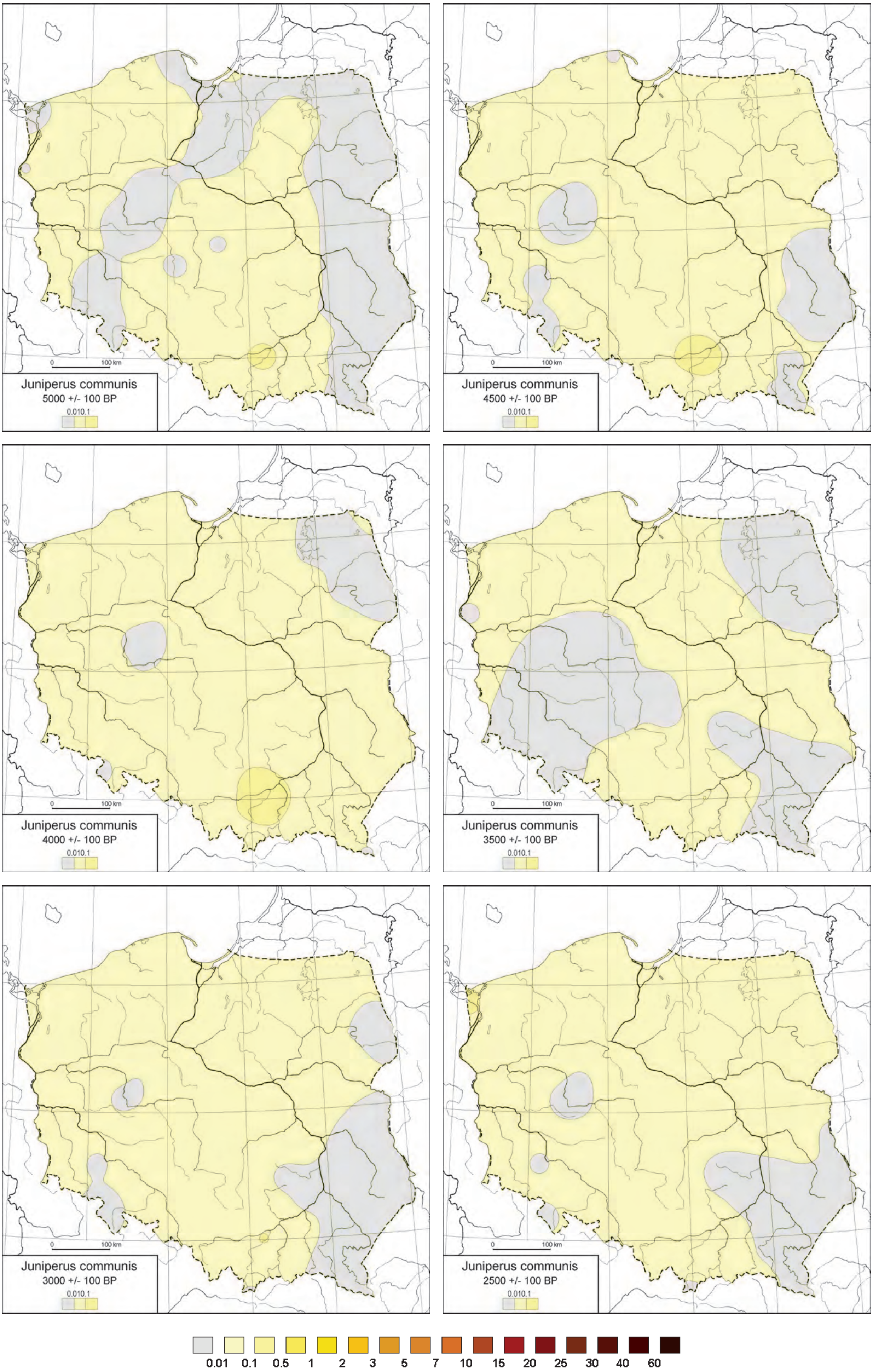

0.3
0.5
0 100 km
Juniperus communis
14000 +/- 100 BP
1.4
Juniperus communis
13500 +/- 100 BP
0.7
0.4
2.5
1.4
1.2
3.3
4.1
Juniperus communis
13000 +/- 100 BP
1.9
0.7
1.7
0.8
0.8
1.1
0.4
0.3
0.3
5.9
3.9
4.2
3.4
1.0
Juniperus communis
12500 +/- 100 BP
Juniperus communis
12000 +/- 100 BP
0.5 1 2 3 5 7
Juniperus communis
11500 +/- 100 BP
0.5 1 2 3
0.01
0.1
0.5
1
2
3
5
7
10
15
20
25
30
40
60


0
100 km
Juniperus communis
11000 +/- 100 BP
0.5 1 2
0
100 km
Juniperus communis
10500 +/- 100 BP
1 2 3 5 7 10 15
0
100 km
Juniperus communis
10000 +/- 100 BP
0.5 1 2 3
0
100 km
Juniperus communis
9500 +/- 100 BP
0.1 0.5
0
100 km
Juniperus communis
9000 +/- 100 BP
0.1
0
100 km
Juniperus communis
8500 +/- 100 BP
0.01 0.1
0.01 0.1 0.5 1 2 3 5 7 10 15 20 25 30 40 60





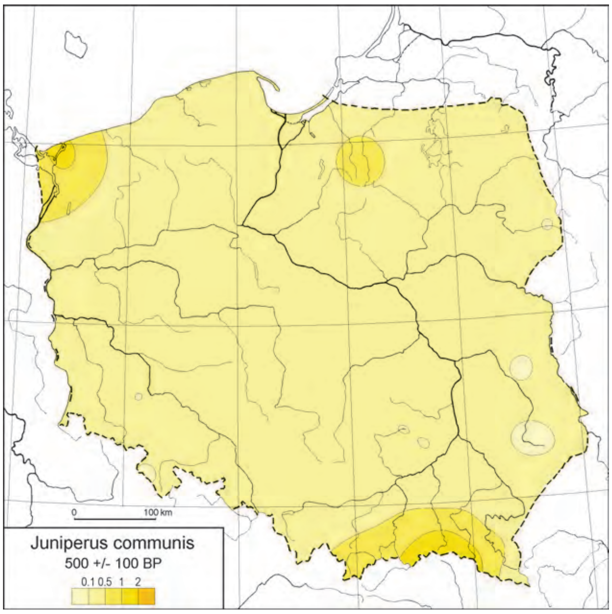
0.01 0.1 0.5 1 2 3 5 7 10 15 20 25 30 40 60

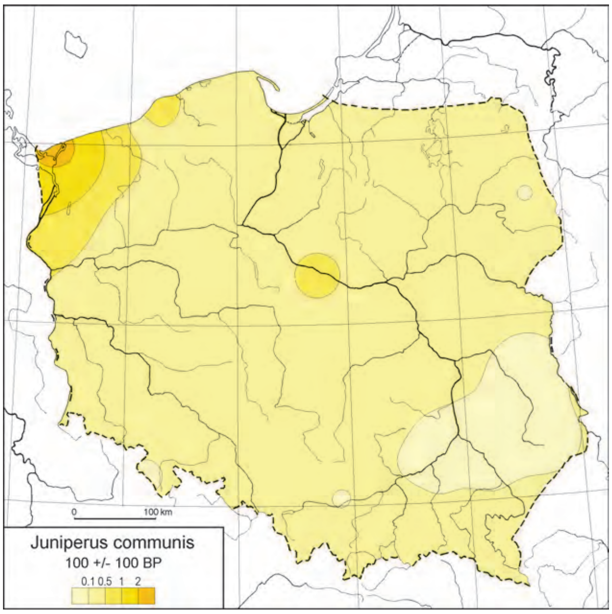

0
100 km
Juniperus communis
5000 +/- 100 BP
0.01 0.1
0
100 km
Juniperus communis
4500 +/- 100 BP
0.01 0.1
0
100 km
Juniperus communis
4000 +/- 100 BP
0.01 0.1
0
100 km
Juniperus communis
3500 +/- 100 BP
0.01 0.1
0
100 km
Juniperus communis
3000 +/- 100 BP
0.01 0.1
0
100 km
Juniperus communis
2500 +/- 100 BP
0.01 0.1
0.01
0.1
0.5
1
2
3
5
7
10
15
20
25
30
40
60


0
100 km
Juniperus communis
2000 +/- 100 BP
0.01
0.1


0
100 km
Juniperus communis
1500 +/- 100 BP
0.01
0.1


0
100 km
Juniperus communis
1000 +/- 100 BP
0.01
0.1


0
100 km
Juniperus communis
500 +/- 100 BP
0.1
0.5
1
2


0
100 km
Juniperus communis
100 +/- 100 BP
0.1
0.5
1
2


0.01
0.1
0.5
1
2
3
5
7
10
15
20
25
30
40
60

Larix decidua Mill. – **European larch**

AGNIESZKA WACNIK, MAGDALENA RALSKA-JASIEWICZOWA AND DOROTA NALEPKA

The taxonomy of the genus *Larix* is quite complicated and in the past has been approached in different ways by taxonomists studying this genus. Flora Europaea (Tutin et al. 1964) lists 2 species of larch native to Europe: *Larix decidua* Miller (*L. europaea* DC.), with two subspecies *L. decidua* subsp. *decidua* and *L. decidua* subsp. *polonica* (Racib.) Domin, the latter formerly considered as a separate species, and *L. russica* (Endl.) Sabine ex Trautv., (formerly *L. sibirica* Ledeb.), an east-European species. Boratyński (1986) in a monographic study of *Larix* Mill. adopts the taxonomy from Flora Europaea, regarding, however, both subspecies of larch in a rather independent way.

PRESENT DISTRIBUTION IN EUROPE AND IN POLAND

Larix decidua is a characteristic species of the subalpine forests of central European mountains (Fig. 53). It may be locally dominant, but more commonly it is a co-dominant taxon with *Pinus cembra* (Huntley & Birks 1983). In the north-eastern part of its range it descends to the montane forelands and neighbouring uplands.

Larix decidua subsp. *decidua* grows only in the Alps and Tatra Mountains, at the upper tree-line and in the highest part of the upper montane forest zone, and, in its variety, var. *sudetica*, in the lower montane forest zone of the eastern Sudetes. *Larix decidua* subsp. *decidua* extends with its highest sites in the Alps at 2900 m a.s.l., about

Fig. 53. *Larix decidua* – map of present-day distribution in Europe: ● – native isolated occurrence, ◒ – status of site unknown or uncertain (after Jalas & Suominen 1973 and Boratyński 1986)

1000 m higher than subsp. *polonica* reaching about 2000 m a.s.l. in the various ranges of the Romanian Carpathians (the highest sites at 2050 m a.s.l. in the Bucegi Mountains) (Rubţov & Mocanu 1958, Rubţov 1965).

Larix decidua subsp. *polonica* is distributed throughout the whole Carpathians, mainly in the foothills and lower montane forest zone, as well as in the region of the Świętokrzyskie Mountains. Moreover, in the lowlands of Poland this subspecies of larch is found in scattered stands along the Warta and Pilica rivers, and a little more frequently in the vicinity of Poznań (Fig. 54, no separation into two subspecies).

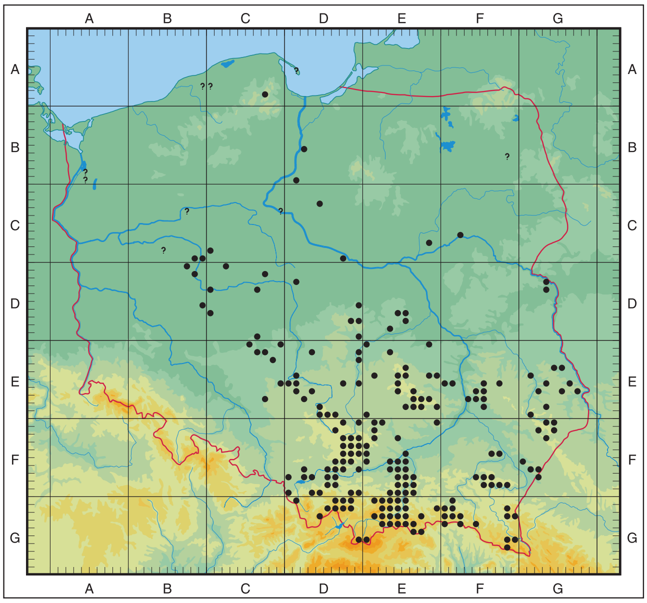


Fig. 54. Present-day distribution of *Larix decidua* Mill. in Poland: **?** – uncertain sites (after Zając A. & Zając M. 2001)

Ecology

Larches frequently occur in forests as a subordinate species; they are pioneering trees, frequently superseded by other species. They are found at elevated sites, exposed to winds, which favours strong transpiration. They grow right up to the alpine tree-line. Larches are the most light-demanding trees of the temperate climate zone, though they demonstrate a great variability depending on ecotype and habitat conditions. A mature European larch requires at least 20% exposure to full light. This results a poor competitive relationships with other trees.

Larches show great thermal tolerance, particularly of high summer temperatures. The growth in size of their shoots is dependent on temperature. They are not particularly sensitive to early and late ground frost (Olaczek 1986).

Larix has the highest transpiration rate of all native trees. Polish larch, *L. decidua* subsp. *polonica*, requires a mean annual precipitation of about 600 mm and average soil moisture. For its optimal growth conditions the relative air humidity should be about 70%, and in the uplands even 80–85% (Jaworski 1994). The height to which larch grows is correlated with the sum of precipitation in each month of the growing season (Kocięcki 1972). It shows a low drought tolerance.

Both subspecies of *Larix decidua* require moderately fertile soils. They show more response to their physical properties. They favour deep friable morainic soils (Olaczek 1986). Polish larch (subsp. *polonica*) particularly favours sandy clays, silty loams, gravels, loess, deep calcareous and chalky soils. It avoids soils with shallow ground water, especially stagnant water. European larch (subsp. *decidua*) can grow on shallow and stony soils (Olaczek 1986).

Larches grow very fast in the juvenile stage. Their reproductive age starts at about 10 years. They produce seeds dispersed by wind. The numbers of seeds are cyclically higher every 3 to 10 years. The average age reached by mature trees is between 100 and 150 years, but ages of 600 years have been reported for alpine larches (McComb 1955).

In the Tatra Mountains *Larix decidua* subsp. *decidua* and *Pinus cembra* grow together as subordinate species in spruce forests of the *Plagiothecio-Piceetum* association (Matuszkiewicz J.M. 2002). Local small patches of this community with larch and stone pine used to be formerly distinguished as the *Cembro-Piceetum* association (Myczkowski 1969, Boratyński 1986). In the lowlands, the following associations may have a native presence of larches: *Pino-Quercetum abietetosum*, *Pino-Quercetum typicum*, *Potentillo albae-Quercetum*, *Abietetum polonicum*, and *Peucedano-Pinetum* (Olaczek 1986).

Pollen production and dispersal

Larix decidua is an anemophilous species, and pollen grains are specially adapted to being wind-dispersed despite their large size and lack of air sacks. After pollen grains are shed from the inflorescence, they lose water rapidly and take the shape of a disc. Once they land on the ovules they absorb water and regain their initial shape (Meeuse & Morris 1984). The intensity of flowering depends on climatic conditions that favour the formation of flower buds. The shedding of pollen begins in late March and early April.

The presence of even single *Larix* pollen grains in a pollen assemblage is a reliable indicator of its local occurrence (Janssen 1966, Huntley & Birks 1983). This has been confirmed by studies from the Asian polar regions of the Ural Mountains and of the Yamal Peninsula where *Larix* forms the alpine and northern tree-lines. In the forest-tundra zone, where larch is the only tree, its pollen grains, despite the proximity of tree stands, are only sporadically found (Jankovská & Panova, unpubl., after Jankovská 1995). Its values in the surface pollen assemblages rarely exceed 10%, even if larch is a dominant component of local forests (Huntley & Birks 1983).

EXPANSION IN EUROPE DURING THE LATE GLACIAL AND HOLOCENE

From the end of the last interglacial throughout the Pleni-Vistulian period larch survived in the Carpathians, where numerous interstadial macrofossils have been found (Środoń 1986). Larch pollen grains, sometimes numerous, were found in the Pleniglacial deposits in Slovakia (Šafárka, from about 52,000 to 16,500 BP) and the Czech Republic (Jablůnka, about 45,000 BP) (Jankovská 2002). *Larix* together with *Pinus cembra* formed probably relict groups of trees at that time in the whole of the Western Carpathians. There exists also probability of *Larix* occurrence in Hungary during the maximum advance of the last glaciation from about 28,700 to 16,750 BP according to radiocarbon dates from wood fragments found *in situ*, identified as *Picea* or *Larix*. Larch pollen found in this area, dated from 14,000–10,000 calendar years BP reached over 10% (Willis et al. 2000). Glacial refugia of *Larix* occurred also in different regions of Siberia (Kremenetsky et al. 1998, Anderson et al. 2002). The presence of *Larix* in central Europe during the Pleniglacial resulted undoubtedly in its quick expansion during the Late Glacial. This situation was favoured by the continental climate (Mamakowa & Starkel 1974, Ralska-Jasiewiczowa 1980, Starkel 1988).

Since the older part of the Late Glacial *Larix* was present throughout the Alps but it declined significantly there as late as about 7000 BP when it was displaced by competitive pressure from other trees and pushed towards higher montane altitudes (Huntley & Birks 1983). Uncovered by the melting front of the Pasterze Glacier in the eastern Alps (Austria), pieces of wood of *Larix decidua* and *Pinus cembra* were found. The age of this larch wood was radiocarbon dated as belonging to the early Holocene, about 9100–8200 BP (Nicolussi & Patzelt 2000). From the late Vistulian and early Holocene *Larix* needles were found in north-west Romania, dated at ca. 12,000 to 11,600 BP (Cârciumaru 1980, Wohlfarth et al. 2001).

In the Late Glacial and early Holocene of Slovakia in the Spiska Valley *Larix* was recorded as both pollen and macrofossils. Pre-Allerød seeds and needles are also recorded from the site of Sivárňa, north-east Slovakia (Jankovská 1998). Larch pollen grains had been found there regularly since the Oldest Dryas. At the beginning of the Late Glacial the forelands of the Tatra Mountains were dominated by forest-tundra with *Larix* as a component. It entered into tundra communities and as a pioneering tree populated mainly terraces of fluvioglacial origin, and the lower slopes of adjacent hills. During the Oldest and Older Dryas this forest-tundra was penetrated also by *Pinus cembra* and *P. sylvestris* (*P. mugo*?). There was a marked expansion of *Larix* in the Allerød, and then at the end of Younger Dryas; this was facilitated by the lack of competitive tree taxa. In the Allerød the amount of *Larix* pollen locally exceeded 10% (Sivárňa, Hozelec, NE Slovakia, Jankovská 1998). Stone pine and larch communities with *Pinus sylvestris* formed there forests of a northern taiga character. At the onset of the Holocene the expansion of *Picea* into the Tatra Mountains region displaced larch at lower altitudes, but larch was able to expand at higher montane positions, as too did *Pinus cembra* and *P. mugo*. The expansion of *Larix* in forests becomes less and less to the west (Jankovská 1991, 1995, 1998, 2002).

MIGRATION PATTERN IN POLAND (Fig. 55)

Larch pollen, due to its morphology and poor preservation in the sediment is difficult to identify during pollen analysis (Janssen 1966, Huntley & Birks 1983). In Poland *Larix* was reported many times from the Late Glacial as pollen and macrofossils (Środoń 1986). Because *Larix* is a deciduous tree and loses its needles every year, they are frequently found on examination of sediments. Wood identified as '*Picea* or *Larix*' is also being found quite often.

Both pollen and needles, as well as *Picea*/*Larix* wood, occur in sites located in the Polish Carpathians, in their forelands and in the Sandomierz Depression, coming from interstadials of the mid-Vistulian Pleniglacial (e.g. ^{14}C dates 35,960±1000, 28,000±1400, 27,745±300 and 22,450 BP, Mamakowa & Starkel 1974, 1977, Mamakowa & Środoń 1977). In the Bieszczady Mountains (Ralska-Jasiewiczowa 1980), in the deposits of a Vistulian interstadial found at Smerek, of undefined stratigraphic position but radiocarbon dated to 16,925±325 BP, a continuous curve of *Larix* pollen up to 7% is accompanied by numerous macrofossils, clearly evidencing larch dominance in the local flora at that time. In another Bieszczady site (Tarnawa Wyżna) both larch pollen (up to 8%) and needles were regularly found from the Older Dryas to the Preboreal period. In the Nowy Targ Basin in the Tatra Mountains foreland *Larix* was present all the time from the Bølling to Preboreal (Na Grelu, Koperowa 1962). All these data document the presence of larch refugia in the northern Carpathians during the last glaciation and its expansion from early stages of the Late Glacial onwards.

13,000 – 12,500 BP

Single *Larix* pollen grains (0.2–0.3%) occur in the mid-Carpathian low altitudes of Jasło-Sanok Depression, together with macrofossils present there since the Oldest Dryas (Harmata 1987, 1995a, b), and at the southern margin of the Małopolska Upland at Wolbrom (Latałowa & Nalepka 1987). They also appear in north-eastern Poland, in the Mazurian Lake District (Wacnik 2003). Their occurrence, shown also on later maps, suggests that during the Bølling *Larix* started to migrate both from the

Carpathians, and from the boreal refugia in the east at the marginal areas of the now retreating Vistulian ice sheet.

12,000 BP

By the end of the Bølling *Larix* seems to have already been a significant component of park-like vegetation in southern Poland, at low altitudes in the Carpathians and their foreland. In the Bieszczady Mountains, shortly after 12,000 BP, its contribution exceeded 5%, which indicates local appearance of open woods dominated by larch. It also grew at that time at least at the margins of the Małopolska Upland (0.5%). Its pollen values from the Western Carpathians are lower (below 1%) than in their eastern part, where the climate continentality was stronger. Isolated islands of low pollen values are found in the Mazurian Lake District, in the Tuchola Forest, Kujawy and Polesie Lubelskie. *Larix* is a tree favouring distinctly a continental, cold montane climate. Its presence in central-north-east Poland at that time can be explained in two ways: the descent of *L. russica* from the north-east or, more probably, the temporary extension of the range of *L. decidua* subsp. *polonica* in response to climatic conditions favourable to its developing there.

11,500 BP

The presence of *Larix* pollen during the Allerød suggests that larch forests were then an important component of vegetation in the Eastern Carpathians, including the mid-Carpathian low positions. From 11,500 BP *Larix* has also been found at Podhale area, at the foot of the Tatra Mountains. Forests with larch occurred in the Małopolska Upland and the Świętokrzyskie Mountains, where it formed a distinct centre, and in the Lublin Upland. There are still isolated, extremely low values of larch pollen in Polesie Lubelskie, Mazurian Lake District and Tuchola Forest, which indicates its presence in those areas.

11,000 – 10,000 BP

The patterns on *Larix* maps for the Allerød/Younger Dryas transition, mid-Younger Dryas and the beginning of the Holocene, despite the strong climatic fluctuations which occurred at those times, do not differ much from each other. Presumably, the climatic preferences of larch, as described earlier, made this tree stronger in competition with pine and birch under the continental, cool and severe climate conditions of mid-Younger Dryas. In addition, a lack of dense woodland or forest cover suited this light-demanding species. Furthermore, with increased temperatures but considerable continentality at the onset of the Holocene (Birks 1986), larch was still strong enough to persist for some time in competition with expanding birches and pine. The highest *Larix* pollen values occur throughout this whole period in the Eastern Carpathians (above 5%), as well as in the Jasło-Sanok Depression and a neighbouring part of Sandomierz Depression, where it is recorded with quite substantial values (up to 3.3%) at a number of sites. Undoubtedly, a centre of larch forests, or forests with a considerable contribution of larch, was situated in those parts of the Carpathians with a suitable climate. Moreover, larch grew in the Silesian Upland, in the region of the present Niepołomice Forest, Małopolska Upland and the Nida river basin. On the 11,000 BP map it also appears in the Roztocze.

There are indisputable traces of *Larix* presence in the lake districts from the Mazurian Lake District westwards, across the Olsztyn Lake District, Kujawy, Tuchola Forest, Drawsko Lake District to Wolin Island at the Odra river estuary. However, everywhere it occurs as single pollen grains which indicates a scattered presence of larch in those regions.

The larch range at the transition from the Late Glacial to the Holocene was similar to the recent distribution of its montane and upland subspecies (Fig. 54). However, the upland subspecies expanded further north-eastwards and westwards.

In response to climatic warming about 10,000 BP, larch started to expand, advantaged by being already present in the local vegetation. It disappeared, however, from its most north-westerly sites and migrated towards those areas with a more continental climate. At that time it was not found to the west of longitude 18°E.

9500 BP

The number of isolated areas with *Larix* diminished. To the west its montane range did not cross the Wisłoka river, and areas with the dominant larch forests persisted only in the eastern parts of the Carpathians (Bieszczady Mountains 5.5%, Jasło-Sanok Depression 2.8%). Larch was still present at the southern margin of the Małopolska Upland. Apart from those regions, single *Larix* pollen grains are recorded in Polesie Lubelskie, Wielkopolska, and at a problematic site down the Odra river (Krupiński 1991).

9000 – 100 BP

The 9000–7500 BP maps confirm the persistence of larch, though gradually declining, in the Carpathians, especially in their eastern part, the Sandomierz Depression, and in the Świętokrzyskie Mountains. Isolated larch pollen finds are recorded at 9000 BP and 7500 BP on the Baltic Sea coast near Gdańsk, at 8500 BP at Tuchola Forest, and at 8000 BP in Wielkopolska. The presence of *Larix* in the region of the Dukla Pass (mid-Carpathian lowering) is regularly confirmed after 6000 BP.

Later maps record single *Larix* pollen occurrences scattered throughout Poland. The 4000 BP map recording the period of advanced post-Neolithic deforestation and the occurrence of scrub-forest communities with oak and abundant hazel differs slightly from the remaining ones. It documents the finding of higher number of sites with larch pollen in eastern Poland, from the Sandomierz Depression through Polesie Lubelskie to the Knyszyn Forest

(Białystok Upland), and westwards in Wielkopolska and the mid-Pomeranian Lake Districts.

The youngest maps (500, 100 BP), apart from single, scattered stands in north-western Poland, confirmed the presence of larch at low altitudes of the Carpathians, the Świętokrzyskie Mountains, and the Roztocze.

CONCLUSIONS

Larix survived the last glaciation in central Europe, as confirmed by numerous macrofossils and pollen from the Carpathians and their forelands, and from Hungary. In the Late Glacial it expanded in the Alpine countries, Romania, Slovakia, the Czech Republic, and in Poland.

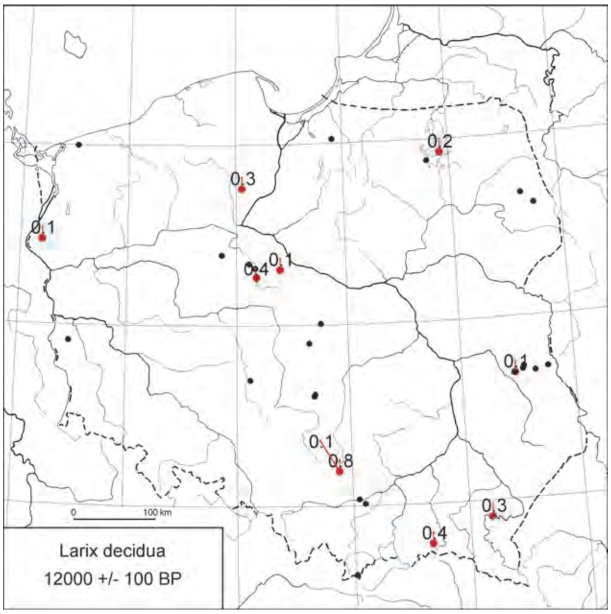
In the Polish Carpathians and in the southern uplands larch became widespread following the early stages of the Late Glacial. It showed also isolated occurrences in other parts of Poland, as far as the lake districts, but did not spread west of longitude 18°E. Its expansion and abundance during the Late Glacial resulted from its preferences for a cool, severe, continental climate, what gave larch a stronger competitive advantage over pine and birch. Also the lack of a dense forest cover suited this light-demanding tree.

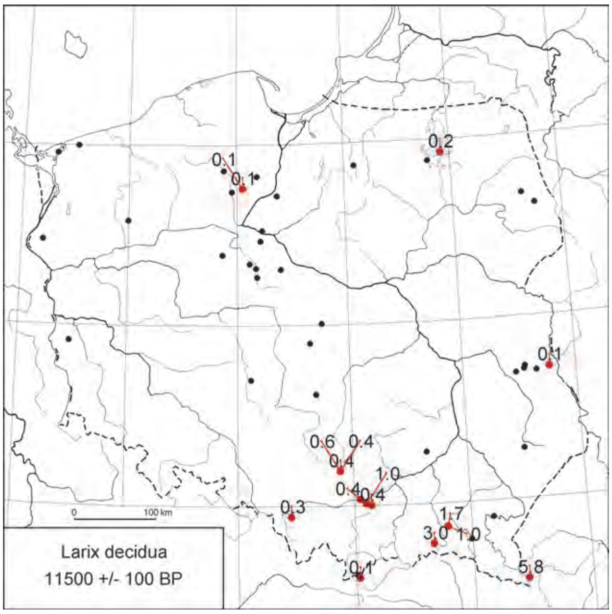
Larch was still a widespread tree in southern Poland at the end of the Late Glacial and the onset of the Holocene, and it then had a distribution range similar to the present-day distribution of its montane and upland subspecies. During the period 9000–7500 BP the occurrence of *Larix* in the Carpathians was gradually declining. On the later maps scattered sites of larch pollen are found in various parts of the country.

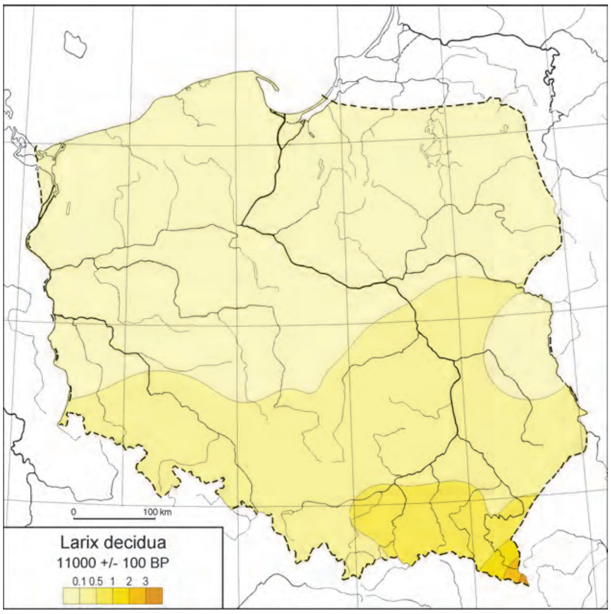
Fig. 55. *Larix decidua*: dot and isopollen maps for 13,000–100 ^{14}C yr BP

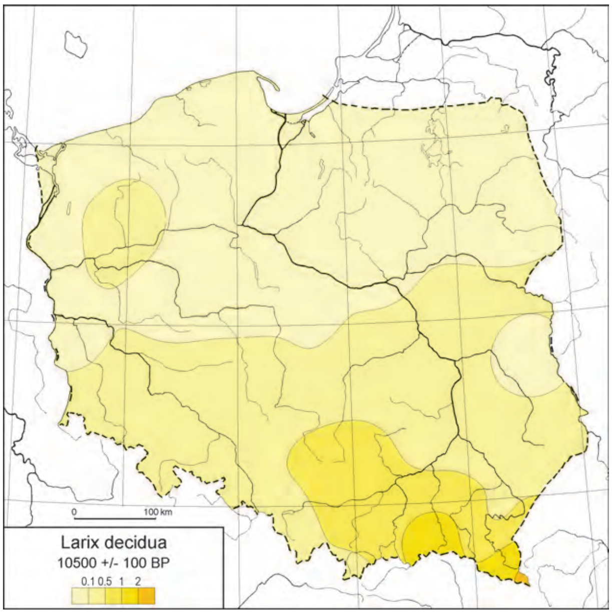

0.3
0.4
0
100 km
Larix decidua
13000 +/- 100 BP


0.0
0.1
0.5
0.1
1.0
0.1
0
100 km
Larix decidua
12500 +/- 100 BP

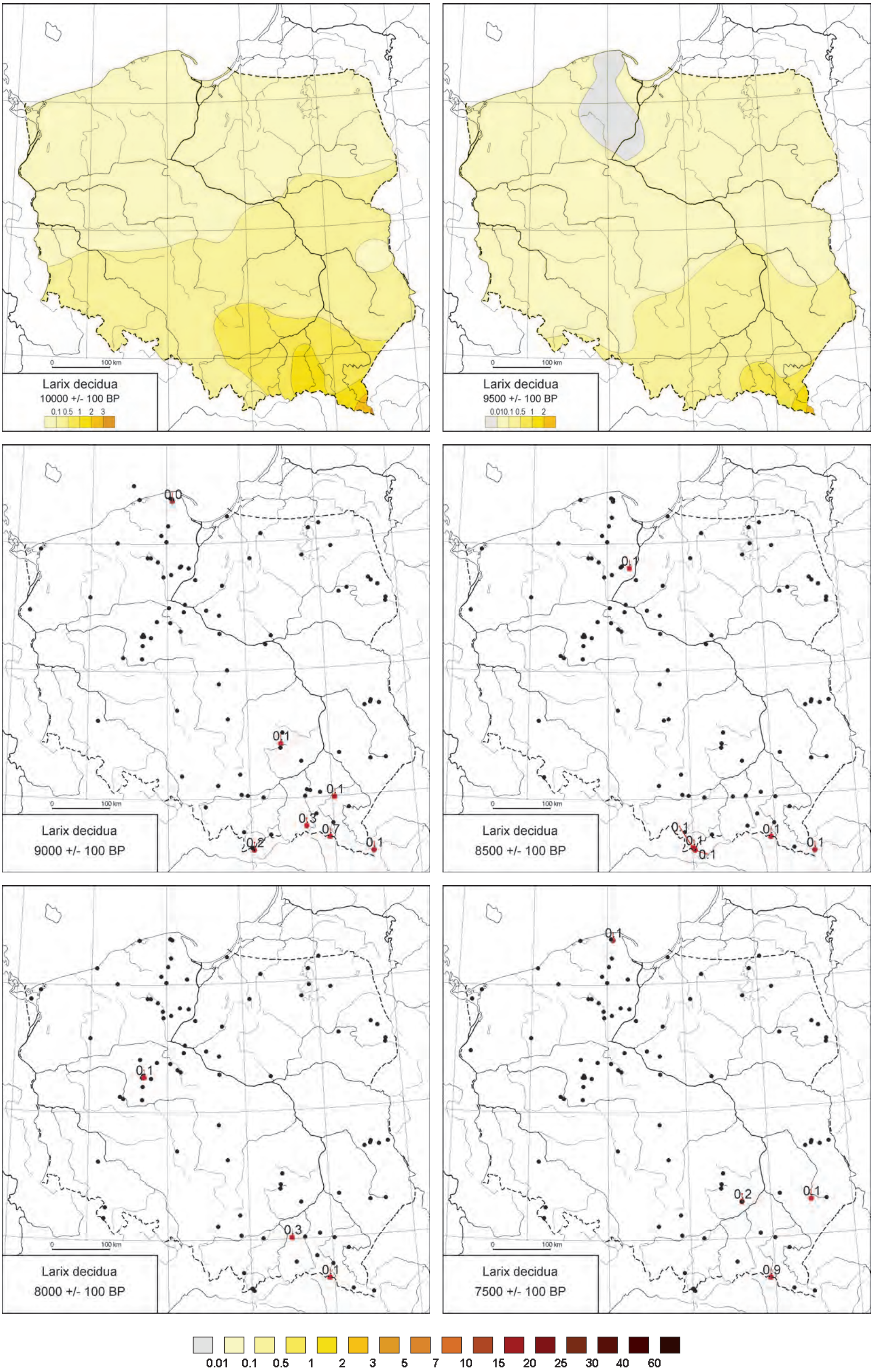

0.2
0.3
0.1
0.4
0.1
0.1
0.1
0.8
0.3
0.4
0
100 km
Larix decidua
12000 +/- 100 BP


0.1
0.1
0.2
0.1
0.6
0.4
0.4
1.0
0.4
0.4
0.3
1.7
3.0
1.0
5.8
0.1
0
100 km
Larix decidua
11500 +/- 100 BP


0
100 km
Larix decidua
11000 +/- 100 BP
0.1 0.5 1 2 3


0
100 km
Larix decidua
10500 +/- 100 BP
0.1 0.5 1 2


0.01
0.1
0.5
1
2
3
5
7
10
15
20
25
30
40
60


0
100 km
Larix decidua
10000 +/- 100 BP
0.1 0.5 1 2 3
0
100 km
Larix decidua
9500 +/- 100 BP
0.01 0.1 0.5 1 2
0.0
0.1
0.1
0.3
0.7
0.2
0.1
0
100 km
Larix decidua
9000 +/- 100 BP
0.1
0.1
0.1
0.1
0.1
0.1
0
100 km
Larix decidua
8500 +/- 100 BP
0.1
0.3
0.1
0
100 km
Larix decidua
8000 +/- 100 BP
0.1
0.2
0.1
0.9
0
100 km
Larix decidua
7500 +/- 100 BP
0.01
0.1
0.5
1
2
3
5
7
10
15
20
25
30
40
60


0,9
0 100 km
Larix decidua
7000 +/- 100 BP

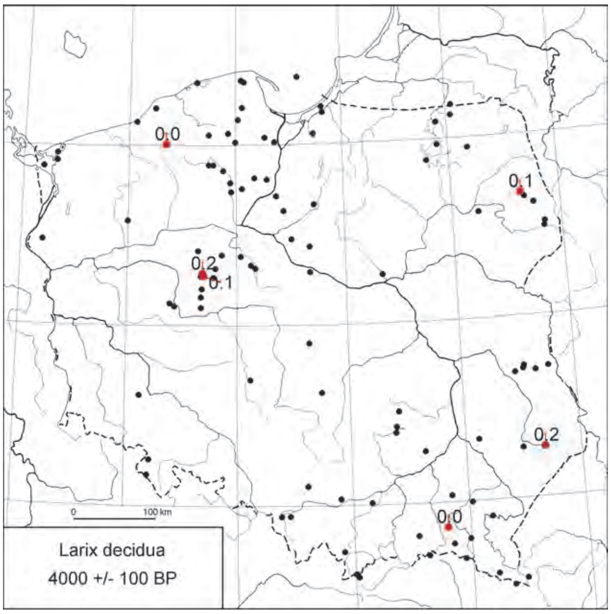

0,7
0 100 km
Larix decidua
6500 +/- 100 BP


0,1
0,1
0,4
0 100 km
Larix decidua
6000 +/- 100 BP


0,0
0 100 km
Larix decidua
5500 +/- 100 BP


0,0
0,1
0,1
0 100 km
Larix decidua
5000 +/- 100 BP


0,0
0,4
0 100 km
Larix decidua
4500 +/- 100 BP


0.0
0.1
0.2
0.1
0.2
0.0
0
100 km
Larix decidua
4000 +/- 100 BP


0.1
0
100 km
Larix decidua
3500 +/- 100 BP


0.0
0.0
0
100 km
Larix decidua
3000 +/- 100 BP


0.0
0.0
0.0
0
100 km
Larix decidua
2500 +/- 100 BP


0.0
0.0
0.1
0
100 km
Larix decidua
2000 +/- 100 BP


0.0
0.1
0
100 km
Larix decidua
1000 +/- 100 BP


0.0
0.0
0.1
0.0
0.1
0.0
0
100 km
Larix decidua
500 +/- 100 BP


0.0
0.3
0.0
0
100 km
Larix decidua
100 +/- 100 BP

Picea abies (L.) H. Karst. – **Spruce**

ANDRZEJ OBIDOWICZ, MAGDALENA RALSKA-JASIEWICZOWA, MIROSŁAWA KUPRYJANOWICZ,
KAZIMIERZ SZCZEPANEK, MAŁGORZATA LATAŁOWA, AND DOROTA NALEPKA

PRESENT DISTRIBUTION IN EUROPE

Spruce (*Picea*) is distributed exclusively in the Northern Hemisphere and according to Gaussen (1966) is differentiated into 48 species. According to Flora Europaea (Tutin et al. 1964) in the European continent it is represented by two species: Serbian spruce (*Picea omorika* (Pančić) Purkyné) and common spruce (*Picea abies* (L.) H. Karst.) as well as by several planted species. Two subspecies belong to *Picea abies*: subsp. *abies* (common spruce) and subsp. *obovata* (Ledeb.) Hultén (Siberian spruce). Serbian spruce is limited to a small area of the Balkan Peninsula. Siberian spruce growing in the Boreal-montane zone of Eurasia (Fig. 56) extends west of the Ural Mountains across western Russia and into northern Scandinavia, whereas common spruce grows in the Dinaric Alps, the Alps, the Sudetes and the Carpathians and almost throughout Scandinavia as well as in the lowlands of north-eastern Europe, where its range intermingles with the range of Siberian spruce (Jalas & Suominen 1973, 1988a).

Within this wide geographical range *Picea abies* is characterised by great individual and regional variability,

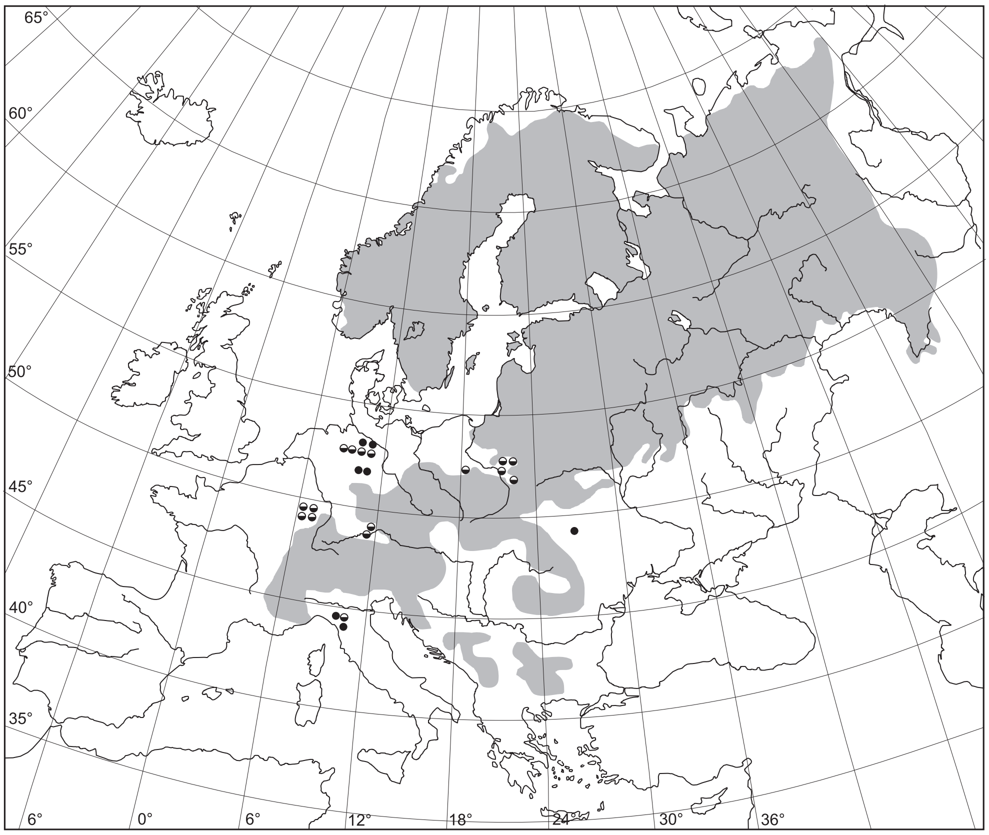


Fig. 56. *Picea abies* – map of present-day distribution in Europe: ● – native isolated occurrence, ◒ – status of site unknown or uncertain (after Jalas & Suominen 1973)

which is the basis for distinguishing lower taxonomic units of various ranks. The greatest importance is attributed to the morphological variability of cones, which form the grounds for distinguishing the basic taxa of a lower rank.

PRESENT DISTRIBUTION IN POLAND

At present *Picea abies* occurs in Poland in two centres – in the mountains of the south and in the north-eastern lowland area (Fig. 57). These distribution ranges are connected with each other only in eastern Poland. Spruce is not native in north-western Poland. In the Beskid Niski range there is a break in its Carpathian range (‘the mid-Carpathian gap’). According to Środoń (1967, 1990b), the breaks and large gaps in its present distribution in central Poland and the Beskid Niski range are probably secondary in most cases, and caused by edaphic factors, but particularly by human interference. In case of the Beskid Niski the low altitude of this range also played a significant role.

Ketner (1966) and Staszkiewicz (1967, 1976) carried out investigations on the morphological variability of *Picea abies* cones, coming from the Carpathian ranges on both sides of ‘the mid-Carpathian gap’, from the Sudetes, from sites situated in the uplands of southern Poland, and from its range in north-eastern Poland. These investigations have shown the occurrence of three main morphological types of cones (Staszkiewicz 1977): *Picea abies* var. *abies* – dominating in the Western Carpathians and at lower altitudes in the Sudetes and comprising ca. 30% of the population in north-east Poland; *P. abies* var. *acuminata* – occurring exclusively in the Eastern Carpathians and forming ca. 70% of north-eastern population; *P. abies* var. *alpestris* – dominating at higher elevations in the Sudetes with a lesser amount occurring in the Western Carpathians.

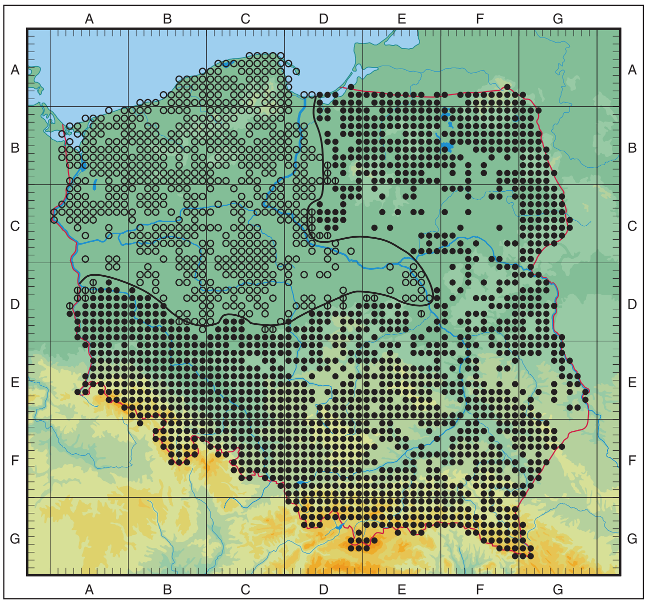


Fig. 57. Present-day distribution of *Picea abies* (L.) H. Karst. in Poland: ○ – synanthropic sites, ⦶ – status of site unknown or uncertain (after Zając A. & Zając M. 2001)

ECOLOGY

Picea abies is a boreal-montane species. This species, being characterised by a wide and fragmented distribution range, shows a very variable relationship to the conditions of the habitats in which its populations occur. In this connection, climatic requirements of spruce cannot be defined by unequivocal indexes (Obmiński 1977). It grows in regions where the January mean temperature is lower than 0°C and July mean temperature is at least 18°C (Bernetti 1995, Zagwijn 1996). It requires a longer period of winter dormancy, the more air temperatures fall below 0°C. A cold climate agrees well with this species, and in the case of a more severe and continental climate, the more snow the better. Spruce, regardless of its age, requires a sufficient amount of moisture both in the air and in the soil. The same sum of annual precipitation may have different ecological effects on spruce in different regions, depending on seasonal rainfall distribution and temperature conditions. The natural range of spruce does not include the areas of Europe influenced by a milder oceanic or Mediterranean climate. It tolerates frost well; in Norway it withstands falls in temperatures to –36(–38)°C, but only in those regions where the minimum total annual rainfall is at least 450 mm (Schmidt-Vogt 1977, Tranquillini 1979). In the upper montane, spruce-dominated forest zone of the Carpathians the total annual rainfall reaches ca. 1600 mm.

Spruce is sensitive to extreme continentality of climate. Reduction of snow cover and strong winter winds exclude it from montane tree stands (Tranquillini 1979). It is also sensitive to late spring ground frosts. Specific races and climatic ecotypes are characterised by different susceptibility to these factors (Obmiński 1977).

Picea abies is a moderately shade-tolerant species and can relatively easily adapt to various light. It can regenerate at 20–30% of full light.

Its soil requirements are moderate, if the degree of soil moisture is sufficiently high. Wet soils with weak aeration are less acceptable for spruce. *Picea abies* reaches its most favourable development on slightly moist, moderately fertile, and not too acid soils, though it tolerates a wide range of pH (Obmiński 1977).

POLLEN PRODUCTION AND DISPERSAL

Spruce flowers in Poland during May and June. In extreme conditions, for example close to the limits of its range, it can flower only every 4 to 10 years (Bortenschlager 1970). Seeds can be set when the temperature during flowering is above 2°C (Folladori 2000, after Ravazzi 2002). Spruce is a wind-pollinated species, producing three times less pollen than pine and more than four times less than oak, and its pollen grains due to their dimensions and weight are not able to float in the air for a long time in spite of being provided with air-sacs.

In palaeoecological reconstructions different pollen values are accepted as evidence for the presence of spruce in forest stands. Pollen values higher than 5% may indicate local presence of this tree (Bortenschlager 1970, Markgraf 1980, Huntley & Birks 1983). The investigations of Hicks (1986, 1994) show that in Finland, recent pollen spectra from forests with spruce as a component have pollen values lower than 4%. Björkman (1996) assumes that a value around 1% may indicate a local presence of single trees of spruce, while increase of the pollen curve up to about 5% probably indicates its regional expansion. Those estimates may be too high, as there are known the sites where *Picea* macrofossils are accompanied by only 0.5% pollen values (Harmata 1987). This tree regenerates from seed.

In the Carpathians spruce forests belonging to the *Vaccinio-Piceetea* class form the upper montane forest zone. At lower montane altitudes and in the lowlands of north-east Poland spruce is present in almost all forest communities (Czerwiński 1973, Matuszkiewicz W. 2001).

EXPANSION IN EUROPE DURING THE LATE GLACIAL AND HOLOCENE

Locations of the glacial refugia of *Picea abies* have been discussed many times (for example Bennett et al. 1991, Combourieu-Nebout et al. 1999, Ravazzi 2002). Generally, all those papers accept the opinion that the locations closest to the Polish boundary, where spruce could have survived the maximum of the last glaciation, are situated in the Romanian Carpathians (Farcas et al. 1999, Björkman et al. 2002, 2003), in Moravia (Damblon et al. 1996, Haesaerts et al. 1996, Damblon 1997), and in the Hungarian Plain (Lang 1994, Willis et al. 1995, 1997, 2000). It is also possible that western Russia was one of the refugial spruce centres (Huntley & Birks 1983).

The map presented by Taberlet et al. (1998) shows the refugial areas of spruce in the Iberian and Apennine Peninsulas and in the northern part of the Balkan Peninsula. Willis et al. (2000) give an account of numerous findings of spruce charcoal in the Palaeolithic sites at the Hungarian Plain, dated between ca. 32,500±2200 BP and 23,500±500 BP as well as *Picea* vel *Larix* charcoal dated after 16,750±400 BP, indicating Vistulian spruce (and/or larch?) refugia in this area.

However, the presence of spruce has also been documented at the inter-pleniglacial sites from the Western Carpathians and in their foothills: a needle of spruce together with a small amount of *Picea* pollen dated to 32,550±450 BP was found in Dobra (Środoń 1968); in a profile from Brzeźnica a pollen zone with a continuous *Picea* curve above 1% has been dated at 35,965±1000 BP (Mamakowa & Starkel 1974). At the site of Jedlicze numerous felled trunks of spruce have been found in a layer dated to 36,700±2100 BP (Krysowska-Iwaszkiewicz & Wójcik 1990). The presence of *Picea abies* macrofossils in the Late Glacial parts of the Carpathian profiles is an additional argument for its survival in the glacial refugia there (Gerlach et al. 1972, Ralska-Jasiewiczowa 1980, Harmata 1987).

MIGRATION PATTERN IN POLAND (Fig. 58)

13,000 – 11,500 BP

On the 13,000 to 11,500 BP maps the *Picea* pollen appears at more and more numerous sites generally at very low values, mostly from silty, bottom sediments of lakes. Spruce is sometimes accompanied by a considerable amount of pollen of thermophilous tree pollen (*Ulmus*, *Corylus*, *Quercus*, *Tilia*, *Alnus*). Only in the Bieszczady Mountains the basal sediment is almost pure and apparently uncontaminated with reworked material (0.5% of *Picea* pollen). At two sites in the north-western part of the Romanian Carpathians, where *Picea* needles have been dated to 12,365±115 and 12,230±105 BP, the peaks of *Picea* pollen after 11,800 BP reach ca. 13% (at 790 m a.s.l.) and nearly 40% (at 730 m a.s.l.) respectively (Björkman et al. 2002, 2003). However, spruce pollen percentages from the parts of those profiles older than 11,800 BP are very low. A similar situation occurs in the case of Tarnowiec site in the Jasło-Sanok Depression where in the Older Dryas *Picea* seeds occur, but the numbers of pollen grains are very low (Harmata 1987). It may be assumed that in the other ranges of the Eastern Carpathians spruce was also present during the Late Glacial.

11,000 – 10,500 BP

The 11,000 and 10,500 BP maps show two centres of spruce distribution in the Tatra Mountains with its pollen values up to 1%, and in the Bieszczady Mountains about 5% (macrofossils found also). They both indicate the *in situ* occurrence of *Picea abies*.

10,000 – 9500 BP

Not earlier than on the 10,000 and 9500 BP maps a distinct expansion of spruce is recorded, spreading from the Carpathians towards the north and north-west. In the Bieszczady Mountains *Picea* pollen values reach ca. 10%. If we assume that its values up to 1% can be an evidence of its local presence, then its range already covered the greater part of the Sandomierz Depression, winning the Sudetes in the west. At the same time on the Slovakian side of Orava pollen values of 20% for this tree occur at a level dated to about 9500 BP (Rybniček & Rybničková 2002).

9000 – 8500 BP

The area of abundant occurrence of spruce already comprises the whole of the Carpathians. Spruce must have expanded also in the area of the recent ‘mid-Carpathian gap’ (Jasiel – 10%, Szczepanek 1987). This was presumably facilitated by rather low competitive pressure from other trees at that time, when the tree-species that later did form the lower montane forest zone were still absent from the Carpathians. Spruce began spreading on the uplands. In the west its distribution includes undoubtedly the Sudetes, though still not in abundance.

8000 – 7500 BP

An abundant centre of *Picea* occurrence is developing in the Sudetes, while in the Carpathians the area of the so-called ‘mid-Carpathian gap’ is distinctly recorded within the range of *Picea*. On successive maps spruce values remain at 3–5% in this area. These values may result from transport of spruce pollen from the adjacent Western and Eastern Carpathians, but it could also result from the impact of isopoll mapping programme, influenced by adjacent high *Picea* values on both sides of the gap.

On the 7500 BP map changes in the distribution of spruce mainly concern the Tatra Mountains centre, from which this tree distinctly expands towards the Western Beskidy Mountains. At lower altitudes in the Carpathians the spruce contribution within the forests increases. In the lowlands the range of *Picea* shifts considerably towards the north-east.

7000 – 6000 BP

In the Carpathian and Sudetian forests spruce has achieved a significant role and locally at higher altitudes it can even become a dominant component. The area of spruce occurrence expands in the lowland parts of Poland approaching the lower course of the Vistula river. In the western part of the lowlands there are no major changes to its distribution.

5500 – 5000 BP

The area with higher values of spruce shifts towards the Świętokrzyskie Mountains and the middle section of Odra river. In the north-east of Poland *Picea* pollen values increase up to 1–2%. However, it is disputable whether this amount really reflects its presence within the local forest stands. The presence of needles of spruce in the sediment from Stare Biele (Białystok Upland) dated at about 5000 BP (Kupryjanowicz 2000, Marek 2000) may support such a suggestion. At this time *Picea abies* reaches and exceeds an altitude of 1500 m a.s.l. on the northern side of the Western Carpathians, as is further confirmed by wood remnants found above this height in the Tatra Mountains (Obidowicz 1996).

4500 – 3500 BP

Since 5500 BP *Picea* pollen values in the ‘mid-Carpathian gap’ were gradually increasing to amalgamate both parts of its range on the 4500 BP map; however on the following maps the outline of this gap has reappeared. On the 4500 and 4000 BP maps in the southern part of Poland spruce shows its maximum occurrence. On the 3500 BP map there are initial signs of separation of the populations between the Sudetes and Western Carpathian areas. However, along the north-eastern boundary of Poland, *Picea* is increasing and forming a new centre. It seems quite probable that from ca. 3500 BP its north and south ranges were temporarily joined together or that they considerably approached each other.

3000 BP

On the 3000 BP map the range of *Picea abies* diminishes in the area in the south-eastern part of the country (the Beskid Niski range and the Bieszczady Mountains together with their adjacent areas), whereas it expands in the north-east of Poland.

2500 – 2000 BP

From 2500 BP the ‘mid-Carpathian gap’ is already clearly visible. At this time the importance of spruce decreases significantly in the forests of north-east Poland, what is also happening in the southern part of its range from ca. 2000 BP.

1500 – 100 BP

There is a re-expansion of the range of spruce in the north that took place between 1500 and 1000 BP. In the south its range was being reduced. Later (500 BP), spruce again forms a distinct centre of expansion in the north-east of Poland. Its range expands slightly also in the Sudetes and their foreland and, to a much lesser degree, in the Western Carpathians. Recently (100 BP), the isopolls do not reflect the real range and role of spruce in the forests of Poland, particularly in the Western Carpathians, where the participation of this tree is still significant (Obidowicz 1996).

At the present day spruce is one of the main forest-forming trees of north-east Poland. The decline in its representation in forest communities, in comparison with the period of ca. 500 BP, is an effect of both forest clearance (mainly since the middle of the 19th century to supply the paper-cellulose industry) as well as of active forest management, which for centuries has promoted pine in this area (Czerwiński 1973).

CONCLUSIONS

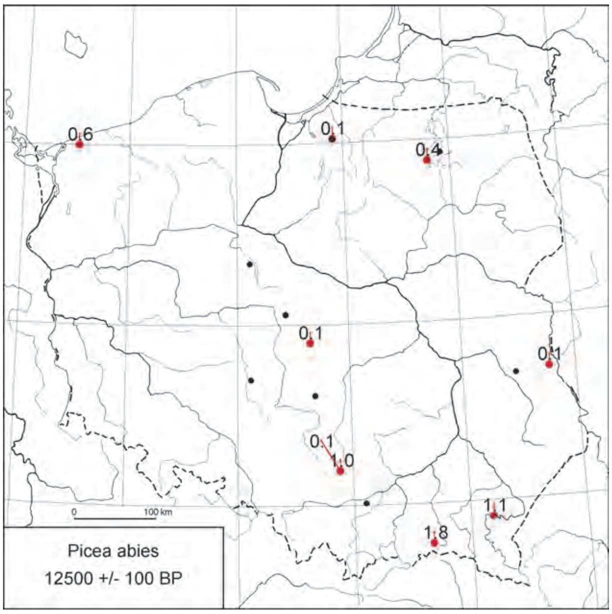
Picea abies migrated over areas of Poland from its refugial regions in the Western and Eastern Carpathians, and in western Russia. Its presence in the Carpathians of north-west Romania from at least 12,400 BP is confirmed by both pollen and macrofossils (Björkman et al. 2002, 2003). In the Polish part of Eastern Carpathians spruce was certainly present in the Late Glacial since the Allerød (Ralska-Jasiewiczowa 1980). The direction of the spruce expansion to the Sudetes about 8000 BP is not quite clear.

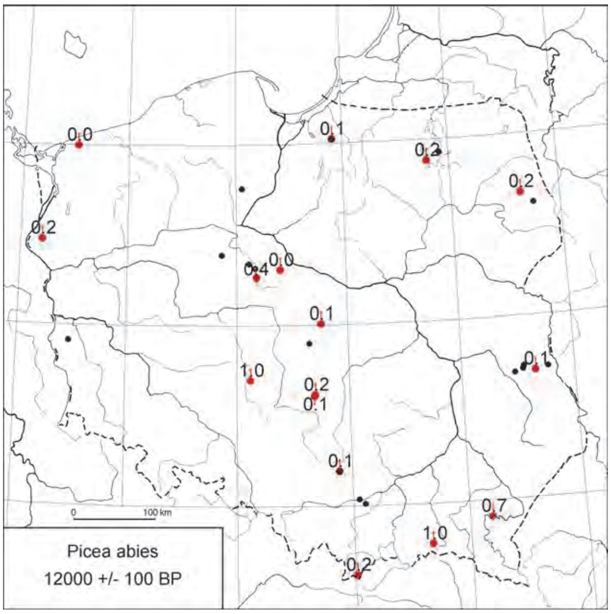
The west and east Carpathian populations expanding since the beginning of the Holocene met in the region of the Beskid Niski range around 7500 BP. At this time the distribution of spruce in the Polish lowlands started to shift towards the north-east. It seems quite probable that in eastern Poland spruce reached the lake districts with scattered sites there since at least 5500 BP. At the time when spruce attained its widest Holocene range in Poland (4500–4000 BP), it might have rebuilt the link between the east and west Carpathian distribution, but for no more than 1000 years.

At that time *Picea* might have approached closer the area of north-western Poland, however this part of Poland has never been occupied by this tree. Otherwise, in the north-eastern areas of the country, a distinct expansion of spruce commenced around, or slightly after 4000 BP and it cannot be excluded that it may still last up till recent times. From the 2500 BP until the present day the changes in the range of spruce, as shown on the maps, have been strongly influenced by human management.

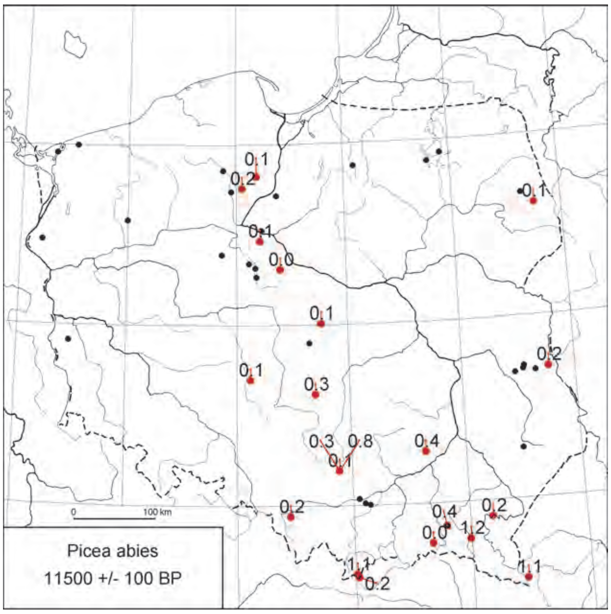
Fig. 58. *Picea abies*: dot and isopollen maps for 13,000–100 ^{14}C yr BP


0.3
0.1
1.2
2.6
0
100 km
Picea abies
13000 +/- 100 BP


0.6
0.1
0.4
0.1
0.1
0.1
1.0
1.1
1.8
0
100 km
Picea abies
12500 +/- 100 BP

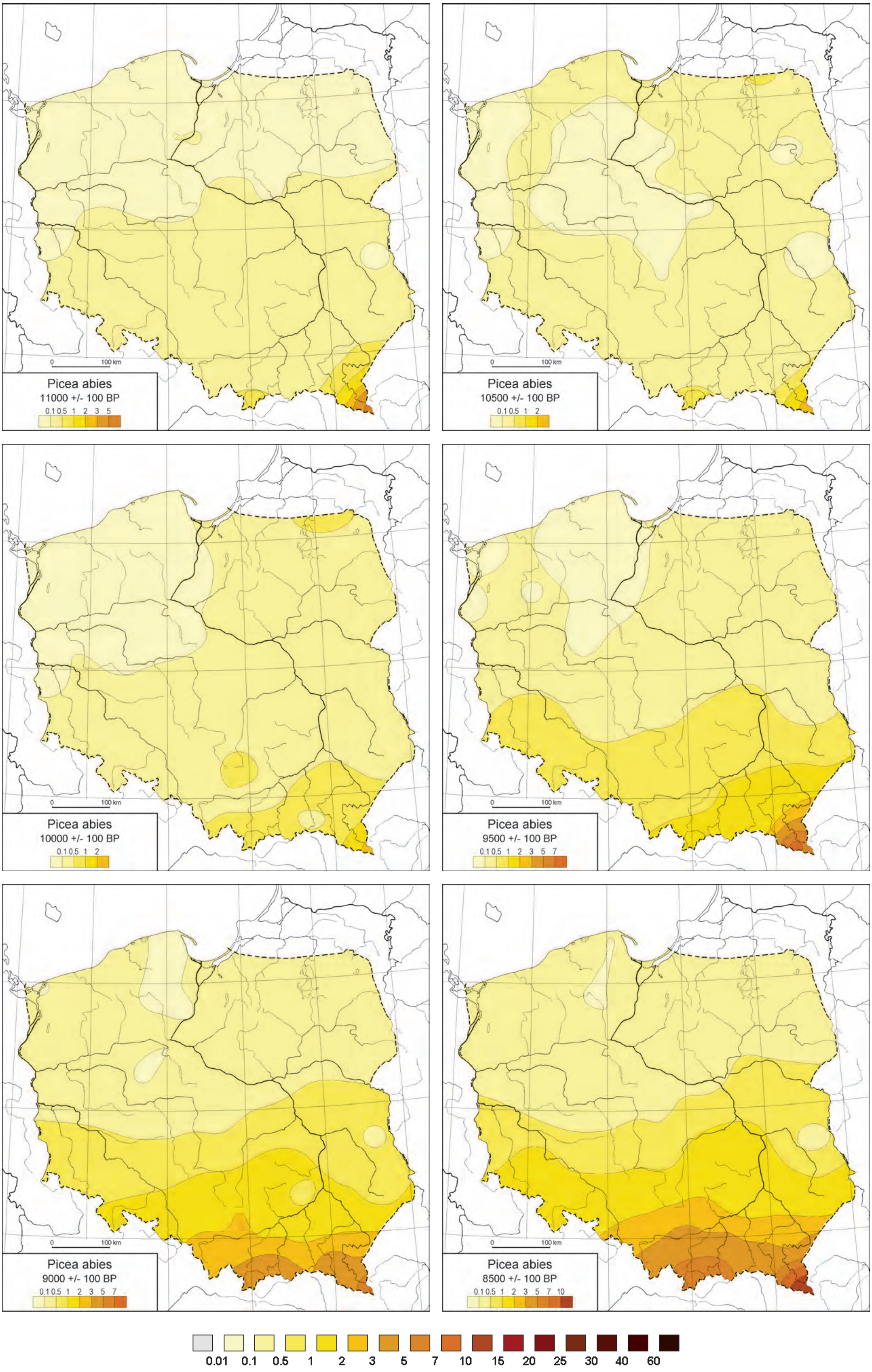

0.0
0.1
0.3
0.2
0.2
0.4
0.0
0.1
1.0
0.2
0.1
0.1
0.1
0.7
1.0
0.2
0
100 km
Picea abies
12000 +/- 100 BP

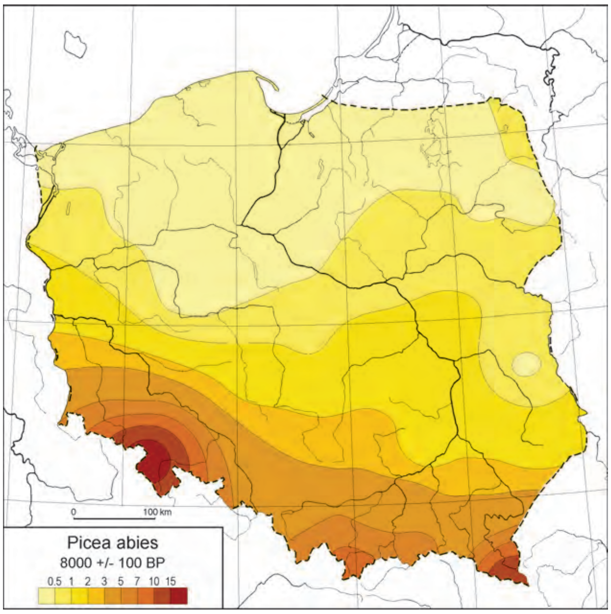

0
100 km
Picea abies
12000 +/- 100 BP
0.1 0.5

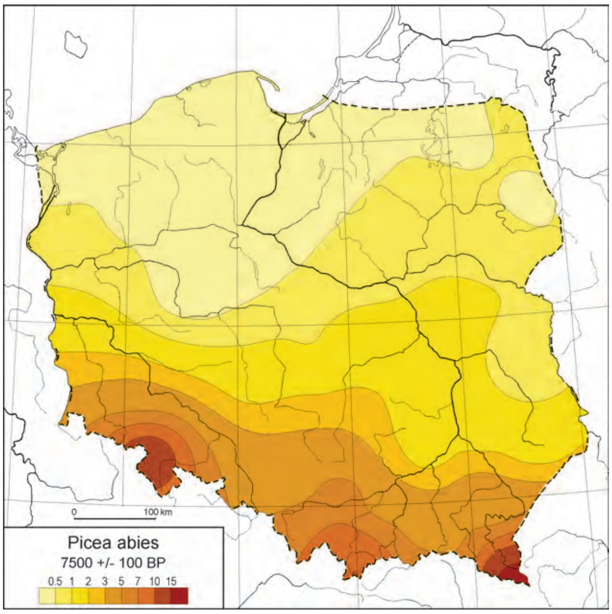

0.1
0.2
0.1
0.1
0.0
0.1
0.2
0.1
0.3
0.3
0.8
0.1
0.4
0.2
0.4
0.2
0.0
1.2
1.1
0.2
1.1
0
100 km
Picea abies
11500 +/- 100 BP

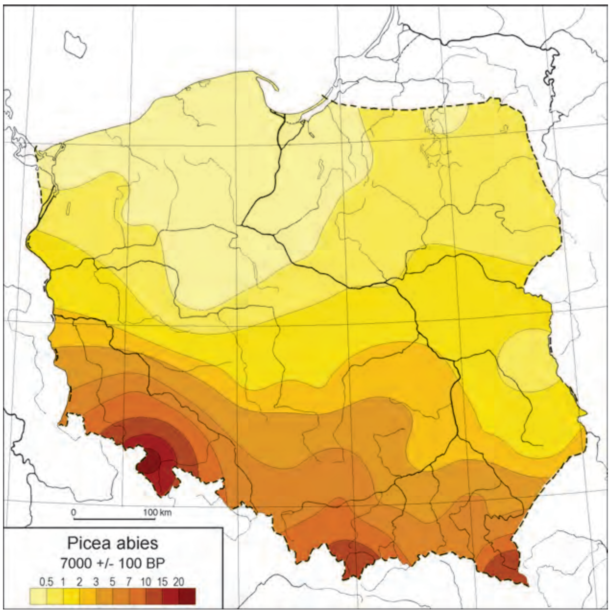

0
100 km
Picea abies
11500 +/- 100 BP
0.1 0.5

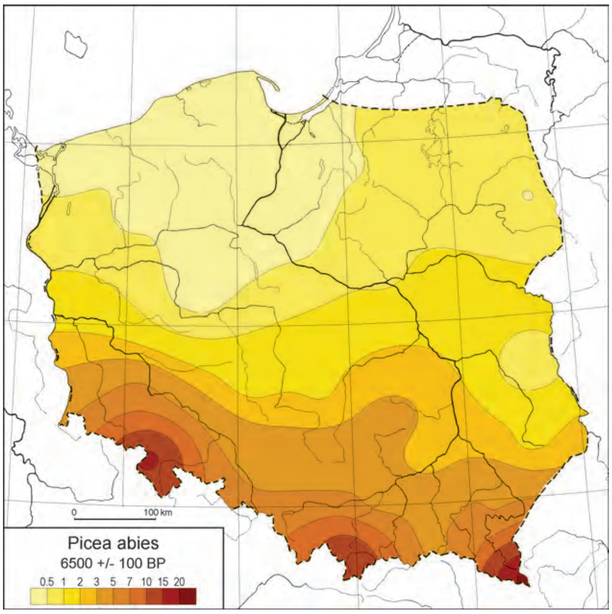

0.01
0.1
0.5
1
2
3
5
7
10
15
20
25
30
40
60

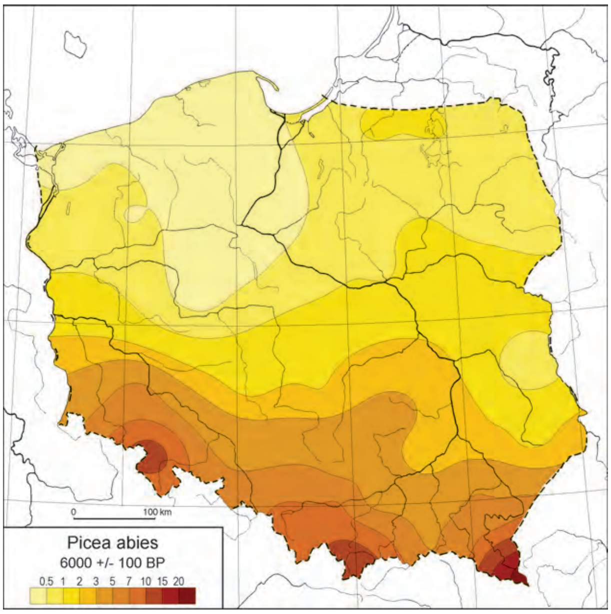

0 100 km
Picea abies
11000 +/- 100 BP
0.1 0.5 1 2 3 5
0 100 km
Picea abies
10500 +/- 100 BP
0.1 0.5 1 2
0 100 km
Picea abies
10000 +/- 100 BP
0.1 0.5 1 2
0 100 km
Picea abies
9500 +/- 100 BP
0.1 0.5 1 2 3 5 7
0 100 km
Picea abies
9000 +/- 100 BP
0.1 0.5 1 2 3 5 7
0 100 km
Picea abies
8500 +/- 100 BP
0.1 0.5 1 2 3 5 7 10
0.01 0.1 0.5 1 2 3 5 7 10 15 20 25 30 40 60

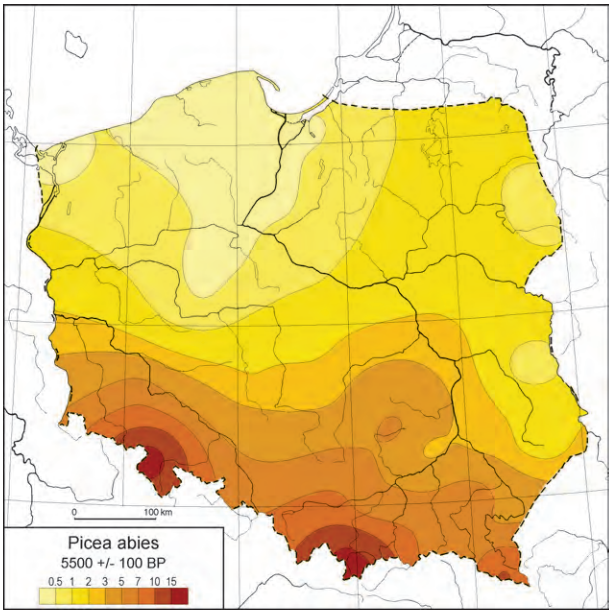

0
100 km
Picea abies
8000 +/- 100 BP
0.5 1 2 3 5 7 10 15


0
100 km
Picea abies
7500 +/- 100 BP
0.5 1 2 3 5 7 10 15

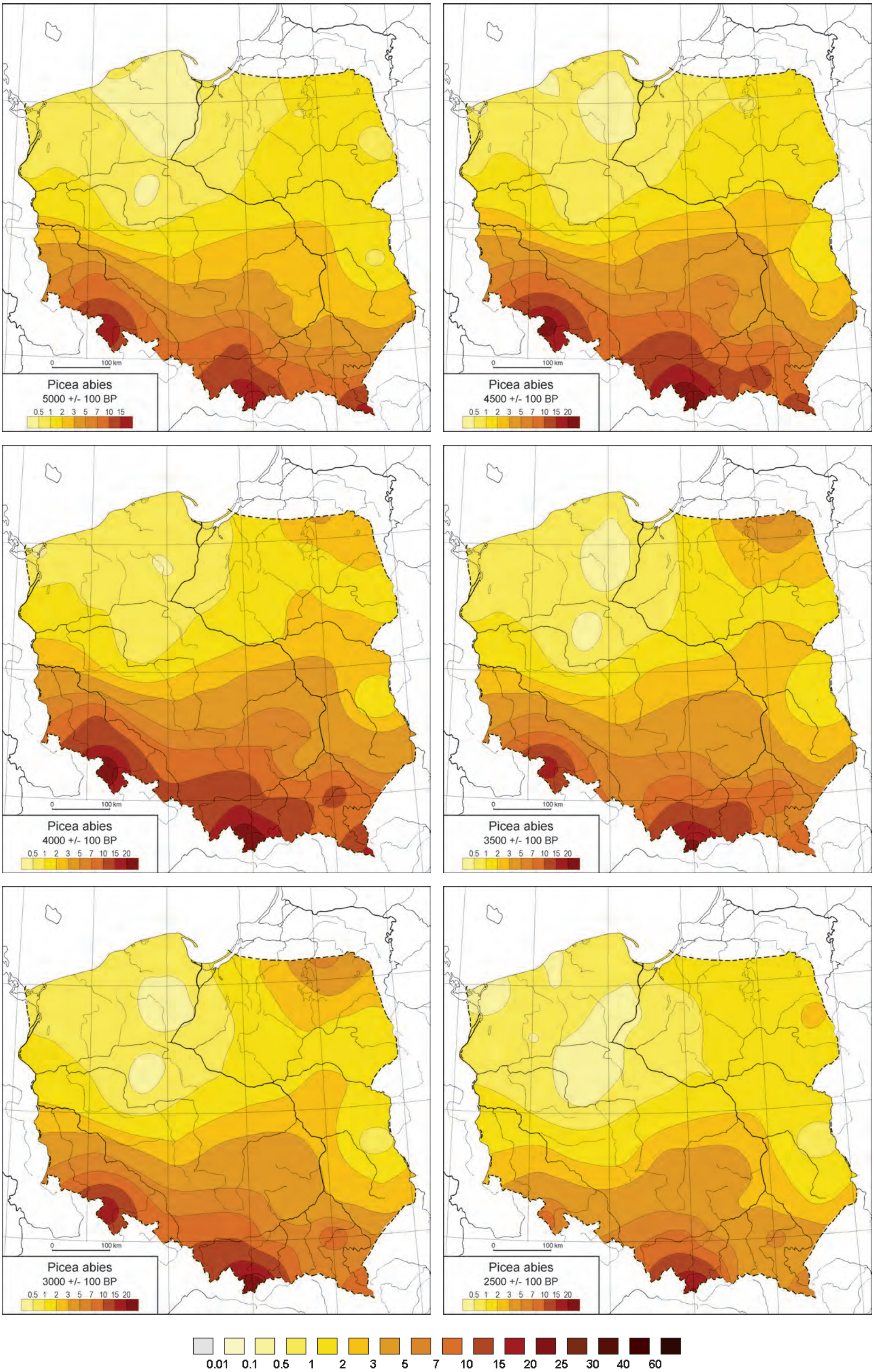

0
100 km
Picea abies
7000 +/- 100 BP
0.5 1 2 3 5 7 10 15 20

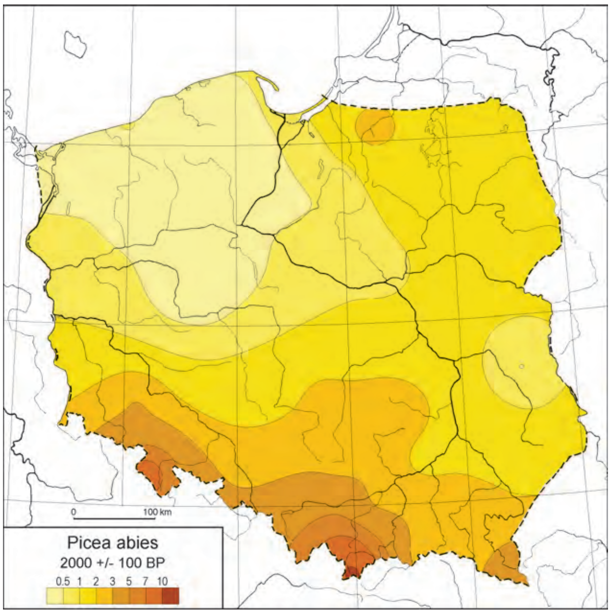

0
100 km
Picea abies
6500 +/- 100 BP
0.5 1 2 3 5 7 10 15 20

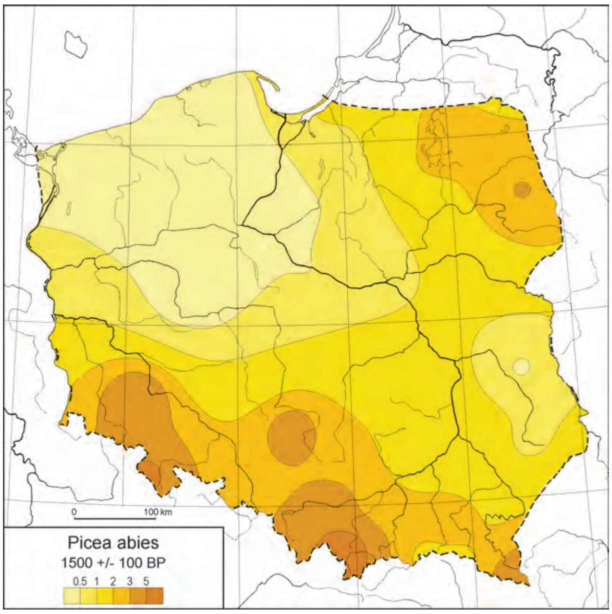

0
100 km
Picea abies
6000 +/- 100 BP
0.5 1 2 3 5 7 10 15 20

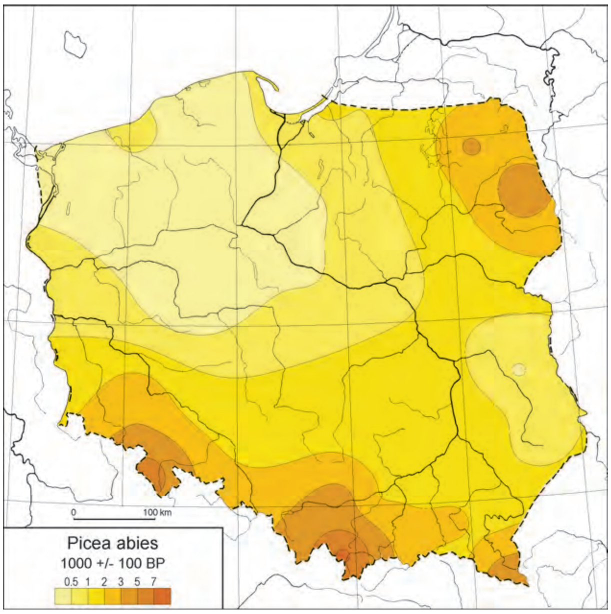

0
100 km
Picea abies
5500 +/- 100 BP
0.5 1 2 3 5 7 10 15

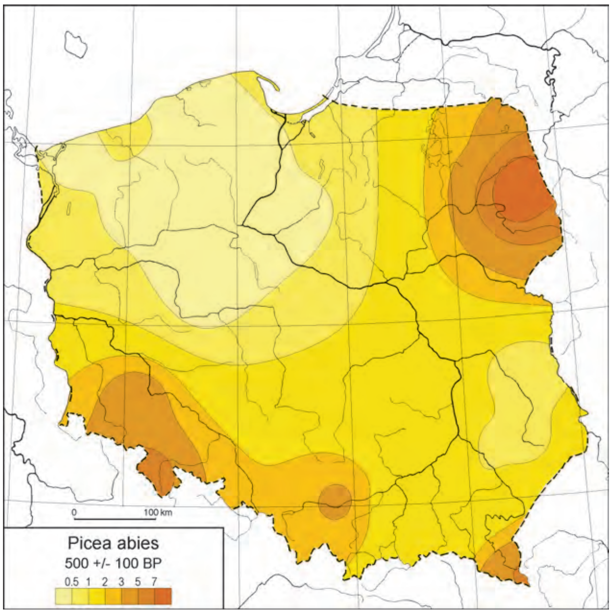

0.01 0.1 0.5 1 2 3 5 7 10 15 20 25 30 40 60

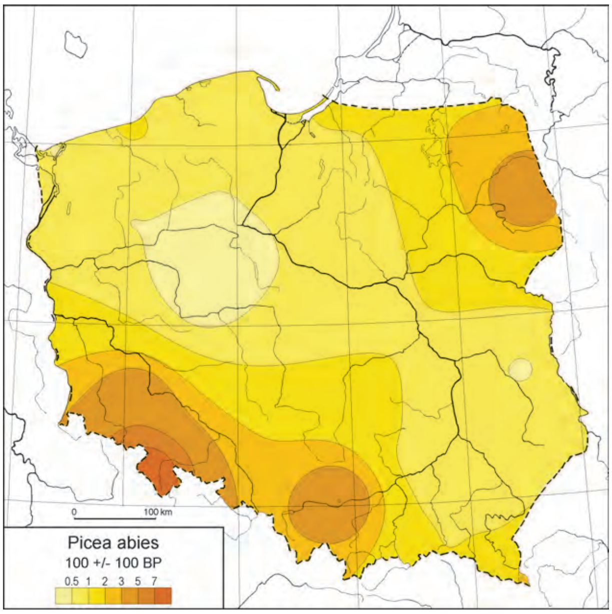

0 100 km
Picea abies
5000 +/- 100 BP
0.5 1 2 3 5 7 10 15
Picea abies
4500 +/- 100 BP
0.5 1 2 3 5 7 10 15 20
Picea abies
4000 +/- 100 BP
0.5 1 2 3 5 7 10 15 20
Picea abies
3500 +/- 100 BP
0.5 1 2 3 5 7 10 15 20
Picea abies
3000 +/- 100 BP
0.5 1 2 3 5 7 10 15 20
Picea abies
2500 +/- 100 BP
0.5 1 2 3 5 7 10 15 20
0.01 0.1 0.5 1 2 3 5 7 10 15 20 25 30 40 60











0.01 0.1 0.5 1 2 3 5 7 10 15 20 25 30 40 60

Pinus cembra L. – European stone pine

ANDRZEJ OBIDOWICZ, KAZIMIERZ SZCZEPANEK AND DOROTA NALEPKA

European stone pine (*Pinus cembra*) belongs to the subgenus *Strobus* (previously *Haploxylon*). This subgenus includes three species in Europe: *Pinus peuce* Griseb. occurring in the mountains of the Balkan Peninsula, *P. sibrica* Mayr. in the north-eastern part of Europe and Siberia, as well as *P. cembra* L. (Lang 1994). The two latter species are considered to be closely related, and Siberian stone pine is often regarded as a subspecies *P. cembra* subsp. *sibirica* (Rupr.) Kryl. Both taxa reveal very close anatomical as well as morphological similarities. Actually, it is quite difficult to distinguish European from Siberian stone pine.

The morphology of *Pinus cembra* pollen is very similar to the *P. haploxylon*-type that is found very often in Tertiary deposits.

PRESENT DISTRIBUTION IN EUROPE AND IN POLAND

European stone pine grows in two main distribution areas: the Alpine and the Carpathian Mountains (Myczkowski & Bednarz 1974). In the Carpathians its range is fragmented and shows features of a relict range. In Poland, the sites of *Pinus cembra* are grouped in the Tatra Mountains (Fig. 59), where the stone pine is a rare characteristic species of the *Piceion abietis* alliance (Matuszkiewicz J.M. 2002), occurring usually between 1300 (1400) and 1650 m a.s.l. (Piękoś-Mirkowa & Mirek 1996).

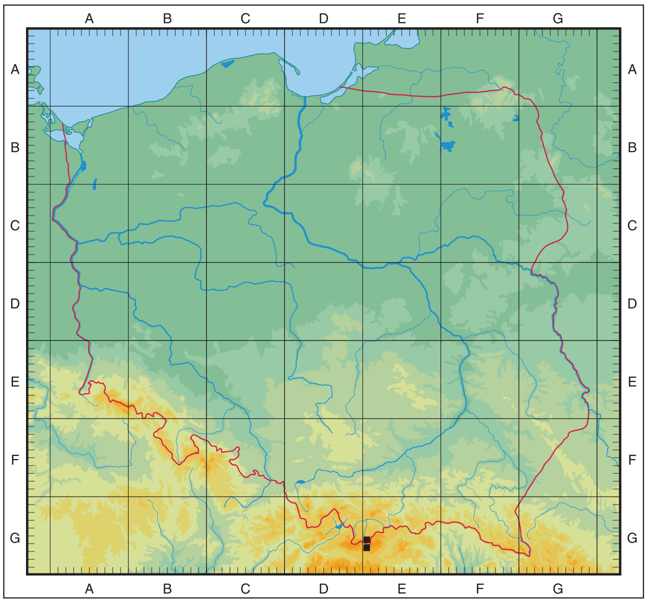


Fig. 59. Present-day distribution of *Pinus cembra* L. in Poland: ■ – relict site presently existing (after Zając A. & Zając M. 2001)

ECOLOGY

Pinus cembra is a tree adapted to conditions of continental climate. It is very resistant to low temperatures, and in mid-winter is able to survive without any damage from frost, down to –40°C. According to Tranquillini (1963, 1969), the frost-tolerance of *Pinus cembra* in the mountains cannot be explained by the normal process of dehydration of both plasma and intercellular spaces during accumulation of saccharides and lipids, but by the exceptionally high viscosity of the protoplasm. This means that, under experimental conditions, the cell content in the needles has been shown to remain unfrozen even during a gradual lowering of temperature to –60°C. Stomatal guard cells of needles are covered with thick cuticle, protecting them from too excessive loss of water.

Observations made in the northern Alps have revealed that *Pinus cembra* forests grow more frequently on the wetter and colder northern slopes. According to foresters this is a secondary phenomenon connected with the development of pasturage resulting in destruction of *Pinus cembra* on more sunny and favourable southern slopes. Where there are rather dry summers *Pinus cembra* may be replaced by pine, where summers are too rainy, it cannot compete with spruce and/or fir (Hofmann 1970). As the growing season at the altitudes occupied by *Pinus cembra* rarely lasts longer than three months, individual specimens of this tree grow slowly, and after 100 years their heights do not exceed 10 m. However, it is a long-lived tree, attaining an age of more than 1000 years (Ellenberg 1978).

In the Alps on the crystalline bed-rock, in the zone of the upper forest limit *Pinus cembra* forms, either an association with larch (*Larici-Pinetum cembrae*), reaching up to 2500 m a.s.l., or a pioneer sub-association on screen together with larch and rhododendron (*Larici-Pinetum cembrae rhododendrotosum ferruginei*). On limestone it grows in the sub-association of *Larici-Pinetum cembrae rhododendrotosum hirsuti* (Mayer 1986). In the Tatra Mountains *Pinus cembra* occurs on poor, non-calcareous bedrock, mainly on granite (Myczkowski & Bednarz 1974). Originally, *Larix decidua* was much more frequent component of forests with stone pine, but at present it occurs there very rarely. The following trees frequently accompany *P. cembra*: *Sorbus aucuparia* var. *glabrata*, *Betula pubescens* subsp. *carpatica*, *Pinus sylvestris*, *Abies alba*, and *Populus tremula*. In the shrub layer there are: *Lonicera nigra*, *Rosa pendulina*, *Juniperus communis*, *Pinus mugo*, *Salix silesiaca*, *Padus avium* subsp. *petraea*, *Ribes petraeum* subsp. *carpaticum*, as well as dwarf shrubs of the genus *Vaccinium* and tall herbs.

The stone pine flowers not earlier than at the age of sixty or later; in the mountains the flowering season starts at the beginning of June, and at the highest sites even at the beginning of July. Ripening of cones lasts until the autumn of the following year. *Pinus cembra* is a species whose seeds are largely dispersed by animals; its seeds can sprout even in fissures of bare rocks. *Pinus cembra* propagates only by seed. Periods of plentiful yield of seeds are usually repeated every 9 to 10 years.

POLLEN PRODUCTION AND DISPERSAL

Pinus cembra pollen is dispersed by wind. The investigations carried out on the largest site of *Pinus cembra* in the Tatra Mountains have shown that in the middle of a stand the representation of *Pinus cembra* pollen in the surface assemblage is more than 27%, while at the margins it decreases to about 5% (Obidowicz, unpublished data). Thus, at least a 5% value of the total pollen sum can be assumed to be an indicator of its presence *in situ*. Wegmüller (1977) has stated that in Late Glacial pollen zones from the French Alps *Pinus cembra* pollen does not exceed 3%. According to this author, it indicates that stone pine did not form close stands then in that part of the Alps. When at the onset of the Subboreal period the curve of *Pinus cembra* exceeds 30%, this author assumes it formed closed stands in the sub-Alpine zone.

EXPANSION IN EUROPE DURING THE LATE GLACIAL AND HOLOCENE

During the Vistulian the refugial areas of *Pinus cembra* occurred in the Alps and Carpathians, beyond the maximum present range of this taxon. They were situated at ice-free, lower altitudes (Lang 1994). Regarding the Carpathians such a supposition is supported by macrofossils of stone pine found in Late Glacial deposits in the foothills on the southern side of the Tatra Mountains (Jankowská 1984, 1995). On the northern side of the Carpathians, the presence of *P. cembra* has been confirmed at several sites by both macrofossils and pollen occurring in interstadial deposits of the Pleni-Vistulian and Late Glacial (Środoń 1952, 1968, Birkenmajer & Środoń 1960, Krauss et al. 1965, Szczepanek 1965, 1971b, Koperowa 1970, Mamakowa 1968, Mamakowa & Środoń 1977, Ralska-Jasiewiczowa 1980, Harmata 1995b, Obidowicz 1996, Gębica 1995, Gębica et al. 1998, 2002). On the other hand, the stone pine pollen found at Late Glacial sites of north-east Poland might have derived from redeposition (difficult to distinguish from Tertiary *Pinus haploxylon*-type), although since the Allerød interstadial it could have been a result of a long-distance transport (Wacnik 2003).

MIGRATION PATTERN IN POLAND (Fig. 60)

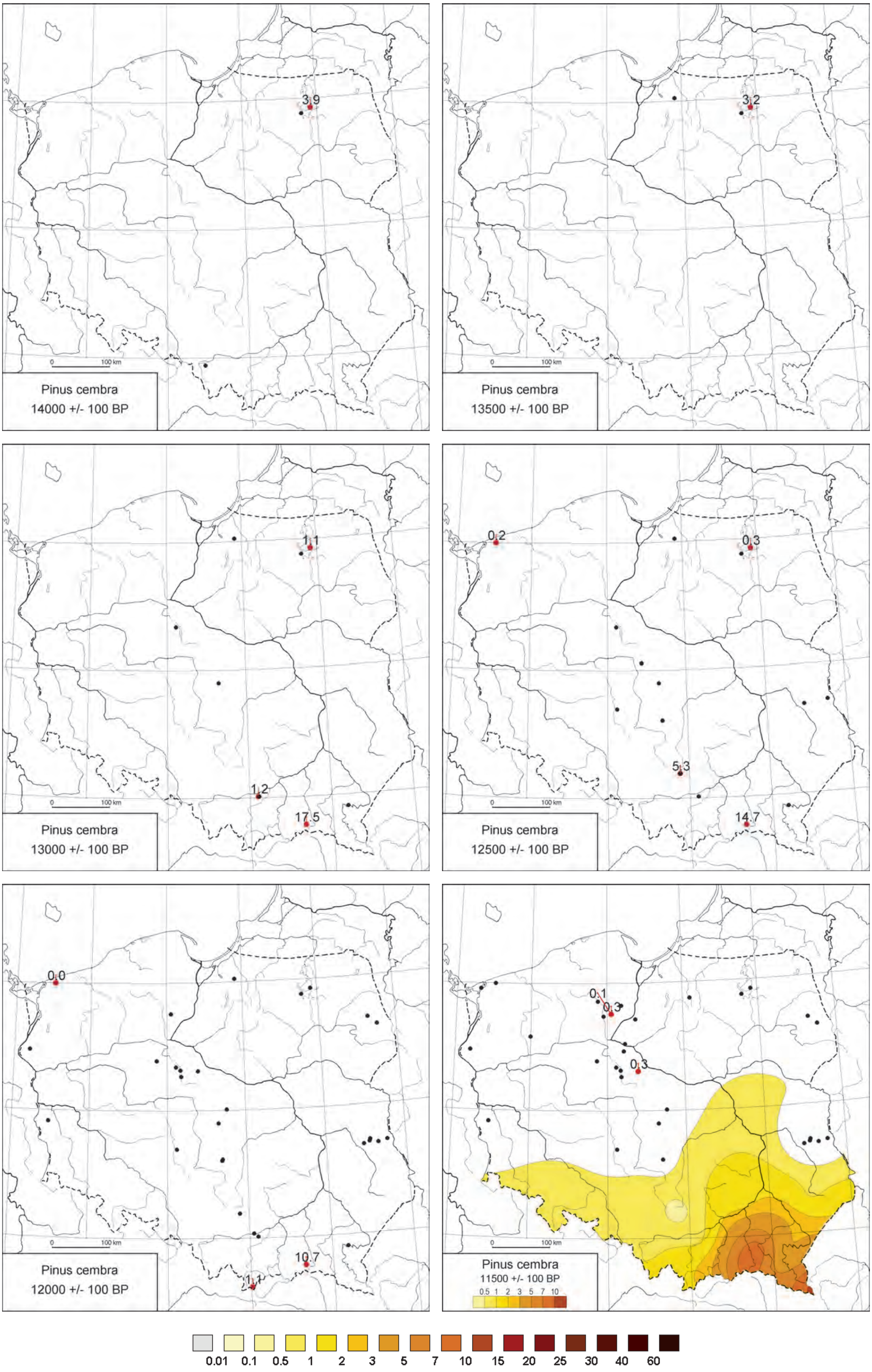
On the 14,000 and 13,500 BP maps *Pinus cembra*-type pollen with values of 3.7 and 3.0% have been found at only one site in north-eastern Poland, and they are interpreted as redeposition from Tertiary deposits (Ralska-Jasiewiczowa 1966). The Late Glacial (13,000, 12,500 and 12,000 BP) is represented by single sites of low *P. cembra* pollen values, except for the site at Jasło-Sanok Depression, where its values, ranging from 9.9% up to 16.5%, indicate the occurrence of this tree in that area. On the 11,500 BP map the number of sites with higher values of *P. cembra* increases, particularly in the Carpathians. Such a situation remains constant on the 11,000, 10,500, and 10,000 BP maps, suggesting the existence of larger populations of this tree in the Carpathians and in their foreland during this part of the Late Glacial. It has been also confirmed by the occurrence of *P. cembra* pollen in the profiles from the region of Gorna Orava on the Slovakian side of the Carpathians (Rybniček & Rybničková 2002). At the same time new sites with low *P. cembra* pollen values appear in the area between the middle and lower course of the Vistula river, but they hardly suggest the presence of *Pinus cembra* in these areas. The 9500 BP map illustrates the maximum of *P. cembra* distribution in southern Poland. On the following 9000 and 8500 BP maps a reduction of the range of *P. cembra* and its restriction to its relict sites in the Tatra Mountains is recorded.

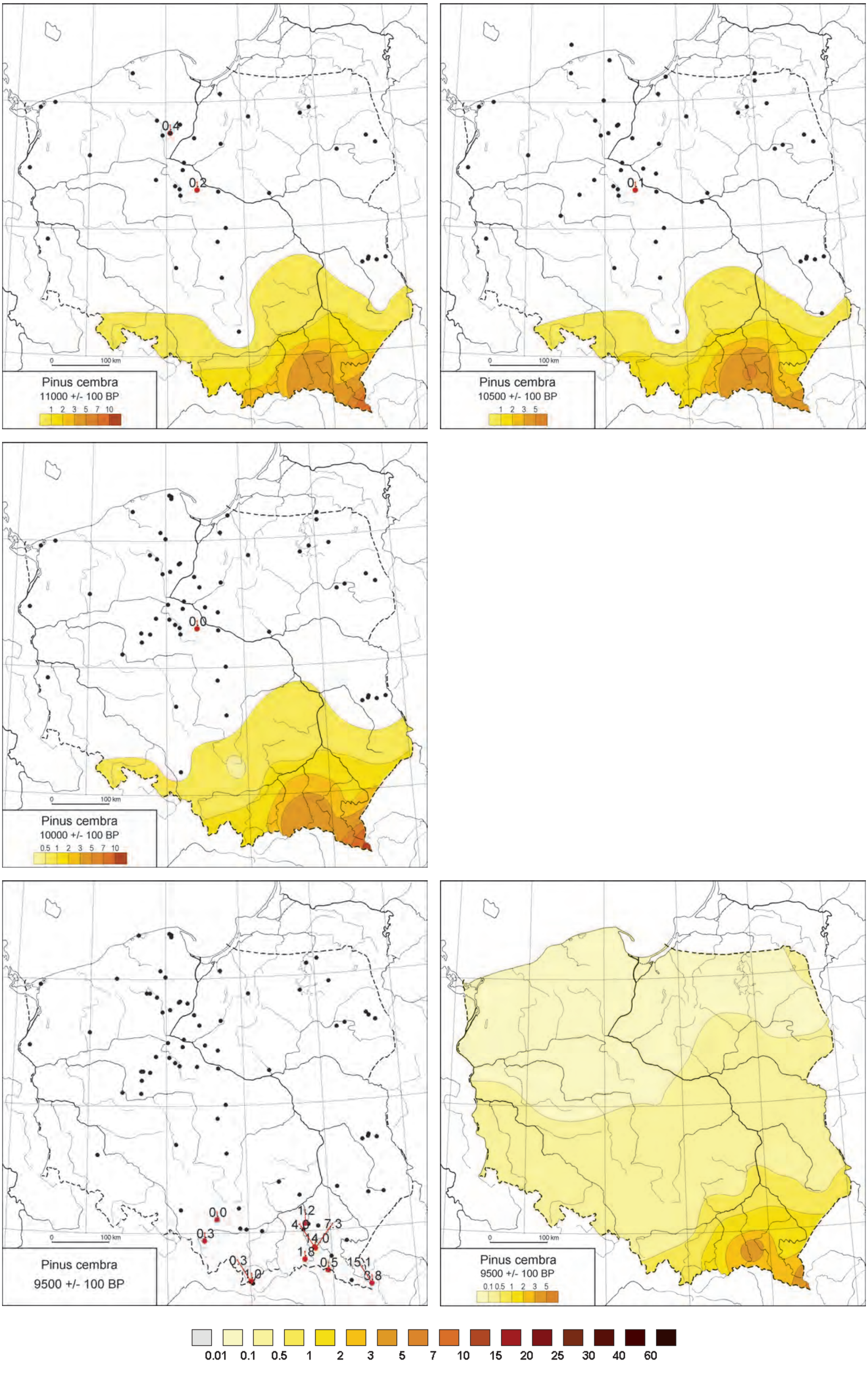
CONCLUSIONS

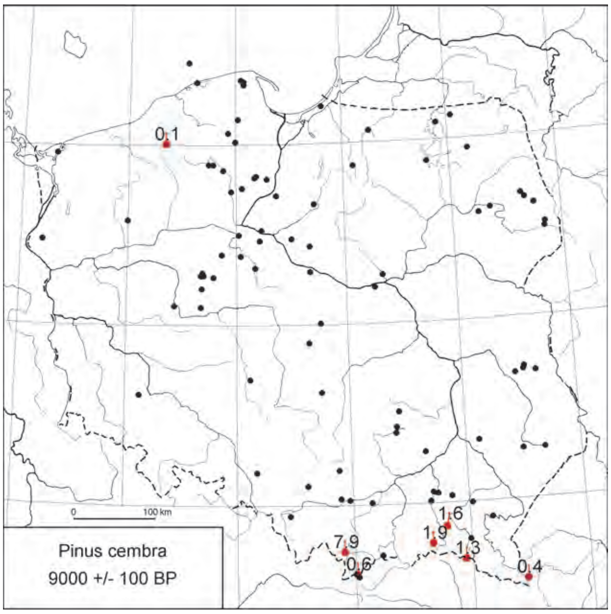
Pinus cembra L. survived the last glaciation in the Carpathians. It expanded quickly during the Late Glacial time, covering its widest area during the period between 11,500 and 9500 BP. In the Holocene, due to the expansion of spruce, *P. cembra* was displaced to its marginal habitats in the high altitudes of the Tatra Mountains.

→

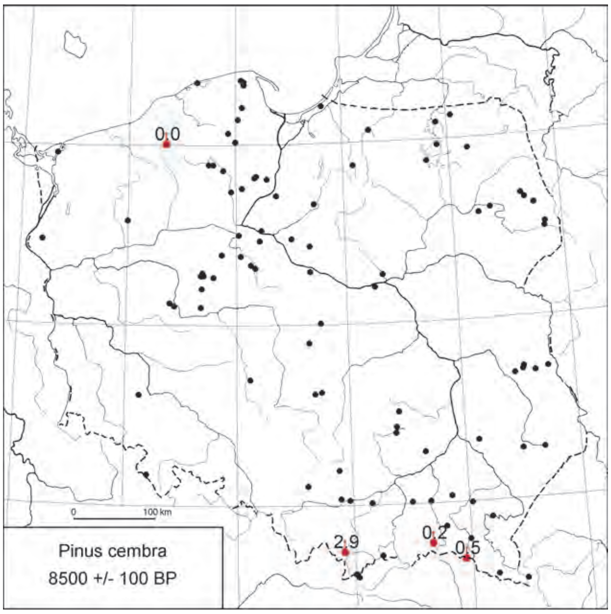
Fig. 60. *Pinus cembra*: dot and isopollen maps for 14,000–5000 ^{14}C yr BP


3.9
0
100 km
Pinus cembra
14000 +/- 100 BP
3.2
Pinus cembra
13500 +/- 100 BP
1.1
1.2
17.5
Pinus cembra
13000 +/- 100 BP
0.2
0.3
5.3
14.7
Pinus cembra
12500 +/- 100 BP
0.0
1.1
10.7
Pinus cembra
12000 +/- 100 BP
0.1
0.3
0.3
Pinus cembra
11500 +/- 100 BP
0.5 1 2 3 5 7 10
0.01
0.1
0.5
1
2
3
5
7
10
15
20
25
30
40
60


0.4
0.2
0 100 km
Pinus cembra
11000 +/- 100 BP
1 2 3 5 7 10
0.1
0 100 km
Pinus cembra
10500 +/- 100 BP
1 2 3 5
0.0
0 100 km
Pinus cembra
10000 +/- 100 BP
0.5 1 2 3 5 7 10
0.0
0.3
1.2
4.0
7.3
14.0
1.8
0.3
1.0
0.5
15.1
3.8
0 100 km
Pinus cembra
9500 +/- 100 BP
0 100 km
Pinus cembra
9500 +/- 100 BP
0.1 0.5 1 2 3 5
0.01 0.1 0.5 1 2 3 5 7 10 15 20 25 30 40 60


0.1
7.9
0.6
1.9
1.6
1.3
0.4
0
100 km
Pinus cembra
9000 +/- 100 BP


0
100 km
Pinus cembra
9000 +/- 100 BP
0.01
0.1
0.5
1


0.0
2.9
0.2
0.5
0
100 km
Pinus cembra
8500 +/- 100 BP


0.5
0
100 km
Pinus cembra
8000 +/- 100 BP


0.8
0
100 km
Pinus cembra
7500 +/- 100 BP


1.3
0
100 km
Pinus cembra
7000 +/- 100 BP


0.01
0.1
0.5
1
2
3
5
7
10
15
20
25
30
40
60


0
100 km
Pinus cembra
6500 +/- 100 BP
0.7


0
100 km
Pinus cembra
6000 +/- 100 BP
0.4


0
100 km
Pinus cembra
5000 +/- 100 BP
0.1

Pinus L. subgenus *Pinus*
(subgen. *Diploxylon* (Koehne) Pilger) – **Pine**

Małgorzata Latałowa, Kazimierz Tobolski and Dorota Nalepka

Pinus is represented by 15 species in Europe from which four are native to the Polish flora (Staszkiewicz 1970). They belong to two subgenera, which differ in the structure of the needles and dwarf shoots as well as in the structure of the pollen grains. *Pinus sylvestris* L., *P. mugo* Turra, and *P.* ×*rhaetica* Brügger belong to the subgenus *Pinus* (previously *Diploxylon*) whereas *P. cembra* L. belongs to the subgenus *Strobus* (previously *Haploxylon*) (Boratyński 1993). In spite of the fact that the morphological features allow one to distinguish pollen grains of both subgenera (Moore et al. 1991), namely *P. cembra* from the pollen of the other three species, such determinations are not regularly applied in some palynological papers. The values of *Pinus* isopolls may be higher, particularly on the Late Glacial maps of southern Poland, where they can be slightly overestimated by inclusion of *Pinus cembra* pollen. *Pinus cembra* is a subject of a separate paper in this volume.

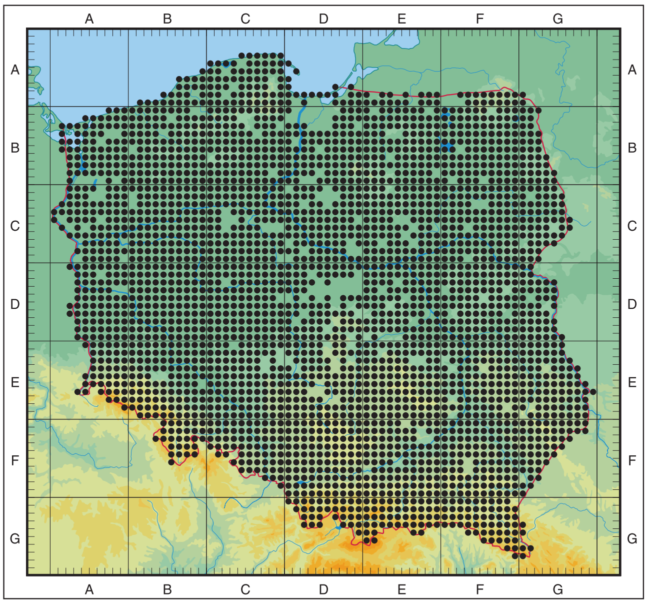


Fig. 61. Present-day distribution of *Pinus sylvestris* L. in Poland (after Zając A. & Zając M. 2001)

Present distribution in Poland

Pinus mugo and *Pinus* ×*rhaetica* are montane species with a small distribution range. *P. mugo* is a low-growing shrub, which in the Carpathians and in the Sudetes forms thick scrub above the upper forest boundary, reaching in the Tatra Mountains 2140 m a.s.l. Sometimes it appears at lower altitudes where it spreads on peat bogs. This species has the northern limit of its range in the Polish mountains (Gostyńska-Jakuszewska & Zieliński 1976). *P.* ×*rhaetica* has a shrubby habit and in Poland is known only from a few peat-bogs occurring in the Podhale area, at the foot of Babia Góra Mountain and in the Sudetes, where it reaches the north-eastern boundary of its range. Outside Poland it grows on submontane peat bogs in Austria, the Czech Republic, Slovakia and in Germany (Boratyńska & Boratyński 1978).

Pinus sylvestris L. belongs to the most common components of the Polish flora, though it is not evenly distributed over the whole country (Fig. 61). It is common in lowland areas, whereas in the Carpathians and in the Sudetes it appears sparsely, but there its stands reach the upper forest limit. A fragment of the southern limit of its collective range runs through south-eastern Poland, in the Bieszczady Mountains (Boratyński 1993).

Ecology

The common pine is an Euro-Siberian species with a widespread range crossing a lot of climatic boundaries (Fig. 62). This is possibly associated with its considerable number of varieties and ecotypes with different climatic requirements (Obmiński 1970). In general pine is one of those species adapted to continental conditions. It can tolerate very well both a very wide annual temperature range and considerable fluctuations in rainfall. Climatic factors restricting the growth of pine include low temperatures during development of its shoots and the relative sensitivity of seedlings to destruction by frost which is a factor limiting *Pinus* regeneration along the northern

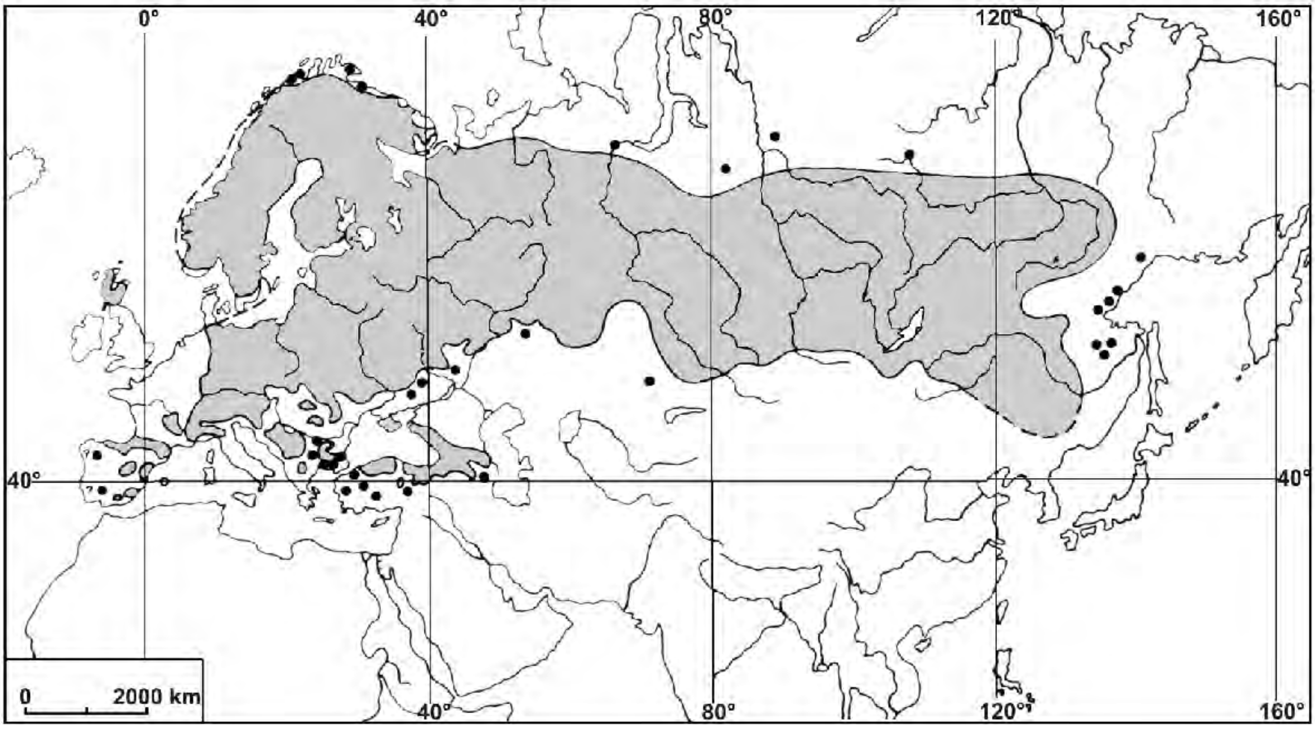


Fig. 62. *Pinus sylvestris* – map of present-day distribution in Eurasia: ● – native isolated occurrence (after Pawłowska 1972 and Jalas & Suominen 1973)

edge of its range (Szafer 1964). According to Iversen (1954) *Pinus sylvestris* in Scandinavia requires a mean July temperature of about 12°C for its development.

Pinus sylvestris is characterised by a high tolerance regarding soil conditions. It grows both, on fertile soils and on extremely poor, boggy soils as well as on dry sands. Due to its wide range of adaptation pine grows also in varied orographic conditions: at various heights and on slopes of different inclinations and exposures (Obmiński 1970). It is a species with typical pioneer features able to expand rapidly in conditions of open and disturbed habitats but not able to withstand competition from other trees that induces more shade. *Pinus* seedlings are particularly light-demanding. A high rate of dispersal is guaranteed by the light, winged seeds (anemochors) as well as by the relatively early age of producing seed, which is about 10–15 years for trees growing in open habitats, and 30–40 years for specimens growing in forest stands (Tylkowski 1993).

Pinus is a species growing above all in coniferous forests, though it is also always present in communities with deciduous trees, particularly with oak (*Querco roboris-Pinetum* and *Serratulo-Pinetum*). In Poland there are two principal coniferous forest associations that occur on slightly moist soils, which have complimentary distributions. The *Leucobryo-Pinetum* association occurs over the greater part of Poland and the *Peucedano-Pinetum* association is widespread mostly in north-western Poland. In dry, acid habitats a different coniferous forest association occurs – *Cladonio-Pinetum*, and on damp, acid habitats *Molinio-Pinetum*, whereas *Vaccinio uliginosi-Pinetum* grows on oligotrophic marshy soils. Other communities of pine forests are of lesser importance in Poland (Matuszkiewicz J.M. 2002). In modern times the widespread presence of *Pinus* in Polish forest communities is mainly a result of forest management with deliberate planting which began almost 200 years ago.

POLLEN PRODUCTION AND DISPERSAL

Pinus flowers plentifully every year. However, under extreme conditions, for example recently along the northern forest limit, its flowering can be set back from a few to several consecutive years (Koski & Tallquist 1978, after Chałupka 1993). In Poland the main pollen season lasts two weeks, generally in May (Uruska et al. 2003). It is estimated that a single inflorescence of *P. sylvestris* can produce as much as 6 million pollen grains (Pohl 1937), and *Pinus* stands may generate a pollen rain amounting to 30–280 thousand pollen grains/cm^2 during a year (Koski 1970). According to Sugita et al. (1999) the productivity coefficient for *Pinus* in comparison with grasses (1) is 5.7. Light and provided with air sacs *Pinus* pollen dispersal is extremely effective, as it is proved by its pollen rain being regularly found in areas far outside its areas of growth (Aario 1940, Johansen 1991, and others). *Pinus* pollen is also a frequent component of the aeroplankton over the surface of the seas and oceans (Harmata & Olech 1991). The capacity of pine pollen for achieving 'long-distance transport' causes difficulties with the interpretation of pollen diagrams and particularly of those pollen zones representing unforested periods. It is also more difficult to estimate a local presence of this taxon based on its participation in pollen assemblages in comparison with other taxa. Huntley and Birks (1983) in their interpretation of isopollen maps assumed pollen values >25% as reflecting an occurrence of small areas of pine in a forested landscape, whilst values >50% were assumed to indicate dominance of pine in local communities. However, it should be emphasized that these values may vary significantly depending on the degree of forest cover as well as on the dimensions of the original basin surface from which a palynological profile has been collected. That is why, in the case of pine, it is essential to obtain data about the occurrence of its macroscopic remains or the presence of stomata, that can be found in palynological slide preparations, indicating unmistakably its local presence (Birks & Birks 2000).

LOCATION OF REFUGIA

It can be assumed that all species of *Pinus* presently occurring in Poland could have survived the period of the last glaciation in refugia situated in the Carpathians and Sudetes and along the northern sides of these ranges. According to Staszkiewicz (1993) the sites of relict populations of the ecotypes *Pinus sylvestris* t. *polonica*, and t. *meridionalis* distributed in the Tatra and Pieniny Mountains provide evidence for a continuous persistence of *Pinus sylvestris* in the Polish Carpathians during the Pleistocene. Rapid expansion of pine during the interstadial periods towards the close of the last glaciation also indicates the presence of *Pinus* refugia along the northern side of the Carpathians and Sudetes.

MIGRATION PATTERN IN POLAND (Fig. 63)

14,000 – 13,500 BP

Low pollen values at single sites do not provide sufficient evidence of *Pinus* expansion into Poland during that time. Those values may relate to long-distance transport of *Pinus* pollen in a treeless landscape during early periods of the Late Glacial.

13,000 – 12,500 BP

Pollen values higher than 40%, which may indicate development of plant communities containing *Pinus* are recorded from scattered sites. *Pinus* presence in Wielkopolska is proved by macrofossils found at the site of Żabinko (Tobolski 1988). However, the very small number of sites does not allow a more thorough interpretation of its participation in plant communities of this period. It may be possible that only around 12,500 BP (Bølling) sparse forests with pine appeared in south and central Poland, whereas most probably communities of this type had not yet developed in the north-west and east of the country. High *Pinus* pollen values at montane sites may indicate spread of communities with *P. mugo* and *P.* ×*rhaetica*.

12,000 BP

The climate cooling during this period (Older Dryas) is reflected by a fall in *Pinus* pollen values at some sites, particularly in west and north Poland, indicating a partial retreat of pine from these areas. However, isopoll lines for 30–40% and >40% values extend across a considerable part of Poland and suggest that the growth of forest communities had not been restricted there. Macrofossils of *Pinus* at the site of Tarnowiec (Jasło-Sanok Depression) are dated to this period (Harmata 1987).

11,500 – 11,000 BP

Isopollen maps illustrate development of pine forests over the whole territory of Poland, with maximum contribution in the younger period. In large areas (Kujawy, the lower Vistula river valley) pollen values exceeding 60% indicate dominance of pine in the forest communities. In the sediments of this period (Allerød) macrofossils of *Pinus* are frequent.

10,500 BP

The Younger Dryas cooling influenced to the highest degree changes in the forest communities in northern and particularly north-western Poland. On Wolin Island the *Pinus* pollen values dropped below 30% which indicates a considerable thinning of tree stands and probably reversion to a vegetation of park-tundra type. Evidence for the local presence of pine in this area is provided by macrofossils (Latałowa 1999b). At that time park-tundra probably dominated the landscape of the whole Pomerania. The contribution of pine declined in the most territory of Poland, including the Bieszczady Mountains and Eastern Carpathian foreland, but except of Pomerania, its role was still important.

10,000 – 9000 BP

At the beginning of the Holocene further expansion of *Pinus* took place, which resulted then in the maximum expansion of pine forest during the Holocene. According to the isopollen maps pine forests, with varying contribution of birch, at that time covered the whole area of Poland.

8500 – 7000 BP

A decline of *Pinus* domination in forest communities began in the Boreal period, mainly due to the expansion of hazel. This first became evident in the Sudetes and Carpathians (including the foreland areas), in the eastern part of the Małopolska Upland and Świętokrzyskie Mountains. During the Atlantic period the *Pinus* decline affected almost all of Poland. The southern regions of Poland and central Wielkopolska are particularly characterised by the considerable and long-lasting participation of hazel in forest communities (compare *Corylus* isopollen maps, this volume). In the following centuries the further decrease of *Pinus* was affected by the development of mesophilous deciduous forests with oak, lime, elm, and ash. This process was most intensive on the fertile soils of the Małopolska area. In the mountains pine was supplanted by spruce.

6500 – 5000 BP

In the younger stage of the Atlantic period further decline of pine followed in the forests across the whole of Poland, but it was particularly intensive in the mountains and the slowest in the lake districts of northern Poland.

4500 – 3500 BP

The beginning of the Subboreal period sees the lowest participation of pine in the forest communities of Poland. Higher amounts appear only along the eastern state boundary where pine spread in the extensive marshy areas (Kulczyński 1939, 1940). In northern Poland, and particularly along the Baltic Sea coast, the *Pinus* decline resulted mainly from Neolithic management of the forest. The pollen diagrams show changes in the structure of forests leading to the development of coppiced woodland, with oak and hazel as the main components. The management techniques applied at that time were unfavourable for pine development (Latałowa 1992). The gradually declining role of pine in the mountains and their foreland areas must have been connected with the beginning of hornbeam and beech expansion.

3000 BP

On the isopollen map from this period the beginning of the reverse process is marked. The amount of pine slightly increases particularly in northern Poland. It is connected with the intensification of settlements on predominantly poor soils; pine expands into the habitats previously deforested and damaged by farming.

2500 – 2000 BP

Isopollen lines divide Poland into a northern part, with significant increase in *Pinus* pollen values and a southern part where this process is much more varied. This period includes the final stage of the Lusatian culture and development of the Pomeranian culture, followed by the expansion of Roman Iron Age cultures. The economy of these cultures was associated with considerable deforestation, which made possible pine expansion, particularly on the poor soils of northern and central Poland, although this process took place also in the southern part of the country (particularly at the beginning of Roman Iron Age – around 2000 BP). On the 2000 BP map a renewed decline of *Pinus* pollen values is marked along the western Baltic coast. It coincides with the beginning of beech expansion in this part of Poland.

1500 BP

At this time a further decline in *Pinus* representation in forest communities is observed almost over the entire country. This was the Migration Period, generating economic collapse in many areas, which resulted in regeneration of forests with deciduous tree species. In central Poland and particularly in Wielkopolska, hornbeam gained a dominant position, and beech spread on the morainic hills along the Baltic Sea coast. In southern Poland, particularly in the mountains, beech and fir expanded. Pine forests remained the dominant type of forest community in Tuchola Forest and in the eastern part of the country.

1000 – 100 BP

Economic developments during the Early Middle Ages initiated a trend of changes in plant communities that has continued to the present day. Deforestation and intensification of agriculture favour pine as a species able to expand into disturbed habitats. For the last 200 years pine has been introduced as the main or the only component of planted forests. At present it is the most frequent element of tree stands in Poland. On the isopollen maps illustrating the youngest period, 500–100 years ago, the Sudetes and Carpathians with their foreland are shown to have a significantly lower representation of pine than previously, and the Bieszczady Mountains display minimum values for this tree.

Isopolls calculated with Cyperaceae included into pollen sum

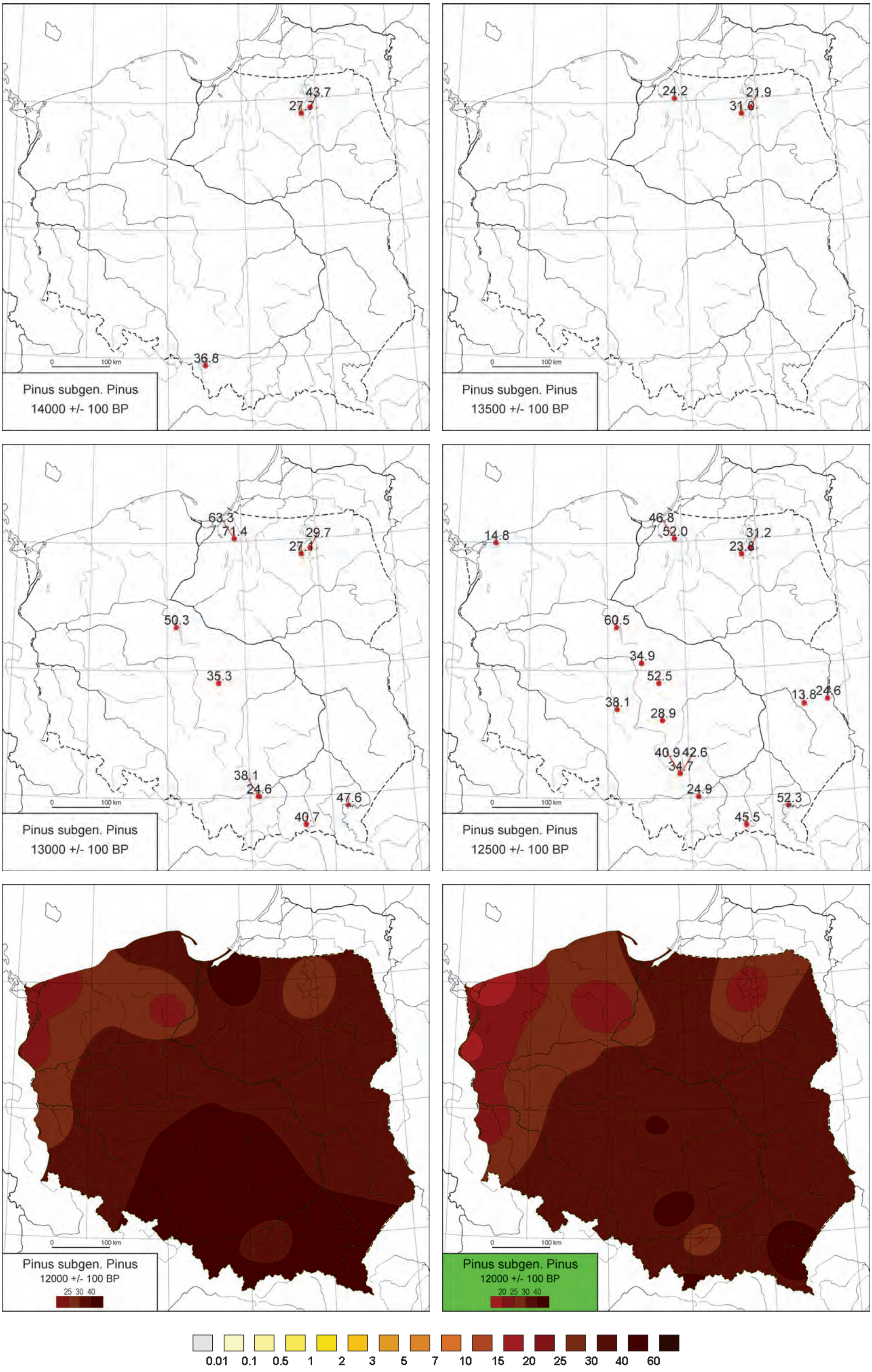
Apart from the main set of maps, several maps showing *Pinus* isopolls calculated with Cyperaceae included into pollen sum are presented on Figure 63. These supplementary maps were selected for those time-horizons which show especially important contribution of Cyperaceae pollen, i.e. for the periods 12,000 – 10,000 BP and 2500–100 BP. They mostly illustrate the methodological problem concerning the importance of the adequate choice of a pollen sum.

The differences between both types of maps (calculated with and without Cyperaceae) are especially striking in the case of the Allerød and the beginning of the Holocene. In both periods due to climate amelioration, *Pinus* expanded on mineral grounds, but in the same time, numerous representatives of Cyperaceae vigorously spread along lake margins and covered different mire types. This strong influence of local pollen on pollen sum gives and effect of a ‘flat’ isopoll picture for the rest of taxa, including *Pinus*. The isopolls calculated with Cyperaceae do not detect one of the most important phenomena in the Late Glacial history of vegetation in Poland, i.e. changes from *Betula* dominated forests in the earlier part of the Allerød to *Pinus* dominated forests during the later part of that period. The new expansion of pine at the beginning of the Holocene (maps 10,000 BP) is also better expressed on the map calculated without Cyperaceae. The comparison of maps for the late Holocene (2500–100 BP) does not present such strong differences, however, the role of pine is better underlined on the maps calculated without Cyperaceae. In contrary to the Late Glacial, Cyperaceae pollen is not the most important constituent of both open-land and local vegetation in the late Holocene.

CONCLUSIONS

Considerable tolerance of a wider range of climatic conditions, as well as its adaptations as a pioneer tree, resulted in a high rate of migration of pine at the close of the last glaciation. Pine belonged to the earliest components of the forest flora and it began to expand from its refugia, situated presumably in mountain valleys within Poland, around 13,000 BP. The Older and Younger Dryas cooling only partly restricted its expansion, particularly in the Pomerania area. Pine reached its maximum abundance in forest communities during the Allerød and in the early Holocene (10,000–9000 BP). Later periods witnessed the decline of *Pinus* as a result of competition with deciduous trees, followed in the late Holocene by the subsequent expansion of pine, because it was particularly well adapted to occupy disturbed habitats. *Pinus* played an important role in regeneration of forests damaged by human management in prehistoric and historic times. Since before 8000 BP the mountainous areas have displayed a separate and distinctive character, in comparison with other regions, expressed by a much lower participation of pine in their forest communities.

Fig. 63. *Pinus* subgen. *Pinus*: dot and isopollen maps for 14,000–100 ^{14}C yr BP. Maps showing *Pinus* isopolls calculated with Cyperaceae included into pollen sum are added for the Late Glacial and late Holocene time horizons and distinguished by green background of map legend


43.7
27.7
36.8
0 100 km
Pinus subgen. Pinus
14000 +/- 100 BP
24.2
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31.0
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Pinus subgen. Pinus
13500 +/- 100 BP
63.3
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35.3
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24.6
47.6
40.7
0 100 km
Pinus subgen. Pinus
13000 +/- 100 BP
46.8
52.0
14.8
31.2
23.8
60.5
34.9
52.5
38.1
28.9
13.8
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40.9
42.6
34.7
24.9
52.3
45.5
0 100 km
Pinus subgen. Pinus
12500 +/- 100 BP
0 100 km
Pinus subgen. Pinus
12000 +/- 100 BP
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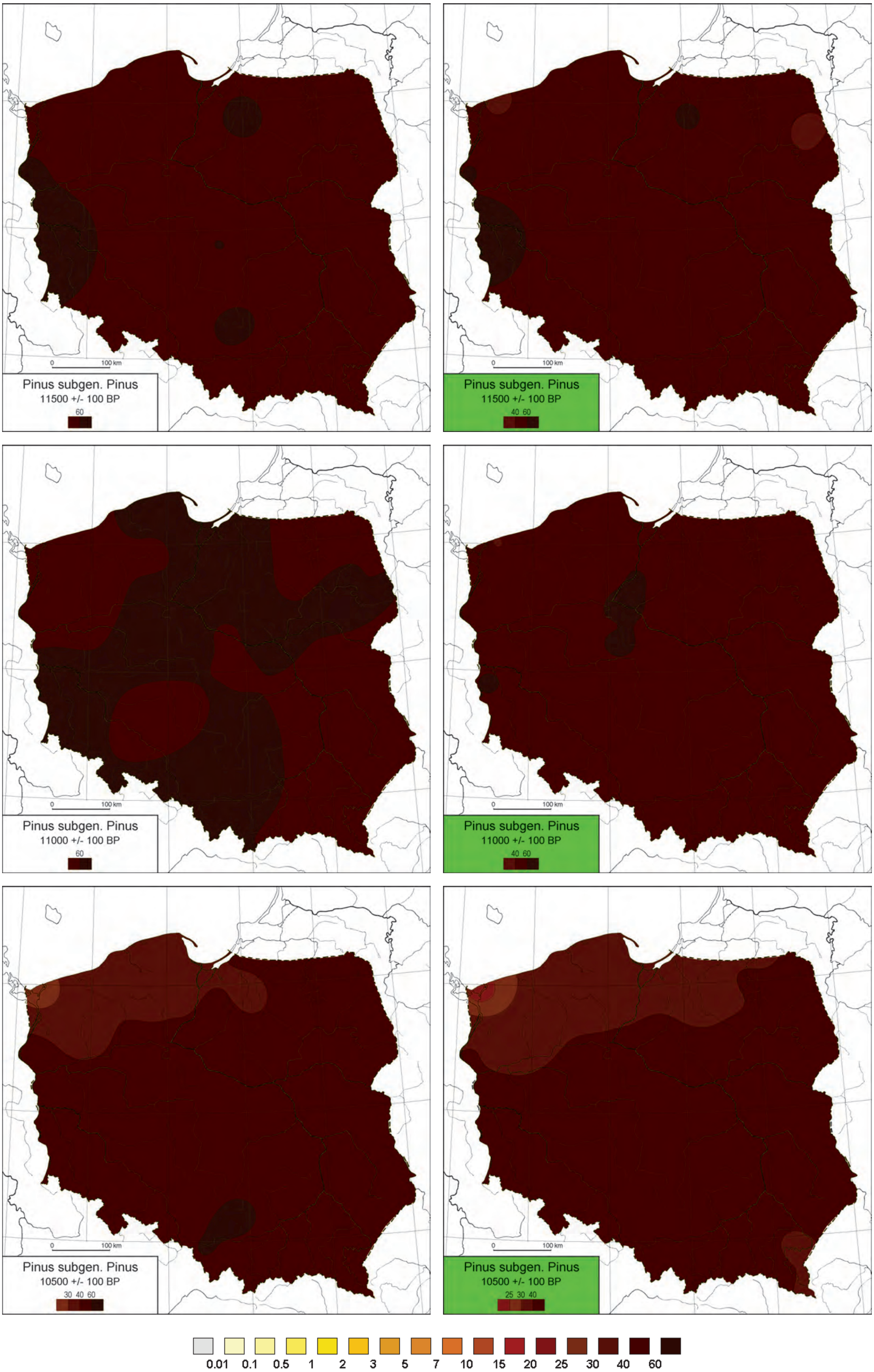
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11000 +/- 100 BP
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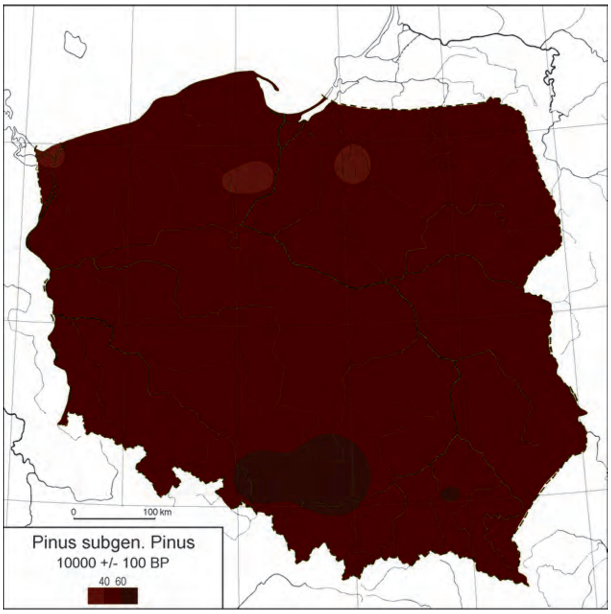
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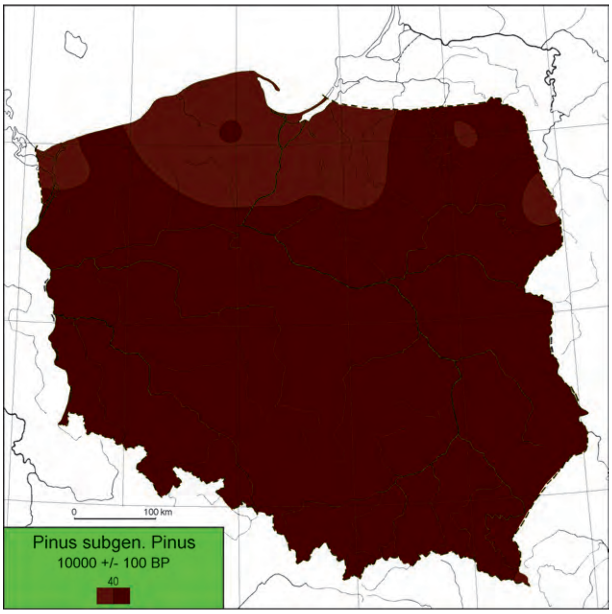
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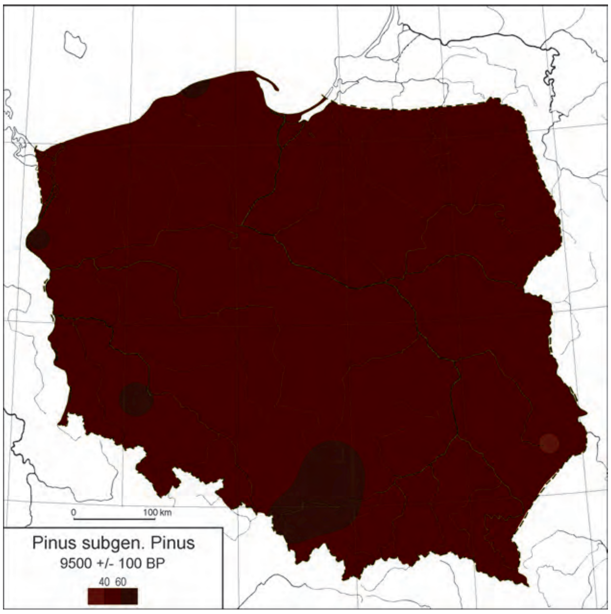
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9500 +/- 100 BP
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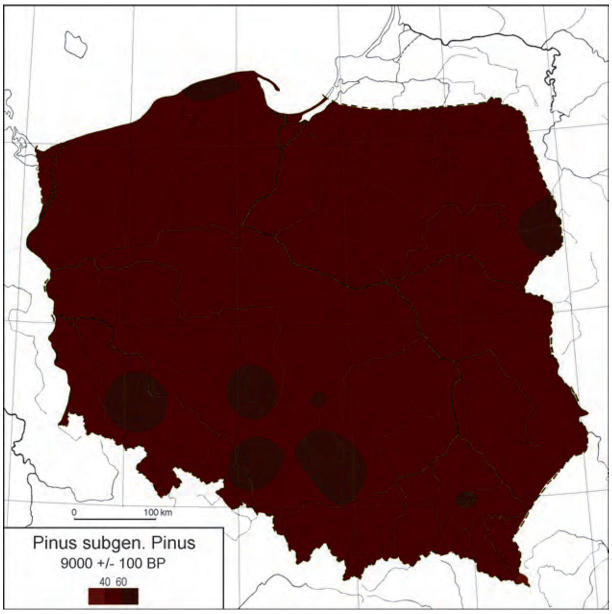
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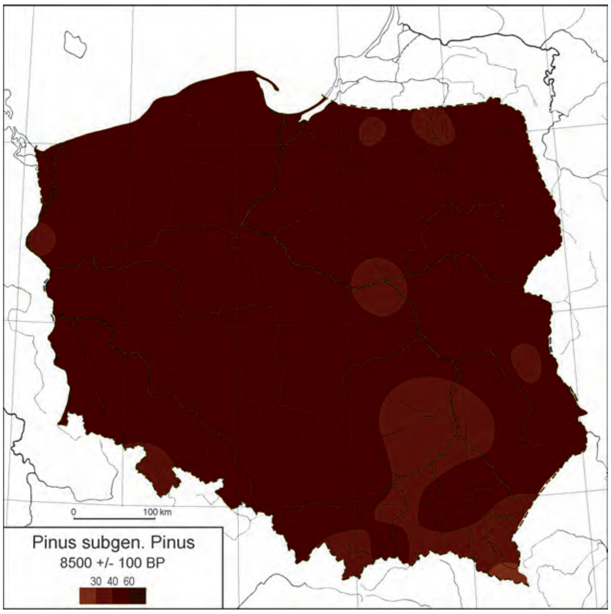
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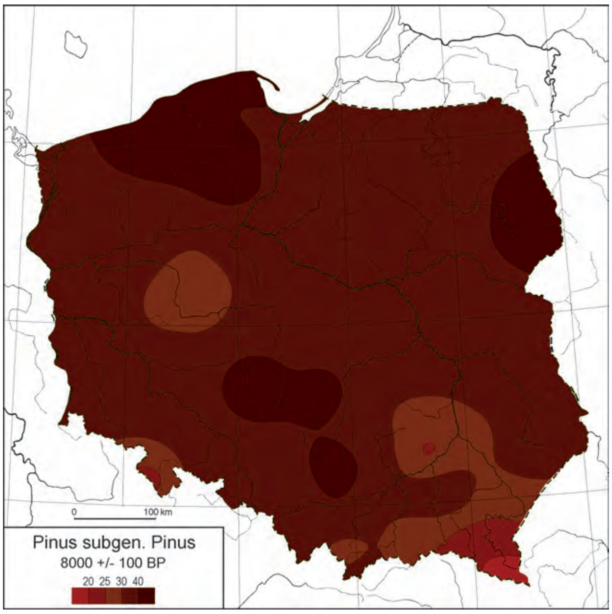
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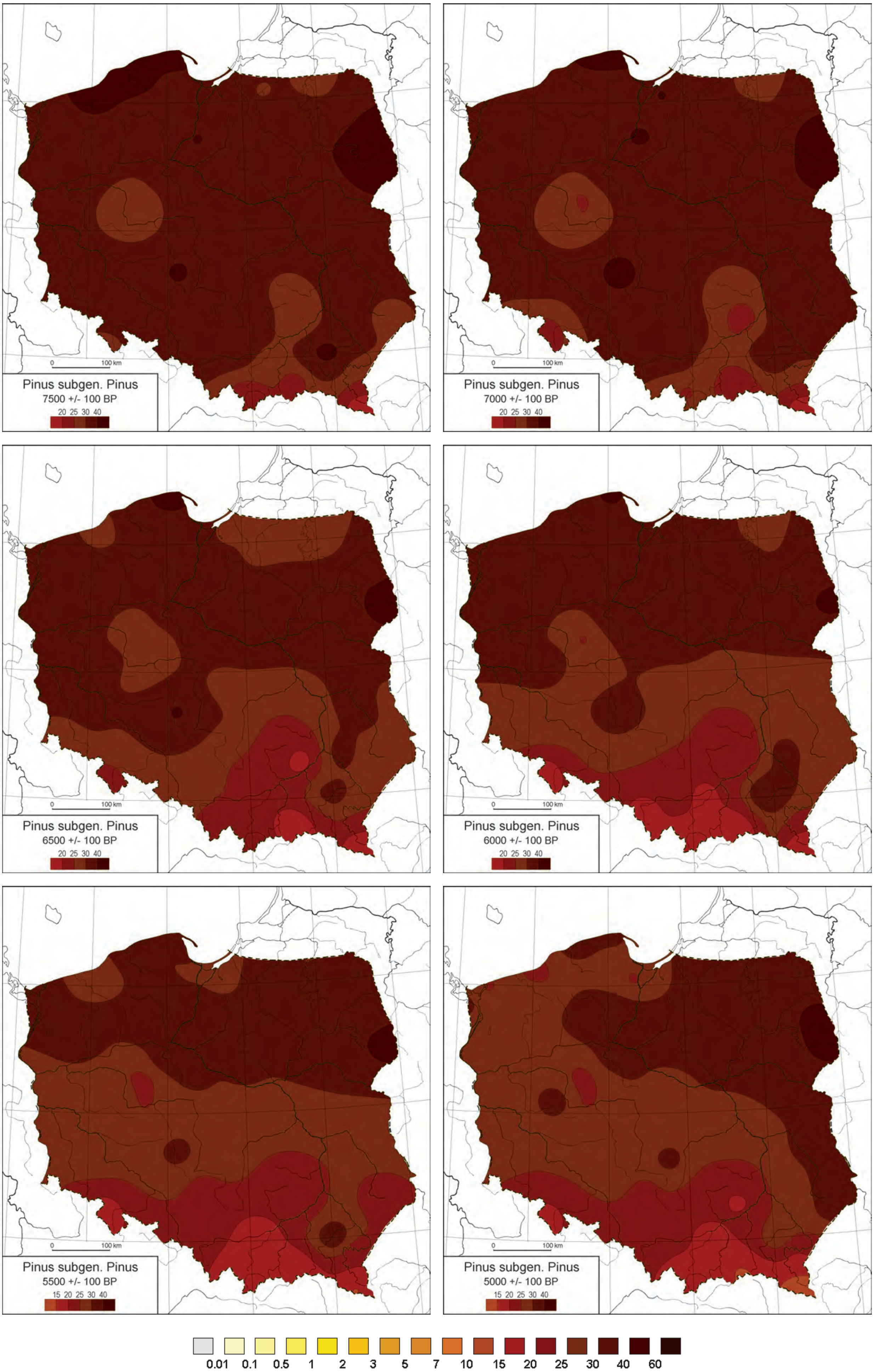
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7500 +/- 100 BP
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Pinus subgen. Pinus
7000 +/- 100 BP
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Pinus subgen. Pinus
6500 +/- 100 BP
20 25 30 40
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Pinus subgen. Pinus
6000 +/- 100 BP
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Pinus subgen. Pinus
5500 +/- 100 BP
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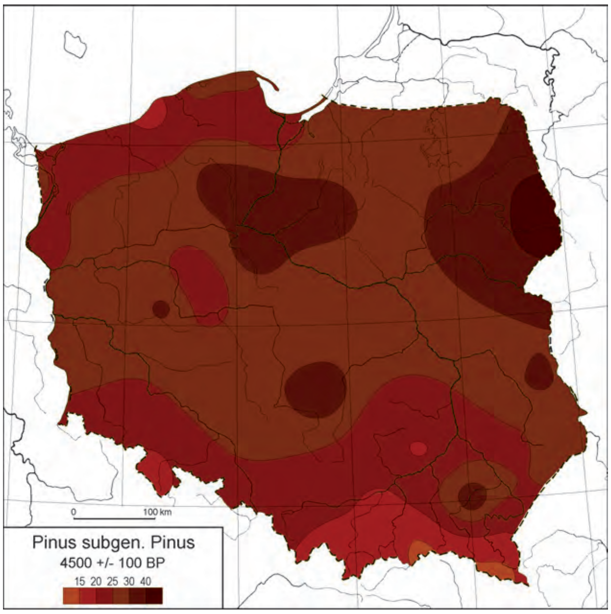

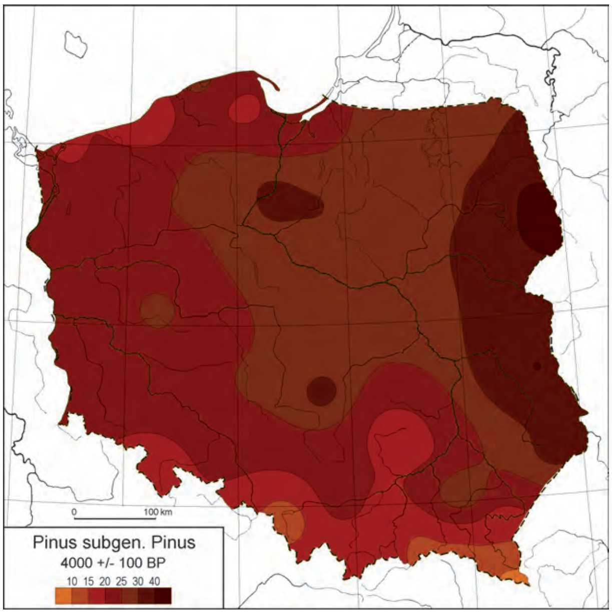

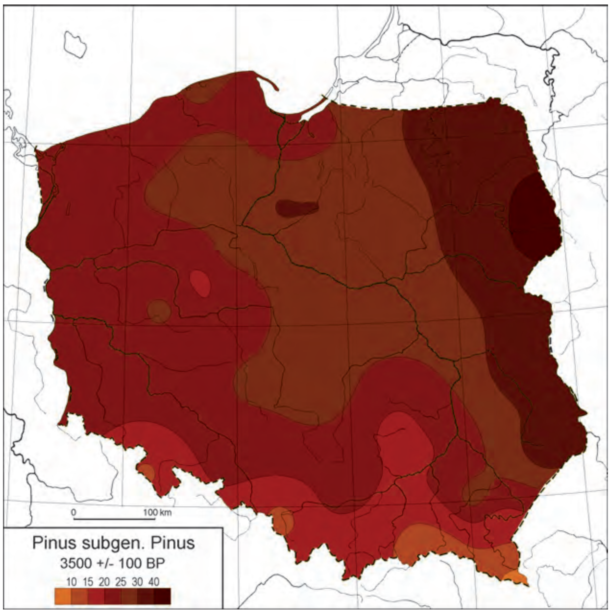

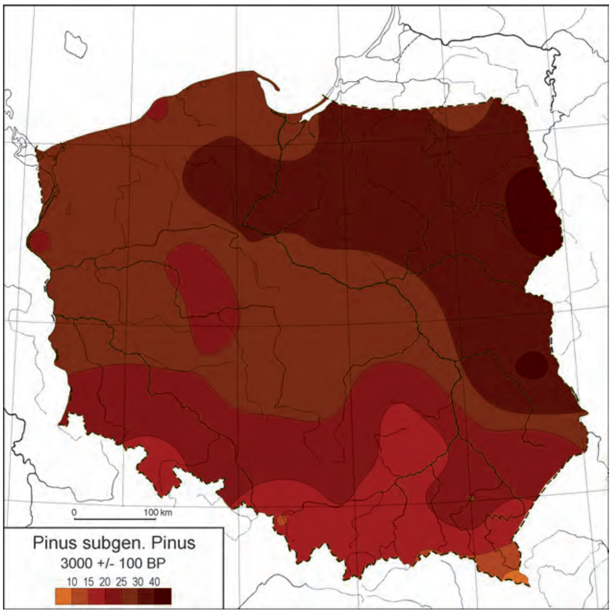

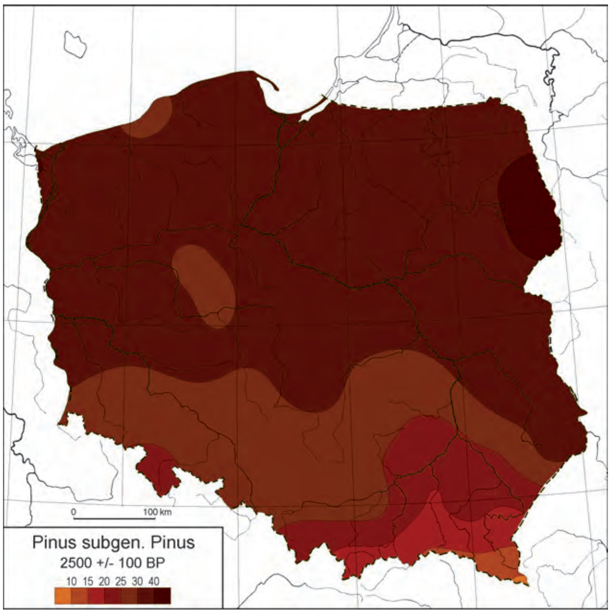

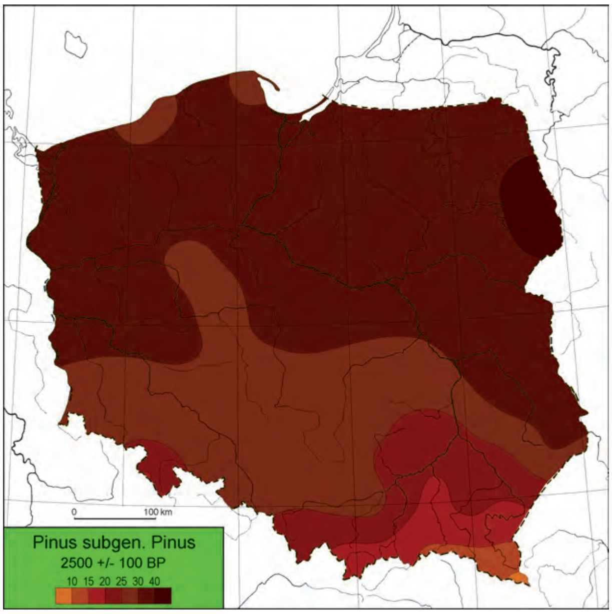

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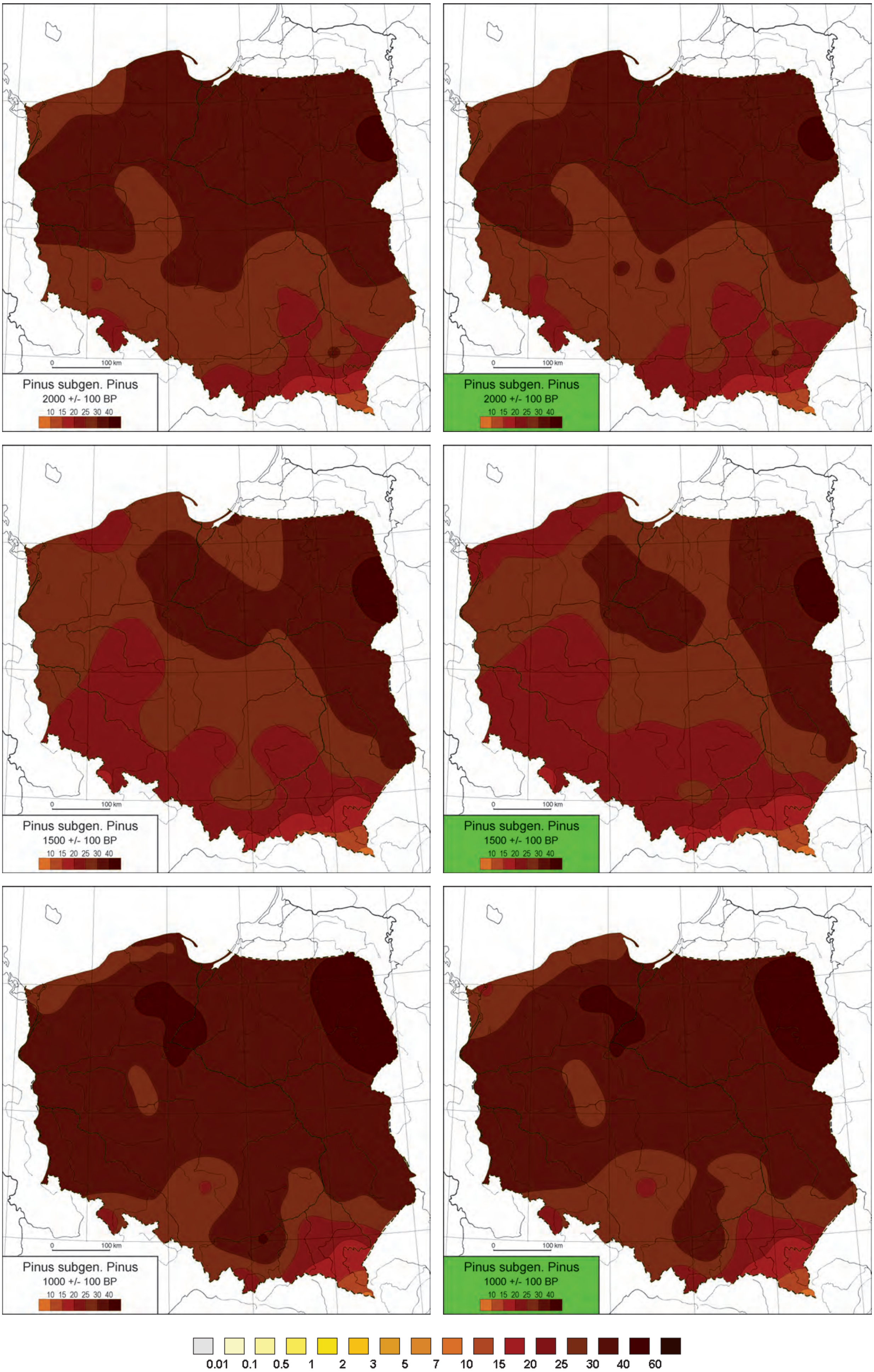
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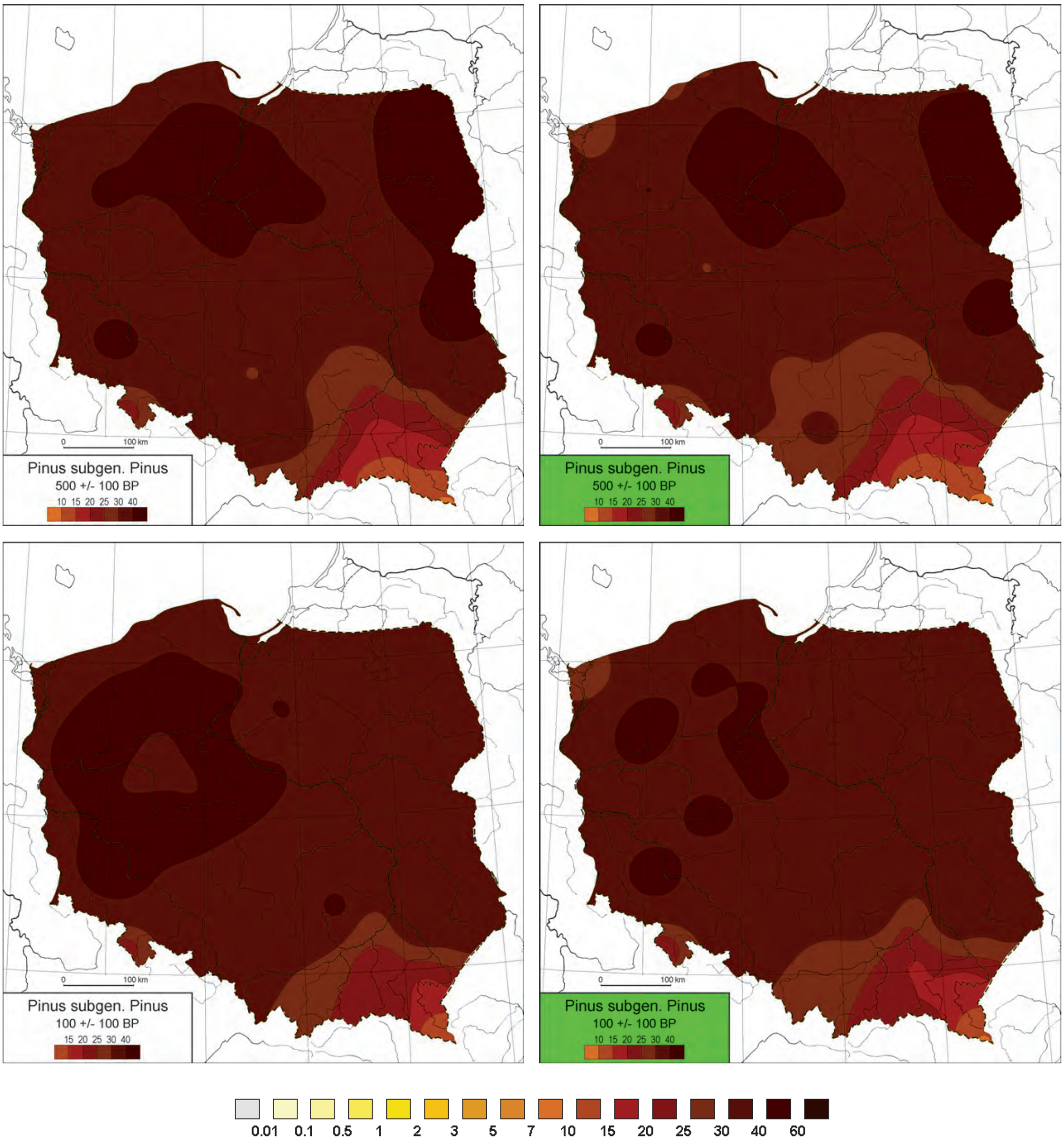
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Populus L. – Poplar and aspen

ANNA FILBRANDT-CZAJA, ZOFIA BALWIERZ, AGNIESZKA M. NORYŚKIEWICZ,
BOŻENA NORYŚKIEWICZ, AND DOROTA NALEPKA

It is estimated that there exist 35 to 40 poplar species (Bugała 1973), but those native to the flora of Europe include three species: *Populus alba* L. (white poplar), *P*. *nigra* L. (black poplar), and *P*. *tremula* L. (aspen), beside a hybrid of black poplar and aspen – *P*. *canescens* (Aiton) Sm. (grey poplar).

PRESENT DISTRIBUTION IN EUROPE

White poplar is native in an area stretching from Spain throughout the Mediterranean and central Europe to Poland; in the south it includes the northern coasts of Africa, Syria, and Iraq as far as the Persian Gulf.

Black poplar is an Euro-Asian species and its natural stands occur from the Pyrenees throughout central, south-eastern and eastern Europe to western Siberia. It reaches its northern limit at latitude 60°N. In the south it extends to the coast of north Africa, Asia Minor and the Caucasus.

Aspen is the most widespread species and occurs throughout Europe from the Iberian Peninsula to the Ural Mountains; in the north of Scandinavia it reaches latitude 70°N, and in the south – north Africa, Asia Minor and the Caucasus.

Grey poplar is found in those regions where its parent species occur. It is frequent in the Balkans and western Europe (Bugała 1973).

PRESENT DISTRIBUTION IN POLAND

Natural stands of white and black poplar are found along river valleys. They are most widespread along the riverbanks of the four most important Polish rivers, the Vistula, the Odra, the Warta and the Bug, and their tributaries. They are rare or absent from the regions of Pomeranian and Mazurian Lake Districts (Zając A. & Zając M. 2001). In Poland black poplar reaches the northern limit of its range (Pawłowska 1959). Grey poplar, together with white and black poplar, is also found in river valleys. Aspen is the most widespread; it extends throughout Poland both in the lowland areas and in the mountains up to 1200 m a.s.l. (Fig. 64).

ECOLOGY

All native species of poplar require a warm temperate climatic conditions and may grow well across the whole of Poland. They are indifferent to continentality of climate. They are light-demanding species growing in sunny places, but are tolerant of seasonal or temporary shade (Zarzycki et al. 2002). *Populus alba* and *P. nigra* have similar habitat requirements. They favour fertile alluvial soils, yet they are also found on much poorer sandy soils (Bugała 1973, Zarzycki et al. 2002). Due to embankment and flow control of most rivers and to the building of dams, the areas of floodplain forest have decreased, which has deprived both species of a lot of habitats where stands formerly grew (Browicz & Gostyńska-Jakuszewska 1970b).

Poplars are dioecious species. Flowers, both male and female, are gathered in pendent catkins. The flowering time of aspen and white poplar is March and of black poplar – the beginning of April, still before the appearance of the leaves. The fruit is a capsule bearing from 4 to 12 minute seeds that ripen in May or at the beginning of June. Poplars are fast-growing trees and bear fruit at the age of 10–15. They flower and bear fruit almost annually, and amply. In comparison with other trees their life is relatively short, the maximum age limit for black poplar is 120–170 years; it is shorter for aspen (60–100 years) but longer for white poplar (200–300 years) (Bugała 1973). The basic method of propagation of poplars growing in Poland is spontaneous seed dissemination (Suszka 1973). They can also propagate in a vegetative way by means of root suckers, especially aspen and grey poplar.

Populus alba and *P. nigra* are species characteristic of the association *Populetum albae* (willow-poplar floodplain forest, Matuszkiewicz J.M. 2002). On drier habitats they occur in forest communities of the alliance *Alno-Padion*. *P. tremula* grows in mixed forests of the *Querco roboris-Pinetum* association and in acidophilous oak woods (Matuszkiewicz J.M. 2002). It is considered a pioneer species in the initial stages of secondary succession,

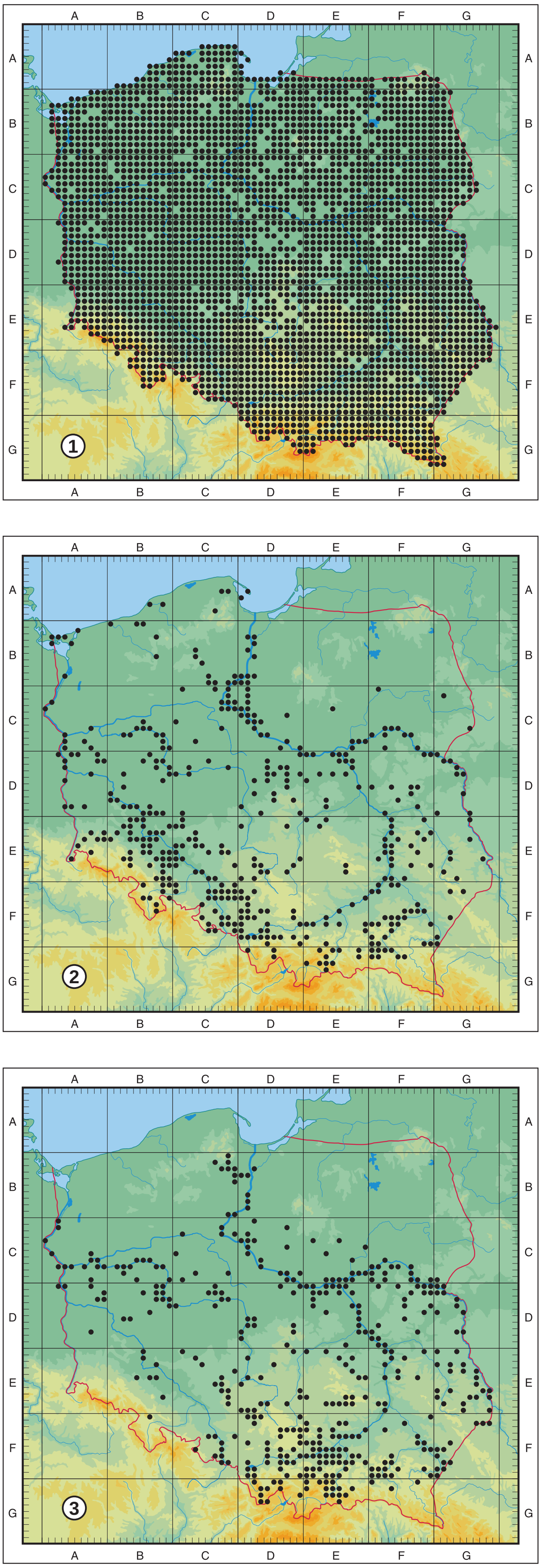


Fig. 64. Present-day distribution of 1 – *Populus tremula* L., 2 – *P. alba* L., and 3 – *P. nigra* L. in Poland (after Zając A. & Zając M. 2001)

such as is found in clearings and fire-burnt forest areas, and sometimes in post-agricultural and post-industrial wastelands (Obmiński 1973).

POLLEN PRODUCTION AND DISPERSAL

Poplars are anemophilous species, producing high amount of pollen. A single male catkin produces about 6 million pollen grains (Dyakowska 1959, Hofman & Michalik 1998). The pollen grains of poplar are thin-walled, which makes them corrode easily in sedimentary deposits under the influence of bacteria and fungi. This may be one of the reasons why in pollen diagrams the representation of poplar is so very low in proportion to its representation in the vegetation. Pollen grains of individual species poorly differ morphologically, yet percentage curves of this genus in pollen diagrams may obviously in some cases represent *Populus tremula* (Środoń 1973). The pollen records relate on the one hand to pollen assemblages representing cold periods, and on the other to the period of anthropogenic destruction of forests when favourable conditions for aspen expansion appeared.

EXPANSION IN EUROPE DURING THE LATE GLACIAL AND HOLOCENE

In view of the edaphic and climatic requirements, as well as the montane distribution of *Populus tremula* the expansion of *Populus* in the Late Glacial and the early Holocene must be related to this species (Huntley & Birks 1983, Delcourt et al. 1984). According to Delcourt et al. (1984) glacial and Late Glacial aspen refugia were probably located in eastern Europe in the vicinity of the northern forest limit. The early Holocene isopollen maps (Huntley & Birks 1983) show *Populus* occurring in the British Isles, the northern European lowlands and southern Scandinavia and probably in the Alps. At this time the taxon expanded towards the north throughout the ice-freed areas of Fennoscandia, and was an important element of plant communities in the Alps. In the mid-Holocene the southern limit of the range of aspen was displaced northwards, perhaps as a consequence of increasing competition with other migrating tree species. Four millennia ago *Populus* reduced its range of distribution, both along its southern and northern boundaries (probably as a result of climatic amelioration). After this time its main range was displaced southwards, along the north-European lowlands. In the last millennia the range of *Populus* has also increased locally in the Alps; both these trends may be related to anthropogenic forest clearance (Huntley & Birks 1983).

MIGRATION PATTERN IN POLAND (Fig. 65)

13,000 – 12,500 BP

At that time a few dispersed sites are found where the presence of *Populus* pollen from 0.1 to 0.3% is recorded.

Due to lower edaphic and climatic requirements of *Populus tremula* it may be suggested that it was this species that was a component of plant communities at these times. It can be assumed that such an early presence of aspen in the Late Glacial documents its survival in Poland during the last glaciation. This has been confirmed by the research carried out by Mamakowa (1968) from the southern Poland. She has shown that in the Paudorf interstadial, corresponding now to the Denekamp oscillation, *Populus* (most probably *P. tremula*) was present in the vegetation of Carpathian forelands. A map for 13,500 BP was not included because there are no *Populus* records from this time.

12,000 BP

Around 12,000 BP the number of *Populus* sites increased. The map shows two areas with slightly increased percentages of *Populus*, in the west and east of central Poland. It may suggest that, irrespective of refugia in Poland, there were two separate directions of *Populus* migration from the east-European lowlands and perhaps from the region of the Alps.

11,500 BP

This period is marked by an increase in poplar percentages (maximum of 1.4%), which suggests a significant role of aspen in Allerød plant communities.

11,000 BP and 10,500 BP

The climatic deterioration of the Younger Dryas may have restricted the flowering of *Populus*, yet in the region of the Mazurian Lakes bud scales of aspen were found from this period (Ralska-Jasiewiczowa 1966).

10,000 – 9500 BP

The onset of the Holocene is again marked by the increase in significance of aspen. It formed a contribution to birch-pine forests, which survived the cooling of the Younger Dryas, and in a short time covered open areas (Ralska-Jasiewiczowa 1999). It is the period of maximum *Populus* occurrence showing pollen values of 0.5% over most of the country. At the estuary of the Odra river on the Baltic Sea and, where the Bug river joins the Vistula river, the percentages of this taxon exceeded 1%. It may suggest the contribution of *Populus nigra* and/or *P. alba* to the pollen assemblages.

9000 – 8500 BP

The consecutive maps record periods of a higher density of forests and register a slight decrease in the presence of *Populus* that might have been caused by its limited access to light. Other species of poplar (*Populus nigra* and *P. alba*) could also have occurred then in moist, periodically flooded areas of river valleys.

8000 – 3000 BP

From 8000 BP percentages of *Populus* decreased significantly. Its pollen over most of the country did not exceed 0.1%, and some islands recording *Populus* values over 0.1% occurred only in the western and central part of Poland, and in the Sandomierz Depression. At 7000 and 6500 BP isopollen maps register a temporary extension of the area with slightly higher *Populus* pollen values. It might have been connected with the appearance of aspen in local clearings caused by Mesolithic man, what is also suggested by some herb indicators (see e.g. *Pteridium*, this volume). During the mid-Holocene (6000–3000 BP) maps depict an insignificant role of *Populus* in the forests. Generally, the 0.1–0.5% pollen values oscillate within the area of central Poland, and appear also in the middle Carpathians and their forelands. On the 3500 BP map they have a range of 0.1–0.5% over the greater part of south Poland, and locally rise in the lower central area of the Carpathians to over 1%.

2500 – 500 BP

At the onset of the Subatlantic period the contribution of *Populus* increases. To some degree this may have been a result of climatic deterioration with rising humidity, which might have provided suitable conditions for the expansion of poplars. However, the main factor contributing to the importance of those trees was increasing anthropogenic activity. Only the 2000 BP map shows a decrease in *Populus* percentage values. It may have resulted from a temporary weakening of settlement processes and increased tree density causing unfavourable conditions for the development of aspen, or it may also result from the time levels selected for this atlas.

100 BP

The modern map illustrates the expansion of *Populus* throughout the country. Percentage values of this taxon come up to 1% or more, in Wielkopolska and in southern Poland. To some degree higher percentage values of this taxon may reflect the introduction and planting of many species and hybrids of poplar.

Conclusions

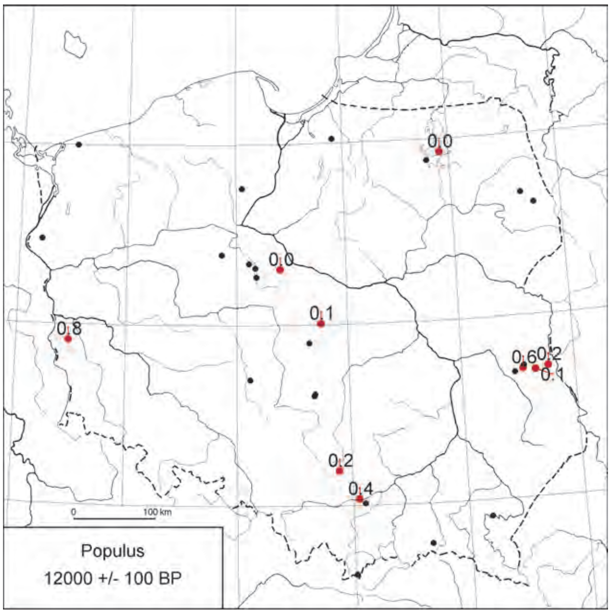
The analysis of isopollen maps shows that *Populus* has continuously been present in Poland from the Late Glacial onwards. However, the interpretation problems of these maps are associated with poor representation of *Populus* in pollen assemblages, intensified by the susceptibility of poplar pollen grains to corrosion processes. The presence of *Populus tremula* in the Late Glacial in Poland is confirmed by the occurrence of its macrofossils. The maximum expansion of *Populus* (*tremula*?) took place at the onset of the Holocene.

Fig. 65. *Populus*: dot and isopollen maps for 13,000–100 ^{14}C yr BP


0.2
0.4
0.3
0
100 km
Populus
13000 +/- 100 BP

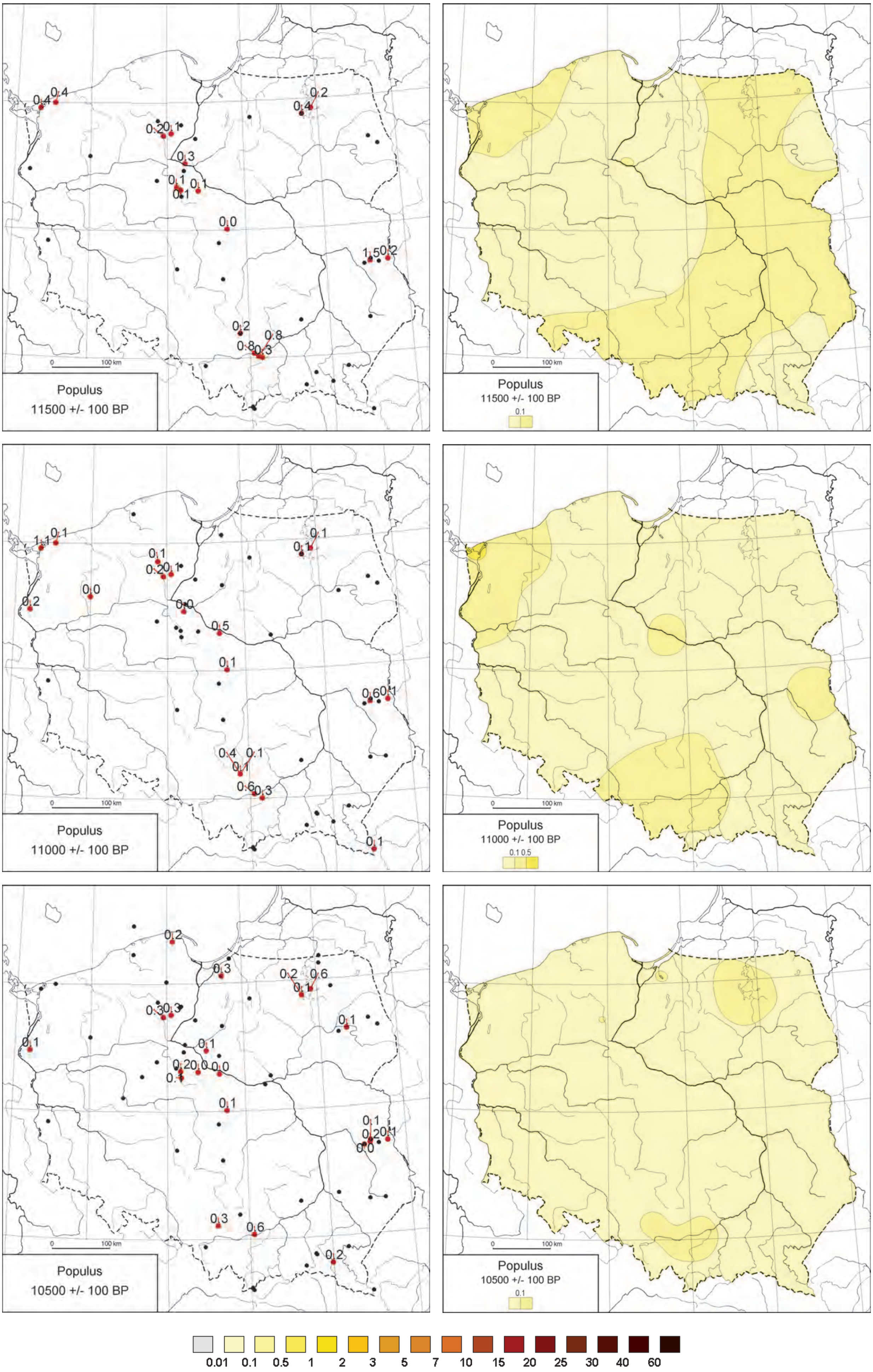

0.1
0.2
0.3
0.1
0.2
0.3
0
100 km
Populus
12500 +/- 100 BP


0
100 km
Populus
12500 +/- 100 BP
0.01 0.1


0.0
0.0
0.8
0.1
0.6
0.2
0.1
0.2
0.4
0
100 km
Populus
12000 +/- 100 BP


0
100 km
Populus
12000 +/- 100 BP
0.01 0.1 0.5


0.01
0.1
0.5
1
2
3
5
7
10
15
20
25
30
40
60


0.4
0.4
0.2
0.4
0.2
0.1
0.3
0.1
0.1
0.1
0.0
1.5
0.2
0.2
0.8
0.8
0.3
0
100 km
Populus
11500 +/- 100 BP
0
100 km
Populus
11500 +/- 100 BP
0.1
1.1
0.1
0.1
0.1
0.1
0.2
0.1
0.2
0.0
0.0
0.5
0.1
0.6
0.1
0.4
0.1
0.1
0.6
0.3
0.1
0
100 km
Populus
11000 +/- 100 BP
0
100 km
Populus
11000 +/- 100 BP
0.1
0.5
0.2
0.3
0.2
0.6
0.1
0.3
0.3
0.1
0.1
0.1
0.2
0.0
0.0
0.1
0.1
0.2
0.1
0.0
0.3
0.6
0.2
0
100 km
Populus
10500 +/- 100 BP
0
100 km
Populus
10500 +/- 100 BP
0.1
0.01
0.1
0.5
1
2
3
5
7
10
15
20
25
30
40
60


0
100 km
Populus
10000 +/- 100 BP
0.1 0.5 1


0
100 km
Populus
9500 +/- 100 BP
0.1 0.5 1


0
100 km
Populus
9000 +/- 100 BP
0.1 0.5


0
100 km
Populus
8500 +/- 100 BP
0.1 0.5


0
100 km
Populus
8000 +/- 100 BP
0.1


0
100 km
Populus
7500 +/- 100 BP
0.1


0.01
0.1
0.5
1
2
3
5
7
10
15
20
25
30
40
60


0
100 km
Populus
7000 +/- 100 BP
0.1


0
100 km
Populus
6500 +/- 100 BP
0.1


0
100 km
Populus
6000 +/- 100 BP
0.1


0
100 km
Populus
5500 +/- 100 BP
0.1


0
100 km
Populus
5000 +/- 100 BP
0.1 0.5

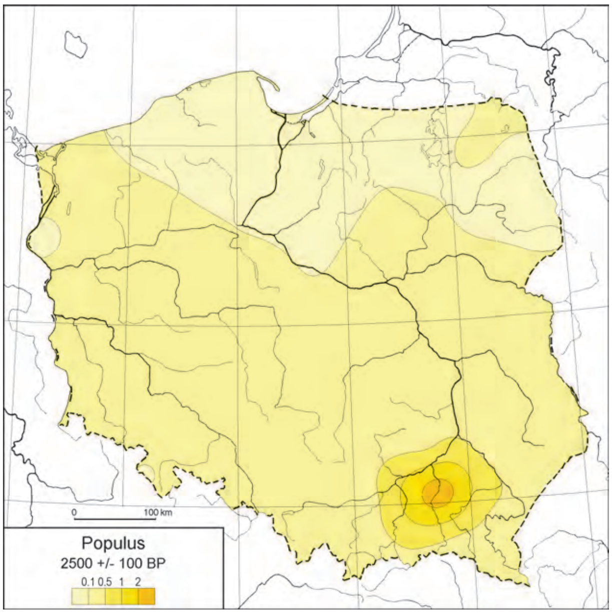

0
100 km
Populus
4500 +/- 100 BP
0.1


0.01
0.1
0.5
1
2
3
5
7
10
15
20
25
30
40
60


0
100 km
Populus
4000 +/- 100 BP
0.1 0.5


0
100 km
Populus
3500 +/- 100 BP
0.1 0.5 1

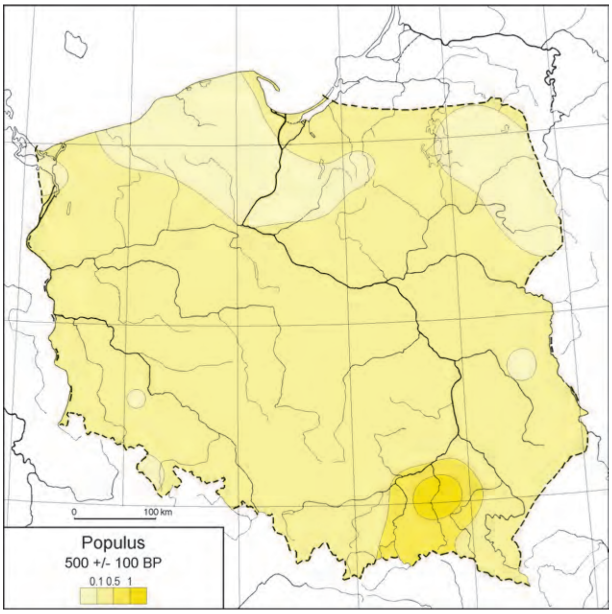

0
100 km
Populus
3000 +/- 100 BP
0.1 0.5


0
100 km
Populus
2500 +/- 100 BP
0.1 0.5 1 2


0
100 km
Populus
2000 +/- 100 BP
0.1


0
100 km
Populus
1500 +/- 100 BP
0.1 0.5


0.01
0.1
0.5
1
2
3
5
7
10
15
20
25
30
40
60



0.01 0.1 0.5 1 2 3 5 7 10 15 20 25 30 40 60

Quercus L. – **Oak**

Krystyna Milecka, Mirosława Kupryjanowicz, Mirosław Makohonienko,
Iwona Okuniewska-Nowaczyk, and Dorota Nalepka

Present distribution in Europe

Three native species of oak occur in central Europe (Tomanek 1994, Jalas & Suominen 1976, 1988b). The range of *Quercus robur* L. (pedunculate oak) comprises the greater part of Europe including almost the whole of western Europe from the northern part of the Iberian Peninsula, the Apennine Peninsula, part of the Balkan Peninsula up to southern Norway and Sweden, the Crimea and the Caucasus, and to the east includes the western part of the Urals. *Quercus petraea* (Matt.) Liebl. (sessile oak) occupies a smaller range from northern Spain, France and northern Italy, the northern part of the Balkan Peninsula excluding the lowland areas on either sides of the Danube up to southern Norway and Sweden. The eastern limit of its range runs along the line Kaliningrad – Białystok – Kowle down to the Black Sea (Tomanek 1994). *Quercus pubescens* Willd. (pubescent oak) occurs mainly in southern Europe but its range extends northwards to most of France, southern Germany and eastwards to the Czech Republic, Slovakia and Romania, but to the south of the Carpathian Mountains.

Among alien species the most commonly met in central Europe are species coming from North America, such as *Quercus rubra* L., *Q. coccinea* Muenchh., and *Q. palustris* Muenchh., as well as *Q. cerris* L., native in the Mediterranean region.

Present distribution in Poland

All three central-European species of oak occur in Poland (Fig. 66). *Quercus robur* is a transgressive species in Poland but is absent from the higher altitudes in the mountains, i.e. above 600 m a.s.l. *Quercus petraea* is also present almost throughout the country except for the north-eastern extremes and the mountain areas (Bugała 1991). *Quercus pubescens* occurs in Poland only at one, isolated site at Bielinek upon the Odra river.

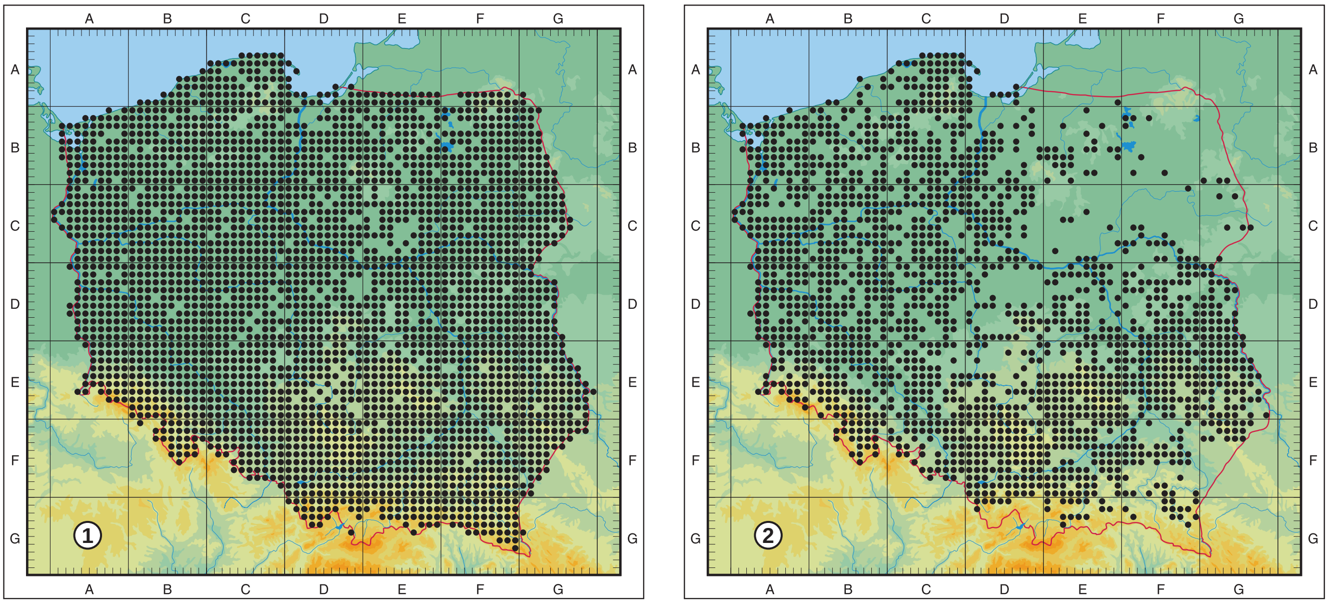


Fig. 66. Present-day distribution of 1 – *Quercus robur* L. and 2 – *Q. petraea* (Matt.) Liebl. in Poland (after Zając A. & Zając M. 2001)

ECOLOGY

Quercus robur requires slightly moist soils rich in organic and mineral nutrients. It grows on loams, calcareous loam and sandy loam soils. Due to its considerable tolerance of soil moisture, and even of early spring floods occurring prior to the development of leaves, it can grow on alluvial river terraces. It occurs equally in areas subject to continental or to oceanic climatic influences. It tolerates low winter temperatures; however, it is sensitive to late spring frosts. The minimum length of the growing season, determining its occurrence, is 130–140 days. In its early stages of life it is shade tolerant but at an older age it becomes light-demanding, and requires full sunlight particularly from above. It starts fruiting at the age of 40–50 years but when it grows in dense forest it bears fruit at an age of about 80 years. Years of heavy acorn production occur every 4–6 years with a tendency to be less frequent towards the limits of its geographical range. It flowers at the end of April or in May, together with the development of the leaves. Its fruits ripen in September or October and their falling is relatively quick. Acorns provide food for many species of birds and mammals.

The capacity for germination immediately after being shed is about 70%. The rate of growth, at first slow, increases about the age of 10 and is most intensive until the tree is 60–70 years old. Growth largely stops after 120 years. An oak-tree can live for about 400–500 years and in some cases even up to 1000 years. Between the age of 20–60 it displays great potential to form side shoots from buds on stumps. A tree exposed to the influence of light after previous shading of its trunk, can forms sucker, which may cause die-back at the top of the tree. *Q. robur* can tolerate urban conditions quite successfully. It often forms hybrids with *Q. petraea*.

Quercus petraea displays similar biological features however, it is less demanding than *Q. robur* in respect of soils (Bugała 1991). It tolerates lower soil fertility and moisture and grows freely even on sandy soils, for example on outwash sands. However, it requires higher temperatures. This last feature probably results in its more limited geographic range as well as in a two-week delay in the opening of its leaves and in flowering, in comparison with the previous species.

Acidophilous well-lit oak forests, and oak-hornbeam forests of the *Carpinion betuli* alliance are the main plant communities, in which oaks play the most important role. *Q. robur* and *Q. petraea* may also occur in mixed coniferous forests, as well as in beechwoods and submontane slope forests of the *Tilio-Acerion* alliance. *Q. robur* occurs also in some types of riverine forest and alder woodland, in subboreal spruce forests and in forest-edge communities of the *Prunetalia spinosae* order (Matuszkiewicz W. 2001).

POLLEN PRODUCTION AND DISPERSAL

Oak is a monoecious, wind-pollinated tree. It does not produce as much pollen as a pine-tree. However, according to Pohl (1937, after Faegri & Iversen 1989), one well-developed crown of oak can yield more than 100 million pollen grains. The amount of pollen production and distance of dispersal depend on whether a tree is growing in dense forest or as an isolated tree, growing in an open area. It is commonly accepted that its relative representation in percentage pollen diagrams reflects more or less its actual proportional frequency in surrounding forest communities (Dyakowska 1959, Andersen 1970, Faegri & Iversen 1989). According to Huntley and Birks (1983) *Quercus* pollen values of >2% in pollen assemblages indicate its local presence, whereas values exceeding 10% suggest that it is playing a considerable role within forest communities.

EXPANSION IN EUROPE DURING THE LATE GLACIAL AND HOLOCENE

The results of both palaeobotanical (Bennett et al. 1991) and genetic research (Taberlet et al. 1998, Hewitt 1999, Mátyás & Sperisen 2001) indicate the existence of at least three or four Vistulian refugia for *Quercus* in Europe. These were the Iberian Peninsula, Italy, the Balkans and, very likely, the Caucasus. The existence of both eastern and western refugia is supported not only by the similarly fast spread of oak northwards in the eastern and western parts of Europe, as reflected on the isopollen maps (Huntley & Birks 1983) but, more recently, also by genetic evidence.

Migration of *Quercus* from its refugia started at or shortly before about 13,000 BP. There have been speculations concerning a possible *Quercus* refugium in western Europe (Belgium), based on finds of oak charcoal, apparently dated to 13,000 BP (Otte 1994, Stewart & Lister 2001). It is possible that oaks from the Balkan and maybe Iberian refugia were those contributing mostly to the colonisation of central Europe. However, recent genetic research points also to the oak expansion from an Italian refugium across the Alps as being of considerable importance (Ferris et al. 1998, Mátyás & Sperisen 2001).

MIGRATION PATTERN IN POLAND (Fig. 67)

12,000 – 10,500 BP

The first oak pollen grains appear at a few sites from various parts of Poland in sediments dated to about 12,000 BP. Their amount never exceeds 0.5% and is usually 0.1%. This is commonly interpreted by palynologists studying those particular sites as the result of redeposition, long-distance transport or contamination of sediment during core collection, thus not reflecting the actual presence of oak in the plant communities of this period.

Oaks most likely did not appear in Poland before the end of the Vistulian, as has been suggested by Huntley (1990a) on the 12,000 and 11,000 BP palaeovegetation maps for Europe. The dot maps for the 11,500–10,500 BP time horizons show on Polish territories scattered sites containing *Quercus* pollen with generally very low pollen percentage values. It can be assumed that this material has been redeposited. The site at Czajków in the Nida Basin, south Poland (Szczepanek 1971a), is an exception. From 11,500 BP on, *Quercus* pollen values are higher there than those at other Polish sites (1% or more), and this tendency has been stable throughout the Holocene. The status of this record must remain uncertain.

10,000 BP

The isopollen map for the transition from the Late Glacial to the Holocene illustrates a division of the area of Poland into two parts: the north, where oak pollen values do not exceed 0.1% and the south with slightly higher values up to 0.5%. It is very likely that this pattern records mainly pollen from long-distance transport, and the higher values in the south of the country may suggest some approach of the advancing oak migration front to southern Poland, thus indicating the direction of that migration. An island of higher *Quercus* pollen values in the Łódź Upland reflects a single maximum of oak pollen (2.4%) at Aleksandrów, resulting, most likely, from some contamination from younger sediments pulled down from the upper part of the profile during boring process.

9500 BP

By 9500 BP the amount of *Quercus* pollen exceeds 0.1% throughout Poland. The find of wood of ‘black oak’ (large oak trunks buried in alluvial gravels) at Lublinek near Łódź, radiocarbon-dated to 9200±70 BP and 9120±50 BP (Goslar & Pazdur 1985), provides firmer evidence for the earliest presence of oak in Poland during the Holocene. In view of the comments above, it may be noted that the increased oak pollen values at Aleksandrów, very close to Lublinek, have disappeared by then. However, in the light of this macrofossil evidence, oak pollen values at Czajków of >1% might actually reflect its local presence there at that time. This may have been promoted by favourable edaphic conditions for oak at that site (Szczepanek, oral communication).

Regarding distribution of oak pollen values on the isopollen maps for the time intervals close to the above date (i.e. 9500–9000 BP), it should be stated that even relatively small values of oak pollen (0.1–1%) do not exclude a local occurrence of this tree.

9000–8000 BP

By 9000 BP three routes of *Quercus* immigration can be recognised in Poland: the north-western one, running along the Baltic Coastal Zone and expressed by higher amounts of oak pollen in the vicinity of Wolin Island (from a west-European refugium?), the southern one, passing through the Moravian Gate towards the Silesian Upland, and the south-eastern route extending as a wide belt from the Wołyń Upland across Roztocze and the Lublin Upland as far as the Świętokrzyskie Mountains and the Kielce-Sandomierz Upland. The second find of the ‘black oak’ at Smolice in the Oświęcim Depression dated to 8400±100 BP (Krąpiec 1992) may support the second route of migration probably through the Moravian Gate.

Between 9000 and 8000 BP oak, migrating from these three directions, very quickly increased its representation in the forests throughout Poland. On the isopollen maps this is shown by about a threefold rise in its pollen values in almost all areas of the country. This expansion must have been particularly rapid in Wielkopolska, where during this millennium the amounts of oak pollen increased ten times. From one direction it was the result of oak migration from the south and east, but at the same time a new migration route from the west appeared. On the 8500 BP map a rise in *Quercus* values is recorded in the western part of the Pomeranian Lake District. This may be regarded as an outpost of its coming advance. The last areas to be colonised by oak were the Białystok Upland with the Biebrza and Noteć river valleys, and the Bieszczady Mountains. Since then and up until modern times, the importance of oak in these areas has been less than in other regions of the country. In the Białystok Upland it has resulted from edaphic conditions. The poor, sandy soils dominating there (Kozłowski 1994) did not meet the requirements of oak. The more severe, continental climate of this part of Poland may have been an additional factor limiting oak expansion.

7500–5500 BP

By 7500 BP the western oak migration route developed widely, and a further north-eastern route appeared, which is illustrated on the isopollen map by the area of relatively high values of *Quercus* pollen (5–7%) in the Mazurian Lake District. In the southern part of Belarus, oak appeared at about 8690±240 BP (Zernitskaya 1997), and it reached southern Finland by 8200±150 BP (Sarmaja-Korjonen 2002). This indicates the relatively rapid northwards migration of this taxon in Eastern Europe and supports the opinion that it arrived in the Mazurian region by 7500 BP from a north-eastern direction. The increase and consolidation of oak forests, continued slowly across almost the whole of Poland from 7500 to 5500 BP which is well recorded on the isopollen maps for this period. This process was slowest in the Carpathians and in the area of the Białystok Upland.

5000–4000 BP

By 5000 BP oak spread widely and abundantly into western Poland and the Vistula delta, as is clear from the 4500 BP map. Evidence for this is well provided by an increase in *Quercus* pollen values up to 15%. 500 years later this taxon had spread across the major part of Poland except for the marginal areas of the north-eastern region and the mountains. On the 4500 and 4000 BP maps local islands of still higher *Quercus* pollen values (15–20%) appeared in central Poland, the central Wielkopolska area and in the north-west. This was the time of the maximum Holocene oak distribution in the forests of Poland. It coincided with the final phase of maximum development of the Neolithic cultures. It seems to be undeniable that humans considerably facilitated the expansion of oak at that time, through the destruction of mixed-species Atlantic forests, supporting more shade-tolerant trees. As a consequence of human activities these were replaced by open well-lit forests with free-standing oak trees flowering abundantly, and with a great amount of hazel scrub (see *Corylus*, this volume). It was probably an anthropogenic, but not quite stable woodland community – an intermediate phase of forest development between the Atlantic forests and the invasion of late-migrating trees, particularly *Carpinus*, and also *Fagus* and *Abies*.

3500 – 1500 BP

The 3500 BP map shows the very high (10–15%) oak pollen values still persisting in north-western Poland, and the lowest percentages occurring in the mountains, particularly in the Bieszczady Mountains. At 3000 BP, synchronously with the development of the Lusatian culture, the north-western centre with high *Quercus* pollen values became fragmented into three local islands – the Wielkopolska, a region along the Odra estuary, and central Baltic Coastal Zone. The remaining areas showed values of 7–10% of oak pollen, except for the still lower values (3–7%) in the mountainous areas. The 2500 BP map corresponding with the decline of the Lusatian culture shows the lowest frequencies of oak pollen, the area of 7–10% values being divided into isolated regions. The largest one in north-western Poland reaches eastwards as far as the junction of the Vistula with the Bug river. The 2000 BP map, corresponding with the onset of the Roman Period, reveals once again increased oak pollen values across nearly whole country, with the higher percentages (7–10%) giving a pattern very similar to the map for 3000 BP. At 1500 BP the decrease in *Quercus* pollen values in the southern mountainous, in marshy regions of north-eastern Poland and an increase in Wielkopolska become more apparent.

1000 – 100 BP

On the *Quercus* isopollen maps for the most recent time levels, there are no clear records showing the influence of human settlements on the distribution of oak. On the 1000 BP map, the region of Wielkopolska, which during Early Medieval times was the central area from which the Polish State developed, displays the highest oak representation in the country. This area forms part of a belt of these high (>7%) pollen values which stretches from the north-west to the east as far as Polesie Lubelskie.

The isopollen maps for 500 and 100 BP suggest a gradual decline of oak throughout Poland. A particularly rapid decline occurred in north-eastern Poland and in the area along the lower Vistula valley. On the 100 BP map the values of oak pollen are reasonably high only in the area of the Nida Basin.

CONCLUSIONS

The *Quercus* pollen found in Late Glacial deposits derives either from long-distance transport or from reworked deposits. The approach of migrating oak populations is marked by a small increase of their pollen values at the onset of the Holocene (10,000 BP). The oldest migration routes approaching from the south, the south-east and the north-west appear on the 9000 BP map. Two younger routes from the west and the north-east become clearly discernible at 8500 and 7500 BP respectively.

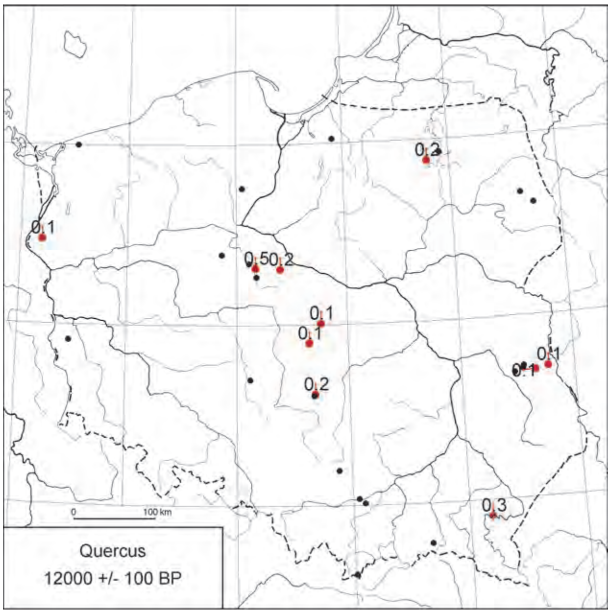
All the younger isopollen maps indicate two, constantly observed trends in the distribution of oak: 1. it was always only of minor importance along the eastern margins of the country, particularly in the north-east, as well as in the mountains, especially the Bieszczady Mountains, 2. it was most abundant in the north-western part of the country, particularly in the Wielkopolska area, throughout the whole Holocene.

The maximum Holocene distribution of oak occurred at 4500–4000 BP, at the time following the maximum development of Neolithic cultures. Oaks formed then, together with hazel, open and well-lit shrubby forests. Its distribution at this time was connected with the destruction of the more deeply shaded mixed Atlantic forests by Neolithic people. Since 3500 BP the importance of oak has displayed a gradual but permanent decline. At the times of the spread, domination and decline of the Lusatian culture, the abundance of oaks diminished gradually. It formed then, together with hornbeam, a new type of forest, the oak-hornbeam forests, one of the most important forest communities in Poland up to recent times.

Comparisons of the isopollen map for *Quercus* relating to the present time (100 years BP) with soil and climatic maps (Kozłowski 1994) indicates that soil conditions were not the main factor determining the distribution pattern of oak, whereas climatic factors may be decisive. Low values of oak pollen are significantly correlated with areas having the most severe climate and with the longest period of snow cover in the country. It is also very likely that, in the past, these climatic factors, particularly applicable to the eastern and mountainous areas, have restricted the distribution of oak in Poland throughout the Holocene.

→

Fig. 67. *Quercus*: dot and isopollen maps for 12,000–100 ^{14}C yr BP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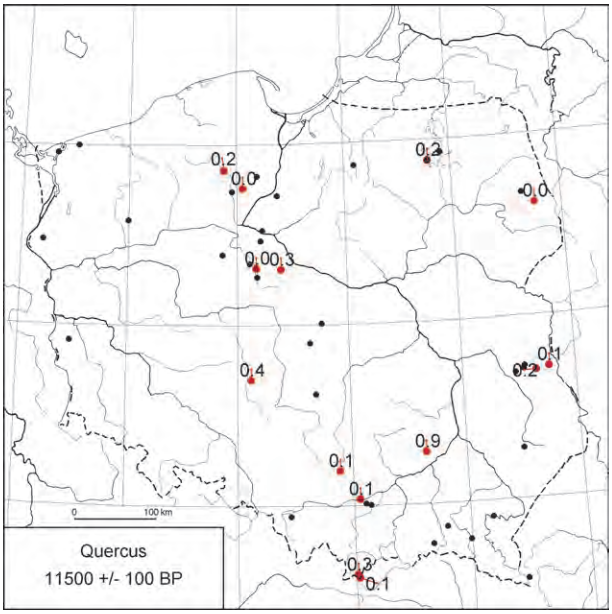
12000 +/- 100 BP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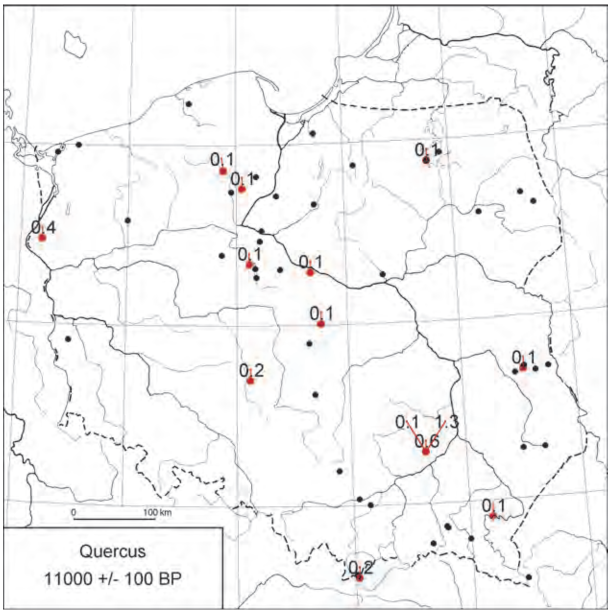
Quercus
11500 +/- 100 BP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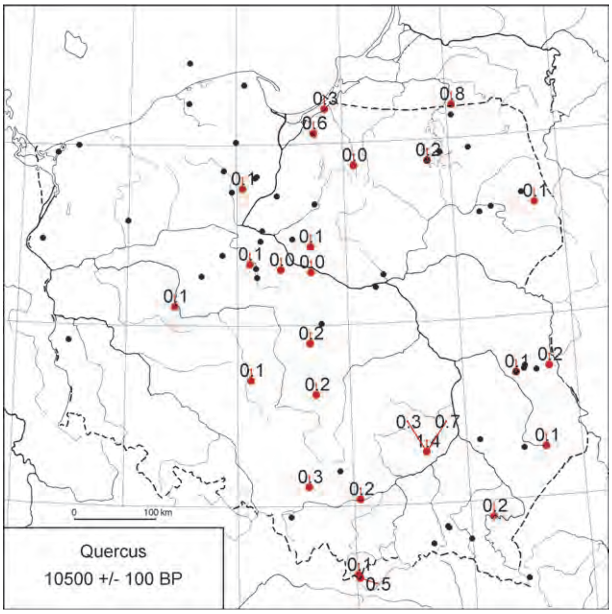
Quercus
11000 +/- 100 BP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0.1 0.2
0.3 0.7
1.4
0.1
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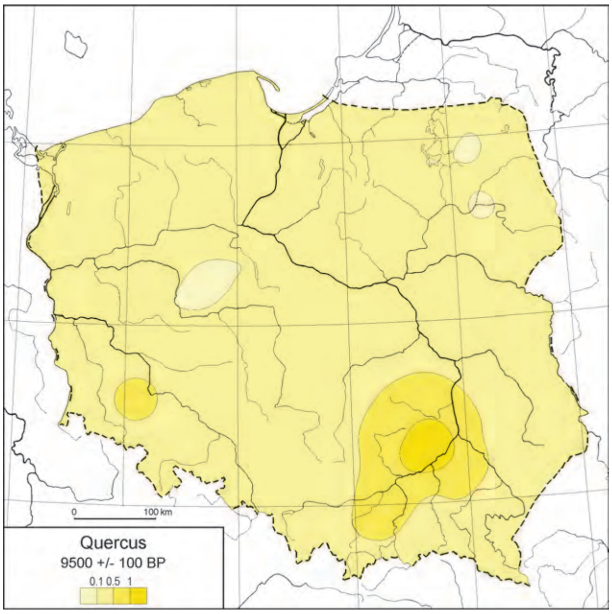
0 100 km
Quercus
10500 +/- 100 BP


0 100 km
Quercus
10000 +/- 100 BP
0.1 0.5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Quercus
9500 +/- 100 BP
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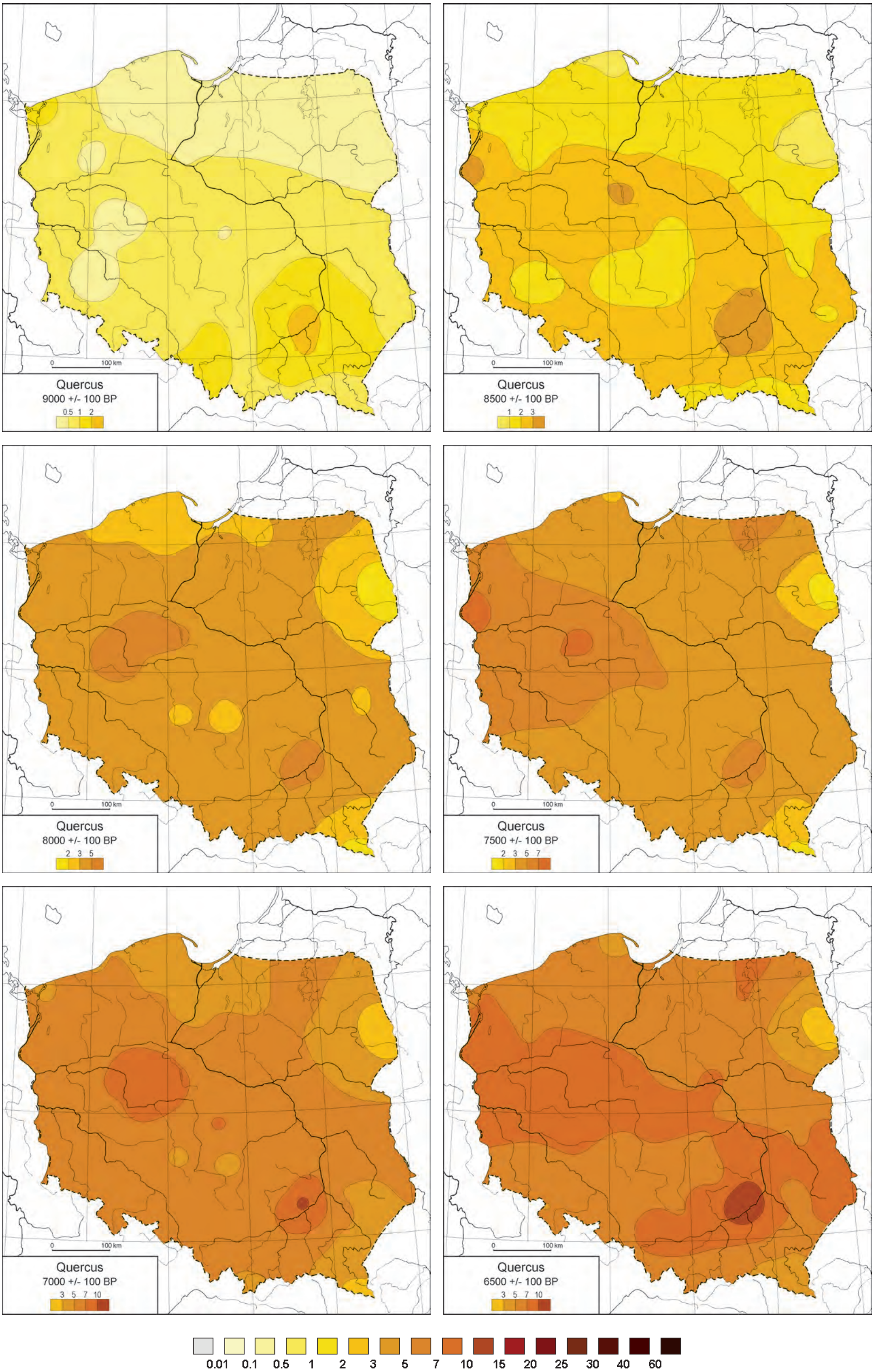
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Quercus
9000 +/- 100 BP
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Quercus
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1 2 3
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100 km
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8000 +/- 100 BP
2 3 5
0
100 km
Quercus
7500 +/- 100 BP
2 3 5 7
0
100 km
Quercus
7000 +/- 100 BP
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100 km
Quercus
6500 +/- 100 BP
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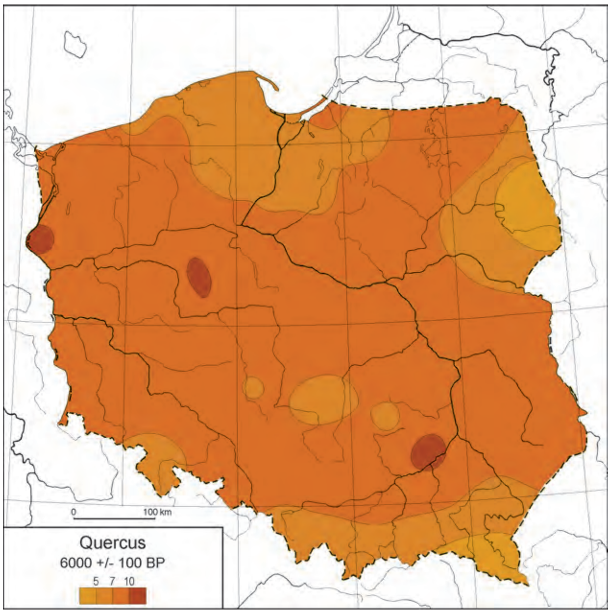
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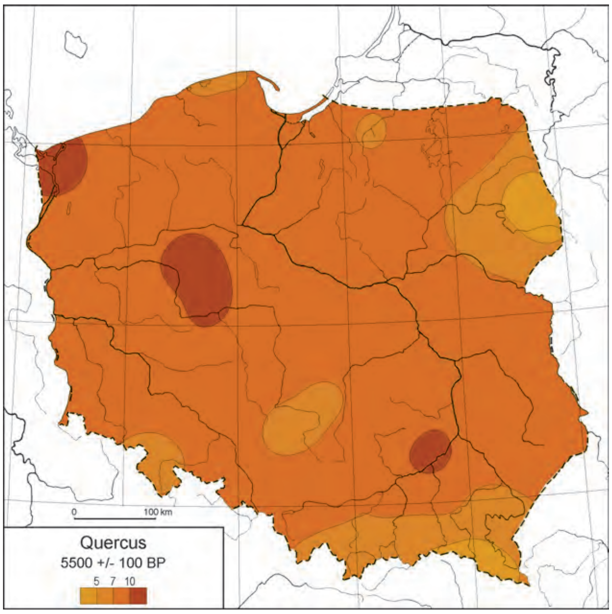
5 7 10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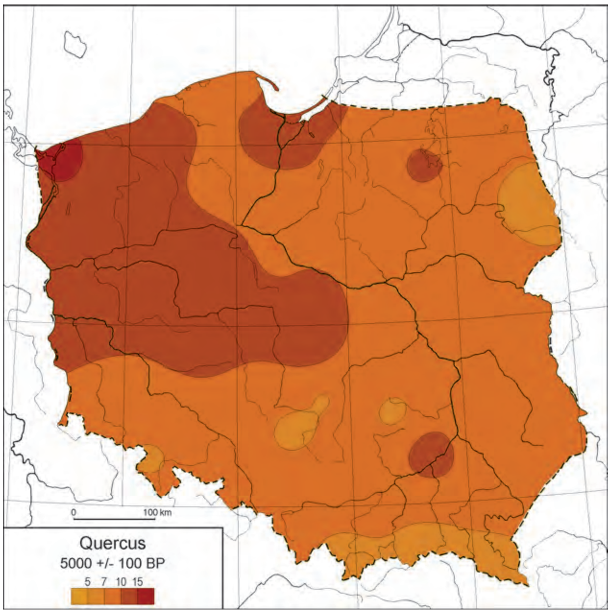
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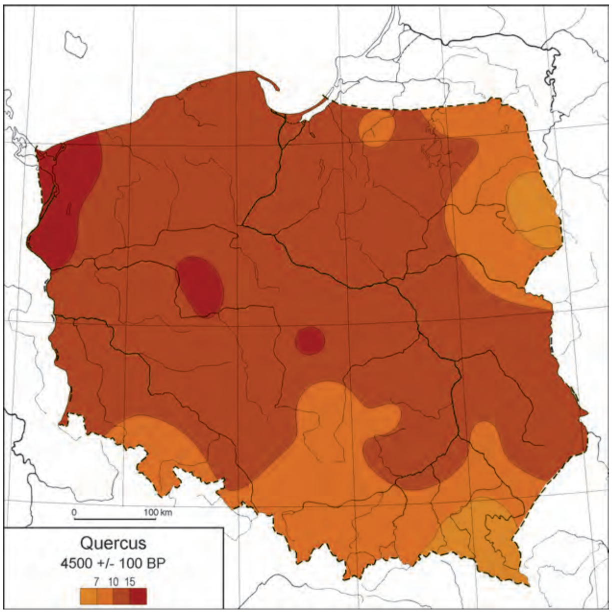
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4500 +/- 100 BP
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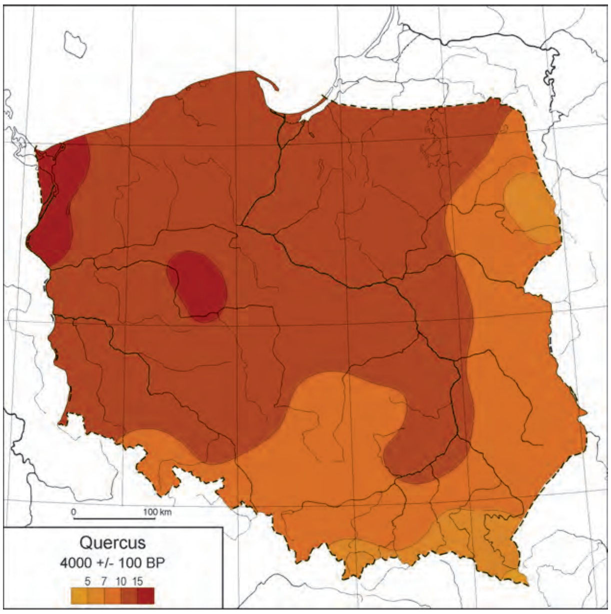
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Quercus
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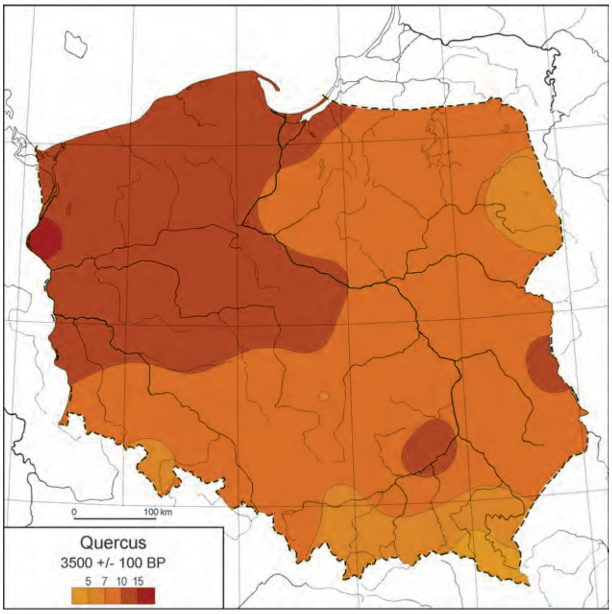
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3500 +/- 100 BP
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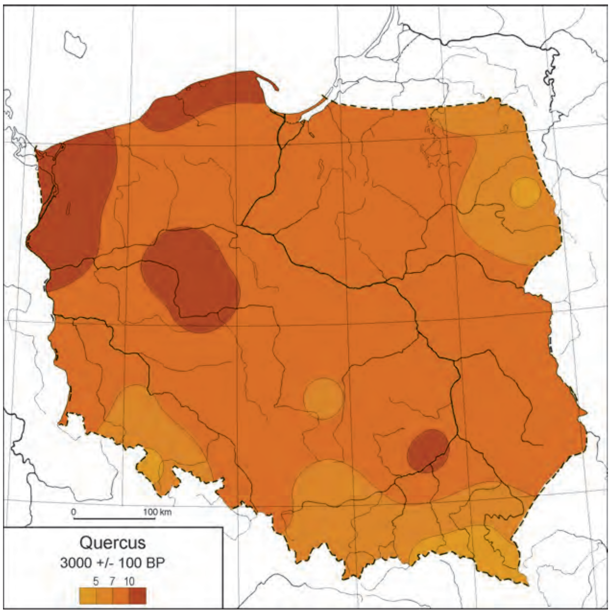
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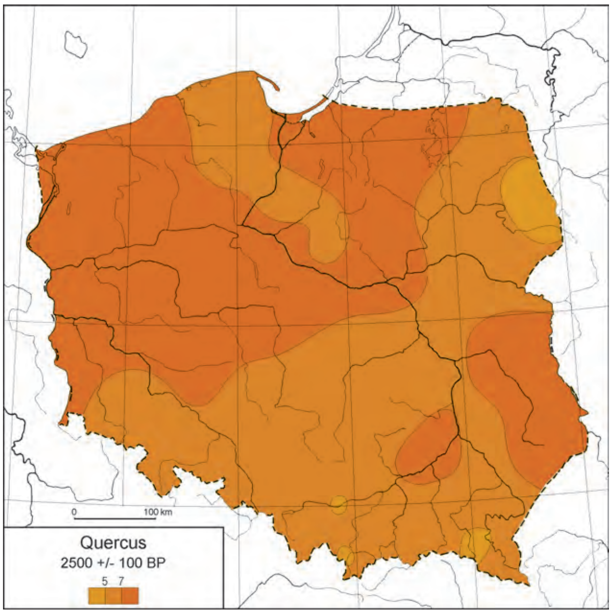
100 km
Quercus
3000 +/- 100 BP
5 7 10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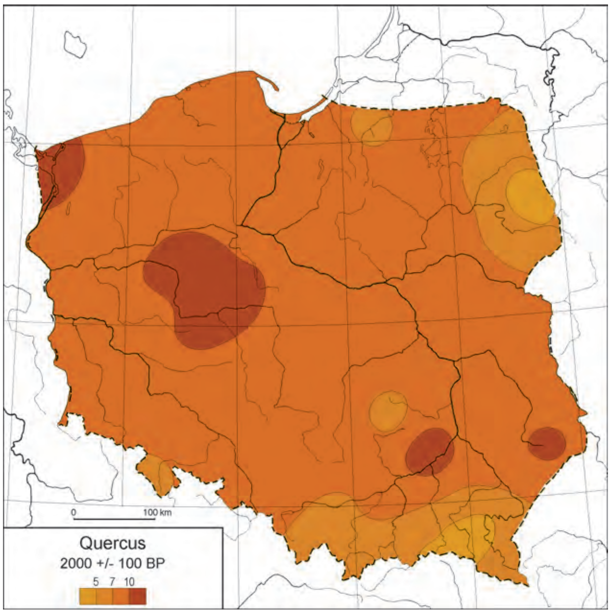
Quercus
2500 +/- 100 BP
5 7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2000 +/- 100 BP
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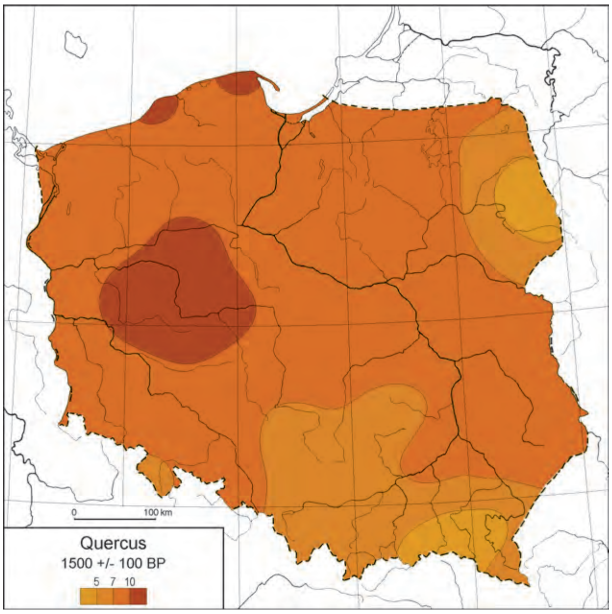
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Quercus
1500 +/- 100 BP
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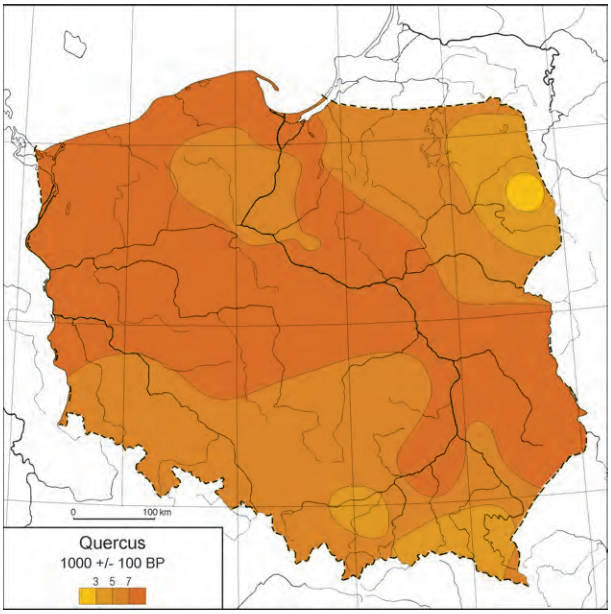
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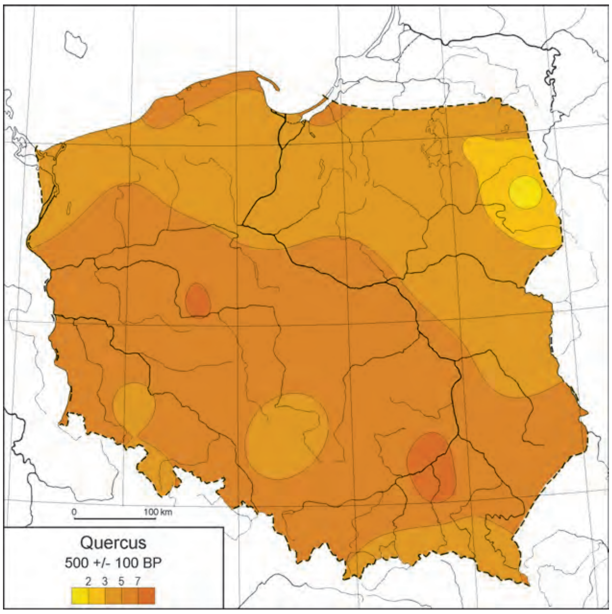
Quercus
1000 +/- 100 BP
3 5 7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500 +/- 100 BP
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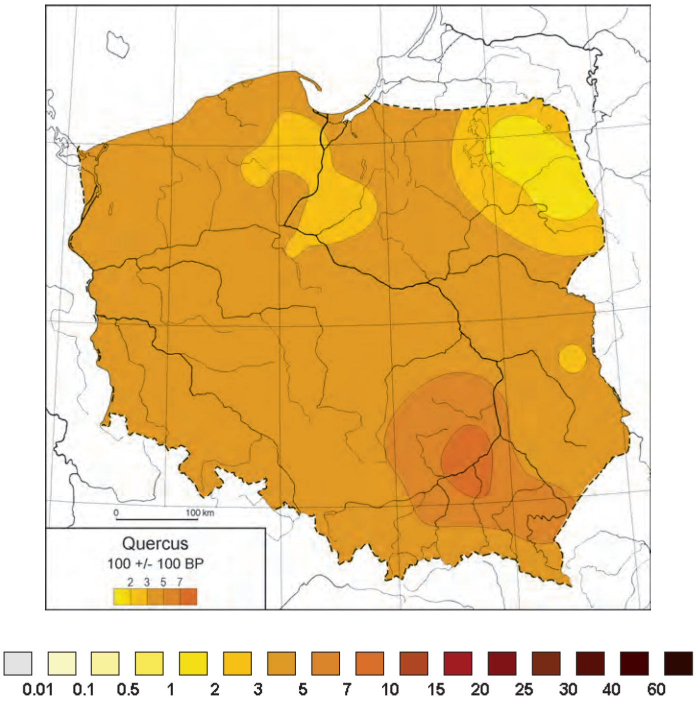
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Salix L. – Willow

Zofia Balwierz, Anna Filbrandt-Czaja, Agnieszka M. Noryśkiewicz,
Bożena Noryśkiewicz, and Dorota Nalepka

Present distribution in Europe

The genus *Salix* comprises about 300 species (Seneta 1973). Of these, 69 species grow wild in Europe as well as many hybrids and varieties. Among willows there are dwarf shrubs (for example *Salix herbacea* L., *S. retusa* L.), low shrubs (for example *S. lapponum* L.), shrubs (for example *S. pentandra* L.) and only a few species of trees (for example *S. fragilis* L., *S. alba* L.). The present day centre of occurrence of *Salix* species lies in the temperate and cool zones of the Northern Hemisphere. This genus is represented by taxa of a very wide Euro-Asiatic range (*S. alba*, *S. caprea* L., *S. viminalis* L.) or Euro-Siberian range (*S. pentandra*, *S. cinerea* L., *S. repens* L.) as well as by the species occurring only in Europe (*S. aurita* L., *S. purpurea* L.). Some of them are restricted just to the southern part of Europe (*S. eleagnos* Scop.), to its northern part (*S. hastata* L.), to the north-eastern (*S. lapponum*) or to the eastern one (*S. dasyclados* Wimmer). The Arctic-Alpine species display a very restricted range, limited either to the high mountains exclusively (*S. alpina* Scop., *S. retusa*) or to the high mountains and the northern subarctic margins of Europe (*S. hastata*, *S. herbacea*, *S. reticulata* L.).

Present distribution in Poland

The Polish flora includes 28 species and many varieties and hybrids (Kościelny & Sękowski 1971). Some of the willow species are very common throughout the country (for example *S. alba*, *S. caprea*, *S. fragilis*, and *S. pentandra*); the others occur in scattered sites or are limited to particular regions, because their range limit runs across Poland (for example *S. daphnoides* Will., *S. eleagnos*, *S. myrtilloides* L., *S. repens*). Some of the species grow only in the Sudetes and Tatra Mountains (for example *S. herbacea*, *S. reticulata*, *S. silesiaca* Willd.). *S. lapponum* and *S. hastata* are glacial relicts.

Ecology

Willows, in spite of being widespread and showing considerable tolerance to unfavourable habitat conditions, vary in relation to their ecological requirements. Most of the species are tolerant of a range of temperature conditions. Only the species of Arctic-Alpine dwarf shrubs occur in the coldest and moderately cold regions of Europe. Others extend their range into the moderately cool zone (*S. reticulata*). However, the majority of willows both of trees and shrubs (for example *S. aurita*) occur in the temperate zone, in a broad sense. Willows are generally demanding with regard to light conditions. Apart from *S. caprea*, which tolerates half-shade, the other species require full light for their development or full light with periodic or temporary shading. With regard to moisture requirements, apart from *S. eleagnos*, *S. reticulata*, and *S. retusa*, which can grow on dry and slightly moist soils, most of the species grow in moist and wet habitats, periodically flooded. Willows have quite varied preferences with regard to soil conditions, such as grain size and the amount of organic matter and humus. *S. alpina*, *S. eleagnos*, *S. reticulata*, and *S. retusa* show extreme requirements for growing in habitats without organic matter such as rocks, rock debris or gravels, whereas *S. lapponum*, *S. myrtilloides*, and *S. nigricans* Sm. grow on peat-bogs. The other species occur on mineral-humic, sandy, and sandy-loamy soils or even on heavy loams and clays. Most of the *Salix* species found in Poland are indifferent to continentality of climate (Zarzycki et al. 2002).

Willows are dioecious plants, whose flowers are clustered to form a catkin, appearing either before the development of leaves or at the same time. The majority of lowland willows belong to species blooming at the beginning of the growing season (March, April) before the development of leaves (Faliński 1990), whereas the flowering of the mountain willows occurs at the beginning of summer (Pawłowski 1956). Fruiting of most of the willow species usually takes place 2 to 3 weeks after flowering, when the seeds are dispersed by wind. The seeds then germinate on the soil surface, sometimes without any resting period. Vegetative reproduction plays an important role. Twigs that are broken off by the wind, by animals or as a result of snow and ice, can be transported quite long distances, and in moist habitats they are able to take root quickly. In nature this method of reproduction is more frequent than sexual reproduction.

All the willow species are characterised by well developed pioneer features, i.e. broad climatic and soil tolerance, high light requirements, rapid growth when young, early flowering, abundant annual seed production, as well as a strong tendency towards vegetative reproduction (Faliński 1990). They are also resistant to frost (Puchalski & Prusinkiewicz 1990). These features allow willows to colonise new areas with ease and to play a critical role in the initial phases of primary and secondary successions.

According to Faliński (1990) it is possible to distinguish in our flora 5 ecological groups of willows: 1. high-mountain dwarf willow shrubs growing on rocks, associated mainly with places with longer-lying snow cover and included in the *Salicetea herbaceae* class (Matuszkiewicz W. 1981a); 2. shrub and tree willows growing on riverine alluvial sediments and sometimes along the margins of lakes, forming the *Salicetea purpureae* class (Borysiak 1990); 3. dune shrub willows; 4. mire shrub willows, forming in the Sudetes relict mountain communities of the *Betulo-Adenostyletea* class, growing, also in the lowlands and in the Lublin Upland; 5. shrub and tree willows with a broad phytosociological and ecological range and with the most strongly developed pioneer features. Some of these contribute to communities of swamp alder woods or reparian forests and subcontinental oak-hornbeam forests with lime, and quite frequently they are found in pine forests on slightly moist or dry soils. The presence of all the species of this group is connected with the initiation or development of secondary successions, leading to formation of forest communities (Faliński 1990). The most common among the Polish tree willows (*S. alba*, *S. fragilis*) grow up to 30 m in height.

POLLEN PRODUCTION AND DISPERSAL

Willows produce huge amounts of pollen. Different views have been put forward about their method of pollination. Some authors (Huntley & Birks 1983, Hofman & Michalik 1998) have stated that willows are wind-pollinated, others (Suszka 1990) that pollen of willows may be spread by wind, but it is mainly distributed by insects. Identification of the different morphological types of the fossil willow pollen (Erdtman et al. 1961, Moore et al. 1991) is rarely performed by palynologists, that is why in the present work the genus *Salix* is treated as a single entity. Correlation between the percentage values of *Salix* pollen in a pollen diagram and the actual abundance of willow species in plant communities is not easy. The values higher than 2% observed at present in the Arctic and in the mountainous areas may be interpreted as widespread occurrence of sub-Arctic or sub-Alpine brushwood or tundra communities (Huntley & Birks 1983). Thus, most of the willow pollen, recorded from Late Glacial sites probably reflects the common occurrence of *Salix* as shrub willows that prefer an arctic climate, and at that time were spreading, together with *Juniperus* and heliophilous species of *Artemisia* and Chenopodiaceae (Tobolski 1998). Interpretation of willow percentage values from Holocene sediments is much more difficult. In fossil pollen assemblages of forest type, willow pollen is generally found only in small quantity because of its insignificant presence within the tree-stands. Sporadically occurring high values may have resulted either from the local presence of carr communities or from the initial phases of secondary succession in areas that had undergone anthropogenic disturbance.

EXPANSION IN EUROPE DURING THE LATE GLACIAL AND HOLOCENE

It is difficult to talk about *Salix* refugia when there are such a large number of willow species of considerable ecological variability. By 13,000 BP willows were present throughout Europe however, their higher pollen values (up to 10%) were noted mainly in northern Europe. In the Allerød the amount of willow pollen decreases, whereas the highest values persist in southern Greenland and in the Scandinavian Peninsula.

The beginning of the Holocene saw a further decrease in *Salix* percentage values. Values higher than 2% occur only in the mountain areas and in the north-western part of Britain; the highest are in southern Greenland. Such a tendency lasted for almost the whole of the Holocene. By 2000 BP the range of 2% values shifted southwards and eastwards from the Scandinavian Peninsula, where the willow percentage pollen values are highest (Huntley & Birks 1983, Delcourt et al. 1984).

MIGRATION PATTERN IN POLAND (Fig. 68)

14,000 – 10,500 BP

The presence of willows has already been noted from 14,000 BP onwards. The small number of sites from the early stages of the Late Glacial does not give the full picture of the distribution of this taxon, since during that time *Salix* species may have been quite common across Poland. In Late Glacial pollen assemblages, some authors (among others: Ralska-Jasiewiczowa, Demske & van Geel 1998, Latałowa 1999a) record the presence of the shrub willows *S. herbacea* and *S. polaris*-type, both characteristic of tundra communities. On the 14,000–13,500 BP maps willow pollen is present at all sites investigated, and from 13,000 to 12,500 BP its values generally reach a few percent. The 12,000 BP isopollen map represents the maximum abundance of *Salix* recorded during the Late Glacial and Holocene. The following 11,500 and 11,000 BP isopollen maps record almost evenly distributed values of willow pollen throughout the country, that are distinctly lower than the previous ones. At this time, during the Allerød, tundra communities became replaced by forests. During the Younger Dryas (10,500 BP) there was again an increase in the importance of plant communities with willows, particularly in northern Poland.

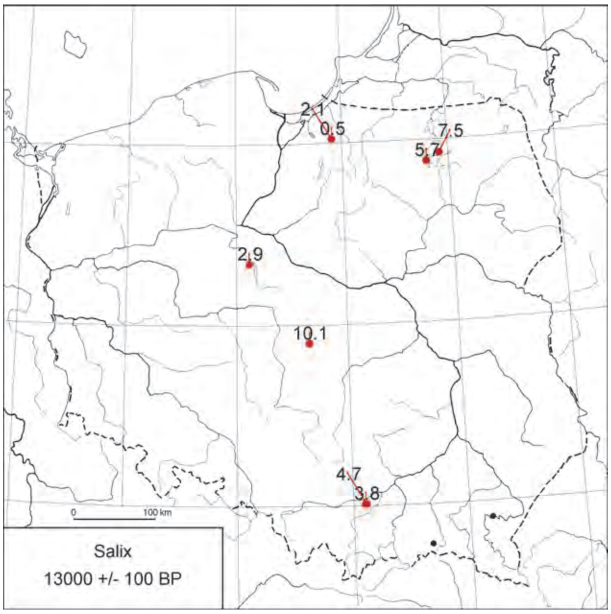
10,000 – 100 BP

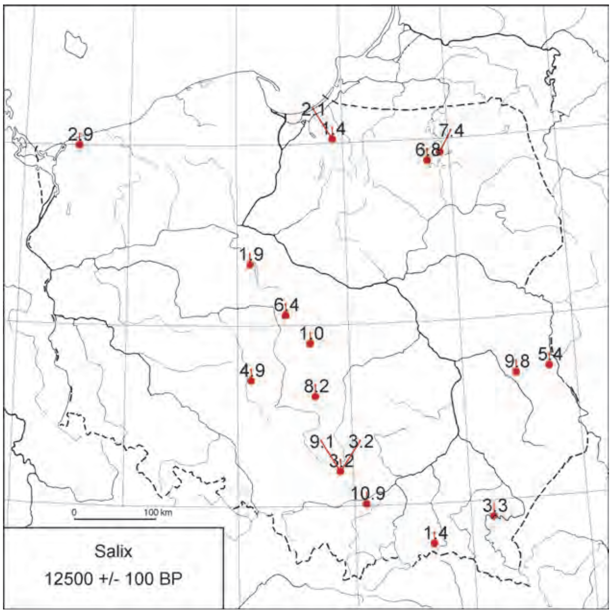
At the beginning of the Holocene (10,000 BP) the amount of *Salix* pollen decreases in central and southern Poland as a result of the gradual spread of forest communities with pine and birch, and subsequently with other species of trees. Small amounts of *Salix* pollen, quite evenly distributed but decreasing with time, can be observed on the subsequent Holocene maps. Since 8500 BP its amount has not exceeded 0.5% in the greater part of Poland, whereas distinctly higher values are observed in the south-eastern part of the country. Such a picture persists for the greater part of the Holocene, and the minor differences may result from the character of habitats that yielded the material for pollen analysis. Since 2000 BP an increase in willow values has been observed from the south-east towards the north-west and the north. At present, percentage values of *Salix* pollen of 0.5% to 2% cover almost the whole territory of Poland apart from the north-western part of the country. The highest values (above 5%) are recorded also in south-eastern Poland.

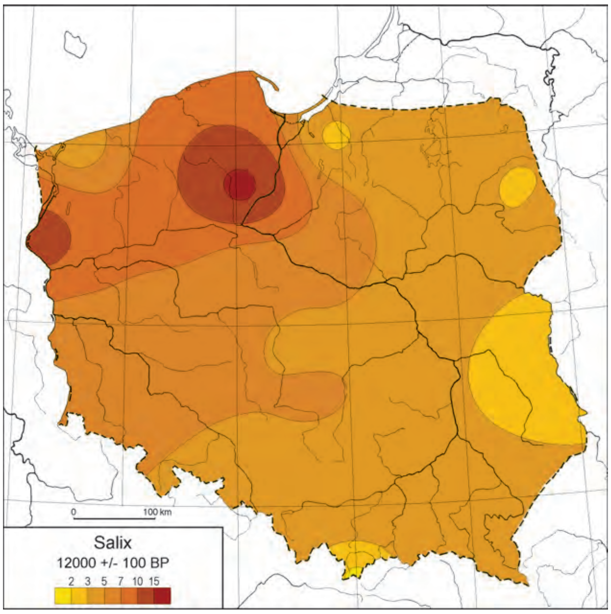
CONCLUSIONS

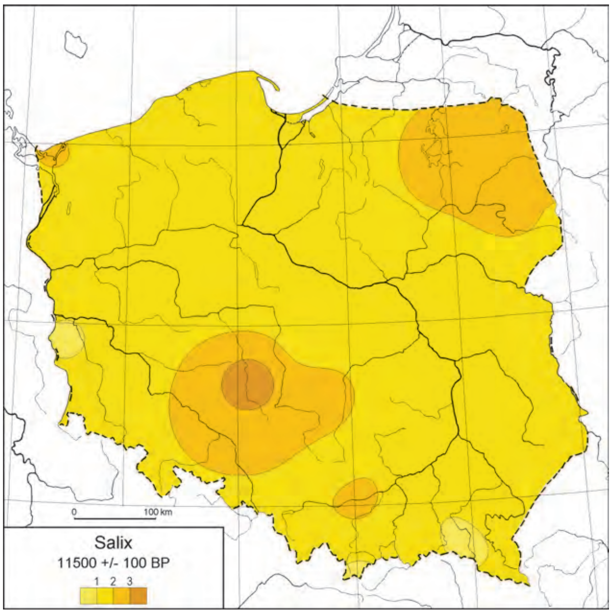
The highest percentage values of willow pollen in pollen assemblages, reflecting their abundance in plant communities, are recorded during the Late Glacial. Willows were a component of the tundra vegetation at that time. At the beginning of the Holocene, as climate ameliorated, these communities retreated because of the expansion of forests. Competition resulting from the spread of mesophilous species of trees restricted the occurrence of willows mainly to riparian communities in the river valleys and to willow scrub around water bodies. In the late Holocene repeated minor expansions of forest and shrub communities in which willows played a role, were probably related to human activity, reflecting secondary successions in areas previously cleared and then abandoned, though climatic change may also have favoured increased wetland areas in river valleys and around lakes.

Fig. 68. *Salix*: dot and isopollen maps for 14,000–100 ^{14}C yr BP









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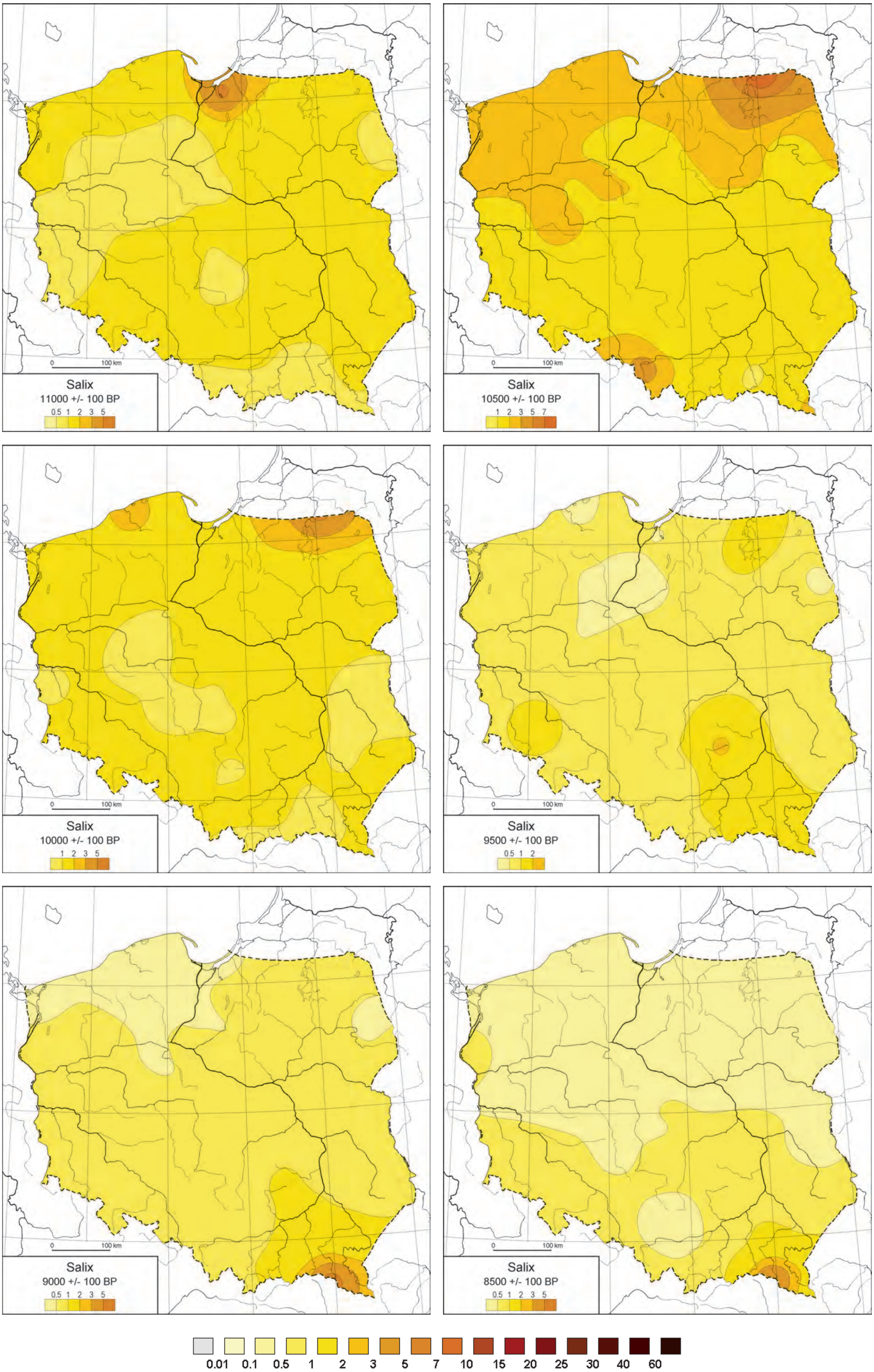
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Salix
11000 +/- 100 BP
0.5 1 2 3 5
0
100 km
Salix
10500 +/- 100 BP
1 2 3 5 7
0
100 km
Salix
10000 +/- 100 BP
1 2 3 5
0
100 km
Salix
9500 +/- 100 BP
0.5 1 2
0
100 km
Salix
9000 +/- 100 BP
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100 km
Salix
8500 +/- 100 BP
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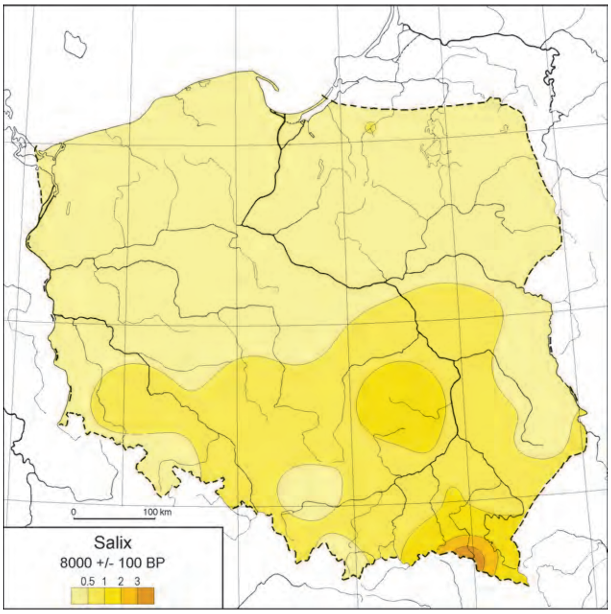
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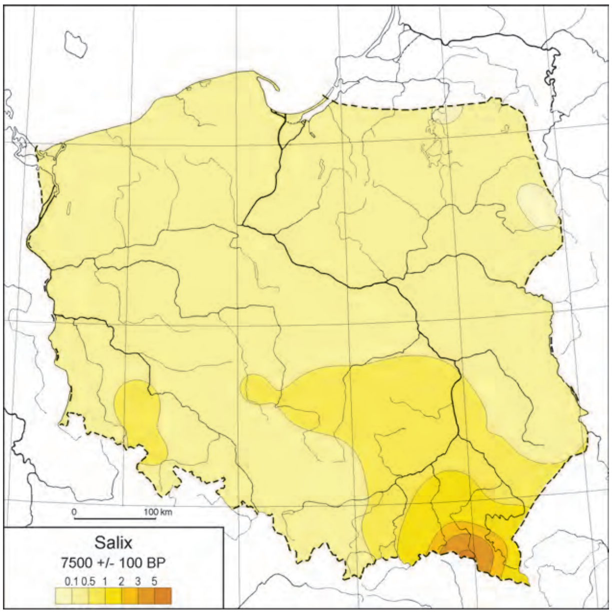
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Salix
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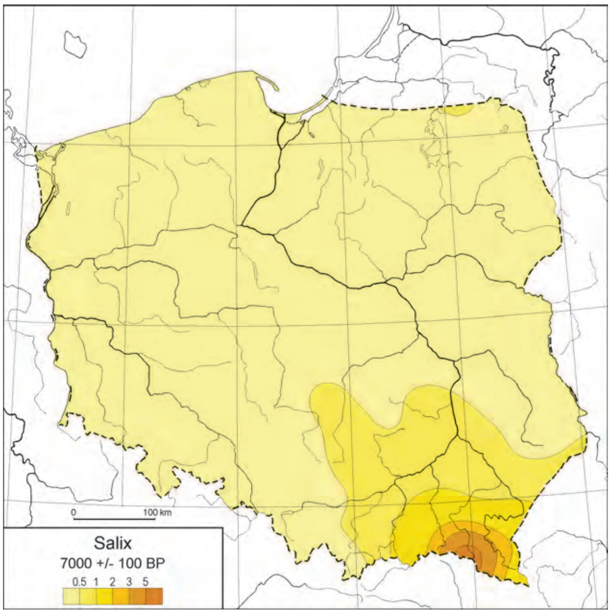
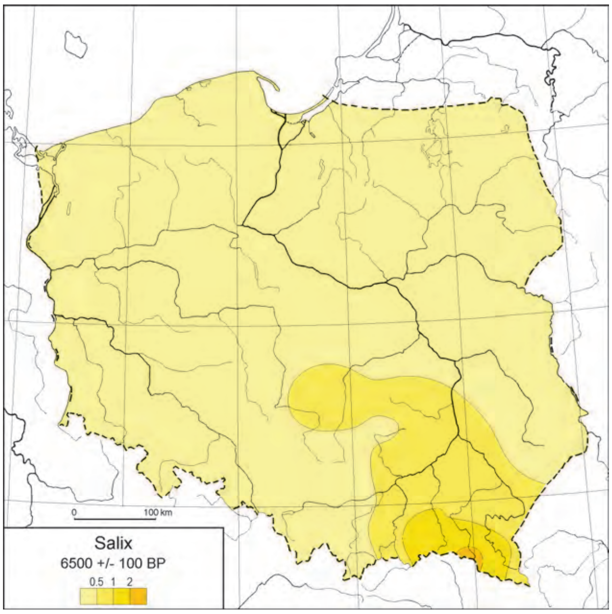
0.1 0.5 1 2 3 5


0
100 km
Salix
7000 +/- 100 BP
0.5 1 2 3 5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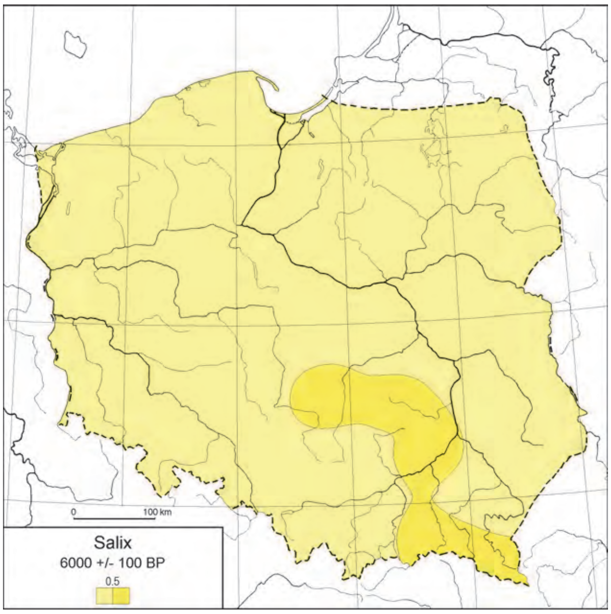
Salix
6500 +/- 100 BP
0.5 1 2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Salix
6000 +/- 100 BP
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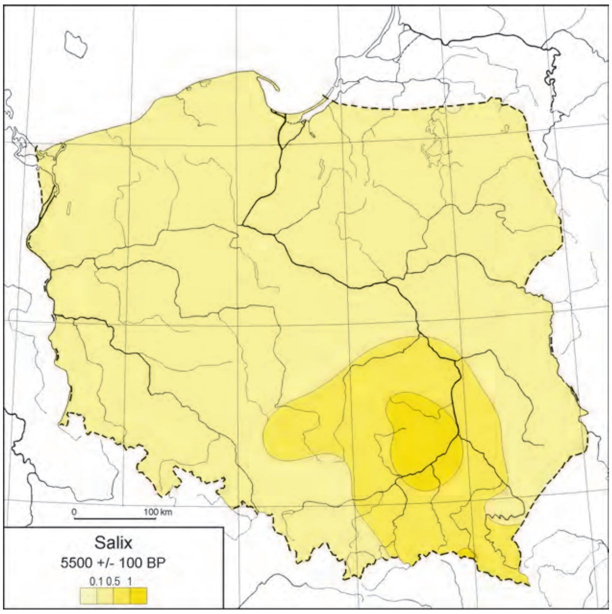
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100 km
Salix
5500 +/- 100 BP
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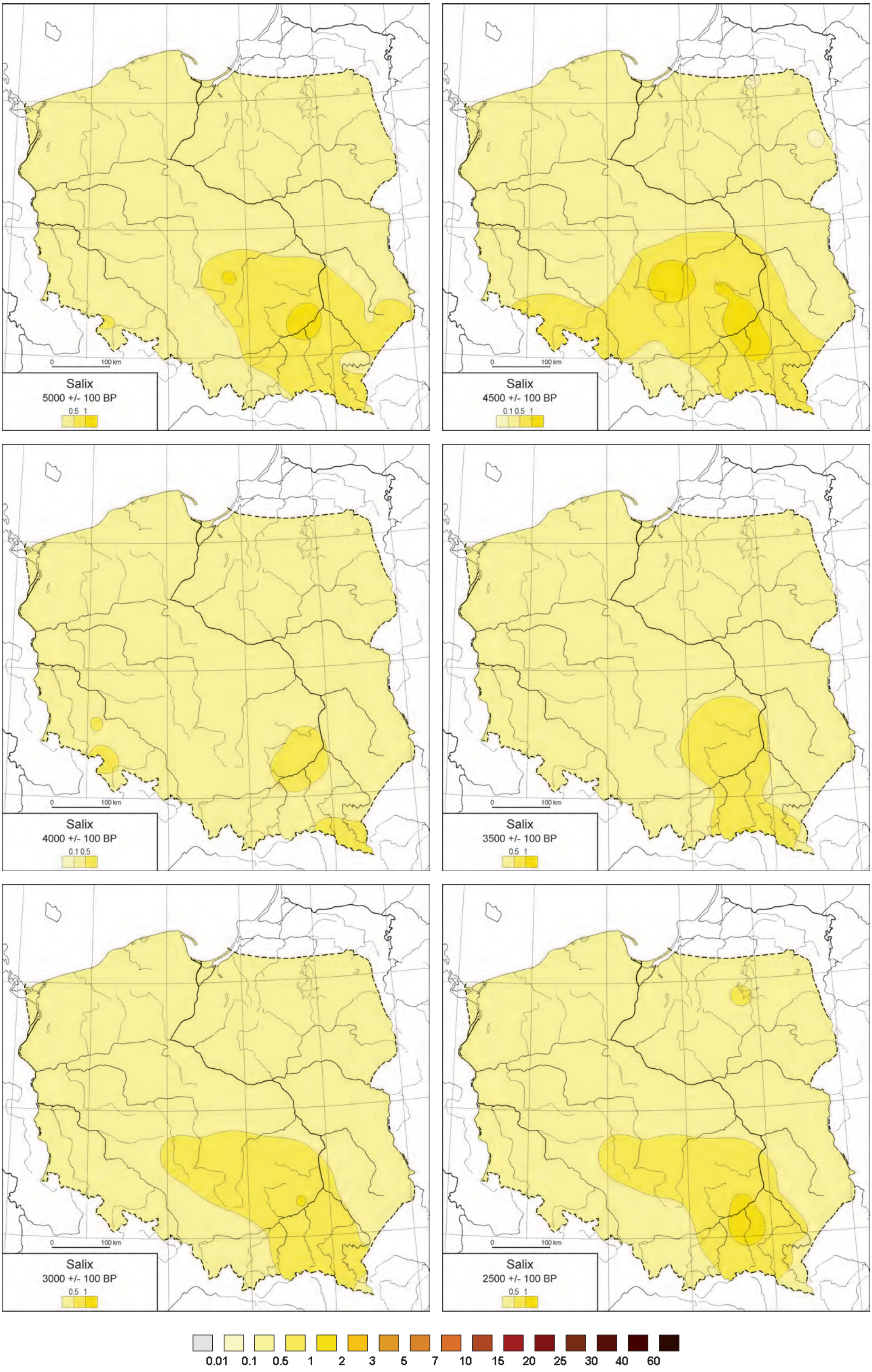
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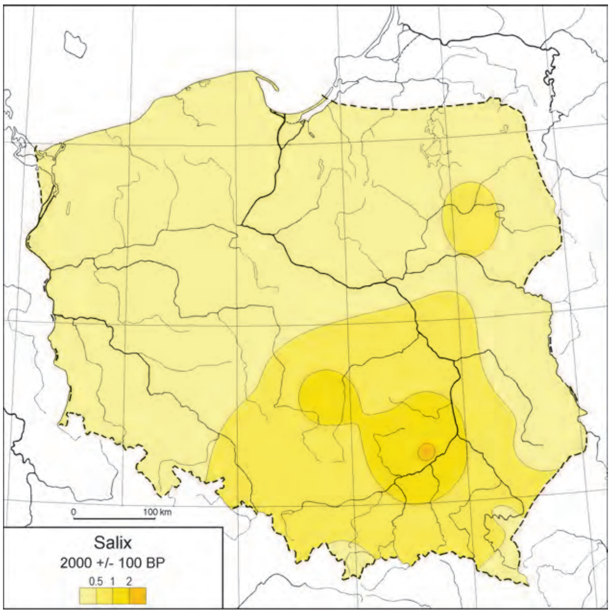
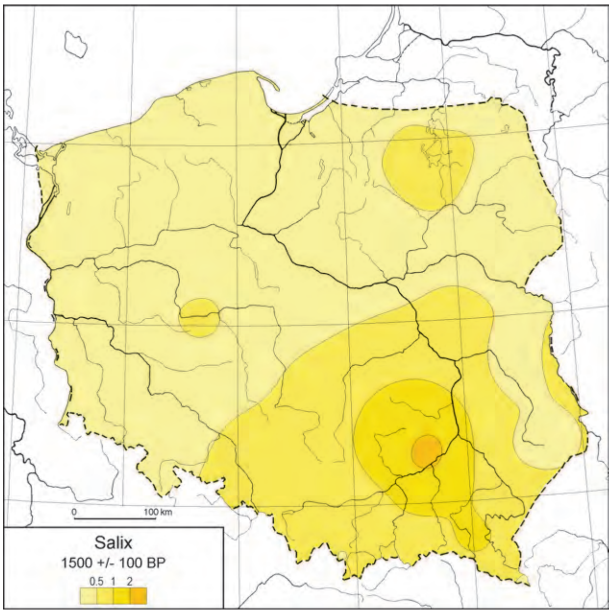
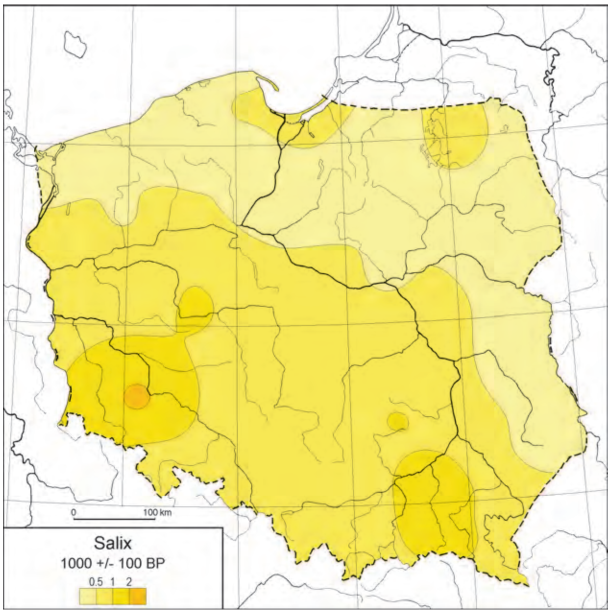
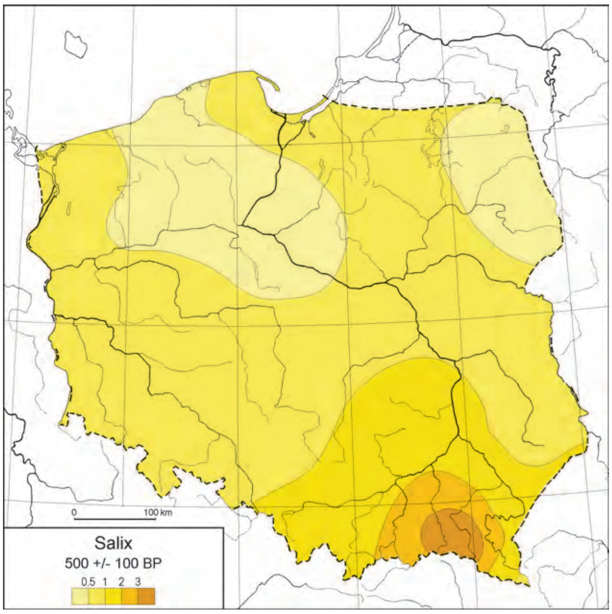
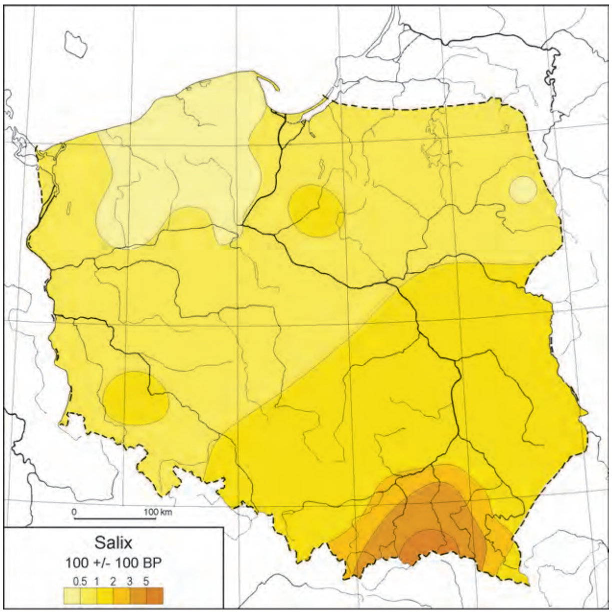
100 km
Salix
5000 +/- 100 BP
0.5 1
0
100 km
Salix
4500 +/- 100 BP
0.1 0.5 1
0
100 km
Salix
4000 +/- 100 BP
0.1 0.5
0
100 km
Salix
3500 +/- 100 BP
0.5 1
0
100 km
Salix
3000 +/- 100 BP
0.5 1
0
100 km
Salix
2500 +/- 100 BP
0.5 1
0.01
0.1
0.5
1
2
3
5
7
10
15
20
25
30
40
60


0
100 km
Salix
2000 +/- 100 BP
0.5 1 2


0
100 km
Salix
1500 +/- 100 BP
0.5 1 2


0
100 km
Salix
1000 +/- 100 BP
0.5 1 2


0
100 km
Salix
500 +/- 100 BP
0.5 1 2 3


0
100 km
Salix
100 +/- 100 BP
0.5 1 2 3 5


0.01
0.1
0.5
1
2
3
5
7
10
15
20
25
30
40
60

Taxus baccata L. – **Yew**

KRZYSZTOF M. KRUPIŃSKI, AGNIESZKA M. NORYŚKIEWICZ AND DOROTA NALEPKA

PRESENT DISTRIBUTION IN EUROPE

In natural forest communities of the Northern Hemisphere the genus *Taxus* occurs rarely or sporadically. It is represented by eight species. *Taxus baccata* L. is the only species occurring in Europe and in Poland (Bugała 1975, Środoń 1975, Seneta 1981a, b, Tomanek 1994). The area of its present occurrence covers almost the whole of Europe (Fig. 69). The north-eastern limit of its range runs along the isotherm of the coldest month –5°C (Król 1975) and the warmest month +16°C (Hultén 1950), corresponding with the area of oceanic climatic influence (Środoń 1975). The limit of yew's scattered distribution range runs across Estonia, Latvia, the eastern margins of Poland down to the western part of Wołyń and Podole. It extends to the Czarnohora Mountains in Ukraine and along the Carpathian arc where it runs parallel to the limit of the range of *Abies alba*. Its northern limit in the Scandinavian Peninsula runs approximately along latitude 61°N, but it extends up the Atlantic coast of Norway to 63°N, its most northerly extent, and in Scotland it reaches latitude 58°N. In the west it reaches the Azores. Its southern boundary runs from Spain, along the Alps and the Apennines to Sardinia, and Sicily, and then from Greece across to Asia Minor with an outlying popu-

Fig. 69. *Taxus baccata* – map of present-day distribution in Europe: ● – native isolated occurrence, ◒ – status of site unknown or uncertain (after Jalas & Suominen 1973)

lation in the Crimean Peninsula and Caucasus (Browicz & Gostyńska-Jakuszewska 1969, Jalas & Suominen 1973, 1988a). Its main centres are associated with regions of western Europe adjacent to the Atlantic Ocean. In central Europe the biggest centre of yew occurs in Hungary (the Bacon Forest – ca. 45,000 trees) (Tomanek 1994).

PRESENT DISTRIBUTION IN POLAND

The eastern limit of natural occurrence of yew runs across Poland (Zając A. & Zając M. 2001) (Fig. 70). In our country yew is a rare species and is under protection. The forest reserves, established for *Taxus baccata* protection, are listed by Fabijanowski (1951). The number of natural single stands or single specimens of this tree in Poland reaches almost 300. They are situated mainly in the south and west and in northern Poland. In the biggest reserve of *Taxus baccata* in Poland at Wierzchlas in the Tuchola Forest, eastern Pomerania, there are about 3000 specimens in an area of about 10 ha (Izdebski 1956, Gieruszyński 1961, Król 1993, Kruszelnicki 2001, Tobolski 2002). In the Tatra Mountains yew extends up to an altitude of 1380 m a.s.l. (tree stumps have been found at 1600 m a.s.l.) (Zembrzuski 1975, Seneta 1981a, b).

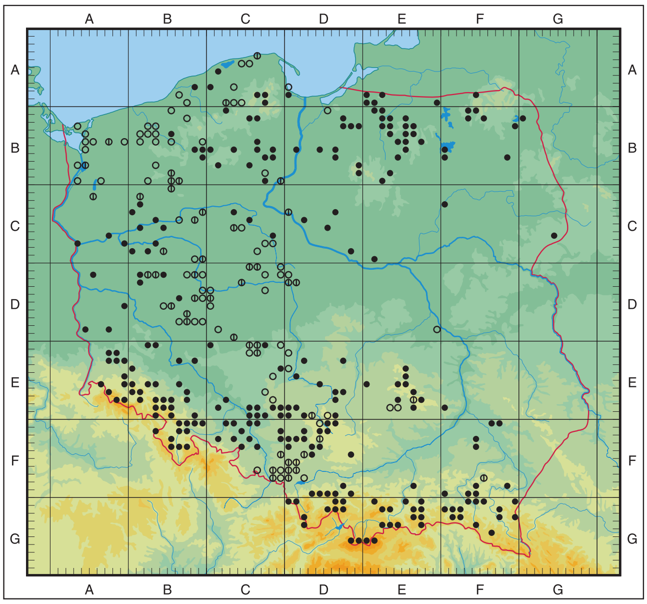


Fig. 70. Present-day distribution of *Taxus baccata* L. in Poland: ○ – synanthropic sites, Φ – status of site unknown or uncertain (after Zając A. & Zając M. 2001)

ECOLOGY

Yew occurring today in Poland is a long-lived, slow-growing tree or shrub with rather broad edaphic preferences. The oldest yew occurring in Europe is said to have reached an age of slightly more than 1000 years (Bugała 1975). Yew occurs in the forest communities of the order *Fagetalia* (Zarzycki et al. 2002). It avoids dry, barren, and acid soils. It grows well on slightly moist and humic soils as well as on peaty soils. It belongs to the shade-demanding or shade-tolerant taxa (more than beech and fir), and it is the most shade-tolerant species amongst the coniferous trees. This feature may result from an adaptation to withstand competition with other forest trees in the conditions of its natural environment. Generally, it occurs in the lower tree layer or in the undergrowth, rarely reaching the upper tree layer. Yew does not tolerate frosty areas and is sensitive to wide fluctuations of temperatures (Król 1975), droughts (Tomanek 1994), and to desiccation by winter winds. It displays considerable adaptive abilities to various environmental conditions. It tolerates air pollution well and even withstands toxic industrial emissions. The distribution of *Taxus baccata* is associated with oceanic climate. It belongs to the group of plants with a European-boreal-montane distribution (similarly to *Fagus sylvatica*).

Yew is a dioecious, occasionally monoecious plant (Suszka 1975, Seneta 1981b, Król 1993). It flowers at the end of April and the beginning of May. Its fruit is a nut ripening in autumn, covered with soft red aril. Birds contribute considerably to their dispersal and germination (Bartkowiak 1975, Czarnowski 1978). Specimens of yew occurring at open sites bear fruit at the age of 20–30 years, while those growing in dense woodland shade only later, at the age of 70–120 years. Years of abundant seed production are cyclic and occur every 2–3 seasons (Szczęsny 1952, Tomanek 1994). Yew trees propagate both sexually and vegetatively.

Intensive grazing by forest animals and felling of yew trees due to demand for its valuable timber are considered to be the main reasons for the contraction of its range in European forest communities (Fabijanowski 1951, Tobolski 2002).

Taxus baccata does not form pure monospecies stands within forests (except in the Caucasus Mountains) but it is one of the elements of diverse forest communities composed mainly of *Abies*, *Fagus*, *Carpinus*, *Alnus*, and *Picea*. At the northern border of its range yew occurs mainly in spruce and fir forests (Król 1975, Seneta 1981a, b).

POLLEN PRODUCTION AND DISPERSAL

Taxus baccata is a wind-pollinated species, flowering rather abundantly. Investigations into the rate of fall of its pollen grains in still air suggest that they can remain airborne for a relatively long time. Mean falling speed of its pollen is about 2.30 cm/s and is slightly less than the speed of other pollen grains with similar dimension. Yew pollen grains belong to a group of pollen types that are difficult to identify because they lack obvious identification features, and in older pollen diagrams they have only rarely been distinguished. That is why pollen values of *Taxus* may be underestimated in relation to their actual presence in the samples. Thus it is quite possible that in the past, yew may have occurred more often in the natural woods of Poland, than has been documented by palynological researches. It has been shown from studies on present-day pollen fall in the 'Cisy Staropolskie' Reserve at Wierzchlas that *Taxus* pollen may have some difficulties with dispersal. Yew was adequately represented in the pollen deposition within the forest and at its margins; however, its values diminished with increasing distance away from male specimens. Studies of surface samples coming from a transect placed under a male specimen of *Taxus baccata* reveal that the majority of its pollen grains fall directly under the tree. Only a few have been recorded beyond the extent of its crown (Noryśkiewicz A.M. 2001, unpubl.).

EXPANSION IN EUROPE DURING THE LATE GLACIAL AND HOLOCENE

In Holocene pollen diagrams *Taxus* pollen has been recorded rather rarely (Środoń 1975, Sarmaja-Korjonen et al. 1991, Ralska-Jasiewiczowa, van Geel & Demske 1998). However, in the mesocratic stages of Masovian and Eemian interglacials it was often an important or even dominant forest element. In this stage of Masovian interglacial in Poland its pollen values can reach 50% (Nita 1999), and in the Eemian 9–12% (Mamakowa 1989, Krupiński 2002). In the Holocene of central Europe yew probably appeared at the end of the climatic optimum, before the appearance of beech (Firbas 1949). Its relatively late arrival in the Holocene in comparison with thermophilous deciduous trees Godwin (1956) is associated with its considerable moisture requirements and intolerance of severe winters. At some sites in central Europe there is palynological evidence for a temporary rise in *Taxus* values before the mass expansion of beech. This early expulsion of yew by beech is observed mainly at the margins of the southern Alps and in the vicinity of Lake Garda (Küster 1996). Palynological studies on the vegetation history of the French Alps and of the Jura (de Beaulieu et al. 1994) have shown the relatively early presence (6500–6000 BP) and wide expansion of *Taxus* pollen particularly in the south and central Jura. Its main spread took place during the younger part of the Atlantic period (pollen values >20%). This resembles its behaviour during interglacial stages, but previously had not been observed from any equivalent sites in the Holocene of Europe. Although *Taxus* expansion during interglacials (climate and maybe also lack of competition from beech) and in the younger Holocene (climate and man) was probably influenced by different factors, the comparison of these processes allows us to draw conclusions about the dynamics of the growth and spread of yew and the dispersal of its pollen. An analysis of prehistoric charcoal proves the considerable role of yew in the areas in question at the end of the Atlantic period (de Beaulieu et al. 1994). Of all the fragments of charcoal studied, 26.8% belonged to *Taxus*. The scarce occurrence of yew pollen in those sites probably documents the restricted distribution of this species, due to its weak competitive abilities. *Taxus baccata* grows slowly and in spite of its broad ecological tolerances it can exist only in niches where fast-growing species are absent (Favre & Jacomet 1998).

In north-western Germany *Taxus* appeared at the end of the Atlantic period and spread at the beginning of Subatlantic. Its pollen values rarely exceed 1% and only in one case reach 4%. The decrease of yew pollen frequency later in the Subatlantic resulted from natural causes (competition for light with beech and hornbeam) and from adverse human activity (Averdieck 1971). In the pollen diagram from Blekinge, south-eastern Sweden, *Taxus baccata* was recorded already in the younger part of the Boreal period (Berglund 1966). Yew is also sporadically present in Holocene diagrams from Denmark (Aaby 1986, Andersen 1989).

MIGRATION PATTERN IN POLAND (Fig. 71)

In Holocene pollen diagrams from Poland, *Taxus baccata* appears sporadically, usually in very small amounts. The method of time intervals applied in this atlas may ignore the sporadic presence of yew at some sites. Due to weak representation of yew in pollen rain and the incomplete identification of its pollen, the maps constructed here display only an approximate picture of the distribution of this taxon and the pollen values presented should be considered as minimal ones.

6000 – 5500 BP

The appearance of single yew pollen grains at two sites suggests the beginning of migration of this species into Poland.

5000 – 3500 BP

On consecutive maps the number of sites with yew pollen rises, but percentage pollen values never exceed 0.2%. A rise of *Taxus* pollen values over 1% between 4500 and 4000 BP in the Lake Gościąż profile (Ralska-Jasiewiczowa & van Geel 1992) has been omitted by time horizons used for mapping. *Taxus* spread was clearly connected there with the activities of Neolithic settlers. The location of *Taxus* sites is limited mainly to central and northern Poland, though this pattern may result from the higher number of sites in that part of the country and not from the real range of *Taxus baccata*.

3000 – 500 BP

New sites appear where yew pollen is determined, suggesting a westward expansion of this taxon. However its percentage values are still relatively low, fluctuating around 0.1% and never exceeding 0.5%.

100 BP

In modern times, a fall in the number of sites at which yew has been noticed is apparent. Locally, in the Tuchola Forest, in the area of the yew reserve, this taxon is recorded with maximum values for the Holocene (0.9–1.3%).

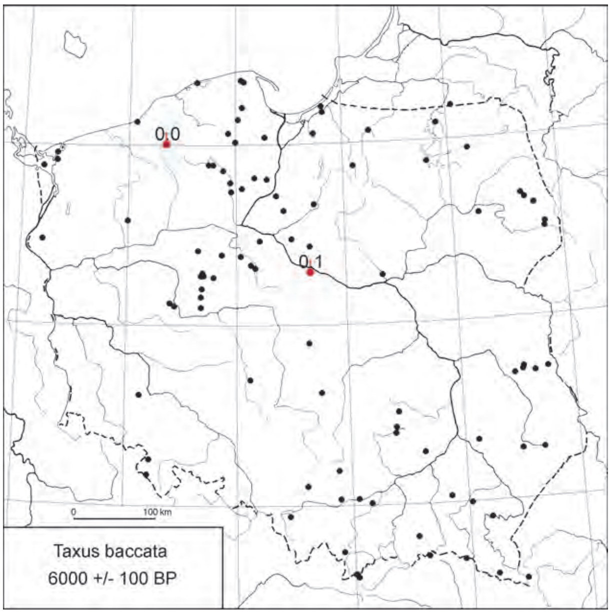
CONCLUSIONS

Taxus pollen is strongly underrepresented in pollen diagrams due to the difficulties in its identification and limited pollen distribution.

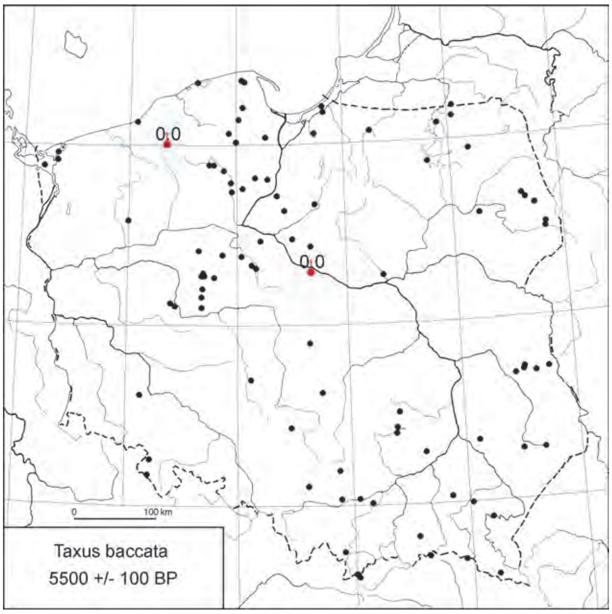
Yew appeared in central Europe at the decline of the climatic optimum. It is a tree associated with oceanic climate. In pollen diagrams from Poland it has been found sporadically and in very small numbers. Thus the maps give only an approximate picture of its real occurrence.

Taxus pollen appears first at 6000 BP, and, from 5000 to 3500 BP, it occurs rarely in central and north Poland. Some westward extension of its range may be suggested after 3000 BP. The maximum yew pollen values have been found on the 100 BP map in its reserve area at Tuchola Forest, Pomerania.

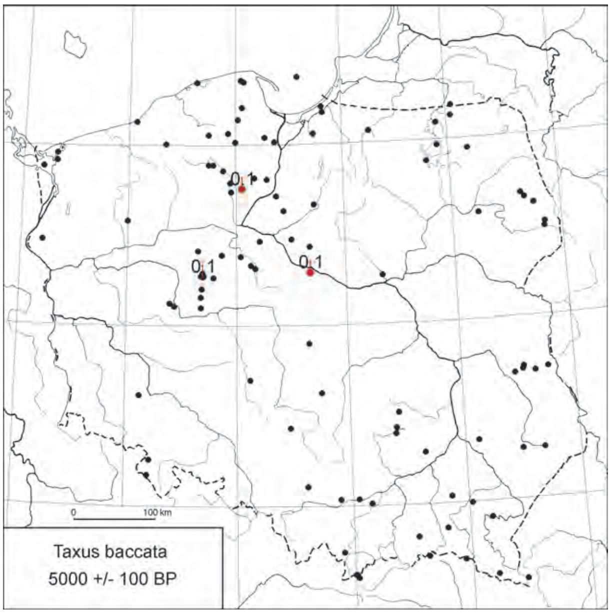
Fig. 71. *Taxus baccata*: dot maps for 6000–100 ^{14}C yr BP



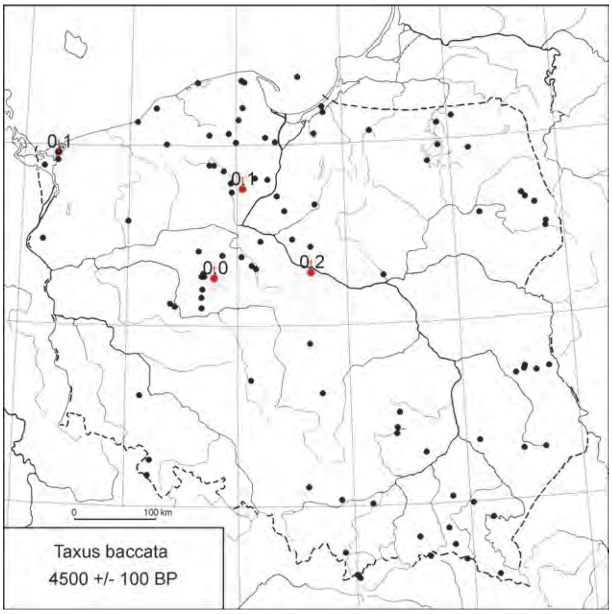
Taxus baccata
6000 +/- 100 BP



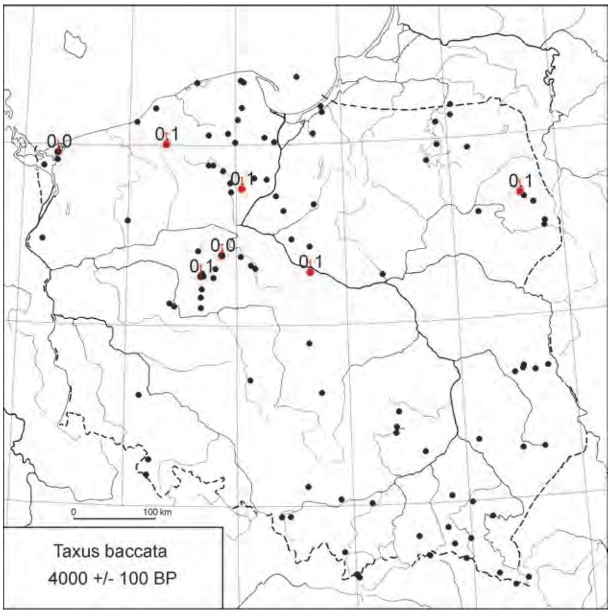
Taxus baccata
5500 +/- 100 BP



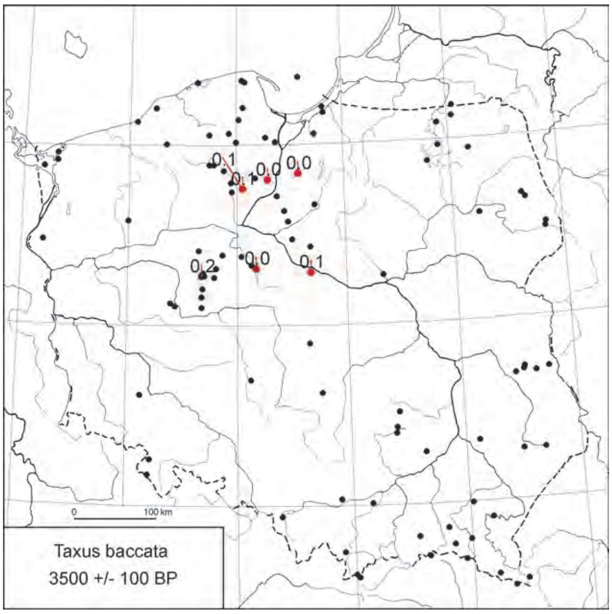
Taxus baccata
5000 +/- 100 BP



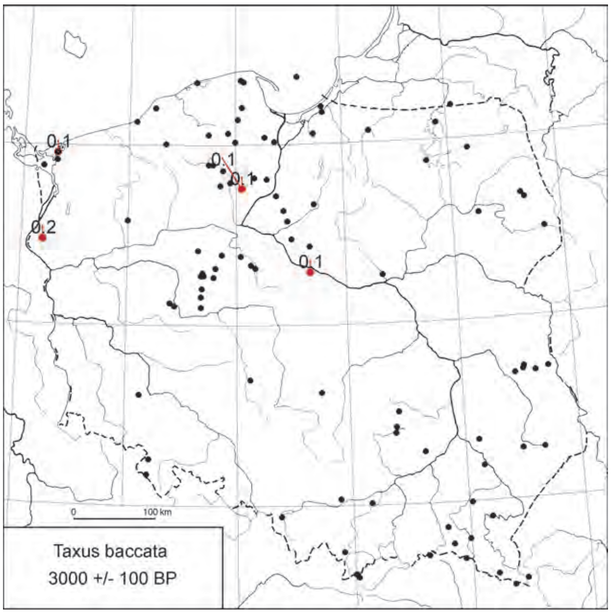
Taxus baccata
4500 +/- 100 BP

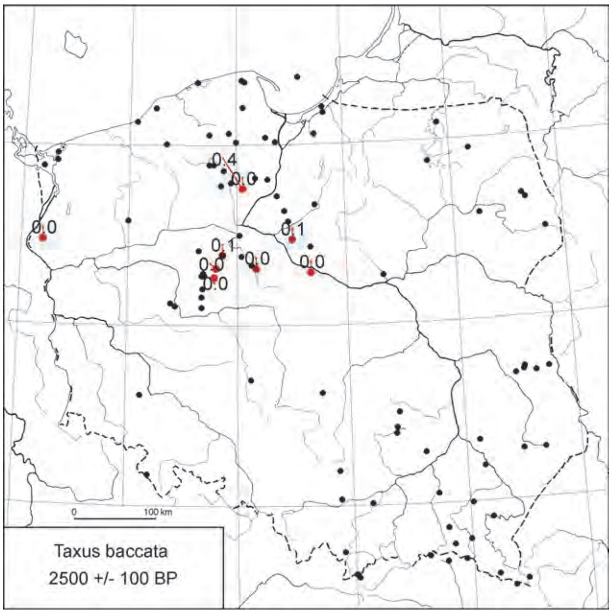


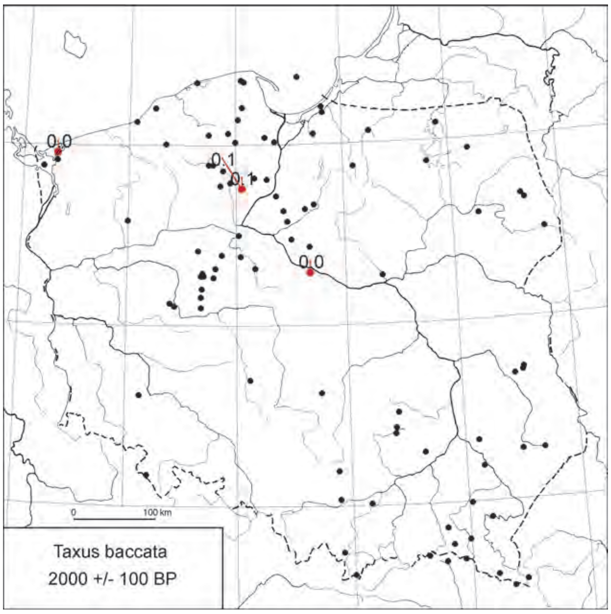
Taxus baccata
4000 +/- 100 BP

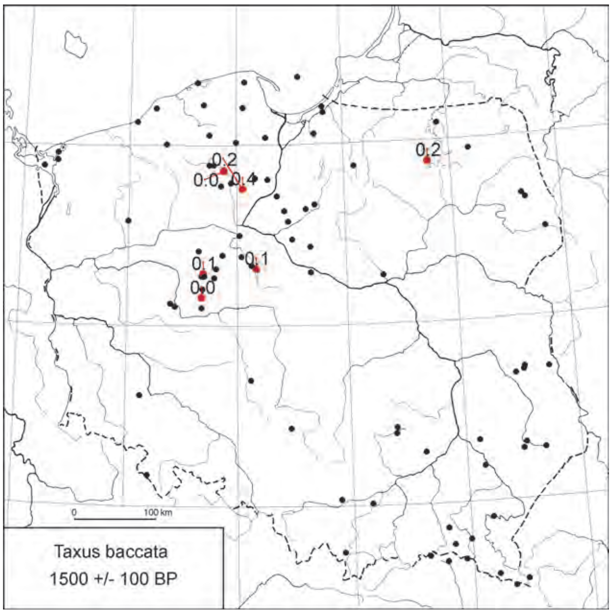


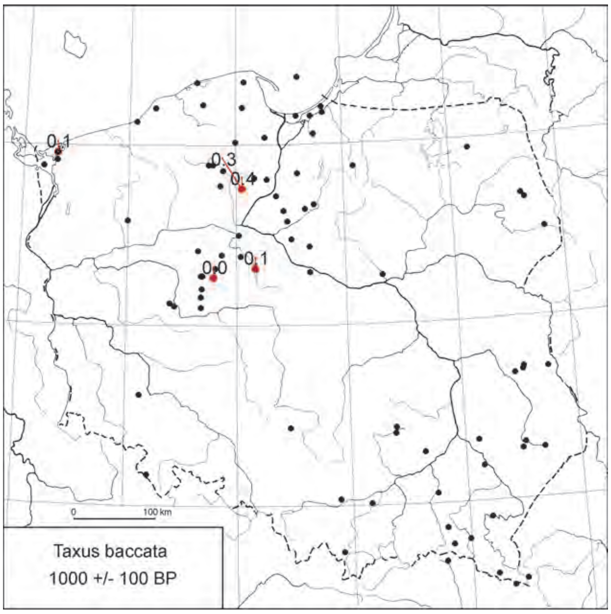
Taxus baccata
3500 +/- 100 BP

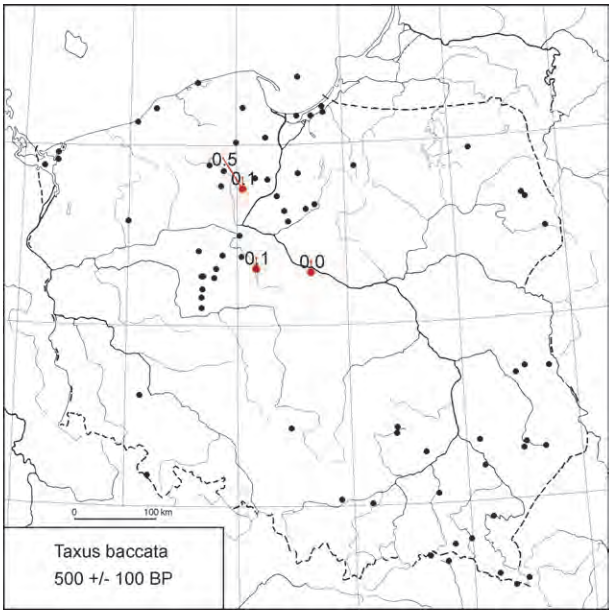

0.1
0.1
0.1
0.2
0.1
0 100 km
Taxus baccata
3000 +/- 100 BP

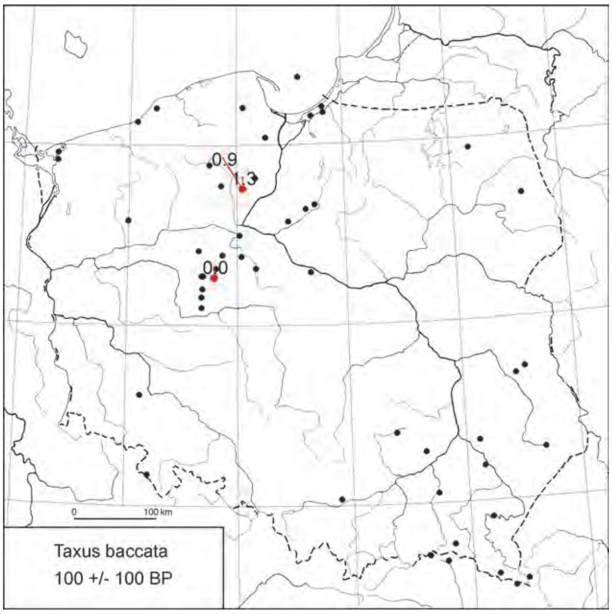

0.4
0.0
0.0
0.1
0.1
0.0
0.0
0.0
0.0
0 100 km
Taxus baccata
2500 +/- 100 BP


0.0
0.1
0.1
0.0
0 100 km
Taxus baccata
2000 +/- 100 BP


0.2
0.2
0.0
0.4
0.1
0.1
0.0
0 100 km
Taxus baccata
1500 +/- 100 BP


0.1
0.3
0.4
0.0
0.1
0 100 km
Taxus baccata
1000 +/- 100 BP


0.5
0.1
0.1
0.0
0 100 km
Taxus baccata
500 +/- 100 BP


0.9
1.3
0.0
0
100 km
Taxus baccata
100 +/- 100 BP

Tilia L. – Lime

Mirosława Kupryjanowicz, Anna Filbrandt-Czaja, Agnieszka M. Noryśkiewicz,
Bożena Noryśkiewicz, and Dorota Nalepka

Present distribution in Europe

At the present day five species of *Tilia* occur in Europe (Tutin et al. 1968). The range of *Tilia cordata* Mill. covers almost the whole continental part of Europe. The northern limit of its range roughly follows latitude 63°N, while its southern border reaches the Pyrenees, southern France, central Italy and the Balkans, the southern margins of the east-European lowland and the southern Ural Mountains (Boratyńska & Dolatowski 1991). It is also present in the Caucasus.

The distribution of *Tilia platyphyllos* Scop., is broadly similar to that of *T. cordata*, with which it can form hybrids (*T.* ×*vulgaris* Hayne, the tree widely planted in parks and gardens), but it does not extend as far north or east in Europe. It is most common in southern and central Europe, south of a line running from northern France, Belgium and central Germany to central Poland. Outlying populations occur in scattered sites in England, the Netherlands and Sweden, and particularly around the western coasts of the Baltic Sea in Denmark and northern Germany. Its eastern boundary extends through Belarus and western Ukraine to the mouth of the Dniestr river, but it does not occur in the Caucasus. Its southern border follows the Mediterranean Sea and the Pyrenees; it is absent from the Iberian Peninsula (Boratyńska & Dolatowski 1991).

Tilia tomentosa Moench and *T. rubra* DC. both occur mainly in the Balkan Peninsula, extending north to Hungary, and in some areas to the east, whilst *T. dasystyla* Steven is endemic to the Crimea (Tutin et al. 1968).

Present distribution in Poland

Two species of *Tilia* occur in Poland (Fig. 72). *Tilia cordata* is a transgressive species, occurring there entirely within the wider range of the species. At the present day it is found scattered throughout the country on suitable soils, but it is most often found in western and southern Poland (Boratyńska & Dolatowski 1991, Zając A. & Zając M. 2001). *Tilia platyphyllos* is here at the north-eastern limit of its range and occurs in the southern part of Poland only up to latitude 52°N (Boratyńska & Dolatowski 1991, Zając A. & Zając M. 2001).

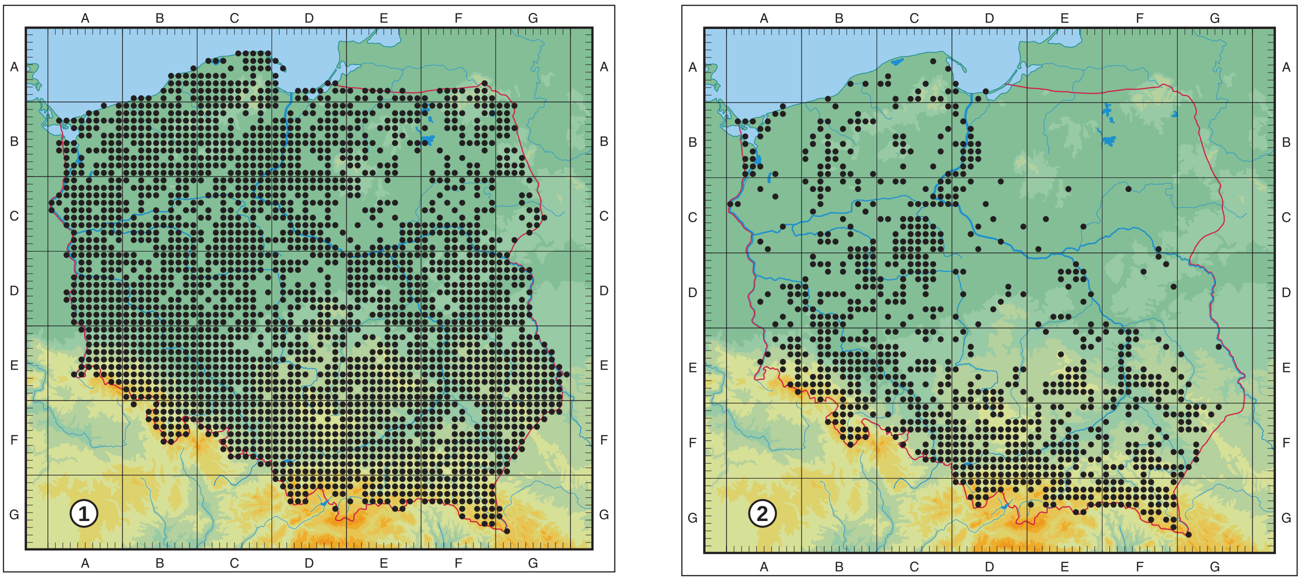


Fig. 72. Present-day distribution of 1 – *Tilia cordata* Mill. and 2 – *T. platyphyllos* Scop. in Poland (after Zając A. & Zając M. 2001)

ECOLOGY

Both species occurring in Poland appear to be indifferent to the degree of continentality of climate. They prefer habitats with rich, mineral-humic soils. The requirements of *Tilia platyphyllos* are greater than those of *Tilia cordata* in respect of both soil richness and moisture. *Tilia platyphyllos* grows on slightly moist, eutrophic soils, while *Tilia cordata* on slightly moist eutrophic to mesotrophic soils (Zarzycki et al. 2002). Both species occupy slightly acid to alkaline habitats, tolerating neither too acid (Jaros 1952, Zarzycki et al. 2002) nor too salty soils (Boratyńska & Dolatowski 1991). In their early stages limes are shade-tolerant, however their requirement for light increases with age.

Limes are monoecious trees with hanging inflorescences consisting of hermaphrodite flowers, clustered in groups of two to eleven, forming a cyme. *Tilia platyphyllos* flowers in the middle of June, usually two weeks earlier than the abundantly flowering *T. cordata* (Hofman & Michalik 1998). Their fruit is 1-, 2- or 3-seeded nut ripening in September (Jaros 1952, Boratyńska & Dolatowski 1991). Limes are long-lived trees reaching an age of 500–800 years (Seneta 1973). Growing alone in open habitats they reach maturity at the age of 20–30 years but within closed woods they bear fruit slightly later, around the age of 40–50 years (Jaros 1952). They reproduce both from seeds and from suckers. Vegetative reproduction of *T. cordata* prevails over sexual reproduction (Kieliszewska-Rokicka 1991).

T. cordata is a characteristic species of the *Carpinion betuli* alliance (Matuszkiewicz W. 2001). It occurs mainly in subcontinental oak-hornbeam forests with lime (*Tilio-Carpinetum*), and also in lowland community *Acer platanoides-Tilia cordata* Jutrz.-Trzeb. 1993, known from many sites in the young glacial areas of northern Poland. Isolated individuals can grow in beech, oak, and mixed coniferous forests as well as in riverine forests. *T. platyphyllos* is a characteristic species of the *Tilio platyphylli-Acerion pseudoplatani*, an alliance that combines two communities, both mountain sycamore forests and sycamore-lime slope forests, that occur on mountain forelands and uplands. In these latter communities *T. cordata* is a characteristic species.

POLLEN PRODUCTION AND DISPERSAL

Limes are principally insect-pollinated trees, though wind-pollination also occurs. They produce relatively numerous pollen grains – one flower produces about 43,500 grains (Dyakowska 1959). The pollen grains are large and relatively heavy (Dyakowska & Zurzycki 1959). These features of *Tilia* pollen grains, together with the entomophily of the tree, result in poor pollen dispersal and consequently underrepresentation of lime in pollen diagrams (Andersen 1970, Środoń 1991). The structure of the exine enables palynologists to distinguish *Tilia cordata* (Praglowski 1962, Andrew 1971, Stockmarr 1974, Christensen & Blackmore 1988) and *Tilia tomentosa* (Mamakowa 1989), and also a morphological type *Tilia platyphyllos*-type, which in Holocene sediments of Poland corresponds with typically formed pollen grains of *T. platyphyllos*. Less typical grains of the latter species may get recorded as *T. cordata*. However, the determination of *Tilia* pollen is very often only made to the genus level.

Pollen grains of *Tilia* are resistant to corrosion, and even if they are slightly damaged they can still be readily identified. Thus, they are often recorded as reworked pollen material from deposits otherwise representing periods with a climate that excludes the possibility of presence of this tree (Iversen 1973). Resistance of lime pollen to destruction can result in overrepresentation of this taxon in dry sediments that have undergone slight oxidation.

EXPANSION IN EUROPE DURING THE LATE GLACIAL AND HOLOCENE

It is clear that the central and southern part of Italy contained important refugia for *Tilia* during the last glacial stage. In pollen diagrams from long continuous lacustrine sequences from Italy *Tilia* appears repeatedly in all the interstadials of the Vistulian (Follieri et al. 1998, Allen et al. 2000), and sometimes even exceeds pollen values of 5% (Bertoldi 1980, after Bennett et al. 1991), though it has not actually been recorded during the glacial maximum itself. Bennett et al. (1991) considered that the Italian Peninsula was the only European refugial area for *Tilia*, but this overlooked its occurrence in the Pleniglacial pollen record from the former Lake Xinias in Greece (Bottema 1979). The early occurrence of *Tilia* during the Late Glacial or Holocene (there are differing views on precise dating) of Tenaghi Phillipon (Wijmstra 1969) and other sites in the Balkans, also demands the existence of nearby refugia. It would be strange if the Balkan Peninsula, which currently holds four species of *Tilia*, was not a major refugial area for this genus, as it was for many other temperate trees. No comparative genetic studies of *Tilia* populations have yet been carried out, but these will probably resolve some of these uncertainties.

Huntley and Birks (1983) suggest that *Tilia* began its expansion in south-eastern Europe and the southern Alps during the Late Glacial, perhaps from about 11,500 BP. Already at the beginning of the Holocene (10,000 BP) the range of this taxon encompassed the whole southern part of the continent, extending from Greece as far as south-western France. A thousand years later (9000 BP) it moved further to the west, extending up to the Pyrenees, and it might have expanded into the lowlands of northern Europe, reaching Poland. During the mid-Holocene (8000–5000 BP) lime became a very important element within the forests over the greater part of Europe, including the British Isles and the southern part of Norway, Sweden and Finland. The maximum Holocene range of lime was reached at about 5000 BP. In the Late Holocene (from about 4000 BP) its range was considerably reduced, mainly in the north and the east of the continent and, to a lesser degree, in the south (Huntley & Birks 1983). Cooling of climate was probably the main reason, but the intensified pressures of human activities may have also influenced this reduction in range.

MIGRATION PATTERN IN POLAND (Fig. 73)

11,500 – 10,000 BP

The dot maps drawn for the accepted time horizons of the Late Glacial and the early Holocene (11,500–10,000 BP) show single sites where low *Tilia* pollen values have been found. They probably reflect the presence of redeposited pollen grains because at the majority of these sites the sediments contain considerable amount of allochthonous material. The amount of lime pollen, which can be recognised, even in a very poor state of preservation resulting from secondary water transport, may be quite high in the assemblages from this type of sediment.

9500 BP

On the 9500 BP map, among the sites in various parts of the country displaying scattered low values of redeposited lime, relatively high values are noticed from a particular horizon at the site of Smerek in the Bieszczady Mountains (3.3%). In this case they can be explained in a different way. The pollen assemblage with high values not only of *Tilia* but also of *Ulmus* and *Corylus* derives from silty sediments with a very low sedimentation rate. Thus the pollen assemblage contains pollen grains which had been accumulating over a long time interval, and does not show the correct picture for this restricted time horizon (Ralska-Jasiewiczowa, oral information). At other sites in this region, also at nearby Tarnawa Wyżna, lime pollen does not occur at this period (Ralska-Jasiewiczowa 1980).

9000 BP

At 9000 BP the north-western part of Poland including the Wielkopolska area, the Pomeranian Lake District, the Baltic Coastal Zone, and the catchment of the lower Vistula river is distinguished by lower values of lime pollen than in other regions. This pattern may record pollen reworked, or brought in by long-distance transport. The actual distribution of its various values across Poland may signify the approach of the front of lime migration towards the southern and eastern borders of Poland, thus, indicating the directions of its future pathways. Relatively high values of *Tilia* pollen (1–2%) recorded in the southern part of the Silesian Upland may illustrate the first and oldest route of lime migration from southern Europe through the Moravian Gate.

8500 – 6500 BP

The 8500 BP isopollen map records the slow expansion of lime across almost the whole area of Poland, apart from the western and north-western parts of the country. Two areas of higher values of *Tilia* pollen are recorded on this map; one in southern Poland, with values exceeding 3% in the Bieszczady Mountains, may suggest a direction of expansion from the south and south-east. The other one in the area of the Mazurian Lake District may indicate a less probable route from the north-east.

On the 8000 BP isopollen map, a small area with the very high *Tilia* pollen values (7–10%) appears for the first time in the areas of the Jasło-Sanok Depression and in the Beskid Niski range. Analysis of the succeeding isopollen maps, from 7500 BP onwards, indicates that this patch persisted there up to historical times. Its relatively weak expression on some of the maps (for example on the 6500 BP map), may have resulted from statistical ‘smoothing’ of pollen percentage values, or from omitting pollen peaks which fall between the time horizons selected for data input (for example, the 30% peak of lime pollen values noticed at Szymbark in the Beskid Niski range just prior to 7500 BP). In the majority of diagrams from this area lime displays higher pollen values than in other places in the Carpathians. Even at the present time this is the region of the Carpathians where lime is most common. For example, in the Beskid Wyspowy range, near Muszyna, there is a unique lime forest reserve with *Tilia cordata* (Fabijanowski 1961). All these facts lead to the conclusion that *Tilia* had, in the past, its migration route from the south across the lower central area of the Carpathians (between the higher western and eastern ranges). This area includes the Beskid Niski and partly the Beskid Wyspowy ranges, as well as the Jasło-Sanok Depression. This migration route was established about 8000 BP and is further reflected in the high percentages of lime pollen in this area on the maps from younger periods.

Between 8500 and 8000 BP the areas of initially low *Tilia* pollen values in western and north-western Poland (up to 0.5%) show an increase of its pollen up to values of 1–2% covering at that time almost the whole country. Later lime expanded into the areas of Wielkopolska, the Pomeranian Lake District, and the Baltic Sea coast. About 7500 BP this led to connection of the western area, where *Tilia* was more abundant (2–3%), with the north-eastern area. The pattern of distribution of *Tilia* pollen values on the 7500 BP isopollen map supports the opinion of Ralska-Jasiewiczowa (1983) that at this stage lime, presumably *T. cordata*, when it expanded into the lowlands, preferentially occupied areas of very fertile soils, associated with deglaciated terrain formerly occupied by the Vistulian ice sheet (the islands of 3–5% values in the lake districts). The shift of values up to 3% to the Western Carpathians and across the Silesian Upland to the Sudetes supports the idea that *T. platyphyllos* was also expanding at that time. At about 7000 BP this expansion was recorded by higher pollen values (5–7%) in the Sudetes and in the Lower Silesia area.

6000 BP

The optimum development of lime occurred at about 6000 BP. The region of its greatest abundance formed a belt across much of northern Poland, which included north-eastern Poland, the catchment of the lower Vistula river, the eastern part of the Baltic Coastal Zone, and the Pomeranian Lake District. Lime pollen values there reached 3–5%, and in the north-western part of the Mazurian Lake District they even exceeded 5%. Lime had also a considerable presence in the Bieszczady Mountains, the Beskid Niski range, Lower Silesia, and Wielkopolska. The areas with lowest pollen values (1–2%) were reduced to the north-western margins of Poland, the Świętokrzyskie Mountains, and the Lublin Upland with Polesie Lubelskie.

5500 – 3000 BP

By 5500 BP the first signs of lime regression appeared. Cooling of climate at the end of the Atlantic period could have been one of the causes of this change together with gradual transformation of soils. Increasing destruction of forests by Neolithic and later Early Bronze settlements could have also been of substantial importance. According to the isopollen maps for 4500 and 4000 BP, this process advanced faster in the eastern Poland, and in the Baltic Coastal Zone. Consequently, it is difficult to explain an expansion of lime at 4000 BP in south-western Poland (statistical effect of Kunice site?). There was a marked increase in the rate of *Tilia* pollen decline between 4000 and 3500 BP. In the Wielkopolska area this rapid fall in *Tilia* values was perhaps influenced by the equally rapid expansion of oak-hornbeam forests. Slightly higher its values persisted for the longest time in the north, in the area of the Vistula estuary, and neighbouring areas of Warmia (2–3%). They also persisted in the south, in the lowest parts of mountains and in their forelands, mainly in the lower central area of the Carpathians, in adjoining mountain ranges, and in the Silesian Upland (7–10%) (*T. platyphyllos*?). However, here also they gradually decreased to 2–3% by 3000 BP.

2500 – 100 BP

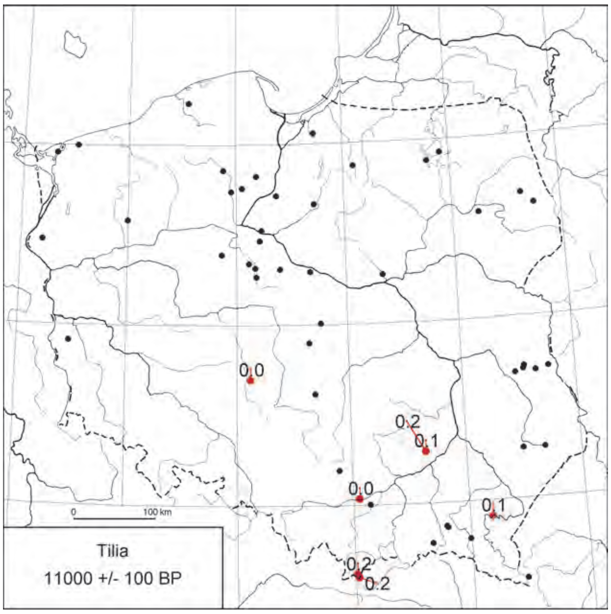
By 2500 BP values of *Tilia* pollen did not exceed 1% over most of the territory of Poland. The analysis of the isopollen maps for the period from 2500 BP up to the present day indicates that the role of lime was gradually reduced. Its elimination from forest communities began in the north-western part of Poland, and this process gradually advanced in a south-eastern direction. In the north-west, during the period from 2500 to 1500 BP, it may have resulted from the expansion of beech. Between 1500 BP – a time horizon representing the period of economic decline during the Migration Period, and 1000 BP – with the founding of the Polish State, the further subsequent reduction in *Tilia* pollen values to below 0.5% is recorded almost across the whole country.

On the maps for different time horizons for the last 2500 years islands of slightly higher *Tilia* pollen values appear in various regions of Poland. The majority of them reflect most probably local phenomena, often connected with temporary changes in settlement processes.

CONCLUSIONS

The isopollen maps for *Tilia*, though not distinguishing the two native species, which probably had different expansion pathways, suggest that the earliest migration routes of this taxon into Poland came from a southerly direction, mainly from the south and south-east. There may also have been a separate migration pathway bringing *Tilia* populations into north-eastern Poland, perhaps from some other undetermined eastern refugium. Though lime spread across most of the country, it particularly favoured areas of rich fertile soils, reaching its maximum abundance at about 6000 BP in a belt across much of northern Poland. The decline of *Tilia* began at about 5500 BP but accelerated from 4500 BP onwards with some regional variations in rate and has continued to the present day. This decline can be ascribed to a combination of different causes. Climatic changes, beginning with the cooling of climate from the end of the Atlantic period, were accompanied by increasing disturbance and destruction of forests by Neolithic and Early Bronze settlements. These in turn favoured conversion of forest communities to oak-hornbeam and beech forests, together with leaching and impoverishment of soils in many areas.

Fig. 73. *Tilia*: dot and isopollen maps for 11,000–100 ^{14}C yr BP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0.2
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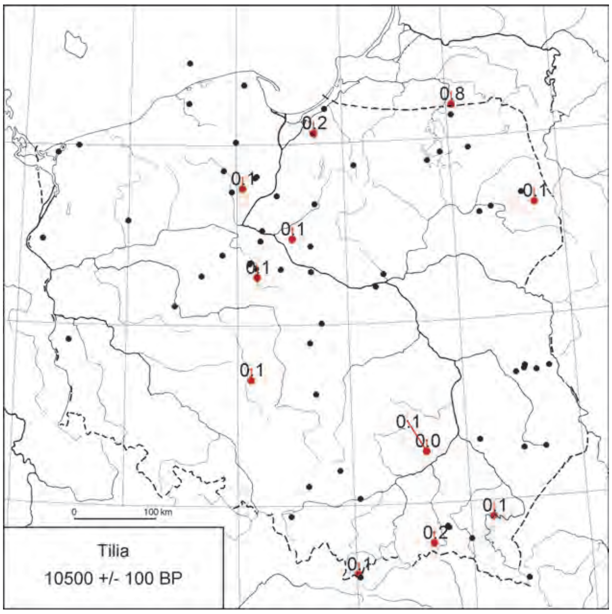
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0.1
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0.1
0.0
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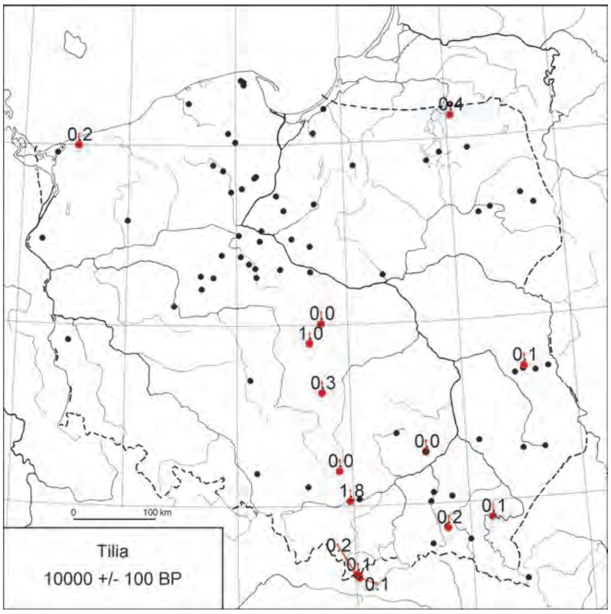
100 km
Tilia
10500 +/- 100 BP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1.0
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0.1
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0.1
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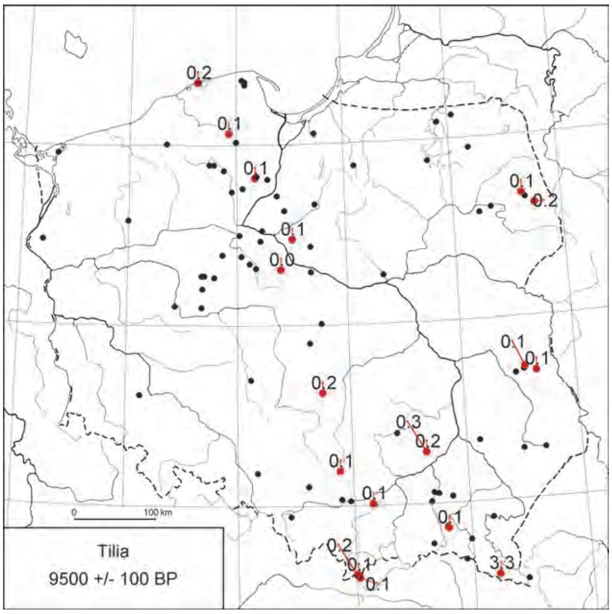
0.1
0
100 km
Tilia
10000 +/- 100 BP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0.2
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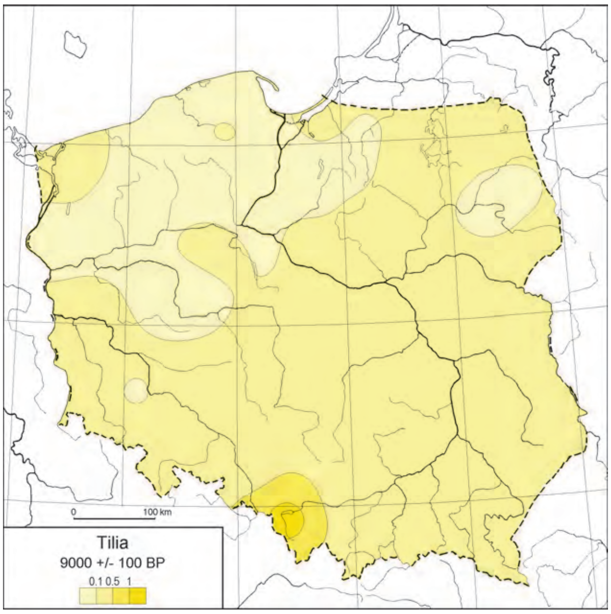
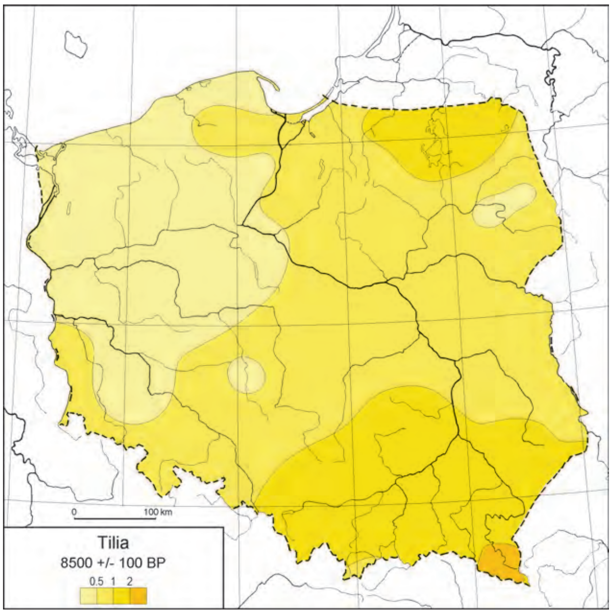
0.1
0.2
0.1
0.1
3.3
0
100 km
Tilia
9500 +/- 100 BP


0
100 km
Tilia
9000 +/- 100 BP
0.1 0.5 1


0
100 km
Tilia
8500 +/- 100 BP
0.5 1 2


0.01
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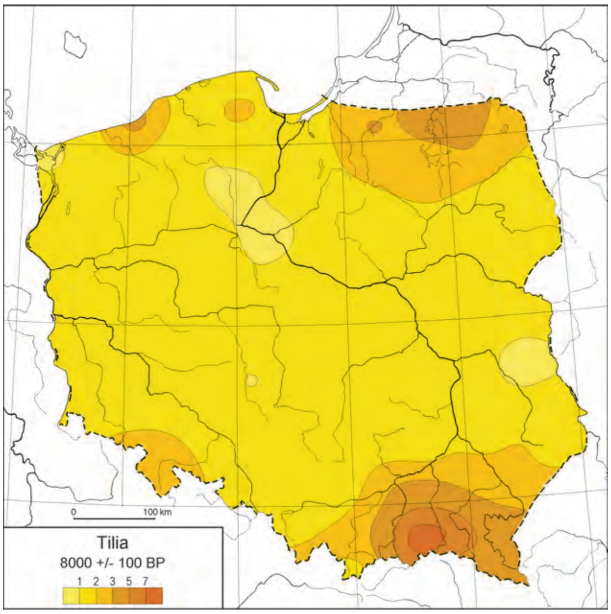
7
10
15
20
25
30
40
60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Tilia
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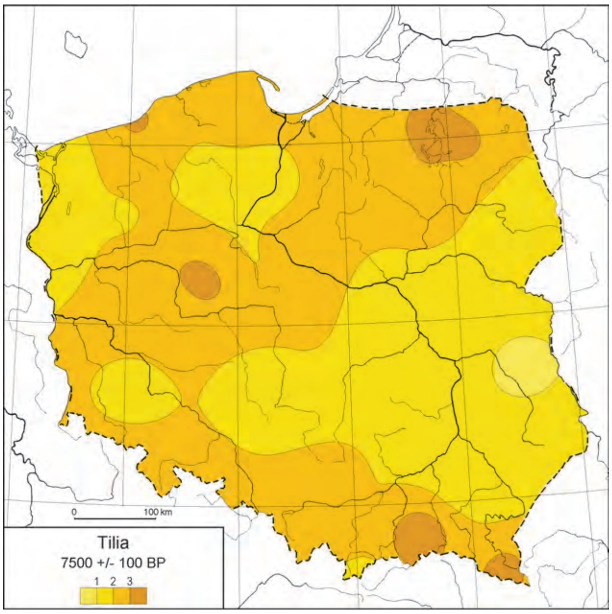
1 2 3 5 7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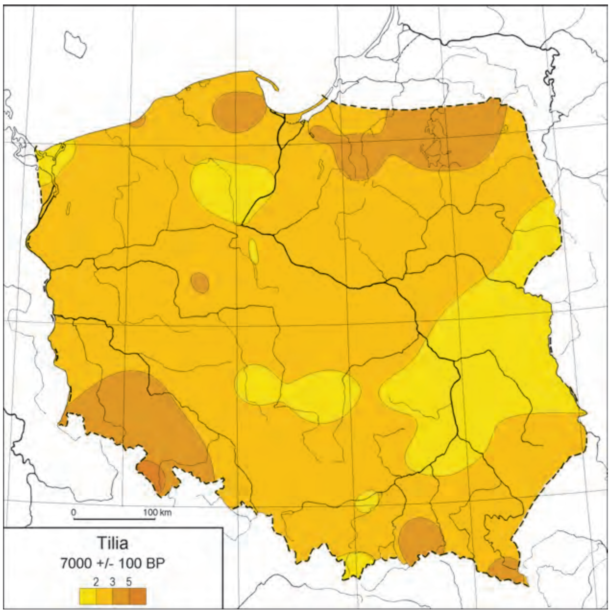
Tilia
7500 +/- 100 BP
1 2 3


0
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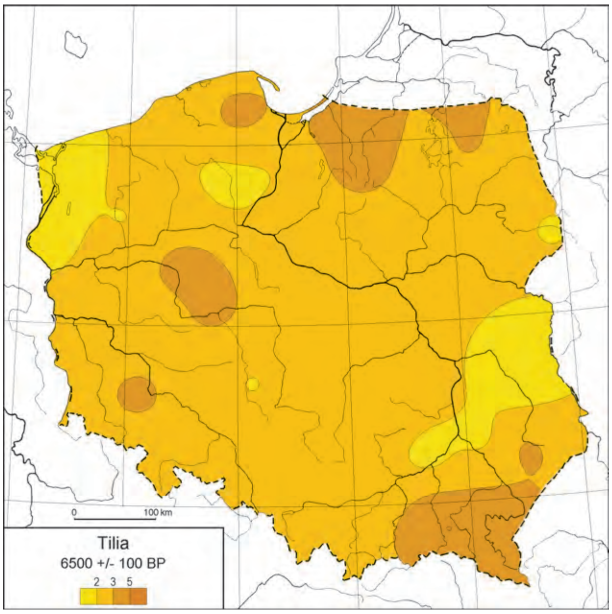
Tilia
7000 +/- 100 BP
2 3 5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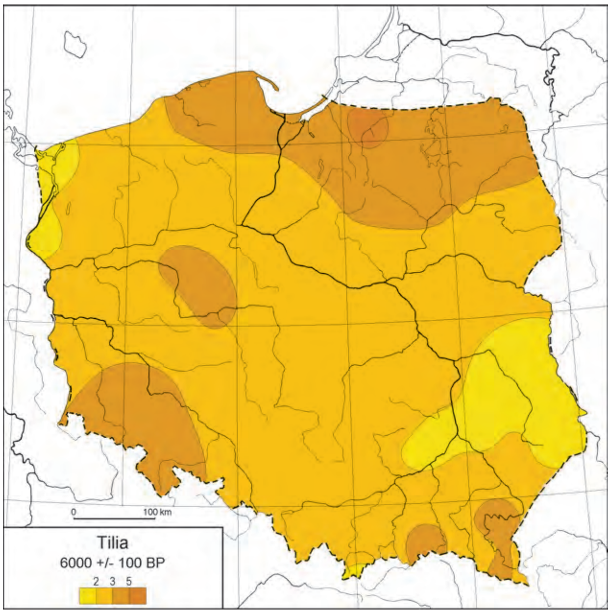
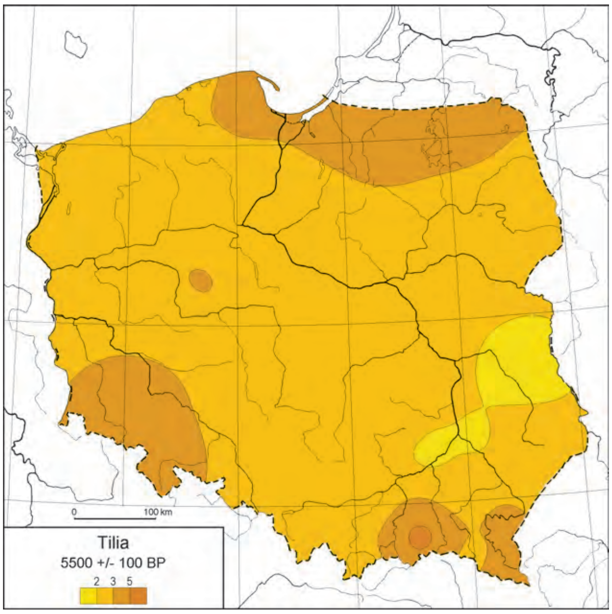
100 km
Tilia
6500 +/- 100 BP
2 3 5


0
100 km
Tilia
6000 +/- 100 BP
2 3 5


0
100 km
Tilia
5500 +/- 100 BP
2 3 5


0.01
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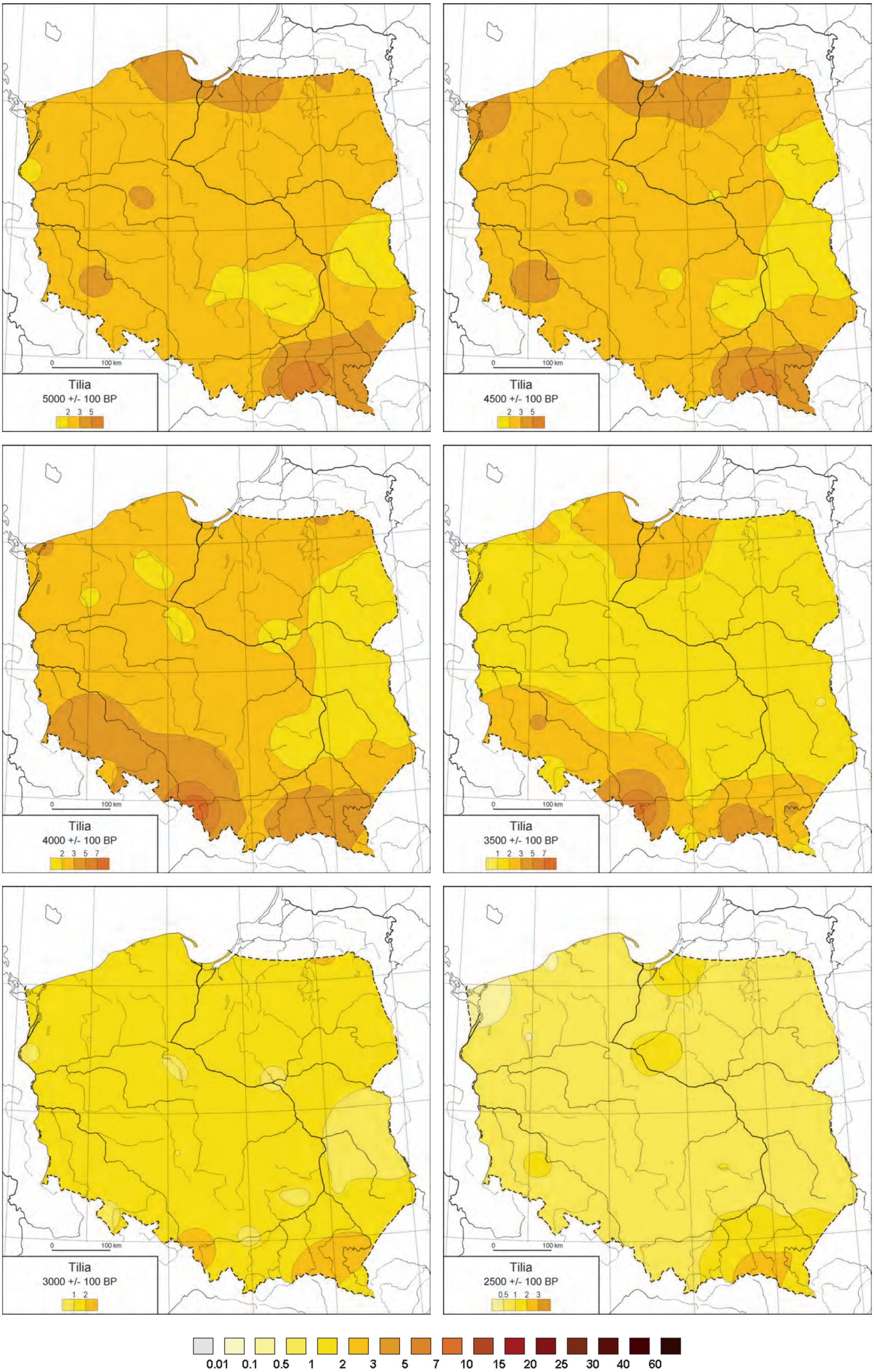
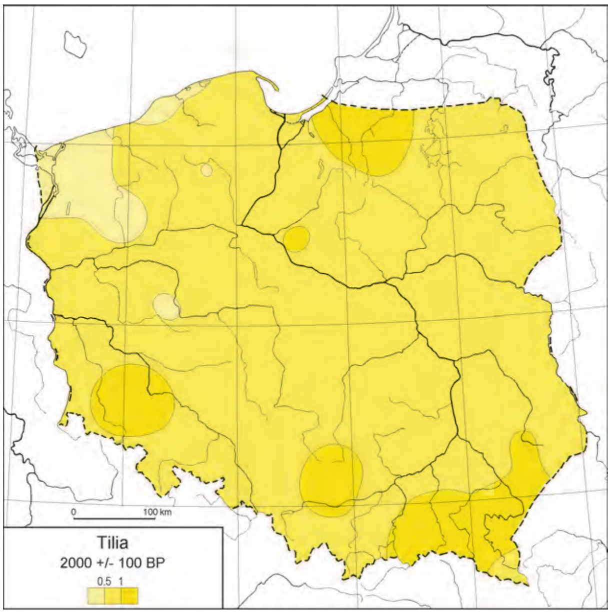
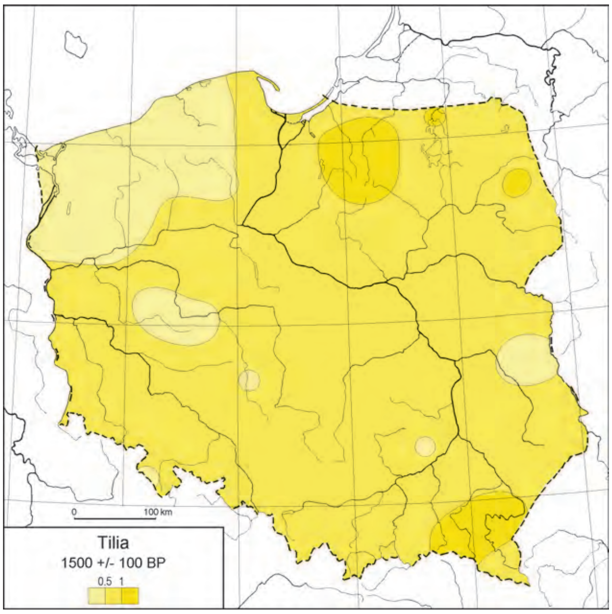

0
100 km
Tilia
5000 +/- 100 BP
2 3 5
0
100 km
Tilia
4500 +/- 100 BP
2 3 5
0
100 km
Tilia
4000 +/- 100 BP
2 3 5 7
0
100 km
Tilia
3500 +/- 100 BP
1 2 3 5 7
0
100 km
Tilia
3000 +/- 100 BP
1 2
0
100 km
Tilia
2500 +/- 100 BP
0.5 1 2 3
0.01 0.1 0.5 1 2 3 5 7 10 15 20 25 30 40 60


0
100 km
Tilia
2000 +/- 100 BP
0.5 1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Tilia
1500 +/- 100 BP
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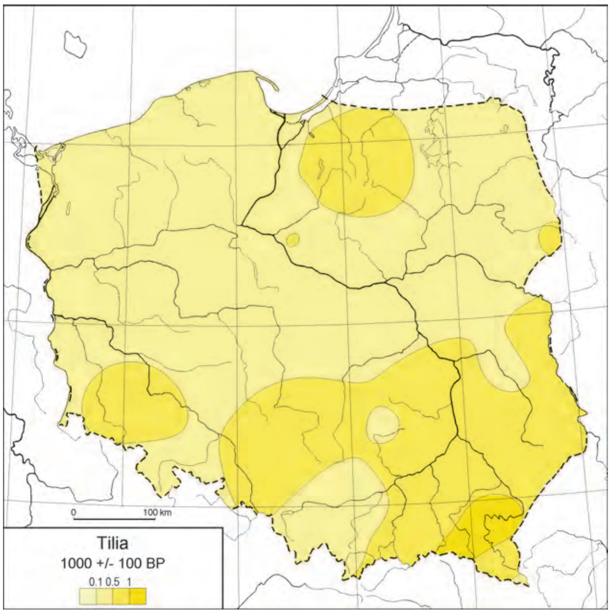
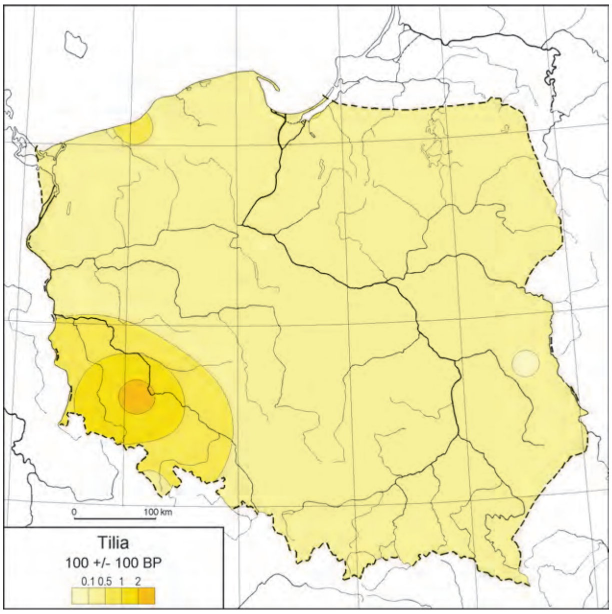

0
100 km
Tilia
1000 +/- 100 BP
0.1 0.5 1


0
100 km
Tilia
500 +/- 100 BP
0.5


0
100 km
Tilia
100 +/- 100 BP
0.1 0.5 1 2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Ulmus L. – **Elm**

JOANNA ZACHOWICZ, MAGDALENA RALSKA-JASIEWICZOWA, GRAŻYNA MIOTK-SZPIGANOWICZ, AND DOROTA NALEPKA

PRESENT DISTRIBUTION IN EUROPE

Today elm is seldom a dominant tree in European forests. It frequently occurs in mixed forests, mainly with *Fraxinus excelsior*, *Quercus robur* and/or *Acer pseudoplatanus* (Huntley & Birks 1983).

Tutin et al. (1964) in Flora Europaea recognises five species of elm (*Ulmus*) as occurring in Europe, although the taxonomy may be more complex, and many hybrids occur too. The most widespread species *U. glabra* Hudson, covers almost the whole of Europe, apart from north-eastern Scandinavia. In the east it extends into Russia and in the south to the Mediterranean countries apart from the western part of the Iberian Peninsula (Zieliński 1979). *U. procera* Salisb. occurs in western and southern Europe, *U. minor* Mill., a taxonomically complex species, is widely distributed from France to Russia, not, however, extending into Scandinavia, northern Russia and some other parts of northern Europe. *U. canescens* Melville grows in the central and eastern Mediterranean region. *U. laevis* Pall. occurs in western-central, central and south-eastern Europe, as far east as the Caucasus (Seneta 1991), but the area of its occurrence becomes progressively restricted in the north and the south as western Europe is approached. Thus its range is wedge-shaped with the apex in central France (Huntley & Birks 1983).

It is quite problematic to distinguish individual species of *Ulmus* basing on their pollen morphology. According to Stockmarr (1970) there are differences in pore numbers in the pollen grains, but they have rarely been recorded in the fossil material due to the unreliability of this method (Tolonen 1980). Thus it is impossible to indicate which species, quite apart from almost ubiquitous hybrids, were growing during the Holocene in the particular regions of Europe.

PRESENT DISTRIBUTION IN POLAND

Three of the above species of elm occur in Poland (Fig. 74) today (Szafer et al. 1969). *U. laevis* is present in mixed deciduous forests throughout Poland, though it is rather rarely found in the south-eastern and north-eastern part. It is exclusively a lowland species (Zając A. & Zając M. 2001). Moreover, it is particularly associated with floodplain forest communities (Seneta 1991).

U. minor, similarly to *U. laevis*, is a lowland species that grows throughout the country but very rarely in the lake districts of northern Poland (Zając A. & Zając M. 2001). It grows in forests and on dry slopes.

U. glabra is the most common species in north-western and southern Poland where it grows both at lower and moderately higher altitudes in the mountains (in the Tatra Mountains it reaches above 1200 m a.s.l.) (Zieliński 1979, Zając A. & Zając M. 2001).

ECOLOGY

All the *Ulmus* species are tall trees reaching 30–40 m. They require moderately warm to moderately cool climatic conditions and generally favour moist and fertile soils but each species displays slightly different soil requirements. They are absent from shallow soils, prone to drought, on either acid or alkaline substrates. They also avoid waterlogged soils.

U. glabra develops well on moist to slightly moist, fertile, neutral, mineral-humic soils, but it particularly favours sandy clays (Zarzycki et al. 2002). It occurs in associations of the *Querco-Fagetea* class, of the *Fagetalia* order, and of the *Tilio-Acerion* alliance (Matuszkiewicz W. 2001). *Ulmus glabra* does not reproduce vegetatively by suckers, whereas the other species frequently do so (Huntley & Birks 1983). Single specimens of *U. glabra* at the age of 20 years may produce 165,000 seeds, whilst, at the age of 40–50 years, as much as 4,965,000 seeds (Boratyński & Filipiak 1999). It is the most resistant *Ulmus* species to Dutch elm disease. *U. laevis* likes moist and fertile soils, neutral and mineral-humic. It grows well on sandy loams and silty soils (Zarzycki et al. 2002). It occurs in associations of the *Alno-Ulmion* alliance (Matuszkiewicz W. 2001). It is relatively resistant to the elm disease. *U. minor* prefers dry to moist soils, rich, neutral and mineral-humic

(Zarzycki et al. 2002). It is the species most tolerant of drought and shade (Seneta 1991). It occurs mainly in the *Ficario-Ulmetum* association and in communities of the *Alno-Ulmion* alliance (Matuszkiewicz W. 2001). It seems to be the most susceptible to the elm disease amongst our native species (Seneta 1991).

POLLEN PRODUCTION AND DISPERSAL

Estimates are not available for the pollen productivity of individual flowers, branches and individual trees of *Ulmus* species, but Andersen (1970) studied the relative pollen productivity and pollen dispersal in forest of a number of tree taxa, including *Ulmus*. His comparisons between pollen assemblages from surface samples and actual forest composition suggested a correction factor of 2 for *Ulmus*, i.e. elm may be twice as abundant in forest vegetation (in percentage terms) than as represented in pollen diagrams. The rate of fall of *Ulmus* pollen grains in air is 0.032 m/s, and its coefficient of productivity in relation to Gramineae (Poaceae) (= 1) is 0.8 (Sugita et al. 1999). According to Huntley and Birks (1983) pollen values >2% indicate the presence of elm within the local vegetation, and pollen values >10% occur only in the areas where elm is an important component of the forest communities. These estimates seem to be too cautious. Values of pollen higher than 1% may already indicate the scattered presence of *Ulmus* in the region.

Ulmus flowers in March and April (Aerobiologic Database, Gdańsk 1994–2002) prior to the appearance of its leaves and those of other forest trees, and that is a reason why its pollen grains can be carried for long distances (Birks & Birks 1980).

EXPANSION IN EUROPE DURING THE LATE GLACIAL AND HOLOCENE

During the Late Glacial *Ulmus* pollen is found in small amounts at scattered sites in ice-free areas of Europe. By 11,000 BP elm was present in south-east Europe, and probably in the southern Alps (Huntley & Birks 1983) as well as in the north-western part of the Eastern Carpathians (Björkman et al. 2002, 2003). In these areas, after the decline of *Ulmus* pollen occurrence during the Late Glacial stadials, its values are already recorded as growing rapidly at the onset of the Holocene. Its range expanded gradually from south-eastern Europe into the north-west. By 9000 BP it had begun its migration towards the north-east, and at about 8500 BP *Ulmus* expanded northwards into Denmark. Later on, its pollen values were declining in south-east Europe and the southern limit of its range was moving northwards. By 5500 BP the area of reduced amounts of *Ulmus* pollen extended northwards, and at 5000 BP pollen values decreased also in northern Europe. Then, elm pollen values declined further, its range became fragmented, and areas

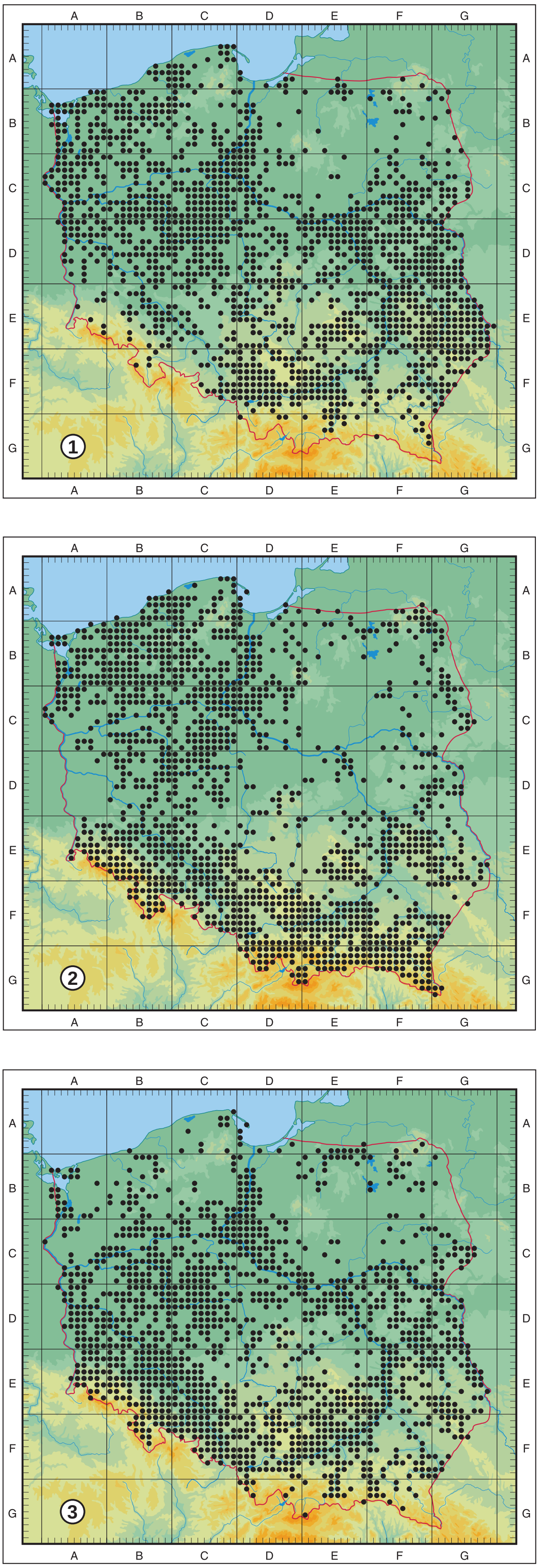


Fig. 74. Present-day distribution of 1 – *U. laevis* Pall., 2 – *Ulmus glabra* Huds. and 3 – *U. minor* Mill. in Poland (after Zając A. & Zając M. 2001)

with high pollen values became increasingly restricted to the east (Huntley & Birks 1983). These were clearly the consequences of spreading epidemic of Dutch elm disease.

The elm migration pattern during the early Holocene indicates the presence of refugia in the Balkans, the southern Alps, southern France, Russia (perhaps in the southern Urals) and in (or close to) south-west Britain. According to Huntley and Birks (1983) the present ranges of the species occurring in Europe suggest that *Ulmus glabra* is the most probably species to have had its refugia close to the British Isles, whereas *U. laevis* survived in eastern Europe in Russia, and *U. minor* expanded from refugia situated in southern Europe. As mentioned earlier, the undoubted occurrence of a refugium in the Eastern Carpathians has also been demonstrated (Björkman et al. 2002, 2003), its location pointing to *U. glabra* as the most probable species. Moreover, the finds of macrofossils of *Ulmus* in the Scandes Mountains in Sweden between 8500 and 8000 BP (Kullman 1998) suggest its appearance there shortly after deglaciation, thus coming from not very distant refugia (Stewart & Lister 2001).

MIGRATION PATTERN IN POLAND (Fig. 75)

11,500 – 10,500 BP

On the 11,500 to 10,500 BP maps there are slightly higher amounts of *Ulmus* pollen (0.6–0.7%) in southern Poland than in the other regions of the country (0.1–0.2%). On the 10,500 BP map they extend up to the basin of the middle Vistula river. However, there is no evidence to suggest that they represent anything other than reworked material or long-distance transport.

The latter suggestion is implied by the fact that at the same time, in two pollen diagrams from the north-western part of the Romanian Eastern Carpathians (Wohlfarth et al. 2001, Björkman et al. 2002, 2003) small maxima of *Ulmus* pollen, reaching a few percent, appear before 11,500 BP and at about 11,000 BP, as well as at about 10,900 BP coincidently with the maximum of *Picea*. In both cases this period is interpreted as the Allerød and the presence of *Ulmus* pollen as indicating trees growing *in situ* (Björkman et al. 2002, 2003). Then, in the Younger Dryas, the *Picea* values fall, and *Ulmus* pollen almost disappears, then emerges quickly again forming a massive curve sometime after the date of 10,325±150 BP. These data might suggest that the low pollen values of *Ulmus* on the Late Glacial maps from southern Poland may derive from long-distance pollen blown in from the Romanian Carpathians.

10,000 BP

The map shows pollen values up to 0.5% across the whole of Poland, with up to 1% in the Western Beskidy Mountains and 1–2% in the Tatra Mountains, as well as up to 1% in the uplands of central Poland as far as Polesie Lubelskie and the state boundary in the east.

9500 – 8500 BP

The pattern of isopolls on the 9500 BP map gives a clear picture of *Ulmus* expansion from the Eastern Carpathians (the Bieszczady Mountains 7–10%) and probably also from the Orava Basin (3–5%) (Rybniček & Rybničková 2002), and of the scattered presence of elm in the south-eastern part of the country.

The maps prior to 8500 BP indicate expansion of *Ulmus* from the three directions: at first, from the south and south-east and then, slightly later (9000–8500), from the north-east. Similar directions of expansion have already been suggested by Ralska-Jasiewiczowa (1983). This author has supposed that these were the migration routes of different elm species: *U. glabra* from the south and *U. laevis* (*U. minor*?) from the east.

8000 – 7500 BP

In the greater part of Poland *Ulmus* is represented by pollen values of 3 to 5%. In south-eastern Poland they reach 10%. These high elm pollen values result probably from the expansion of *Ulmus glabra* from its southern and south-eastern refugia. The representation of elm occurrence in the north-eastern areas also increases (5–10%), and this may confirm the existence of an eastern refugium.

Small, local islands of higher pollen values (5–7%) also appear in other areas of Poland. On the 8000 BP map the lowest elm values are found in the north-western part of Poland but already by 7500 BP they had become reduced to a small area in the middle part of the Baltic Coastal Zone. In this area *Ulmus* was probably losing its habitats in competition with hazel migrating from the north-west.

7000 – 6500 BP

Expansion of elm observed on the 7500 BP map in the south and north-eastern part of the country resulted around 7000 BP in the amalgamation of the southern and north-eastern ranges. The highest pollen values occur in the Sudetes and Carpathians and in their foothills, whilst the lowest are in the Szczecin Lowland. On the 6500 BP map *Ulmus* reaches its maximum for the Holocene in Poland, and only in north-western Poland and in the uplands of southern Poland do its values fall below 5%. The remaining parts of the country show values up to 7%, except for the Sudetes and Carpathians where they reach up to 10% and locally even higher (the Pieniny Mountains up to 15%). It can most likely be attributed to a considerable presence of *U. glabra* in the forests of the mountainous areas.

6000 – 5500 BP

The area of lower *Ulmus* pollen, centred on the upland of southern Poland, expands. In the west it merges with the north-western area and in the east reaches the state frontier. In the north-eastern part of the country values higher than 5% persist only along the middle Vistula and Narew valleys and in the eastern lake districts. On the 5500 BP map the area with elm pollen values of up to 7% and more is mainly restricted to the south. This covers the mountain regions (locally up to 10%), the adjacent Sandomierz Depression, in the south-west the Silesian Lowland and, in the south-east, the Lublin Upland with Wołyń and Polesie Lubelskie. The whole remaining parts of the country yield elm pollen values up to 5%.

5000 – 4500 BP

Across the greater part of lowland Poland as far as where the Bug river flows into the Vistula river *Ulmus* pollen values fall below 3%, apart from the northern part of the eastern lake districts which display values up to 5%. This fall results undoubtedly from the development of elm disease. The expanded 'corridor' on the 5000 and 4500 BP maps apparently connecting these lake districts in the north-east with the middle and southern parts of Poland, and marked by elm values up to 5% is probably a statistical artefact of the map-writing programme. On the additional 4800 BP map (Ralska-Jasiewiczowa et al. 2003b and Fig. 75, this volume) the northern boundary of the 3% isopoll for elm runs continuously almost parallel to the 52°N, separating the southern part of Poland with its higher elm values. This suggests that to the north Dutch elm disease may have spread at that time from the west to the east across the mid-Polish lowlands and the lake districts. Higher values of elm (5–7%) still persist in the Carpathians and in their foreland (most likely *U. glabra*). A similar pattern on the 4500 BP map in this account differs only by the low pollen values in north-western Poland having expanded southwards.

4000 BP

On 4000 BP map there is an important change in the distribution of elm pollen values in the territories of Poland. Values of 5% or more are found only in the Carpathians and their foreland, including Roztocze and the Wołyń region in the east, and in the Sudetes in the west. In all other regions of the country the maximum *Ulmus* pollen values reach only up to 3%, and in north-western Poland and in the marshy areas of eastern Poland they are 1–2%. If this is to be explained by a further spread of Dutch elm disease, then its main attack might have shifted southwards from the areas decimated earlier. However, it should also be born in mind that the period of 4500–4000 BP was the time of the maximum development of Neolithic cultures that may also have contributed to the destruction of elm.

3500 BP

The area with more abundant elm in the forests was restricted to the Carpathians and their forelands. In south-western Poland elm pollen values up to 3% still occur. Beyond these areas, everywhere else elm pollen values below 2% indicate only local and scattered occurrence of elm.

3000 – 2500 BP

As the changes in the isopoll pattern show, the importance of elm in the plant communities was submitted to further decline. At first, the pollen values of elm are 2% throughout the country. Slightly higher values (2–3%) are still found in the Carpathians. In the central part of the Baltic Coastal Zone the values of elm do not exceed 1%. This area of very low values extends gradually, and on the 2500 BP map comprises the whole northern part of Poland with its limit at 52°N, as on the 5000 BP map.

2000 – 500 BP

The further decline of elm advanced from the north-western direction, where at this time an intensive expansion of beech was initiated, and later also from the north-east. Generally, over the whole Poland values of elm pollen do not exceed 2%, and in the greater part of the country they are <1%. Thus the 500 BP isopollen map somehow repeats the pattern of the 5000 and 2500 BP maps but with drastically lowered values of *Ulmus* pollen.

100 BP

On this map a slightly different pattern of *Ulmus* isopolls is observed. Values of 0.5 to 1% are recorded from almost the whole territory of Poland with a few small 'islands' with up to 2%. Elms are virtually absent from the Baltic Coastal Zone and the whole of eastern Poland (values <0.5%).

CONCLUSIONS

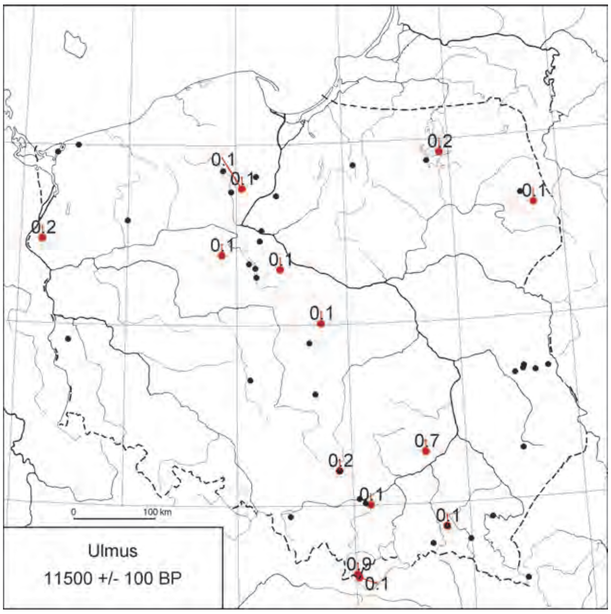
Elms migrated into Poland from different directions: between 10,000 and 9500 BP elm, probably *U. glabra*, arrived in the Carpathians, from the south-east. Elm is known to have been present in the mountains of north-west Romania already during the Allerød. Also elm may have immigrated via Orava. Slightly later (9000–8500 BP) the direction of *Ulmus* migration from the north-east is clearly detectable, which would agree with the suggestion by Huntley and Birks (1983) that *Ulmus laevis* had refugia in Russia. The maximum Holocene distribution of *Ulmus* was reached around 6500 BP.

It is now commonly accepted that the elm disease caused by fungus *Ceratocystis ulmi* (Ascomycetes) and spread by beetles of the genus *Scolytus*, was the cause of the elm decline recorded in pollen diagrams by the end of mesocratic phase (Rackham 1980, Groenman-van-Waateringe 1983, Peglar 1993, and others). According to the central-European literature the elm decline occurred generally at about 5000 radiocarbon years BP. Basing on the isopollen maps it can be assumed that the first signs of this disease may have already appeared in Poland around 6000 BP. Such early collapses of *Ulmus* pollen values have already been reported from the area of north-western Poland (Wolin Island, at about 5800 BP Latałowa 1992) and also from north-western Denmark (at about 6500 cal BP = ca. 5750^{14}C BP, Andersen & Rasmussen 1993), thus generally from the expected direction of approach of this disease. We can also assume that destruction of elm was additionally increased by the agricultural and pastoral activities of Neolithic populations (for example see Peglar 1993). When comparing the maps of settlement distribution in early Neolithic time (6000–5000 BP) with the maps recording elm pollen decline, we cannot exclude the joint influence of both these factors. However, the belt of elm destruction in the lowland area of Poland (west-east) suggested by the 5000 BP map and observed on both the 4800 BP map and on the following ones may indicate further a shift in the progress of this disease.

The next sudden drop in elm decline recorded on the 4000 BP map may have resulted principally from human activities, such as farming and nomadic shepherding of the late Neolithic populations. Decimation of all three species of elm, expressed by the pollen values reduced to 1–2% on the 3000 BP map, and 0.5–1.0% over the whole northern part of Poland on the 2500 BP map, must have been caused mainly by the settlement and economic activities of the Lusatian tribes. The picture on both these maps suggests destruction of *U. glabra* in the forests of the Carpathians and the 2500 BP map implies slightly less intensive destruction of elm species over the whole upland area of southern Poland.

The 4800, 2500 and 500 BP maps shows strong similarities in the pattern of *Ulmus* maps: the lower pollen values occur in the lowland, and higher values in the upland and mountains parts of Poland. It might be explained by the higher sensibility of lowland elm species – *U. laevis* and *U. minor*, than that of mountain elm, *U. glabra*, to both – elm disease, and economic activities during the period of intensified human impact, and generally by more intensive human activities on lowland areas.

Fig. 75. *Ulmus*: dot and isopollen maps for 11,500–100 ^{14}C yr BP. The map for time-horizon 4800 BP is added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0.1
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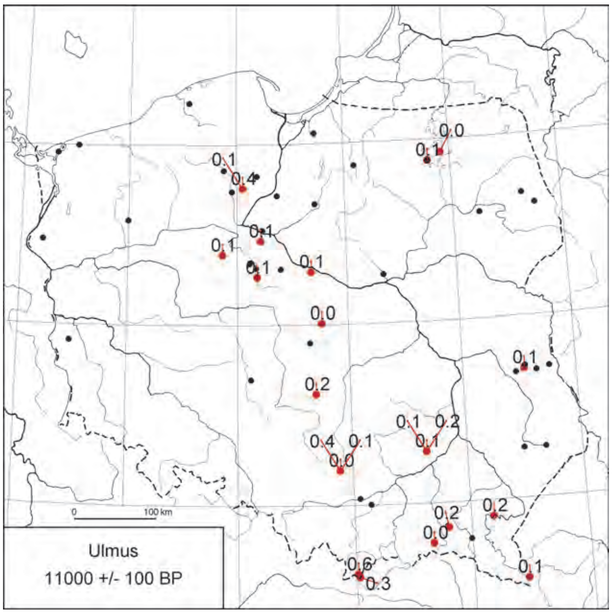
0.2
0.1
0.1
0.9
0.1
0 100 km
Ulmus
11500 +/- 100 BP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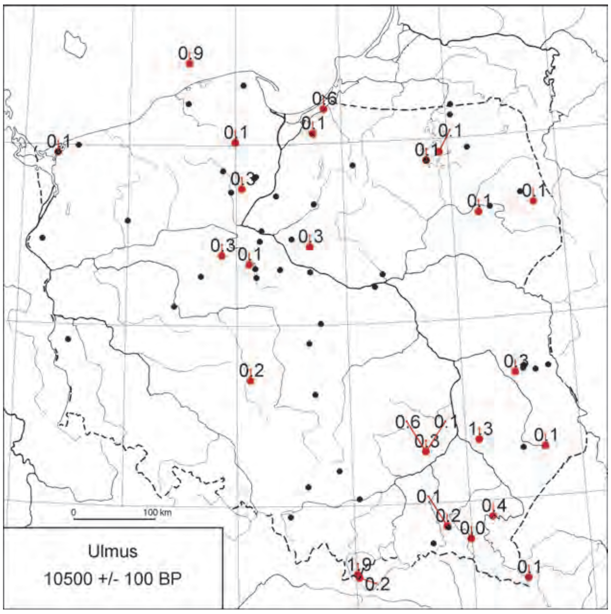
0.1
0.4
0.1
0.1
0.1
0.1
0.0
0.1
0.2
0.1
0.2
0.4
0.1
0.0
0.1
0.2
0.2
0.2
0.0
0.6
0.3
0.1
0 100 km
Ulmus
11000 +/- 100 BP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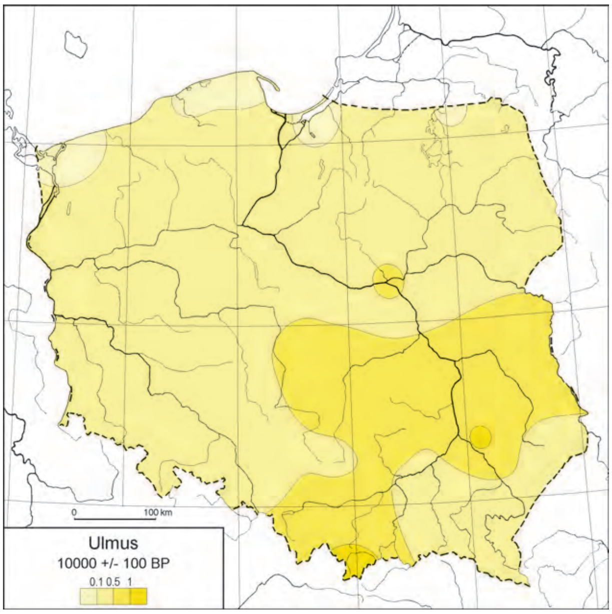
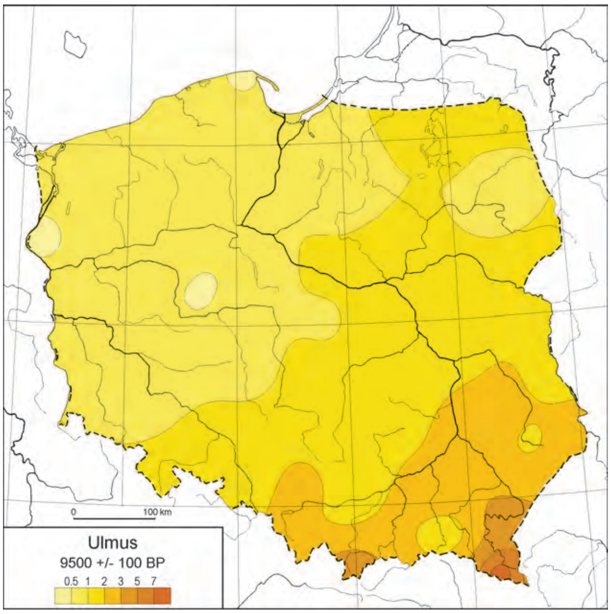
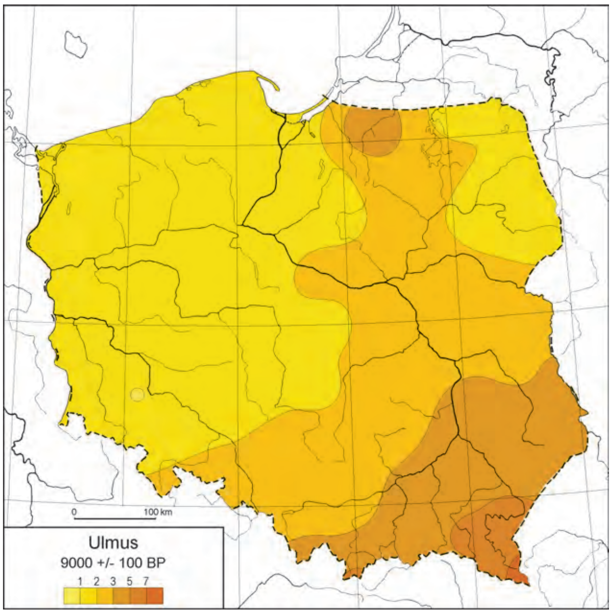
0.6
0.1
0.1
0.1
0.1
0.1
0.3
0.1
0.1
0.3
0.1
0.3
0.2
0.3
0.6
0.1
1.3
0.3
0.1
0.1
0.4
0.2
0.0
1.9
0.2
0.1
0 100 km
Ulmus
10500 +/- 100 BP


0 100 km
Ulmus
10000 +/- 100 BP
0.1 0.5 1


0 100 km
Ulmus
9500 +/- 100 BP
0.5 1 2 3 5 7


0 100 km
Ulmus
9000 +/- 100 BP
1 2 3 5 7


0.01
0.1
0.5
1
2
3
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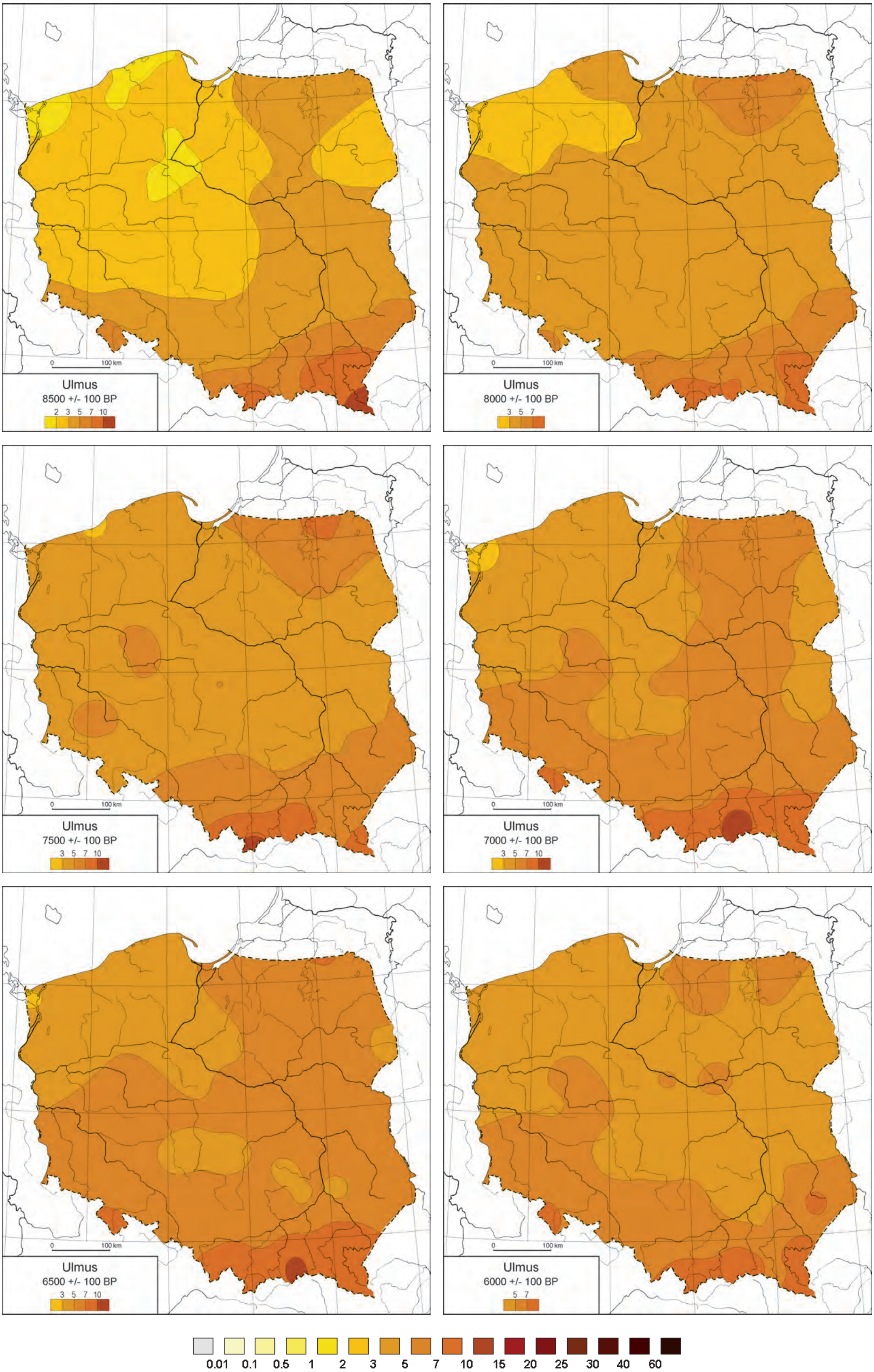
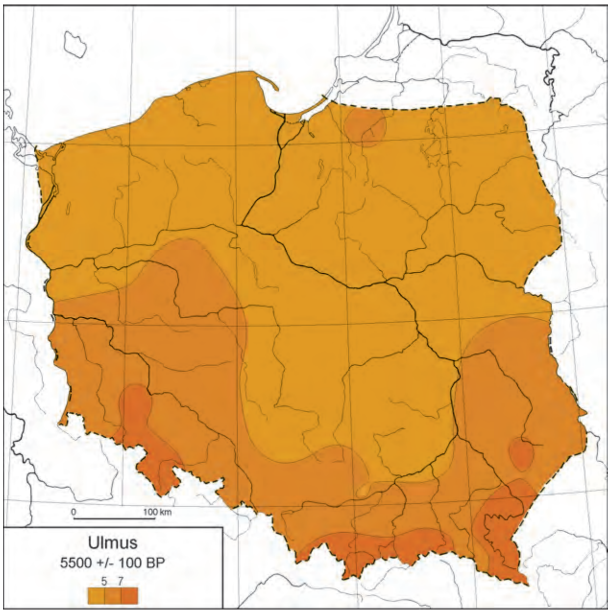
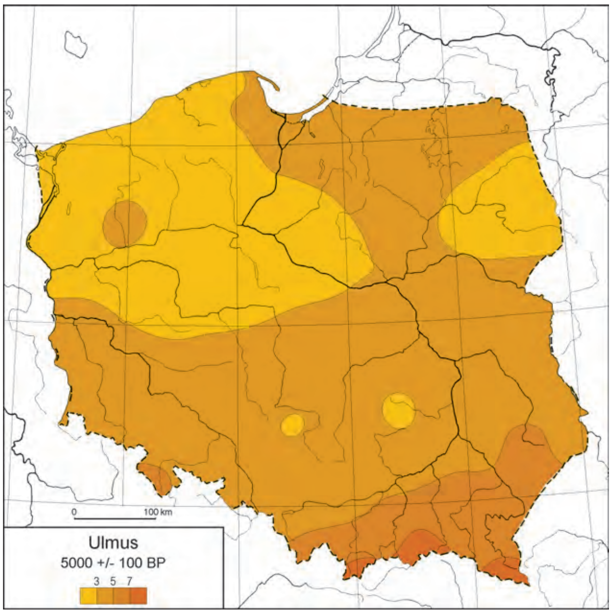
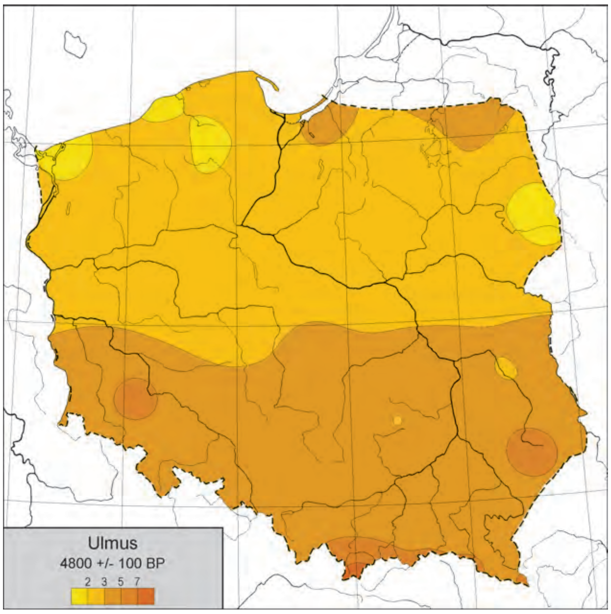
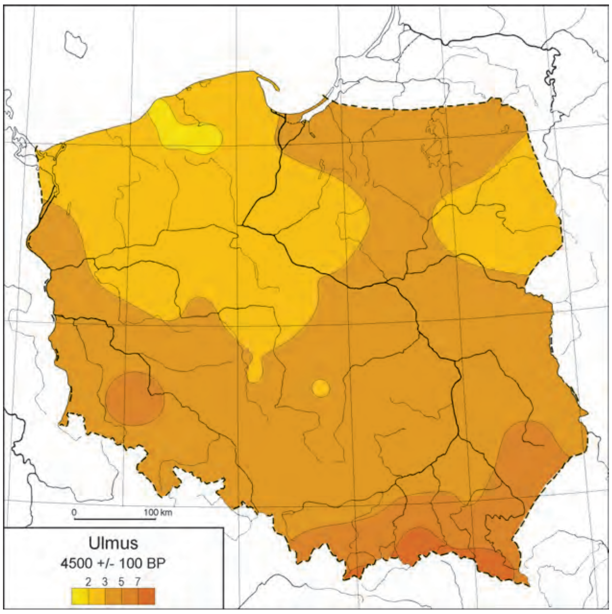
7
10
15
20
25
30
40
60

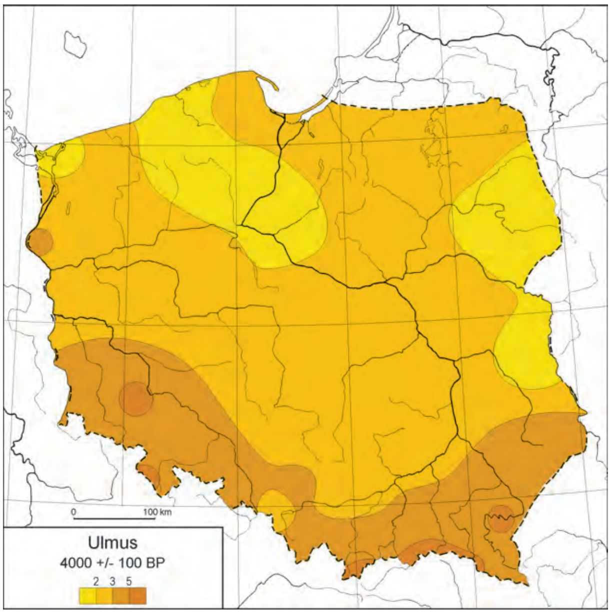

0 100 km
Ulmus
8500 +/- 100 BP
2 3 5 7 10
0 100 km
Ulmus
8000 +/- 100 BP
3 5 7
0 100 km
Ulmus
7500 +/- 100 BP
3 5 7 10
0 100 km
Ulmus
7000 +/- 100 BP
3 5 7 10
0 100 km
Ulmus
6500 +/- 100 BP
3 5 7 10
0 100 km
Ulmus
6000 +/- 100 BP
5 7
0.01 0.1 0.5 1 2 3 5 7 10 15 20 25 30 40 60

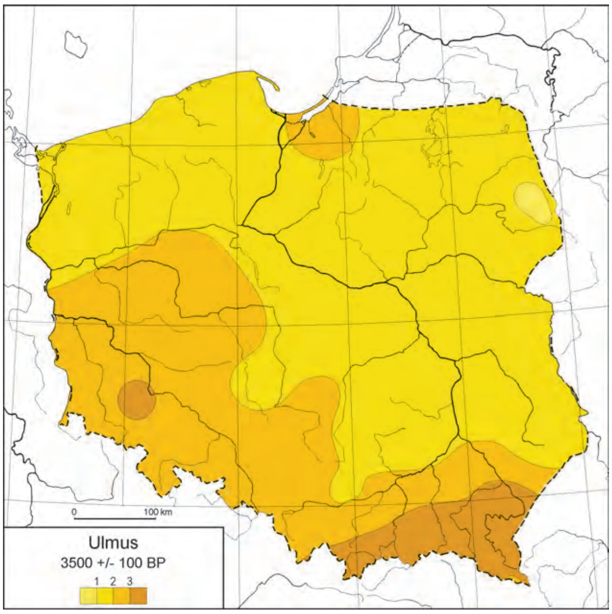












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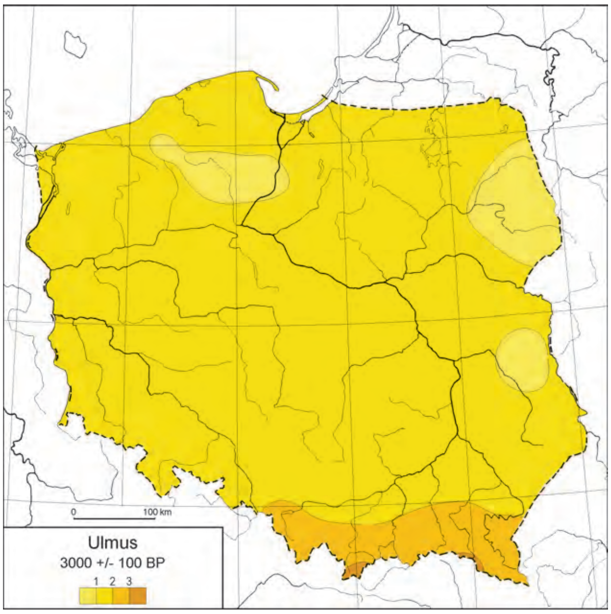
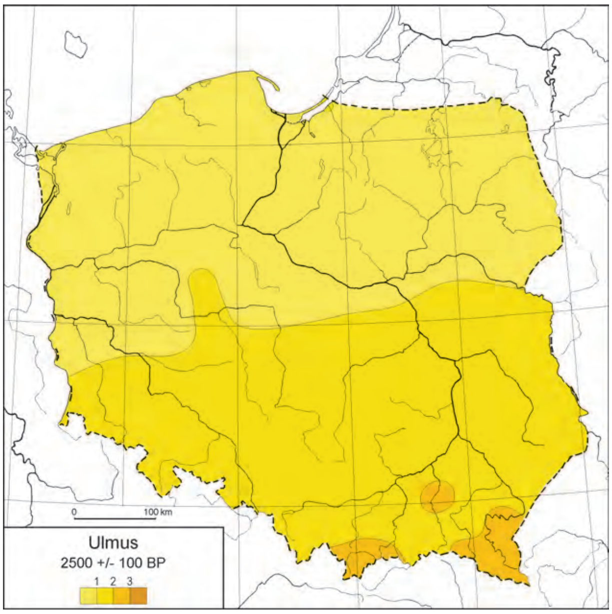
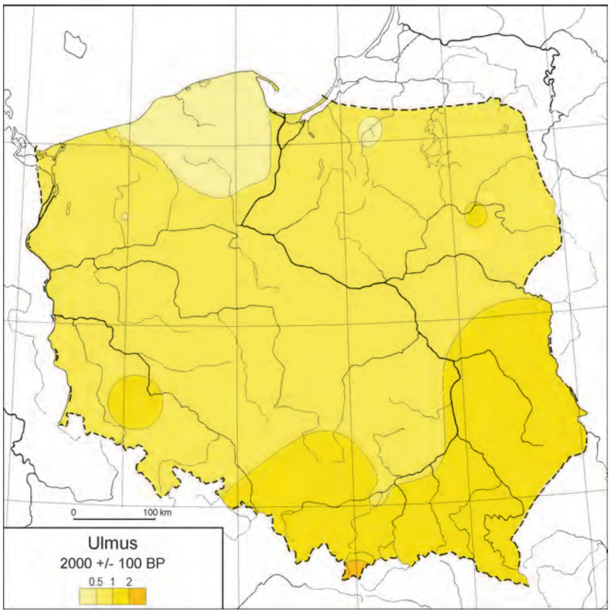
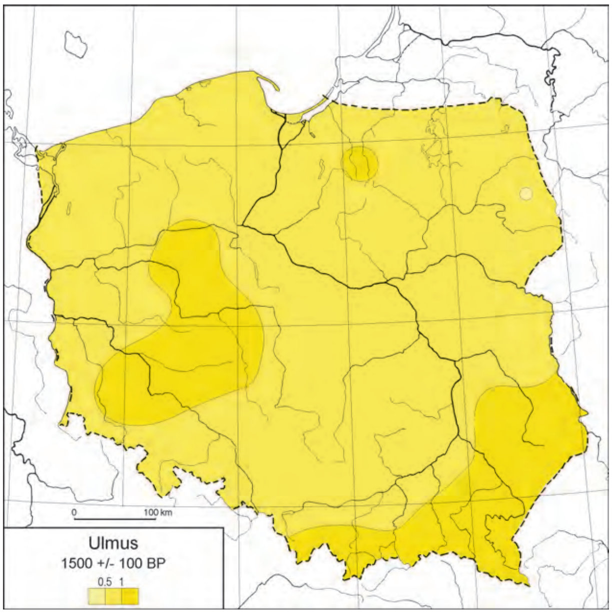
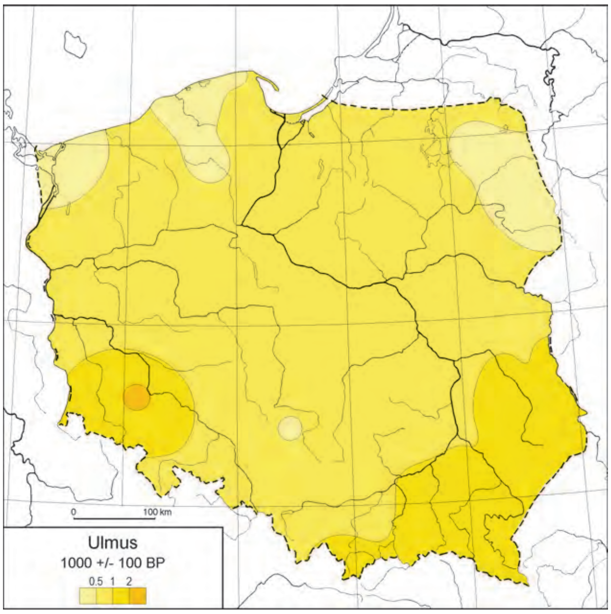
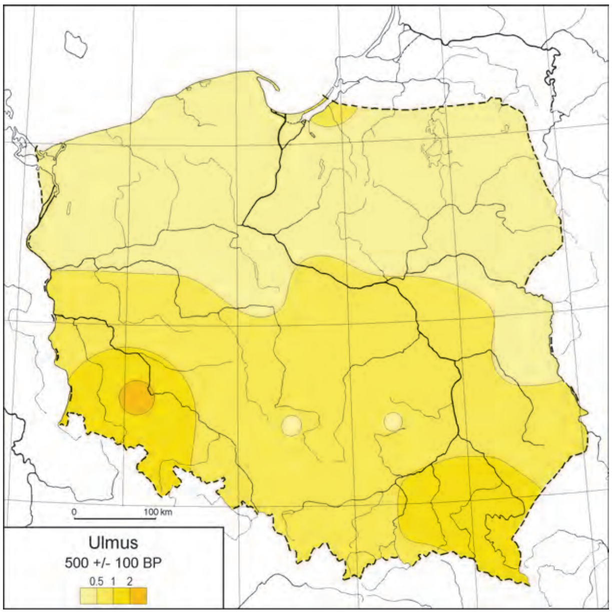

0
100 km
Ulmus
3000 +/- 100 BP
1 2 3


0
100 km
Ulmus
2500 +/- 100 BP
1 2 3


0
100 km
Ulmus
2000 +/- 100 BP
0.5 1 2


0
100 km
Ulmus
1500 +/- 100 BP
0.5 1


0
100 km
Ulmus
1000 +/- 100 BP
0.5 1 2


0
100 km
Ulmus
500 +/- 100 BP
0.5 1 2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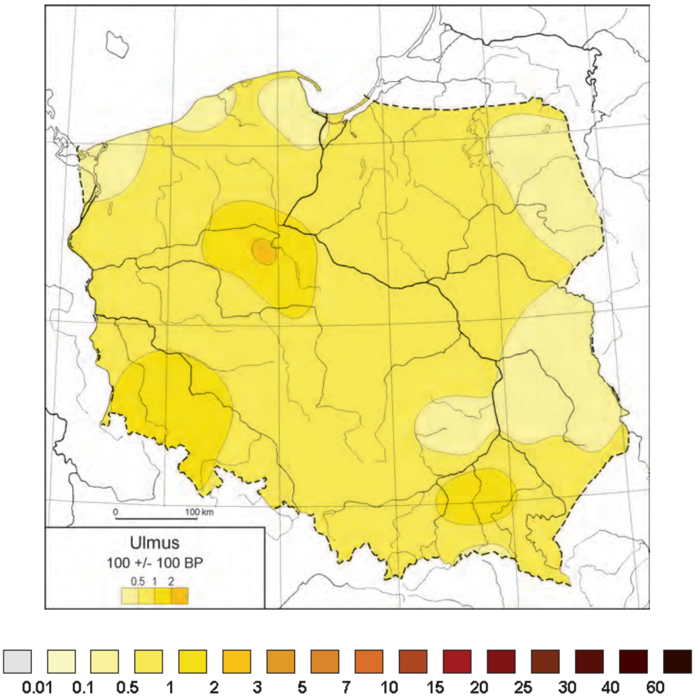
0
100 km
Ulmus
100 +/- 100 BP
0.5 1 2
0.01
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60

Viscum album L. – **Mistletoe**

WOJCIECH GRANOSZEWSKI, MAŁGORZATA NITA AND DOROTA NALEPKA

One species of mistletoe, *Viscum album* L., occurs in the area of Poland with three subspecies distinguished within it: *V. album* subsp. *album*, *V. album* subsp. *abietis* (Wiesb.) Abromeit, and *V. album* subsp. *austriacum* (Wiesb.) Vollmann.

PRESENT DISTRIBUTION IN EUROPE AND IN POLAND

This genus is widespread in Europe as far north as southern Scandinavia. To the east it has a scattered distribution in western Russia up to about longitude 39°E; further south-east it reaches the Crimean Peninsula and the northern Caucasus Mountains (Jalas & Suominen 1976, 1988b, Hultén & Fries 1986) (Fig. 76), and in the south of North Africa (Boratyńska & Boratyński 1976). In Poland (Fig. 77) this genus occurs over the whole country, more sparsely in the Carpathians and their forelands, on the Małopolska Upland, and in north-eastern Poland (Stypiński 1997, Zając A. & Zając M. 2001).

ECOLOGY

Viscum is a semi-parasite plant with high light requirements, tolerating periodic or temporary shading (Zarzycki et al. 2002). Temperature requirements vary slightly within the species. *V. album* subsp. *album*, and

Fig. 76. *Viscum album* – map of present-day distribution in Europe: ● – native isolated occurrence (after Jalas & Suominen 1976 and Hultén & Fries 1986)

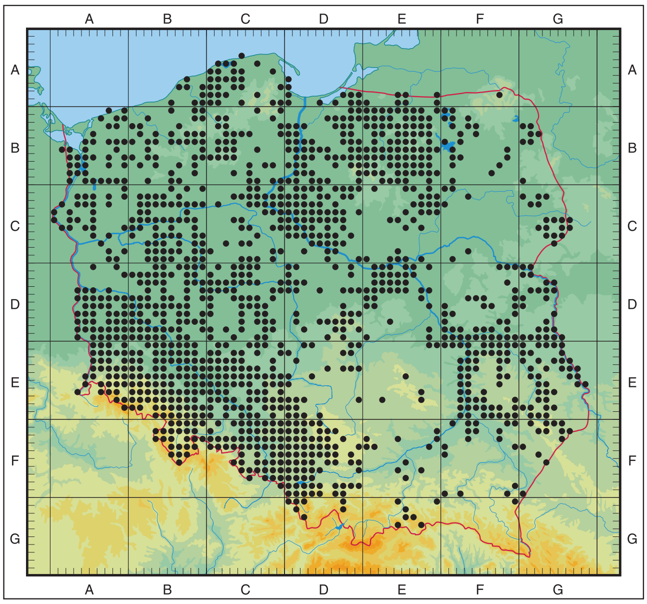


Fig. 77. Present-day distribution of *Viscum album* subsp. *album* L. in Poland (after Zając A. & Zając M. 2001)

V. album subsp. *austriacum* are indicators of a moderately warm climate, whilst *V. album* subsp. *abietis* may also indicate a moderately cold climate (Zarzycki et al. 2002). According to Iversen (1944) the presence of *Viscum* pollen points to a mean temperature of the warmest month above 16°C, and it is treated as an indicator of very warm summer seasons. All the subspecies of mistletoe are neutral in respect to continentality of climate (Zarzycki et al. 2002).

In the area of Poland its flowering, according to various authors, occurs from February to April. Distribution of seeds is mainly by birds, but also by small forest mammals (Stypiński 1997).

The plant communities in which particular subspecies occur, depend on the species of host. *V. album* subsp. *album* displays the widest spectrum of hosts (118 species of trees and shrubs). The most common hosts are *Tilia cordata*, *Betula pendula*, *Acer platanoides*, *Sorbus aucuparia*, *Populus* ×*canadensis*, *P. nigra*, and *Salix alba* (Stypiński 1997). This subspecies occurs in communities of the *Querco-Fagetea* and *Quercetea robori-petraeae* classes. *V. album* subsp. *austriacum* parasitizes mainly *Pinus sylvestris*, less frequently *Picea abies*, and only occasionally deciduous trees. Its occurrence is restricted to communities of the *Dicrano-Pinion* alliance. Only *V. album* subsp. *abietis* is tied in Poland to a single host (*Abies alba*) and occurs in communities of the *Vaccinio-Piceetalia* and *Fagetalia* orders.

Humans influence the distribution of mistletoe because of management activities and planting strategies that favour particular tree species (Stypiński 1997).

Pollen production and dispersal

Mistletoe is a sparse pollen producer. Pollen of all three subspecies is morphologically indistinguishable. Pollen grains of mistletoe are adapted for distribution by insects. However, some researchers are of the opinion that mistletoe is, at the same time, both an insect- and a wind-pollinated plant (Stypiński 1997).

Expansion in Europe during the Late Glacial and Holocene

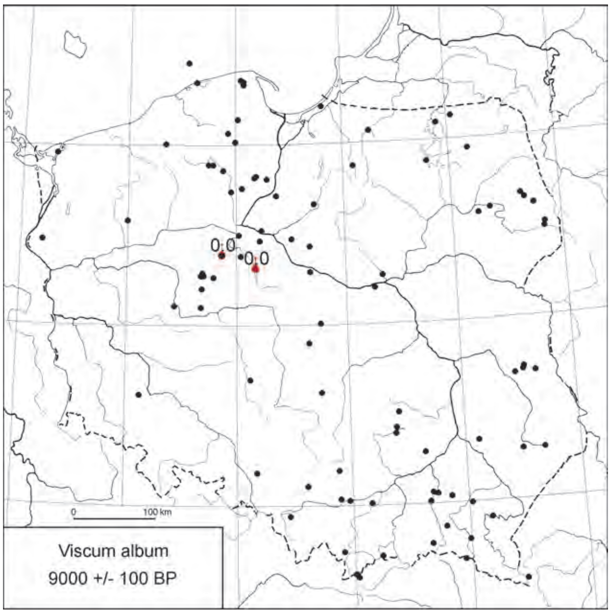
Mistletoe survived the glacial stages in the Mediterranean region and after the melting of the last ice-sheet, it migrated northwards together with its hosts (Stypiński 1997). According to Huntley and Birks (1983), in the middle Holocene mistletoe had a more restricted range in the west and south of Europe, whereas it reached further north in comparison with its present contiguous distribution. It is also possible that such a picture of mistletoe distribution during the Holocene results from an insufficient amount of data from southern and western Europe.

Migration pattern in Poland (Fig. 78)

While interpreting the isopollen maps, it should be emphasized that the low percentage values of *Viscum* pollen in the pollen assemblages (<0.6%) and its discontinuous occurrence at the selected time horizons may result from low pollen production and inefficient pollen dispersal, or else it may actually have been absent from sites at those time horizons.

Viscum pollen appeared at about 9000–8500 BP in central Poland, at the foot of the Tatra Mountains and in the Sudetes. At some sites it was recorded even earlier (about 8700 BP). In the period between 8500–7500 BP mistletoe expanded gradually in Poland, and by 3500 BP its range covered the whole country. Significant reduction in mistletoe pollen values occurred between 3000 and 500 BP. On the 100 BP isopollen map its pollen has been recorded only in the Małopolska Upland. Such considerable decline in the occurrence of mistletoe may have resulted from the cooling of climate during the Little Ice Age. At present, mistletoe is a species commonly occurring in the central lake districts, in the Lublin Upland and particularly in south-western Poland (Zając A. & Zając M. 2001).

Fig. 78. *Viscum album*: dot and isopollen maps for 9000–100 ^{14}C yr BP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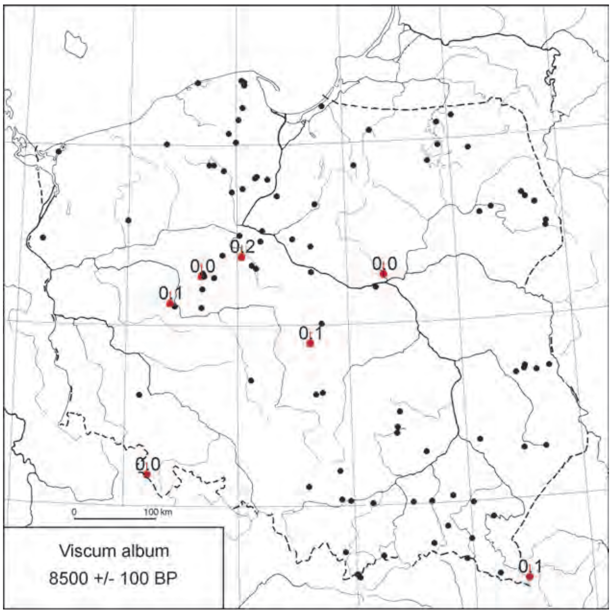
0.0
0
100 km
Viscum album
9000 +/- 100 BP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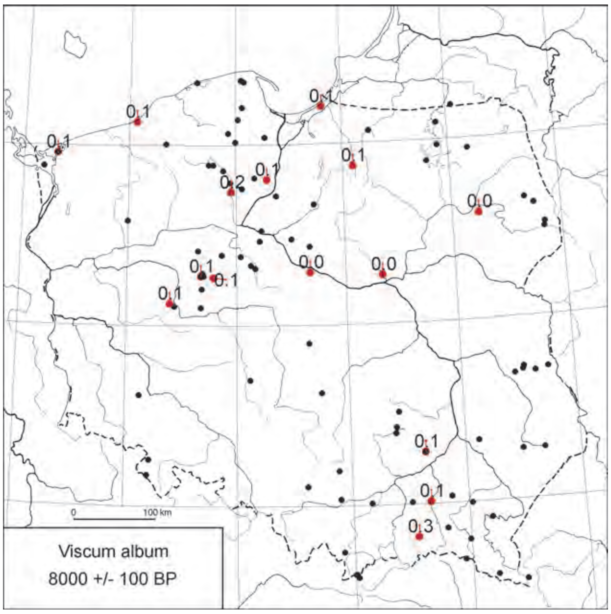
0.0
0.1
0
100 km
Viscum album
8500 +/- 100 BP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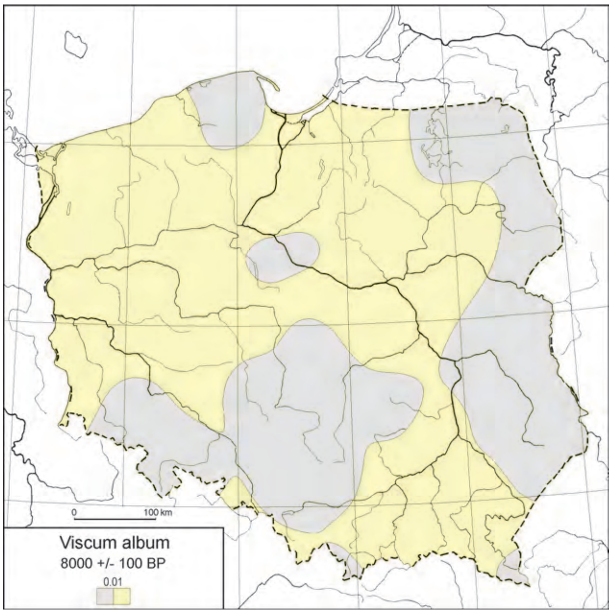
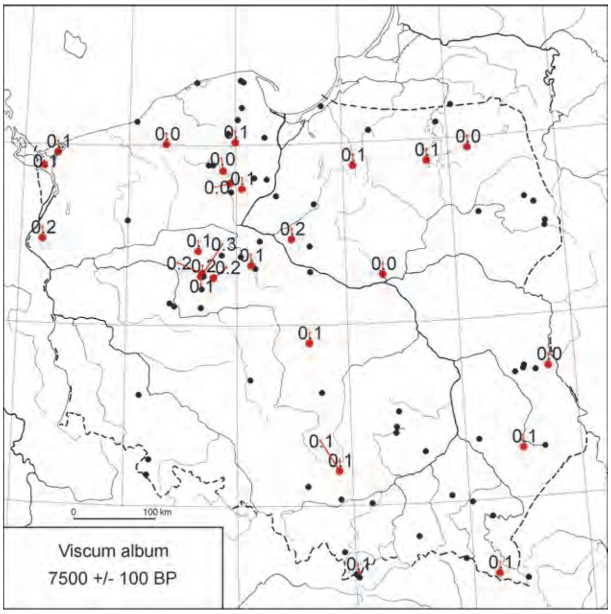
0.1
0.2
0.1
0.0
0.1
0.1
0.1
0.0
0.0
0.1
0.1
0.3
0
100 km
Viscum album
8000 +/- 100 BP


0
100 km
Viscum album
8000 +/- 100 BP
0.01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0.1
0.1
0.1
0.0
0.0
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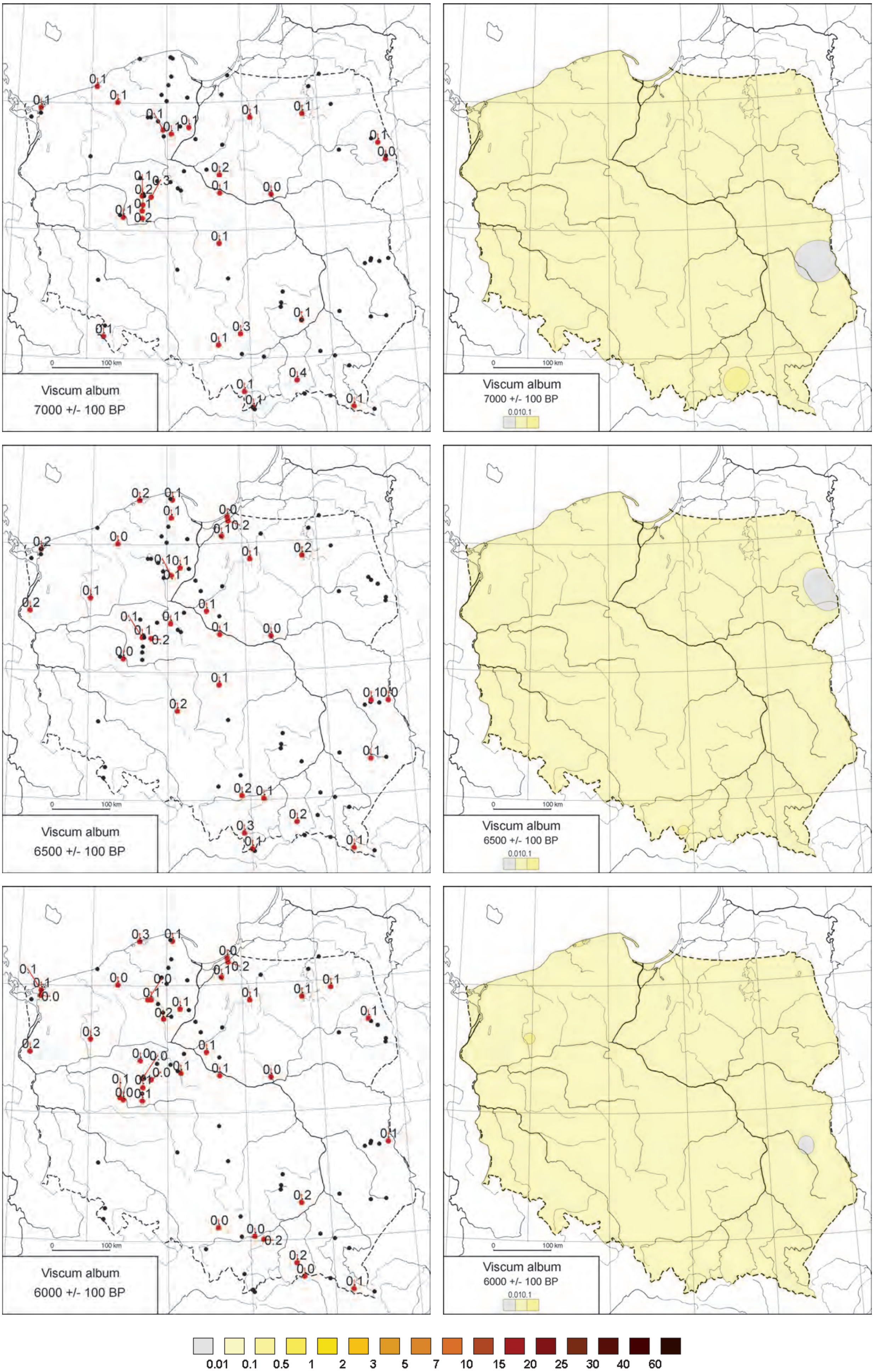
0.3
0.1
0.2
0.2
0.2
0.1
0.0
0.1
0.0
0.1
0.1
0.1
0.1
0.1
0
100 km
Viscum album
7500 +/- 100 BP


0
100 km
Viscum album
7500 +/- 100 BP
0.01


0.01
0.1
0.5
1
2
3
5
7
10
15
20
25
30
40
60


0 100 km
Viscum album
7000 +/- 100 BP
Viscum album
7000 +/- 100 BP
0.01 0.1
Viscum album
6500 +/- 100 BP
Viscum album
6500 +/- 100 BP
0.01 0.1
Viscum album
6000 +/- 100 BP
Viscum album
6000 +/- 100 BP
0.01 0.1
0.01
0.1
0.5
1
2
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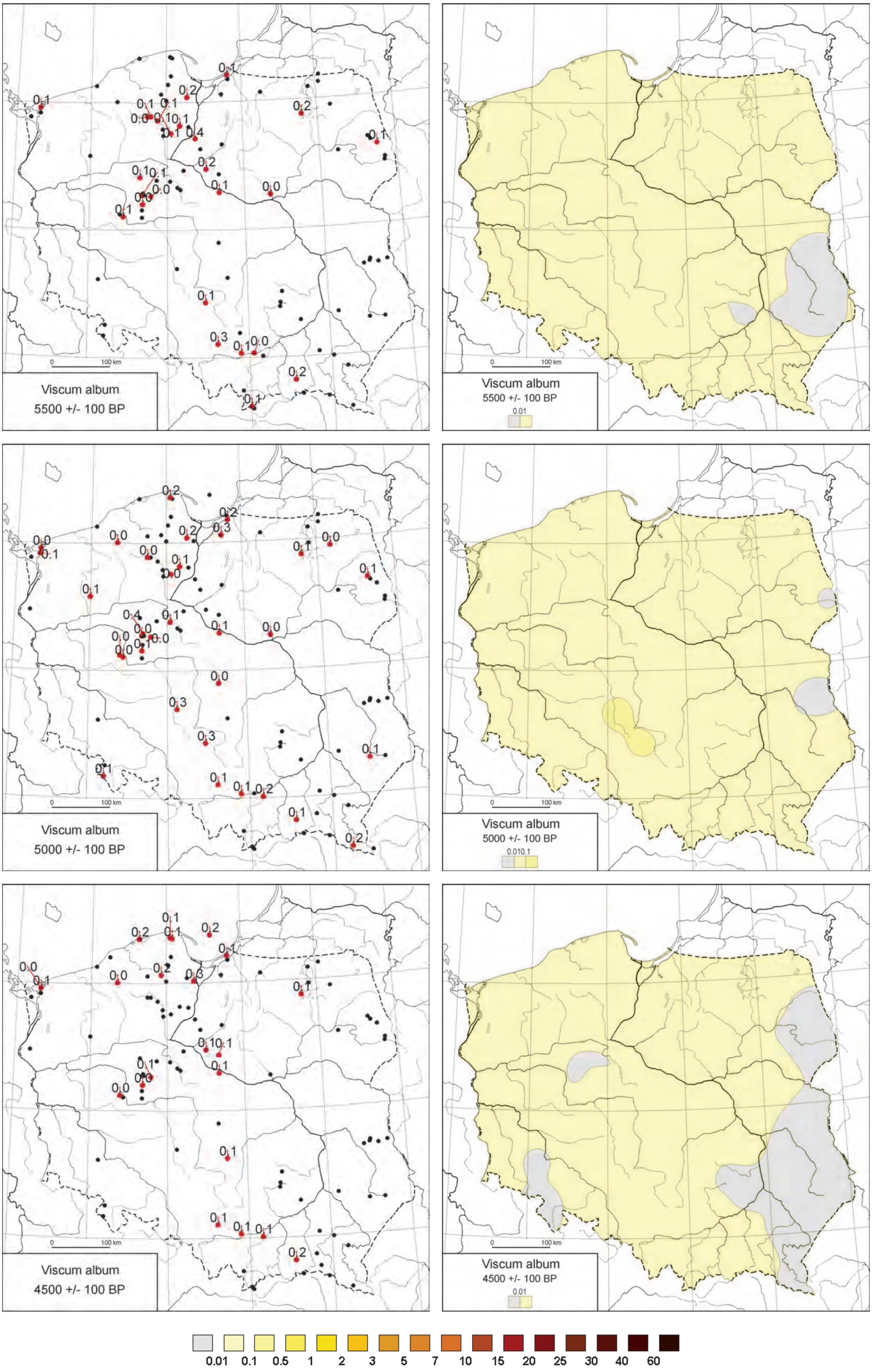
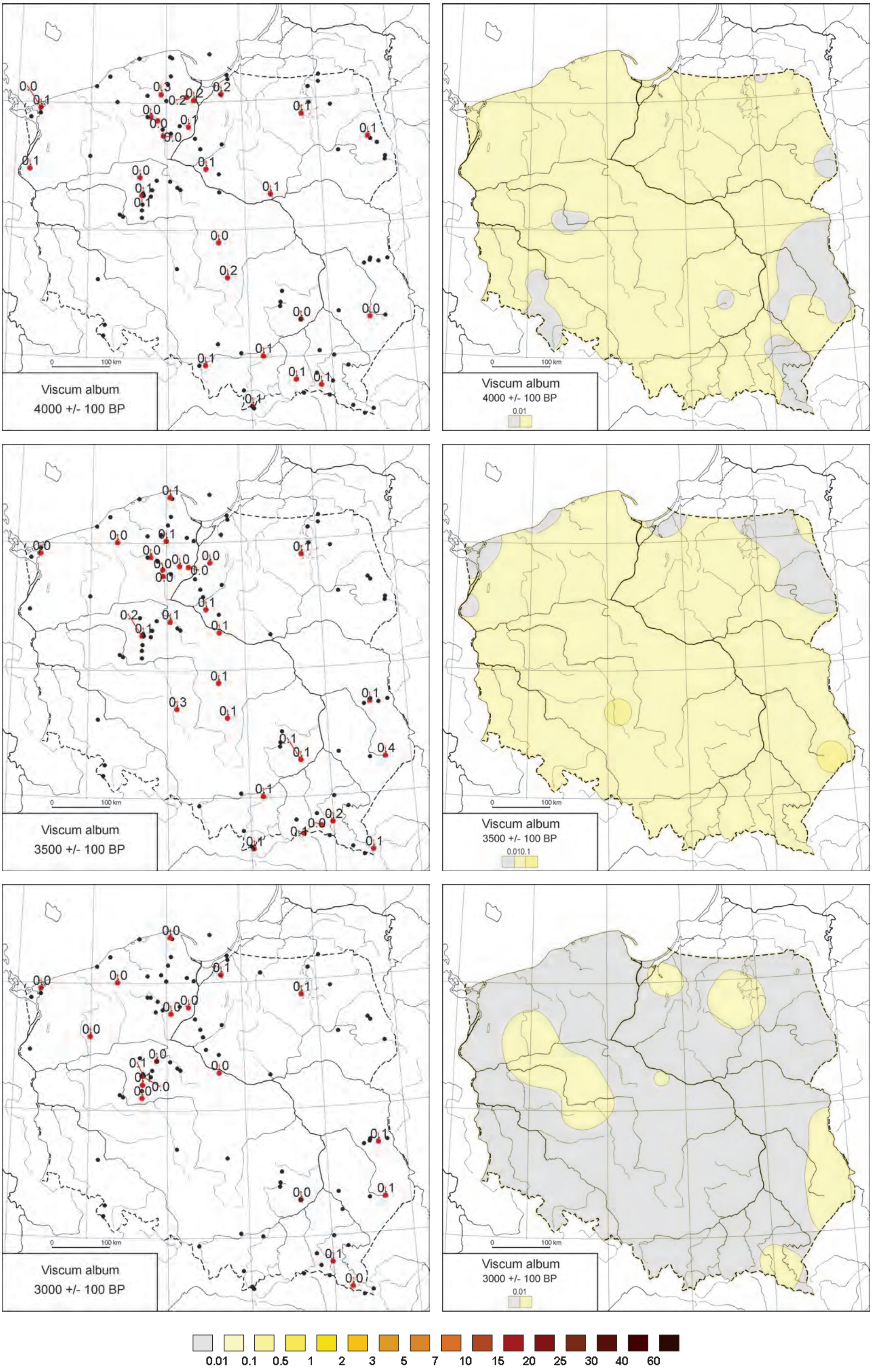
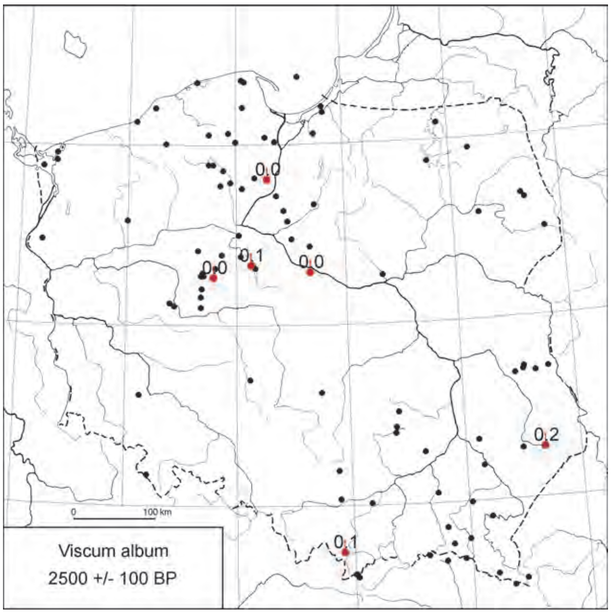
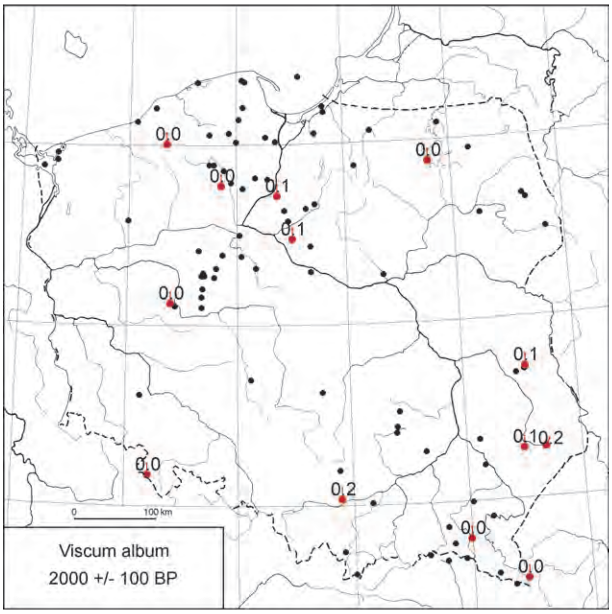
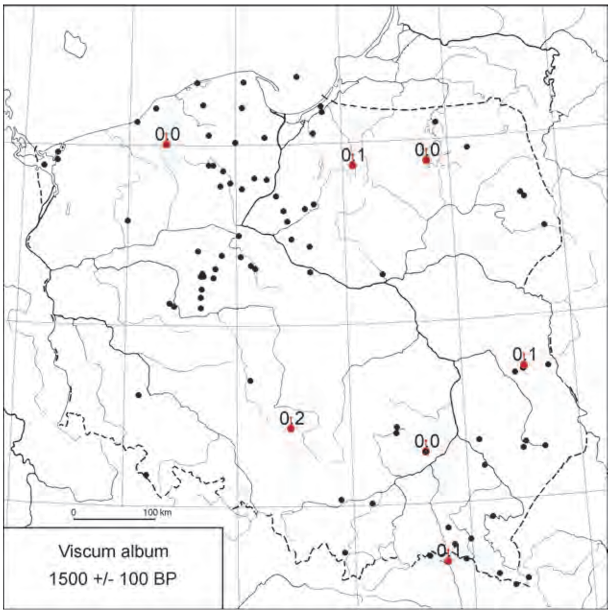
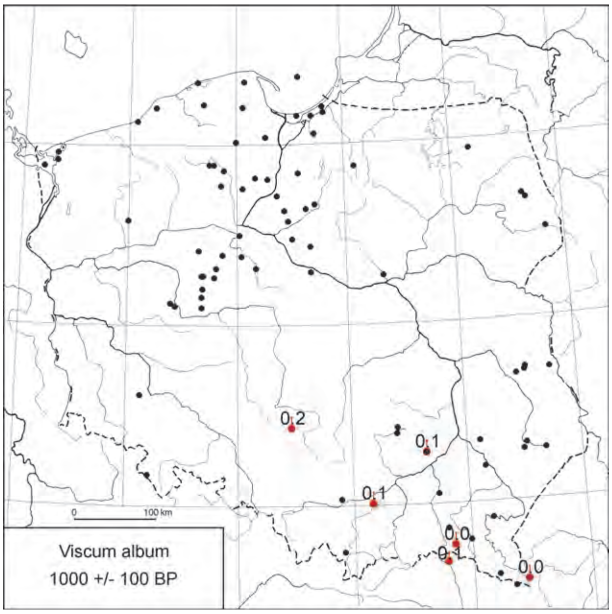

Viscum album
5500 +/- 100 BP
0.01
Viscum album
5000 +/- 100 BP
0.01 0.1
Viscum album
4500 +/- 100 BP
0 100 km
0.01
0.1
0.5
1
2
3
5
7
10
15
20
25
30
40
60

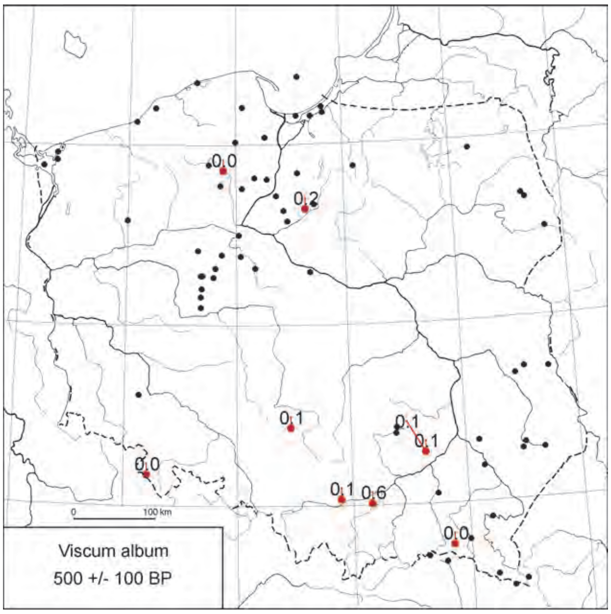

Viscum album
4000 +/- 100 BP
0.0
0.1
0.3
0.2
0.2
0.2
0.1
0.0
0.0
0.1
0.0
0.1
0.1
0.1
0.0
0.1
0.1
0.1
0.0
0.2
0.0
0.0
0.1
0.1
0.1
0.1
0.1
0
100 km
Viscum album
4000 +/- 100 BP
0.01
Viscum album
3500 +/- 100 BP
0.1
0.0
0.0
0.1
0.1
0.0
0.0
0.0
0.0
0.0
0.0
0.1
0.2
0.1
0.1
0.1
0.1
0.3
0.1
0.1
0.1
0.1
0.4
0.1
0.2
0.0
0.4
0.1
0.1
0
100 km
Viscum album
3500 +/- 100 BP
0.010.1
Viscum album
3000 +/- 100 BP
0.0
0.0
0.0
0.1
0.1
0.0
0.0
0.0
0.0
0.1
0.0
0.1
0.0
0.0
0.1
0.0
0.1
0.1
0.0
0
100 km
Viscum album
3000 +/- 100 BP
0.01
0.01
0.1
0.5
1
2
3
5
7
10
15
20
25
30
40
60


0,0
0,1
0,0
0,0
0,2
0,1
0
100 km
Viscum album
2500 +/- 100 BP


0,0
0,0
0,0
0,1
0,1
0,0
0,1
0,1
0,2
0,0
0,2
0,0
0,0
0
100 km
Viscum album
2000 +/- 100 BP


0,0
0,1
0,0
0,1
0,2
0,0
0,1
0
100 km
Viscum album
1500 +/- 100 BP


0,2
0,1
0,1
0,0
0,1
0,0
0
100 km
Viscum album
1000 +/- 100 BP


0,0
0,2
0,1
0,1
0,1
0,0
0,1
0,6
0,0
0
100 km
Viscum album
500 +/- 100 BP


0,1
0
100 km
Viscum album
100 +/- 100 BP

Vitis vinifera L. subsp. *sylvestris* (C. C. Gmelin) Hegi – **Wild grape-vine**

WOJCIECH GRANOSZEWSKI, MAŁGORZATA NITA AND DOROTA NALEPKA

PRESENT DISTRIBUTION IN EUROPE

Wild grape-wine is a sub-Mediterranean-Atlantic taxon growing in southern Europe (Fig. 79) and at isolated sites in the valleys of big rivers in the lowland areas of Austria, south Germany and south-west Switzerland (Hegi 1965). In the south-eastern part of its range it occurs in the Dniepr, Dniestr and Prut river basins (Różaniec 1950). In Poland it has not occurred recently.

ECOLOGY, POLLEN PRODUCTION AND DISPERSAL

Vitis is a liana. It grows under the conditions of warm and very warm climate (Ellenberg et al. 1991), in regions within the area of mean annual isotherms of 10–20°C (Sobolewska 1954). It is a hygrophilous plant, occurring on slightly moist and moist to wet soils (Ellenberg et al. 1991). It grows in partly shaded or half-shaded sites. It is a sub-oceanic species (Ellenberg et al. 1991).

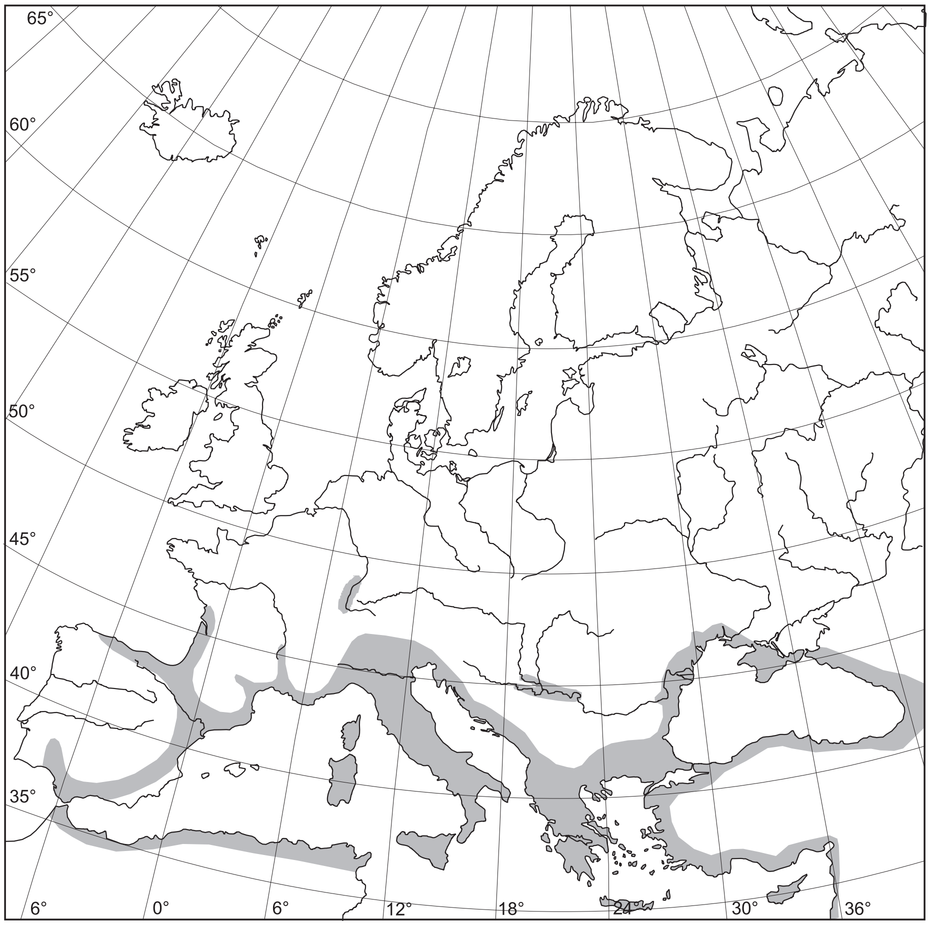


Fig. 79. *Vitis vinifera* subsp. *sylvestris* – map of present-day distribution in Europe (after Negrula 1946, in Sobolewska 1954 and after Zohary & Spiegel-Roy 1975, in Zohary & Hopf 2000)

According to Oberdorfer (1953, after Matuszkiewicz & Borowik 1957) *V. vinifera* subsp. *sylvestris* is a characteristic species of *Ficario-Ulmetum* floodplain forest in some parts of western Europe (Matuszkiewicz J.M. 2002).

Wild grape-vine is a dioecious plant with a very strong capacity for vegetative reproduction (Paczoski 1912). It is usually self-pollinated, sometimes insect pollinated (Ralska-Jasiewiczowa 1980).

DISTRIBUTION IN EUROPE DURING THE LATE GLACIAL AND HOLOCENE

In the post-glacial period wild vine migrated from southern European refugia along the Rhone valley through the Burgundian Gate to the Rhine valley. According to some authors (for example Kubitzki 1961) during the Holocene climatic optimum its range may have reached as far as the Baltic area (Schleswig-Holstein), and in the Neolithic it may have been widespread in north-west Europe. It is probable that due to human intervention it extended as far as Denmark and southern Sweden (Sobolewska 1954).

MIGRATION PATTERN IN POLAND (Fig. 80)

Pollen of *Vitis* is represented by very low percentage values (0.2% at most) in pollen assemblages. For the first time it appears on the 8000 BP map in the Pomeranian Lake District and in the Małopolska Upland. In the middle and younger Holocene *Vitis* pollen is sporadically recorded at single sites in different parts of Poland. However, some sites of *Vitis* pollen have unfortunately but unavoidably been omitted, since they occurred between the 500 years time horizons used for drawing the pollen maps. At the time of the Holocene climatic optimum *V. vinifera* subsp. *sylvestris* was the only likely source of *Vitis* pollen (Ralska-Jasiewiczowa & van Geel 1998). Between ca. 7000 and 3000 BP pollen of *Vitis* occurs sporadically in the Bieszczady Mountains, and more regularly it appears there during the younger Holocene (Ralska-Jasiewiczowa 1980). It is possible that it derived then from long-distant transport from the vineyards on the south side of the Carpathians. Pollen of *Vitis* is also recorded in central Poland (the 7500, 4500 and 100 BP map) as well as in the Mazurian Lake District (1500 BP).

Fig. 80. *Vitis vinifera* subsp. *sylvestris*: dot maps for 8000–100 ^{14}C yr BP


0.2
0.1
0
100 km
Vitis vin. ssp. sylvestris
8000 +/- 100 BP

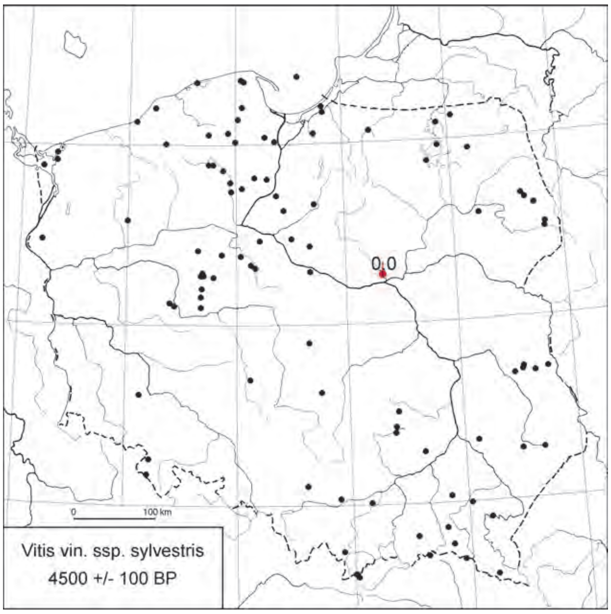

0.0
0.1
0
100 km
Vitis vin. ssp. sylvestris
7500 +/- 100 BP


0.1
0
100 km
Vitis vin. ssp. sylvestris
7000 +/- 100 BP


0.2
0
100 km
Vitis vin. ssp. sylvestris
6000 +/- 100 BP


0.1
0.2
0
100 km
Vitis vin. ssp. sylvestris
5500 +/- 100 BP


0.1
0.1
0
100 km
Vitis vin. ssp. sylvestris
5000 +/- 100 BP


0,0
0 100 km
Vitis vin. ssp. sylvestris
4500 +/- 100 BP


0,1
0 100 km
Vitis vin. ssp. sylvestris
4000 +/- 100 BP


0,1
0,1
0 100 km
Vitis vin. ssp. sylvestris
3500 +/- 100 BP


0,1
0 100 km
Vitis vin. ssp. sylvestris
3000 +/- 100 BP


0,1
0,0
0 100 km
Vitis vin. ssp. sylvestris
2000 +/- 100 BP


0,0
0,0
0,0
0,1
0 100 km
Vitis vin. ssp. sylvestris
1500 +/- 100 BP


0.1
0.1
0.0
0
100 km
Vitis vin. ssp. sylvestris
1000 +/- 100 BP


0.1
0
100 km
Vitis vin. ssp. sylvestris
500 +/- 100 BP


0.0
0.1
0.1
0.1
0.1
0
100 km
Vitis vin. ssp. sylvestris
100 +/- 100 BP

ISOPOLLEN HISTORY
OF
HERBACEOUS PLANTS

Artemisia L.

MIROSŁAW MAKOHONIENKO, MAŁGORZATA LATAŁOWA, KRYSTYNA MILECKA,
IWONA OKUNIEWSKA-NOWACZYK, AND DOROTA NALEPKA

There are about 50 native species of *Artemisia* in Europe. 18 species grow in Poland, half of them are alien species naturalised in our flora and/or ephemerals (Mirek et al. 2002). Of the nine other species, six are regarded as native (*A. absinthium* L. var. *calcigena*, *A. campestris* L., *A. eriantha* Ten., *A. pontica* L., *A. scoparia* Waldst. & Kit. and *A. vulgaris* L.), and other three species are cultivated.

PRESENT DISTRIBUTION IN EUROPE

The genus *Artemisia* is found almost throughout the whole Europe, from the Mediterranean zone in the south to the sub-Arctic zone in the north. The majority of European species of *Artemisia* grow in southern and south-eastern regions with a continental climate. They are important components of the steppes of south-east Europe, especially in the most southern belt of dry steppes called ‘absinthium steppes’, which in some areas become an ‘absinthium semi-desert’ (Podbielkowski 1991). In inland saline habitats of eastern Europe *Artemisia maritima* is found, a species that also occurs in coastal habitats in western Europe. Some species of *Artemisia* are connected with the mountainous regions of southern and central Europe, e.g. *A. eriantha*. The Arctic-sub-Arctic zone of northern Europe has only one species *Artemisia norvegica* whose pollen may be identified to the species level (Godwin 1975). It occurs in open, disturbed habitats and on unstable screes. A number of species in Europe frequently occur in habitats transformed by human activities, and so can be described as being components of synanthropic communities.

PRESENT DISTRIBUTION IN POLAND

Only three native (or perhaps long naturalised) species of *Artemisia* are commonly found in Poland, that is *A. absinthium*, *A. campestris*, and *A. vulgaris* (Szafer et al. 1986). *Artemisia vulgaris* occurs throughout the country, but *A. campestris* and *A. absinthium* are found mainly in lowland regions. The Carpathian region is beyond the range of *A. campestris*, and the sites of *A. absinthium* are sporadic in the region of the Carpathians and Sudetes with their foothills (Zając A. & Zając M. 2001). The smallest distribution ranges are those of *A. eriantha*, a high altitude species restricted to the Tatra Mountains, and *A. pontica* whose native sites are restricted to the relict steppe communities in the southern part of the Małopolska Upland. *A. scoparia* and *A. austriaca* Jacq. show distinct preferences for eastern regions of Poland.

ECOLOGY

The occurrence of *Artemisia* species is associated with open habitats with full exposure to light. *A. vulgaris* tolerates temporary or transitory shade (Zarzycki et al. 2002). The three most common Polish species of *Artemisia* (*A. vulgaris*, *A. campestris*, and *A. absinthium*) are indifferent to the degree of climatic continentality, whereas *A. austriaca* and *A. scoparia* are essentially associated with habitats characterised by continental influences, lying east of the Vistula river valley (Zarzycki et al. 2002).

Artemisia species grow on soils with varied grain-size composition, from rocky through gravelly and sandy sites to heavy loams and clays. As regards moisture, they prefer dry or slightly moist habitats. They have no particular preferences as regards soil fertility and occur on poor soils (especially *A. campestris*) as well as on moderately fertile and rich ones (*A. absinthium* and *A. vulgaris*). They grow on both moderately acid and alkaline soils (pH from 5.5 to over 6.6). The most tolerant is *A. campestris* subsp. *campestris*, which can grow on both alkaline and strongly acid soils (pH 3.5–4.5). Native *Artemisia* species favour soils poor in humus. In Poland they are most common in strongly anthropogenic communities of perennials constituting the second phase of colonisation of ruderal areas (subclass *Artemisietea*) whose characteristic species, apart from *Artemisia vulgaris* are, among others, *Arctium tomentosum* and *Cirsium vulgare* (Matuszkiewicz W. 2001). *A. vulgaris* occurs most abundantly in the association *Arctio-Artemisietum*, found at moderately nitrophilous ruderal sites on clayey soils, which are found throughout Poland near housing estates, along roadsides, refuse dumps, etc. *A. absinthium* is a species characteristic of the order *Onopordetalia,* which includes thermophilous communities of tall ruderal perennials in dry habitats. *A. campestris* is a species characteristic of the class *Festuco-Brometea*, including communities of thermophilous grasslands of steppe character (Matuszkiewicz W. 2001). In Poland *Artemisia* species at present show a tendency, in some cases weak, in others strong, to expand into fresh sites, particularly those associated with anthropogenic transformation of habitats.

Pollen grains of *Artemisia* are easily identified to the genus level. Webb and Moore (1982) suggest the possibility of differentiating pollen types within the genus. However such a differentiation is not commonly attempted. In central Europe an increase in *Artemisia* pollen representation in Holocene sediments is frequently associated with anthropogenic activity. In Behre's classification (1981), *Artemisia* pollen is an indicator of ruderal habitats and, to a lesser extent, of fallow ground and forest grazing.

POLLEN PRODUCTION AND DISPERSAL

The *Artemisia* species most commonly represented in Poland have show similar flowering behaviour. Their pollen is present in the air for over 10 weeks, generally from mid-July to mid-September (Szczepanek 1994a, b, Latałowa & Góra 1996, Stach 1996). In central and northern Europe the optimum time of pollination falls in mid-August. *Artemisia* is one of the very few genera in the family Asteraceae comprising wind-pollinated plants. Their adaptation to air transportation is indirectly manifested by the reduction of sculpture elements of their pollen grains. Despite wind dispersal and high pollen productivity, *Artemisia* pollen is relatively poorly distributed (Wolf et al. 1998). Much of pollen does not rise higher than 3–10 m above ground level, which limits its wider distribution (von Wahl & Puls 1989). Therefore, *Artemisia* pollen is likely to be underrepresented in subfossil pollen assemblages.

According to the suggestion made by Huntley and Birks (1983), *Artemisia* pollen values over 2% are a reliable indication of its local presence in the neighbourhood of the site, whereas values over 10% occur where open conditions prevail and *Artemisia* is abundant in the vegetation. In modern pollen spectra from areas transformed by human activity in which *Artemisia* constitutes a local component of synanthropic communities, its pollen values oscillate around 1% (sum of AP+NAP) or do not exceed this value (Latałowa 1992, Makohonienko et al. 1998, Latałowa & Święta 2002). Therefore, it must be assumed that values around 1% undoubtedly confirm the local occurrence of the taxon. It seems that even lower values, around 0.7%, as is found during the historic period in many regions of western Poland (see the *Artemisia* 100 BP map), provide information about its local representation.

EXPANSION IN EUROPE DURING THE LATE GLACIAL AND HOLOCENE

Isopollen maps published by Huntley and Birks (1983) show that *Artemisia* was widespread in the ice-free areas of Europe during the Late Glacial. The highest values are over 25%, and are recorded at 13,000 BP in the central part of southern Europe. *Artemisia* values declined at the beginning of the Holocene. A higher representation was present for a longer time in south-eastern and eastern Europe, and locally in Scotland and the Alps. By 7000 BP in regions of Europe, for which information was available in 1983, values over 2% were recorded only sporadically. 5000 BP saw a slight increase in *Artemisia* values in the Balkans.

MIGRATION PATTERN IN POLAND (Fig. 81)

14,000 – 12,500 BP

The oldest and very rare sites with sediments dated at 14,000 and 13,500 BP document the presence of *Artemisia* with values of about 6 and 11.7% in north-east Poland and about 5% in southern Poland. Slightly more numerous sites, dated at 13,000 BP and corresponding to the Oldest Dryas/Bølling, show a representation of *Artemisia* throughout Poland with values of 2–8%. Locally higher values over 5% are recorded at this time in the north-eastern region of the Great Mazurian Lakes and in southern Poland. At 12,500 BP, i.e. during the Bølling warming, the values of *Artemisia* pollen reach still 5–8.5% in east Poland and 3% in some areas of southern and central regions of Poland.

12,000 – 11,500 BP

At the 12,000 BP map the pattern of isopolls shows a gradient in the distribution of *Artemisia* in Poland, with a decline westwards. Isopolls for the easternmost regions represent values over 3% (locally 7%), in most of Poland they reach values of 2–3%, whereas in the north-west they are below 2%. The pattern of pollen representation for the Allerød (11,500 BP) illustrates a successive retreat of communities with *Artemisia* towards the east, with the most parts of Poland, except for the easternmost regions, yielding its pollen values below 2%.

11,000 – 10,500 BP

On the map relating to the Younger Dryas (11,000 BP), the contribution of *Artemisia* in south-eastern Poland reaches values of 3–5%, and locally over 7%, yet north-western regions have values not exceeding 2%. It indicates a renewal of steppe communities containing *Artemisia* at the beginning of the Younger Dryas, with their expansion coming from the south-east. In the mid-Younger Dryas (10,500 BP), representation of *Artemisia* throughout Poland increases to 3–5%, and in south-eastern regions and the Tatras exceeds 7%. High values are reached in Pomerania and central Baltic Sea coast whose separate character is marked even today by the survival of a greater number of 'Late Glacial relict species'. *Juniperus* pollen values during the Younger Dryas fluctuated in the opposite direction to those of the genus *Artemisia* (*Juniperus*, this volume).

10,000 – 9500 BP

At the onset of the Holocene (10,000 BP), the pollen contribution of *Artemisia* was reduced throughout Poland. The isopoll patterns distinctly reflect the restriction of communities with *Artemisia* to the south-east; from which direction its species had expanded during the Younger Dryas. At the beginning of the Holocene, pollen contributions of *Artemisia* in the south-east have values between 3 and 5%, locally over 5%, whereas in western Poland and in a substantial part of central Poland they are below 2%. The 9500 BP map shows a decline in *Artemisia* pollen values below 3% throughout Poland, with the lowest values reaching 0.5% in northern Poland. Plant communities with *Artemisia* were still best represented in the south-eastern part of the country.

9000 – 6000 BP

Between 9000 and 6500 BP the contribution of *Artemisia* underwent only slight fluctuations. Its isopolls have values below 0.5% throughout most of the territory of Poland. Pollen values between 0.5 and 2% occur in the south-eastern region of Poland, including the Carpathians and their forelands, part of the Małopolska Upland, the Lublin Upland and Polesie Lubelskie, and are only sporadically exceeded. However, slightly higher *Artemisia* pollen values (at 8000–7500 BP) occurred temporarily in the region of Lake Gopło at Kujawy, where chernozem soils prevail. About 6000 BP *Artemisia* reaches their minimum values throughout Poland; even in south-east Poland, it did not exceed 0.7%.

5500 BP

This gradual fall in the pollen contributions of *Artemisia*, starting from the beginning of the Holocene, with a longer period of stable low values from 9000–6500 BP and their minimum falling at around 6000 BP, was reversed at about 5500 BP. In the south of Poland, particularly in the upland zone, there appear local 'island' areas where *Artemisia* pollen values increase up to 0.7–1%. They occur in the basin of the upper Vistula river, the region of Kraków, the Silesian and Kraków-Częstochowa Uplands and the Lublin Upland. This increase is probably associated with an increased activity of the Early Neolithic populations of the Lengyel-Polgar cycle cultures in the loess areas of those uplands. Islands of higher *Artemisia* pollen values are also found in the river basin of the upper Warta and the Podlasie Upland, and they persist at Kujawy.

5000 BP

At 5000 BP three regions in Poland can be detected with heliophilous plant communities in which *Artemisia* had persisted or even increased in importance. These are still: 1. a region in the basin of the upper Vistula river, 2. the Lublin Upland with neighbouring areas of the Sandomierz Depression and part of Polesie Lubelskie, and 3. the region of Kujawy. The development of vegetation containing *Artemisia* is indicated locally along the lower Odra river, in the neighbourhood of Pyrzyce, where chernozem soils occur and where advanced Neolithic settlements have been recognised (Kulczycka-Leciejewiczowa 1996).

The period discussed above corresponds with the Middle Neolithic, when populations associated with the Linear Pottery culture were reduced and then disappeared, and the Funnel Beaker culture started to develop, apparently from local Mesolithic communities (Kośko 1980, Czerniak 1994).

4500 BP

On the 4500 BP map the highest *Artemisia* pollen values are restricted to the Lublin Upland and lowland regions, especially to the clearly isolated region of Kujawy and to a weakly marked region of the lower Odra river. In this period (the Late Neolithic), the Funnel Beaker and Globular Amphorae cultures developed.

4000 – 3500 BP

The 4000 BP (the Late Neolithic) and 3500 BP maps (the Early Bronze Age) show the spread of *Artemisia* into wider parts of the country, and the pattern of isopolls indicates the progressive expansion of the area with increased Artemisia values (>0.7%) from the south-east through Wołyń and Lublin Upland, and along the valley of the middle Vistula river to link with the Kujawy region, where such values were already present.

3000 – 2000 BP

Isopolls for 3000–2000 BP, which cover the Bronze Age and Early Iron Age through to the Roman Period, illustrate an increase in *Artemisia* pollen throughout Poland. The development of *Artemisia* species at that time was probably associated with the expansion of existing settlement zones and intensification of agriculture and pastoralism.

1500 BP

About 1500 BP, during the Migration Period or the early stage of Slavonic settlement, plant communities with *Artemisia* were reduced. Isopolls show the lowest values (up to 0.5%) in northern Poland, western Pomerania, central Pomerania, and the northern part of Mazovian Lowland. The western, central and eastern parts of Poland, and the south-eastern uplands together with the Carpathians shows higher values of *Artemisia* pollen.

1000 – 100 BP

In the last millennium *Artemisia* species expanded again throughout Poland as a consequence of the growth of human settlements. Isopollen maps show its pollen values of 1–2% occurring in most parts of the country. The 1000 BP map shows values of >2% in central Wielkopolska, representing the tribal centre of Polanie, which was a region where the foundations of the Polish State were being formed. The next map presents a similar picture (about 500 BP), but the region of central Wielkopolska is no longer distinctly differentiated. In times close to the present (100 BP), isopolls show a smaller importance of *Artemisia* in north-western Poland, where the influence of the Atlantic climate is higher. The palynological picture in this case corresponds with the present distribution of *Artemisia* species in Poland (Zając A. & Zając M. 2001).

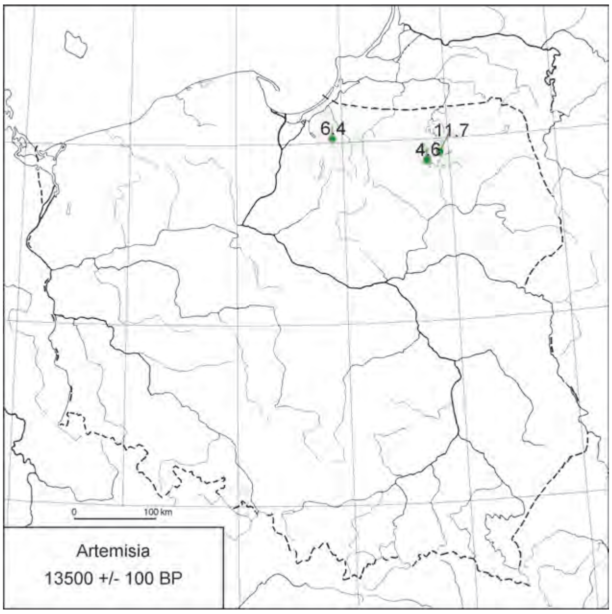
CONCLUSIONS

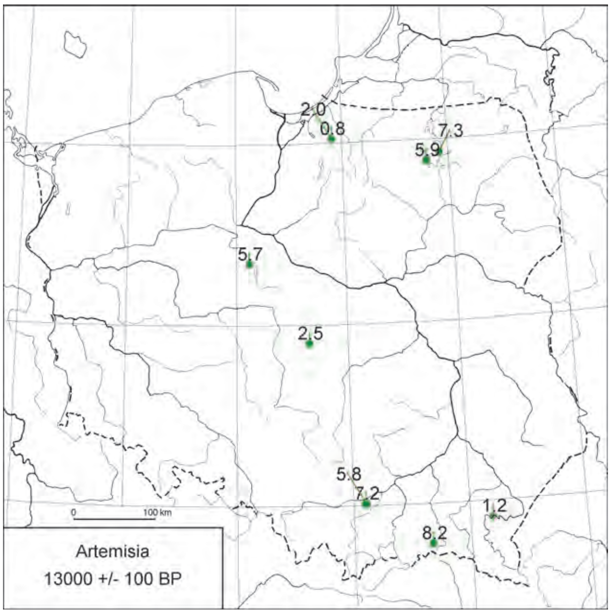
The expansion of *Artemisia* species in Poland in the last 14 thousand years was conditioned first by climatic and later by anthropogenic factors. During the Late Glacial they were important natural components of the flora, indicating a continental climate. Their pollen contribution in Poland at those times exceeded values of 11%, a level never observed later, in the Holocene. At the time of the disappearance of the Vistulian glaciation, apart from species occurring in Poland at the present day, other species characteristic of dry and cool climates may have been present. In particular, species associated with the sub-Arctic zone, such as *A. norvegica* might have also occurred in Poland. During the Younger Dryas, as the direction of *Artemisia* expansion shows, species from eastern regions, such as *A. austriaca*, *A. annua* or *A. scoparia* might have immigrated. In the Late Glacial, and especially during the Allerød and the Younger Dryas, the major gradient of change in *Artemisia* pollen values ran east to west, with significantly higher *Artemisia* contributions in the east reflecting the influence of a more continental climate. The high contribution of *Artemisia* in plant communities during the cool periods of the Late Glacial emphasizes the differences between contemporary tundra communities of the sub-Arctic zone and the Dryas-vegetation of central Europe at the end of the last glacial stage.

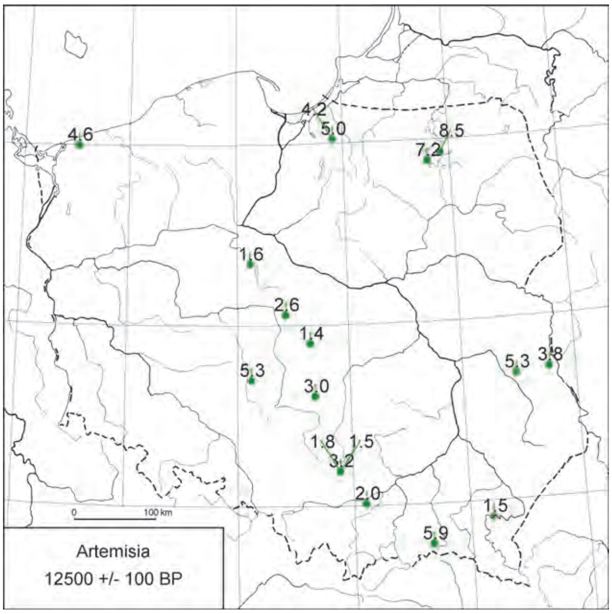
The Holocene development of forest communities restricted the occurrence of *Artemisia*, which is illustrated by its pollen values falling to a level of 0.2–0.5%. These low contributions may represent local stands of *Artemisia* that survived in habitats better exposed to sunlight and on soils poor in humus. A higher contribution of *Artemisia* is characteristic of the south-eastern region of Poland during the early and middle Holocene, the area the closest to the east-European steppe zone. In the lowlands, slightly higher pollen values of *Artemisia* appear in the region of Kujawy. About 5500 BP there was a change in the Holocene history of *Artemisia*, which is shown by its local development, first in the zone of the south-Polish uplands and then in the lowlands. This development at that time was directly related to settlement and farming processes of the Neolithic communities. A significant presence of *Artemisia* in the cultural landscape has persisted throughout the Bronze Age and Iron Age into recent times, illustrating the intensity of the development of anthropogenic plant communities.

Fig. 81. *Artemisia*: dot and isopollen maps for 14,000–100 ^{14}C yr BP


6.0
4.4
4.9
0 100 km
Artemisia
14000 +/- 100 BP


6.4
11.7
4.6
0 100 km
Artemisia
13500 +/- 100 BP


2.0
0.8
7.3
5.9
5.7
2.5
5.8
7.2
1.2
8.2
0 100 km
Artemisia
13000 +/- 100 BP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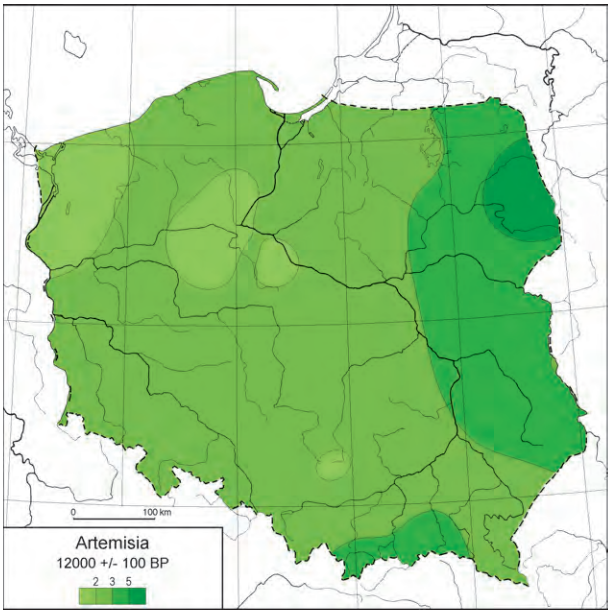
12500 +/- 100 BP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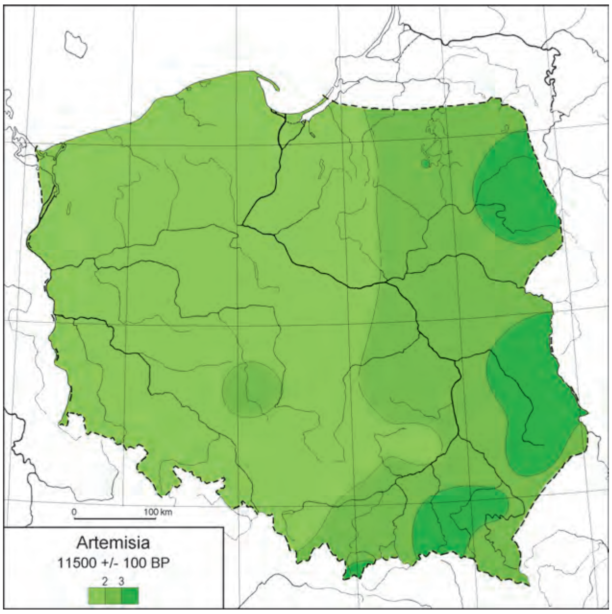
12000 +/- 100 BP
2 3 5


0 100 km
Artemisia
11500 +/- 100 BP
2 3


0.01
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1
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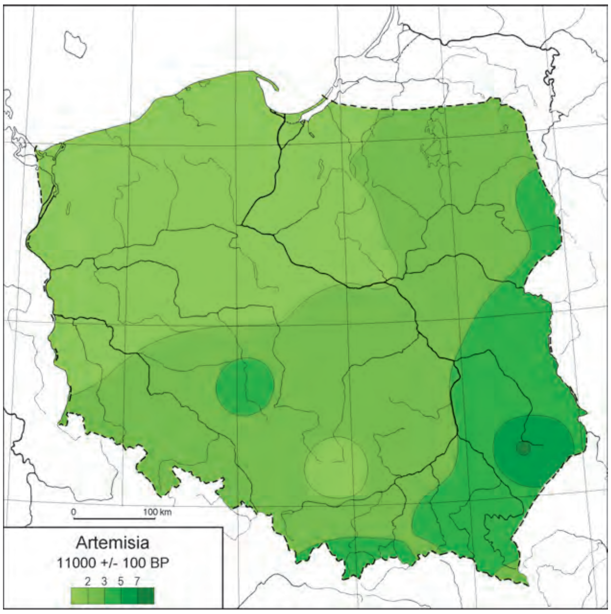
60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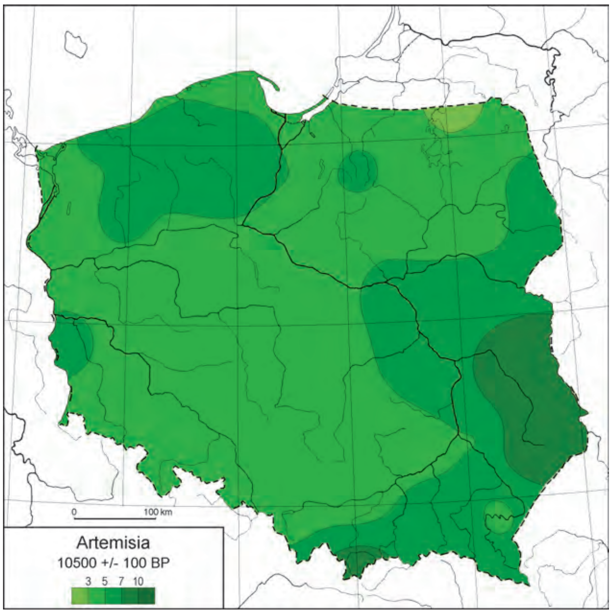
2 3 5 7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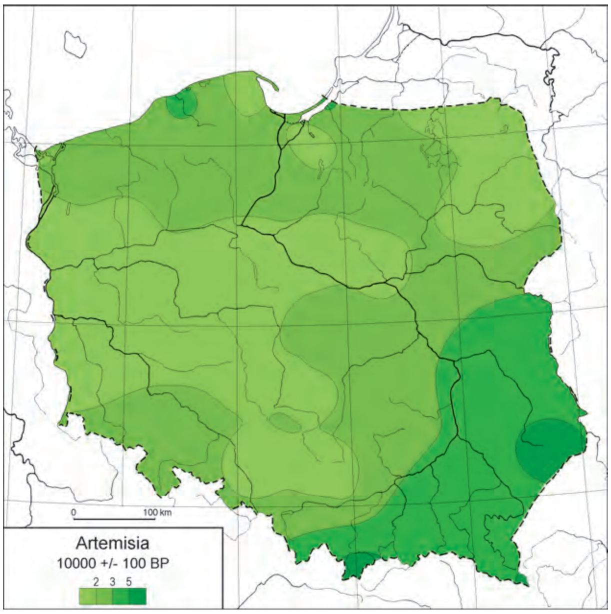
10500 +/- 100 BP
3 5 7 10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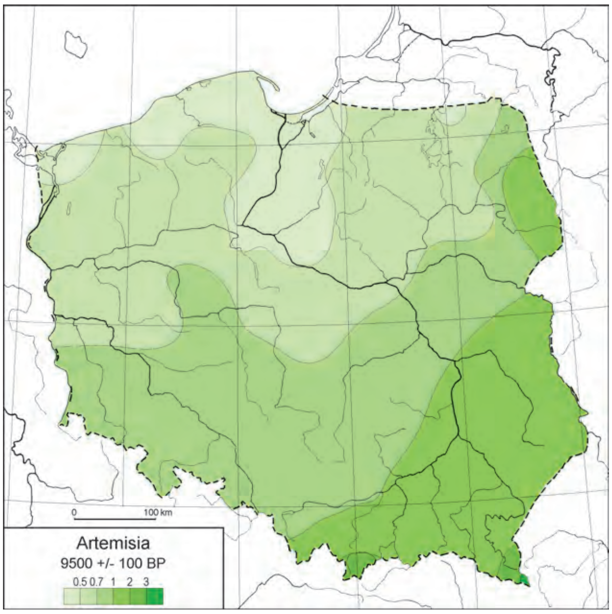
Artemisia
10000 +/- 100 BP
2 3 5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100 km
Artemisia
9500 +/- 100 BP
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0
100 km
Artemisia
9000 +/- 100 BP
0.5 0.7 1


0
100 km
Artemisia
8500 +/- 100 BP
0.2 0.5 0.7 1 2


0.01
0.2
0.5
0.7
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20
30
40
60


0
100 km
Artemisia
8000 +/- 100 BP
0.2 0.5 0.7


0
100 km
Artemisia
7500 +/- 100 BP
0.2 0.5 0.7 1


0
100 km
Artemisia
7000 +/- 100 BP
0.2 0.5 0.7 1


0
100 km
Artemisia
6500 +/- 100 BP
0.2 0.5 0.7 1


0
100 km
Artemisia
6000 +/- 100 BP
0.2 0.5


0
100 km
Artemisia
5500 +/- 100 BP
0.2 0.5 0.7


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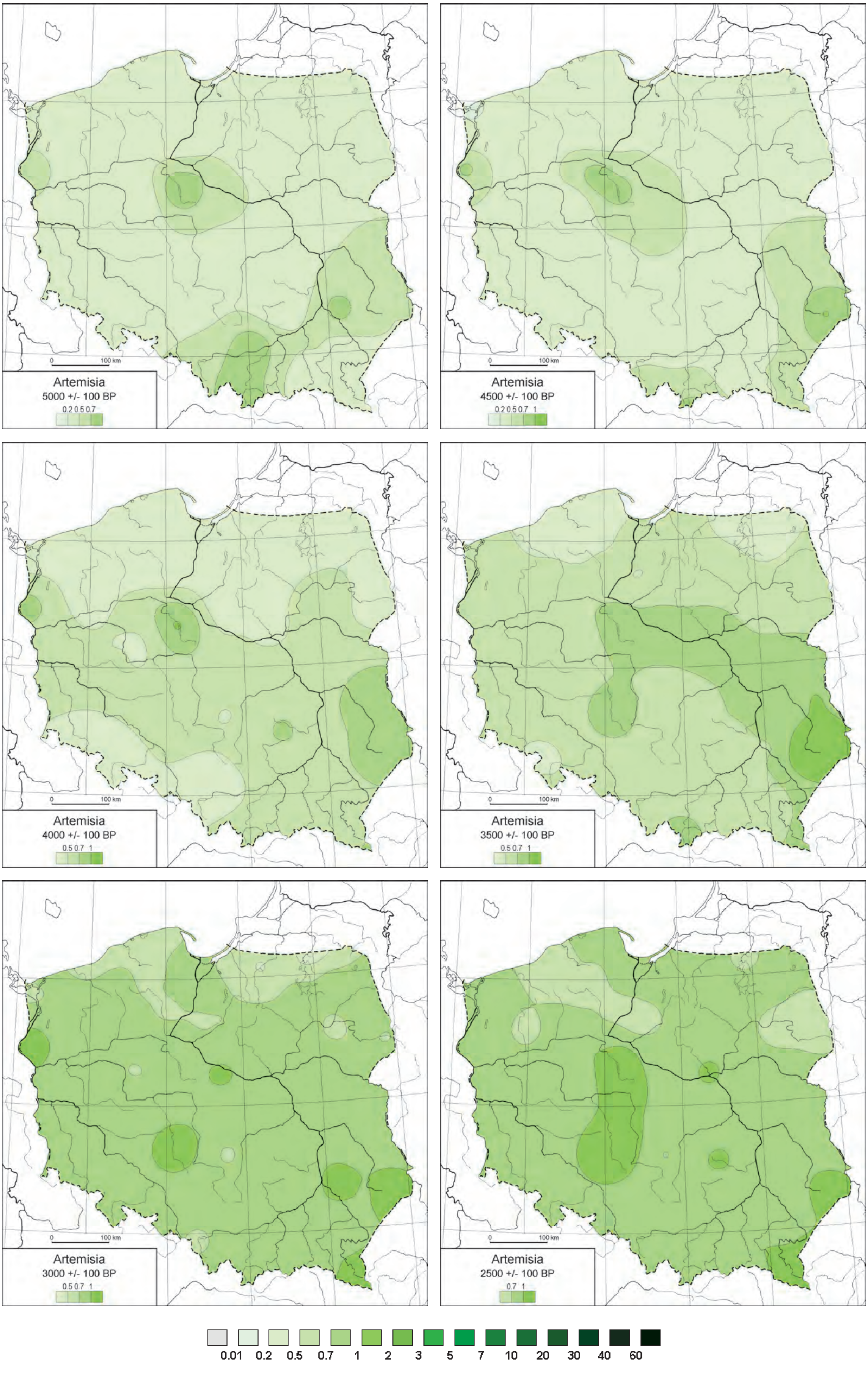
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100 km
Artemisia
5000 +/- 100 BP
0.2 0.5 0.7
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100 km
Artemisia
4500 +/- 100 BP
0.2 0.5 0.7 1
0
100 km
Artemisia
4000 +/- 100 BP
0.5 0.7 1
0
100 km
Artemisia
3500 +/- 100 BP
0.5 0.7 1
0
100 km
Artemisia
3000 +/- 100 BP
0.5 0.7 1
0
100 km
Artemisia
2500 +/- 100 BP
0.7 1
0.01
0.2
0.5
0.7
1
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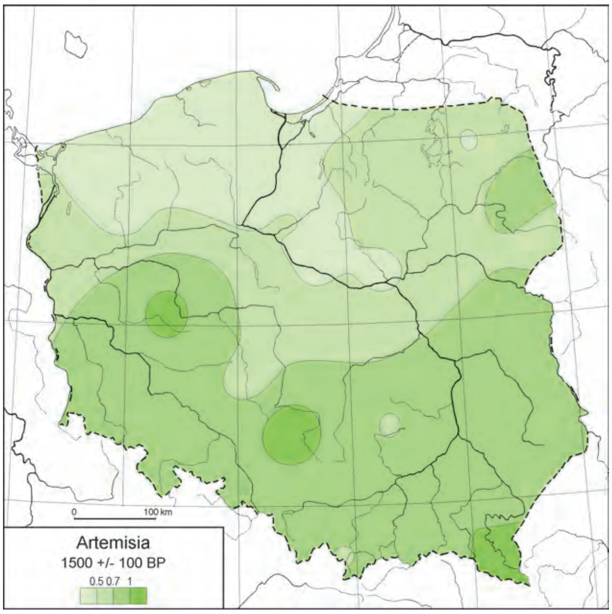
7
10
20
30
40
60


0
100 km
Artemisia
2000 +/- 100 BP
0.5 0.7 1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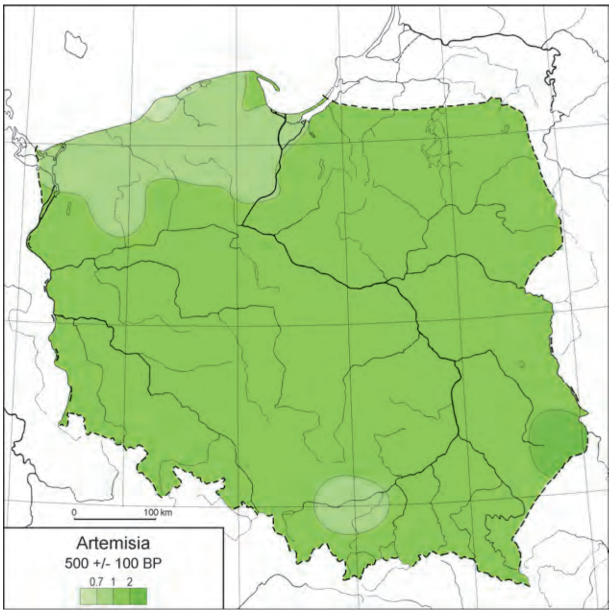
100 km
Artemisia
1500 +/- 100 BP
0.5 0.7 1


0
100 km
Artemisia
1000 +/- 100 BP
0.7 1 2


0
100 km
Artemisia
500 +/- 100 BP
0.7 1 2


0
100 km
Artemisia
100 +/- 100 BP
0.7 1 2


0.01
0.2
0.5
0.7
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60

Cerealia (*Secale cereale* L. excluded) – **Cereals**

KRYSTYNA MILECKA, MIROSŁAW MAKOHONIENKO, IWONA OKUNIEWSKA-NOWACZYK,
AND DOROTA NALEPKA

The morphological pollen type Cerealia comprises pollen grains of cultivated cereals distinguished on the base of their size and exine structure, as well as the shape and dimension of the porus, according to the criteria defined in a key published by Beug (1961). Three genera have been included to this type here: *Triticum* L., *Avena* L., and *Hordeum* L. The pollen grains of *Secale* L., on the basis of their elongated shape and a characteristic annulus, are identified separately (see *Secale cereale*, this volume). *Panicum miliaceum* L. has pollen grains smaller than other cereals. The occurrence of millet may be determined only on the basis of macrofossil analysis. A few wild grasses, such as *Leymus arenarius* (L.) Hochst. and some *Glyceria* R. Br. species have large pollen grains also, which might be confused with those of cereals. Determination to genera can only be achieved using high-grade oil-immersion microscopy and the use of phase contrast (Grohne 1957, Beug 2004). This is seldom carried out because archaeologists, who are most interested in the spread of cereal culture, have a far richer and more reliable source of evidence from charred or otherwise preserved macrofossils of cereal grains and spikelets.

The origins of the majority of the cereals are connected with the regions, known collectively as the Fertile Crescent, extending from the eastern coastlands of the Mediterranean Sea basin (the Levant), through southern Turkey to Mesopotamia (modern Iraq). The origin of individual species of cereals, particularly of wheat, from wild forms, is quite well documented, and the area of their present-day occurrence indicates provenance of some of today cultivated species (Zohary & Hopf 1988). The history of cereals is essentially closely connected with the activity of humans during the last few thousand years.

PRESENT DISTRIBUTION OF CEREAL CULTIVATION IN EUROPE

Triticum – **Wheat**

The only wild species of wheat in Europe is *Triticum baeoticum* occurring exclusively in the Balkans and the Crimea. Seven species, varying in number of chromosomes, are cultivated. The only diploid form, *Triticum monococcum*, is sporadically cultivated in mountainous areas of Europe, in the Balkan countries, Romania, Germany, France, Switzerland, Spain, and Italy (Hanelt 2001). Tetraploid glume wheat *T. dicoccon* can be found again sporadically cultivated in the mountainous areas of Germany, Switzerland, France, Spain, the Balkan countries, and the Czech Republic. Tetraploid free-threshing wheat, *T. durum*, is widely cultivated in the Mediterranean region but it rarely appears elsewhere. In southern and parts of central Europe, as well as in England, the other tetraploid naked wheat, *T. turgidum* is occasionally cultivated. In the Mediterranean countries *T. polonicum* is sporadically grown. The hexaploid species include *T. spelta* planted on a small scale in central, southern, eastern and north-western Europe, and also the most widely farmed common wheat *T. aestivum* which is cultivated throughout Europe except for the extreme north (Hanelt 2001).

Hordeum – **Barley**

At present six wild and two cultivated species of barley occur in Europe. Wild species can be found throughout Europe in varied habitats according to the ecological preferences of individual species. *Hordeum spontaneum* occurs in dry habitats, for example on the island of Crete; *H. murinum* is common in dry grasslands and in disturbed habitats; *H. marinum* is a plant of sandy maritime habitats and sometimes of disturbed places; *H. hystrix* occupies dry sites in south-eastern Europe and again disturbed habitats; *H. bulbosum* can be found in dry grasslands of the Mediterranean region and south-eastern Europe, and *H. secalinum* is widespread in meadow communities. The cultivated species *H. distichon* and *H. vulgare* are diploid forms cultivated throughout the continent (Huntley & Birks 1983).

Avena – **Oat**

Wild species of oats are characterized by various habitat requirements, determining the area of their occurrence in Europe. *Avena clauda*, *A. eriantha*, *A. saxa-*

tilis, and *A. prostrata* prefer dry, rocky areas in the south. *A. longiglumis* is connected with the sea coasts of Spain and Portugal. Some of the wild forms, *A. barbata*, *A. sterilis*, and *A. murphyi*, occur as weeds within cultivated and ruderal habitats, also mainly in southern Europe. The most commonly occurring throughout the continent is the wild oat *A. fatua*. The most widespread and frequently cultivated species of oats is *A. sativa*. The other planted species, according to Huntley & Birks (1983), are of local importance and have restricted areas of cultivation: *A. strigosa* in northern, western, and central Europe, *A. brevis* in north-western regions, *A. nuda* in central, and *A. byzantina* in southern Europe.

ECOLOGY

In general, cereals are 'long-day plants', which require long hours of daylight to achieve flowering and setting seed. Under short-day conditions they persist for much longer in a vegetative stage before, finally, flowering (Roszak 1997). The cultivated species of oat *A. sativa* is particularly characterised by a long vegetative period, which is why its cultivation fails in the north (Podbielkowski 1992). All cereals are light-demanding, and shading of the lower parts of young plants, when sowing is too dense, causes poor growth and diminished hardiness. Young cereal plants are quite resistant to low or even sub-zero temperatures, though getting more sensitive to frosts with time. The cereal most resistant to low temperatures is rye, whereas wheat and barley display higher warmth requirements. Excessively warm conditions are also unfavourable. Barley is the most tolerant of high temperatures. Among winter crops wheat is the most demanding and barley slightly less so in respect of water availability. Among the summer crops, oat is very demanding in this respect, wheat has moderate requirements, and barley is the least demanding (Roszak 1997).

Common wheat, *Triticum aestivum*, is very particular about soil conditions. It develops most successfully on deep, permeable soils, rich in humus, and with pH close to neutral. Dry, sandy and peaty soils are inadequate for wheat. Soil requirements of barley are lower, and it grows well on various types of soils except for acid, wet soils and light sand. The least demanding is oat, which can develop successfully on every soil type, even on peaty soils, if moisture is sufficient.

Wheat, depending on the species, can reach a height of up to 1.2 m (*T. monococcum*, *T. dicoccon*), 1.5 m (*T. polonicum*, *T. aestivum*), and even 1.7 m (*T. spelta*). Wheat flowers in June and July. It is an annual plant, cultivated as summer crop, or biennial as a winter crop, sown in autumn of the year preceding its harvest. Oat reaches over 1 m in height, and it flowers from June to August. Cultivated barley may be 1 m tall and flowers in June or July. Wild species are only up to 40–70 cm tall and their flowering lasts longer, until August or even into September (Szafer et al. 1986).

POLLEN PRODUCTION AND DISPERSAL

The cereals mentioned above are self-pollinating plants. Pollination of wheat takes place prior to opening of the flowers, self-pollination of oats may occur even during the opening of the florets, whereas barley is generally self-pollinated, though cross-pollination is also possible (Podbielkowski 1992). This process and its very high biological efficiency determine very low pollen productivity. Thus, the cereals discussed are usually underrepresented in the pollen diagrams.

EXPANSION IN EUROPE DURING THE LATE GLACIAL AND HOLOCENE

The oldest pollen grains of Cerealia-type found in Europe have been dated to 11,000 BP. A few scattered sites with cereals values not exceeding 1% are located in southern Europe (present-day Greece and France). Since the beginning of the Holocene the range of occurrence of cereals has expanded slowly northwards, encompassing the Balkans, Crete and the Apennine Peninsula, and at 8000 BP reaching values of 7% at some sites (Huntley & Birks 1983).

The expansion of cereal cultivation, initially of barley and wheat species is inextricably bound up with the spread of Neolithic culture. By 6500 BP farmers using pottery characteristic of the Linear Pottery culture had occupied areas of fertile, light soils across Europe to western Germany. By 5000 BP well-marked regions with a regular presence of cereal pollen in their pollen assemblages appear in south-eastern Europe, in the Alps and in an area stretching from central Germany to the extreme north-west of Poland. Their presence was first indicated in the pollen record by brief episodes with very small temporary increases in pollen of Poaceae (Gramineae), herbs such as *Plantago lanceolata* and *Rumex*, and sometimes a few pollen grains of cereal-type. From about 5500 BP these 'landnam' episodes (Iversen 1941) spread to sites in the British Isles and southern Scandinavia. Up to 2500 BP, into the Bronze Age, a gradual and slow extension of the areas of cereal cultivation proceeded, apart from the major part of the Iberian Peninsula, the northern regions of Scandinavia, and Great Britain and Ireland.

A very distinct increase in the contribution of cereal pollen to pollen assemblages is reflected on the 2000 BP isopollen map (Huntley & Birks 1983). This increase is most intensive in the central part of the continent as a result of the extensive spread of cereal cultivation during the growth and expansion of the Roman Empire. In the present-day area of Switzerland there were sites where exceptionally high cereal pollen values, reaching 17% have been found. However, it should be mentioned that for the construction of maps presented by Huntley and Birks (1983) the pollen of all the cereals including also *Secale* was taken into account. Rye in contrast with the other species is a wind-pollinated plant producing a considerable amount of pollen, and that is why including *Secale*, cultivated since the Roman times, into the group of other Cerealia results in an increase of pollen percentages in comparison to the preceding time intervals. The following maps illustrate the presence of cereals in pollen assemblages almost throughout Europe, except for the northern and western extremes. The highest pollen values are still recorded from the central part of the continent in Germany, Poland and the Czech Republic, and from southern France. As noted above, macrofossil remains can provide a much more detailed picture of the extent of cultivation of individual cereal crops, and it is clear from that evidence that, because of the low dispersal of pollen of all cereal crops, except for rye (*Secale*) which is treated here in a separate account, the pollen record gives a poor representation of the importance of cereals in the landscape over much of the late Holocene.

However, tracing the range and spread of cereals in the Holocene, one must bear in mind that their occurrence has been strictly associated with the presence of humans. As was mentioned earlier, none of the species of cultivated cereals is native to the Polish or European floras, and their presence, ever since they first appear in the pollen record, has been influenced by the development and directions of the migrations of human communities during the Holocene.

SPREAD OF CEREALS CULTIVATION IN POLAND (Fig. 82)

6500 – 4500 BP

Early occurrences of cereal pollen grains have been reported in Poland at about 6500 BP. These come from scattered sites situated in the north, on either sides of the lower course of the Vistula river. These records are difficult to explain, since the oldest agricultural Linear Pottery and Lengyel cultures settled in southern Poland. However, in that area there is no trace of cereal cultivation as early as 6500 BP.

The subsequent time intervals up to 4500 BP illustrate a growing number of sites with traces of cereal cultivation. They are concentrated in the central and southern parts of Poland. They are particularly dense in the Kujawy area, although this may partly be a result of the large number of sites investigated in that region and recorded in the data base. In the whole western part of the country, from the middle course of the Warta and Noteć rivers, there are no pollen records of human agricultural activity associated with cereal cultivation, since there is lack of sites there (apart from one in the Sudetes, where cereal pollen may have come by long-distance transport). That is why no Early Neolithic settlement centre on the upper Odra has been noted.

4000 BP

The isopollen map for the 4000 BP time level records the representation of cereal pollen in assemblages with values between sporadic and 0.2%. Throughout the Polish territories these values are very low but nevertheless occur regularly, indicating widespread cultivation of cereals by Late Neolithic/Early Bronze Age populations.

3500 – 2500 BP

The succeeding maps illustrate a similar picture of cereal pollen representation. At the majority of sites the percentages of Cerealia do not exceed 0.2%. Only a few, small areas, where higher values occur, are shown. They are mostly situated in the north-western and north-eastern parts of the country as well as in the Carpathians.

2000 BP

Not until the 2000 BP time level are there noticeable changes in the isopoll patterns. By then the percentages of cereals have increased, particularly in a belt across central Poland and in the north-western part of the country. At the mouth of the Vistula river pollen values for Cerealia reached 0.5–0.7%.

The cultivation of cereals in Poland during the Roman Period has been confirmed by a great number of macroscopic finds, mainly of caryopses (Lityńska-Zając 1997). Based on the list of all the sites at which the remains of cereals from pre-Roman and Roman times have been found this author concluded that the cultivation of cereals was a very important part of agricultural activities at that time. She also pointed out that it is quite difficult to reconstruct the early structure of agricultural production throughout Poland, as the observed pattern may reflect only the present state of research and not real crop preferences in particular geographical regions. In spite of these limitations she stated that barley was commonly cultivated throughout the country, wheat played an important role, but in various parts of the country different *Triticum* species were used, and these preferences were changing with time. Oats have been found at a relatively small number of sites but at these were not abundant. However, the role of this cereal was increasing over time, particularly during the Roman Period. Cultivation of millet and rye was also important, but they are not discussed in this chapter.

1500 BP

The 1500 BP map does not reflect any considerable change. The representation of cereals decreased in the eastern part of the Baltic Coastal Zone, in the neighbouring part of Western Pomerania and in the basin of the upper Vistula river. Sites with cereal pollen values only exceptionally exceeding 0.5% are still dominant throughout the country. The most abundant sites are located in the north-western part of Poland, in the region of Wolin Island. The poor representation of cereals at this time is not surprising at this time level, as, at about the middle of the first millennium AD, during the Migration Period, there was a general decline in settlement. Pollen diagrams relating to this time reflect regeneration of forest communities and a fall in the pollen sum for those taxa associated with human activity. This was the interval between the end of the Roman Period, a period when such indicator taxa were abundant, and the Early Middle Ages, when there was a resurgence of activity, particularly at sites associated with the early development of the Polish State. However, the patterns representing cereal cultivation, both in this and the previous map, may only be giving a poor reflection of economic activity in the Roman Period and illustrate a general underrepresentation of this group of cereals in the pollen record.

1000–100 BP

The 1000 BP time level reflects the cultivation of cereals and management of Polish lands during the Early Middle Ages. A distinct division into the north-western and south-eastern regions is recorded on the isopollen map. This first region, characterised by a higher degree of cultivation and more intensive management, comprises lands, which were the cradle of the Polish State such as Wielkopolska, Kujawy, and part of Western Pomerania, as well as the area around the mouth of the Odra river on the Baltic Sea. The second region, the south-eastern, shows a lower representation of cereals, especially in the regions to the east of the Vistula river.

The 500 BP map illustrates the cultivation and management of the Polish lands in the 15th and 16th centuries. The pattern of division of the country into north-western and south-eastern parts is similar, although with a different distribution of percentage values. Most of north-western Poland which is shown on the 1000 BP map with cereal pollen percentage values of 0.7–1%, on the 500 BP map is covered with values of 1–2%, and this area of higher values is extended south-eastwards, reaching Polesie Lubelskie in the east, and the Moravian Gate in the west. It is difficult to give reasons for the lower values of cereal pollen in the east of Poland. In these areas, the data are derived mostly from peat bogs and rarely from lakes, and probably that is why the pollen assemblages show a lower regional representation. At this time all regions of Poland were inhabited and cultivated. The soils of the Lublin Upland are amongst the best in Poland, and cultivation of wheat was very successful there, however the studied sites from that region are scarce and poor.

High amounts of cereal pollen, above 3%, are characteristic of two areas associated with the mouths of the two largest Polish rivers. The first, situated on the eastern side of the lower course of the Vistula river, was clearly related to the area of the former State of the Teutonic Knights. The high level of agriculture, and the management of the Teutonic Knights, who levied tributes by force, which stimulated more intensive cultivation, result in this area being distinct from its neighbours (Długokęcki 2001, Kaczmarek 2001). The second area connected with the lower course and mouth of the Odra river was related historically to the Land of the Pomeranian Princes.

The present-day picture (100 BP map) is slightly different and shows more intensive cultivation of cereals in the Polish Lowland regions with values >2%. The areas connected with the mouths of the biggest rivers, the Vistula and the Odra, are again distinguished by values of >3%. The amounts of cereals in the upland and mountainous parts of Poland are at a level of 1–2%, locally lower.

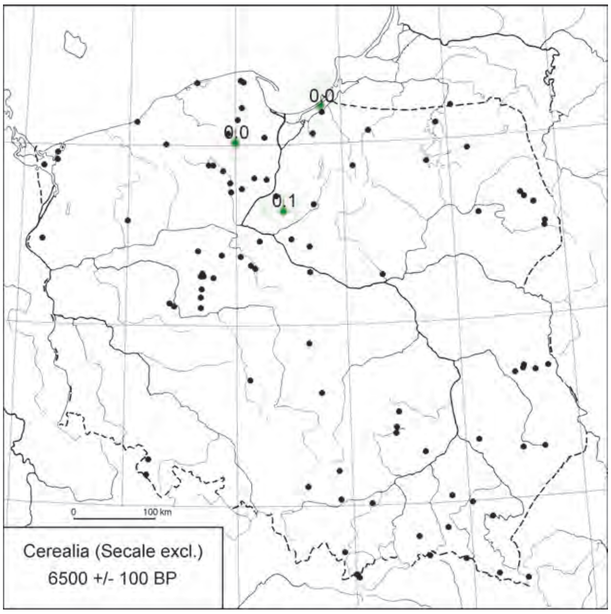
CONCLUSIONS

The isopollen maps for cereal pollen may provide a lot of interesting data, however some additional information is necessary. First of all, the data concerning the pollen types connected with the human activity should be analysed using time horizons expressed in calendar years (see Table 1) making possible comparisons with archaeological and historical data. It should also be taken into account that time horizons, giving maps every 500 years, do not allow the recording or recognition of many characteristic changes, that nevertheless occurred during the history of settlements, as the timescale of the development of different cultures does not correspond with such coarse time divisions. Isopollen data related to the Neolithic and the Bronze Age cultures reflect a not very intensive cultivation of cereals. This results from both poor pollen production and limited dispersal of the pollen grains of the species under discussion and from the far too distant location of some sampling sites from the centres of settlement.

The 2000 BP isopollen time level, is in general slightly too early to reflect accurately and effectively the agricultural management of the Roman Period, and indicates poorly the increased cereal cultivation of that period in relation to preceding horizons. It may partly be a result of the more widespread cultivation of rye, which is not included in the cereal sum but which played quite an important role during the Roman Period. Thus the 2000 BP map does not reflect the most intensive economic development of this settlement phase. This results in a rather small difference between this map and that for 1500 BP, although the latter actually reflects a time of economic decline during the Migration Period.

Isopollen data illustrating the cultivation of cereals during the last millennium indicate intensive agriculture in the areas connected with the valleys of the largest rivers. This resulted from the interaction of several factors, such as: new areas of settlement following the founding of the Polish State, the impact of migration routes along the rivers and of communication routes between the inland areas and the Baltic ports, the intensive development of the peri-Baltic areas, and the location and impacts of the State of the Teutonic Knights. Exploitation of the favourable soil conditions of the fertile riverside lowlands may have also played some role.

Fig. 82. Cerealia (*Secale cereale* excluded): dot and isopollen maps for 6500–100 ^{14}C yr BP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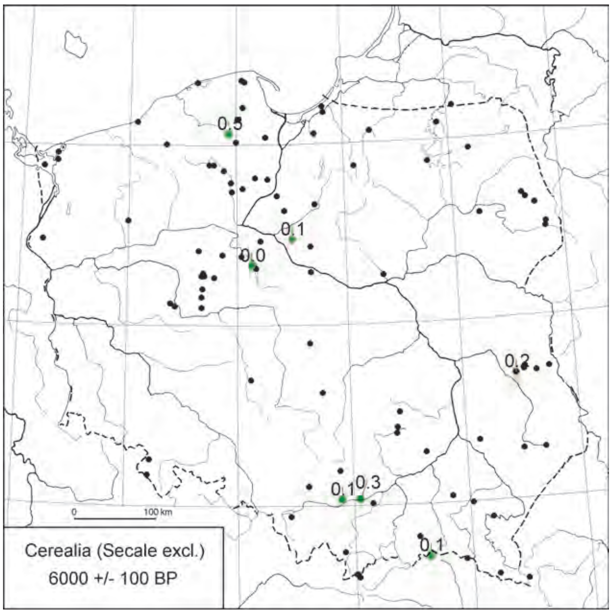
Cerealia (Secale excl.)
6500 +/- 100 BP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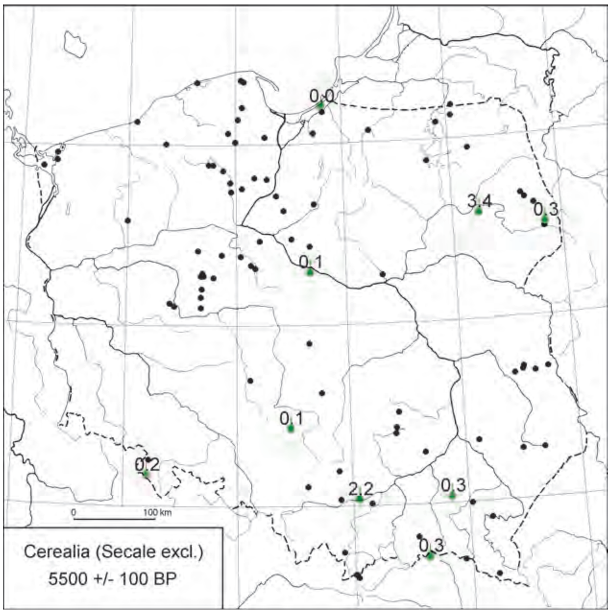
0.1
0
100 km
Cerealia (Secale excl.)
6000 +/- 100 BP


0.0
3.4
0.3
0.1
0.1
0.2
2.2
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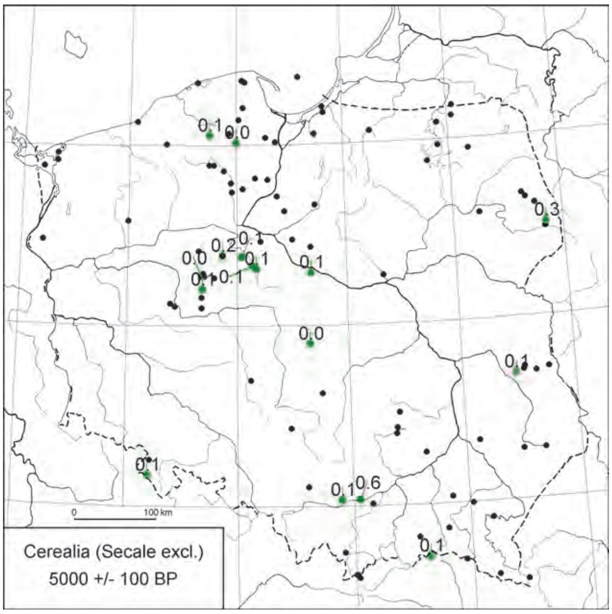
0.3
0
100 km
Cerealia (Secale excl.)
5500 +/- 100 BP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0.1
0.1
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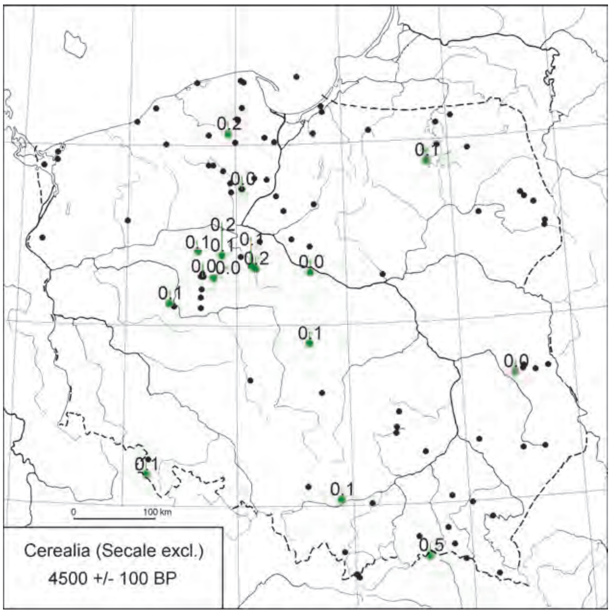
0.1
0.1
0.6
0.1
0
100 km
Cerealia (Secale excl.)
5000 +/- 100 BP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0.1
0.0
0.0
0.2
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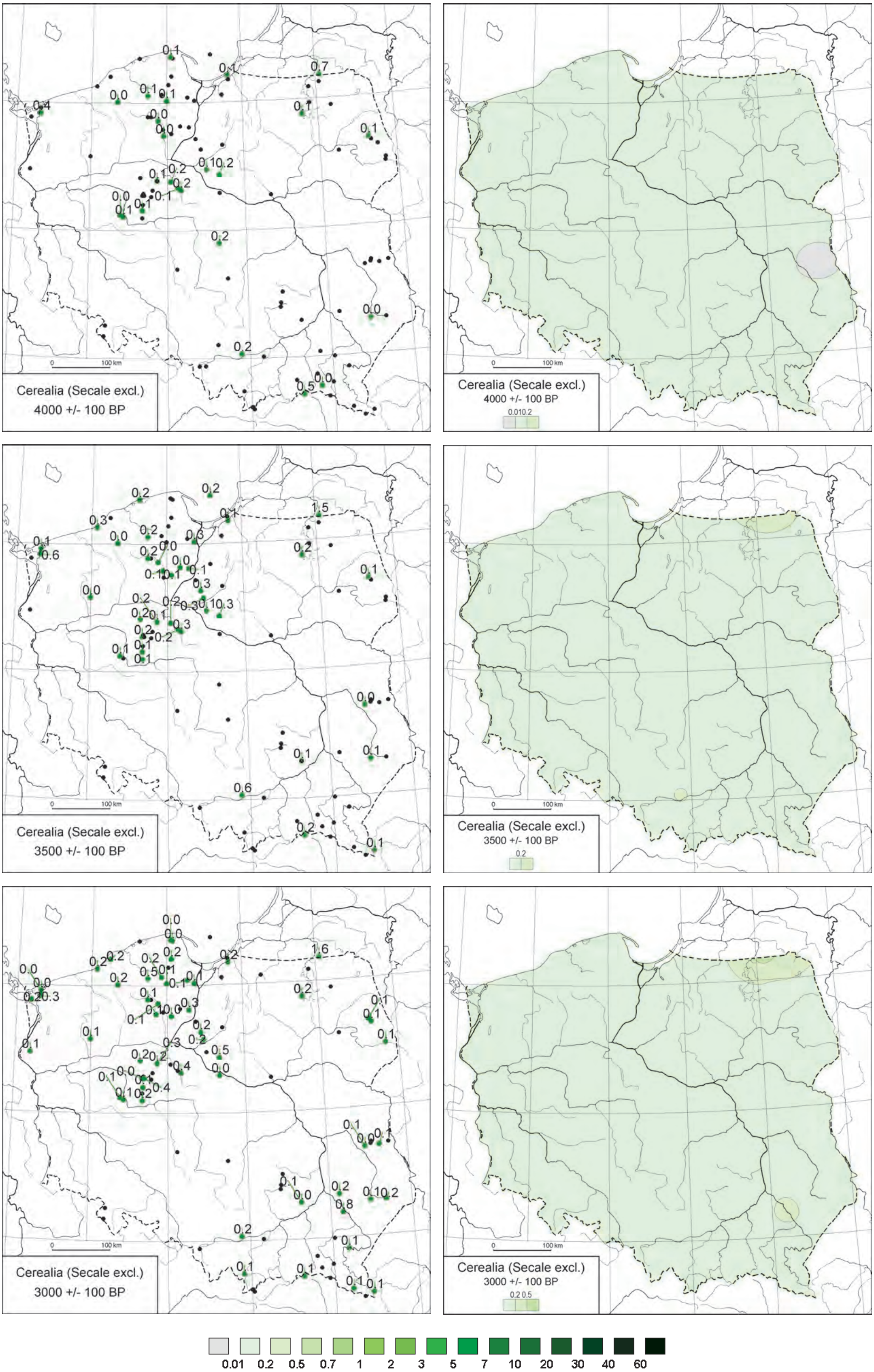
0.1
0.0
0.1
0.1
0.5
0
100 km
Cerealia (Secale excl.)
4500 +/- 100 BP


0
100 km
Cerealia (Secale excl.)
4000 +/- 100 BP
0.01 0.2
Cerealia (Secale excl.)
3500 +/- 100 BP
0.2
Cerealia (Secale excl.)
3000 +/- 100 BP
0.2 0.5
0.01
0.2
0.5
0.7
1
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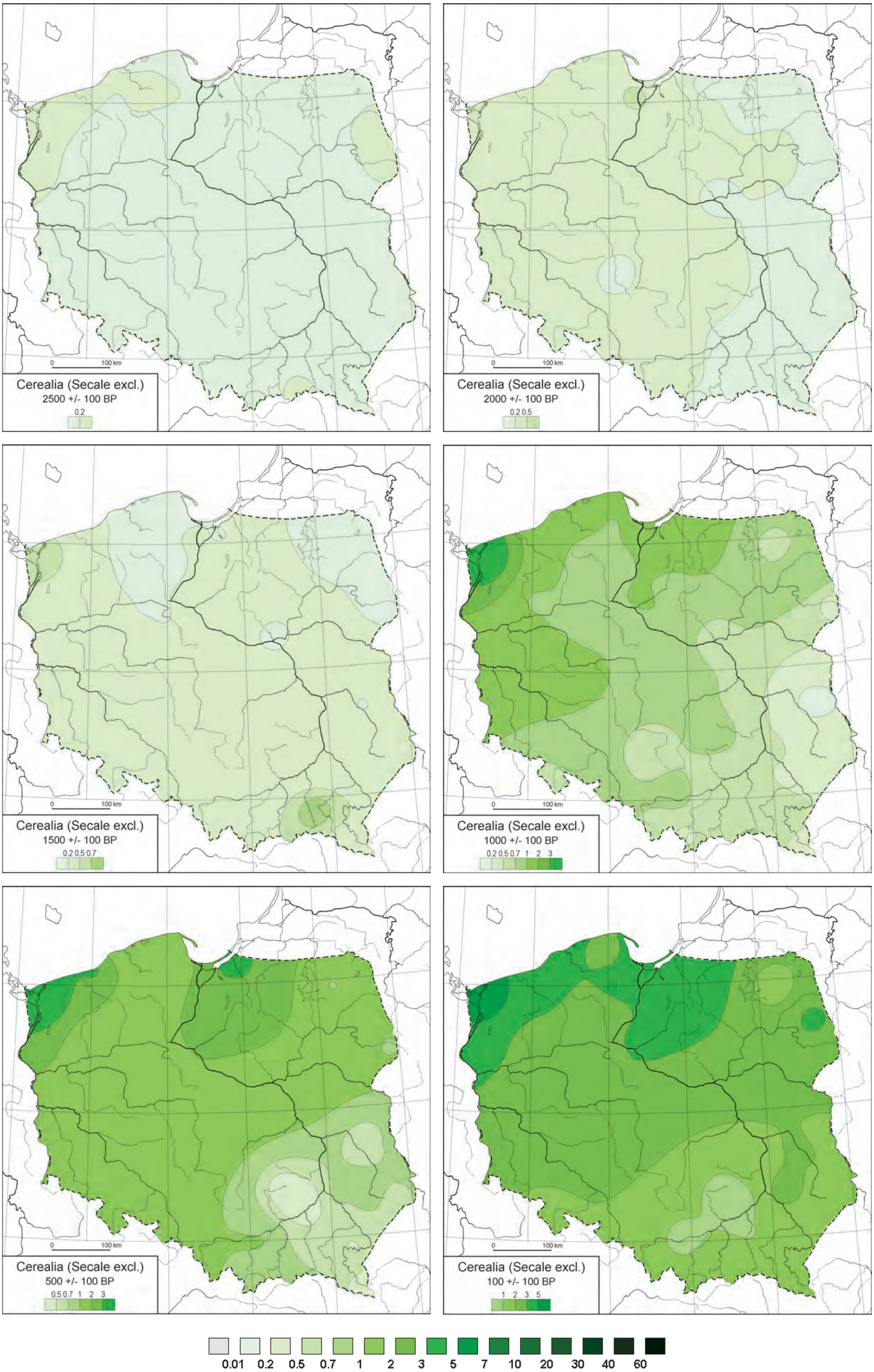

0 100 km
Cerealia (Secale excl.)
2500 +/- 100 BP
0.2
0 100 km
Cerealia (Secale excl.)
2000 +/- 100 BP
0.2 0.5
0 100 km
Cerealia (Secale excl.)
1500 +/- 100 BP
0.2 0.5 0.7
0 100 km
Cerealia (Secale excl.)
1000 +/- 100 BP
0.2 0.5 0.7 1 2 3
0 100 km
Cerealia (Secale excl.)
500 +/- 100 BP
0.5 0.7 1 2 3
0 100 km
Cerealia (Secale excl.)
100 +/- 100 BP
1 2 3 5
0.01 0.2 0.5 0.7 1 2 3 5 7 10 20 30 40 60

Chenopodiaceae – Goosefoot family

Małgorzata Latałowa, Mirosława Kupryjanowicz
and Dorota Nalepka

The Chenopodiaceae is one of those families that show only slight variation in their pollen morphology, and, in spite of attempts at more precise identification of their pollen (Monoszon 1973), only identifications at the family level seem to be possible. The pollen of Amaranthaceae, very similar in respect of their morphology, is also included in this type.

Present distribution in Europe

In Europe the family Chenopodiaceae includes more than 30 genera and about 150 native species (Tutin et al. 1964), with many of them being widespread on this continent (for example *Chenopodium album*, *Ch. glaucum*, *Ch. hybridum*, and *Ch. polyspermum*). However, the majority of species has the northern boundaries of their continuous ranges reaching no farther than southern Scandinavia. A considerable diversity of members of this family occurs in areas of continental climate, but also, due to their tolerance of saline soil and subsoil conditions, in various communities of marine coastal zones. At present, many Chenopodiaceae species are characteristic components of the anthropogenic vegetation both as ruderals and as agricultural weeds.

Present distribution in Poland

In Poland, the Chenopodiaceae family is represented by 10 genera including at least some which are native species. However only within the genera *Chenopodium* L. and *Atriplex* L. are there quite a large number of species that are common over the whole or almost the whole country (*Chenopodium album*, *Ch. glaucum*, *Ch. hybridum*, *Atriplex patula*, and *A. prostrata*). The members of the other genera occur as rare species, occupying specific, mainly sandy habitats (*Polycnemum arvense*, *Kochia laniflora*) or are halophytes (*Halimione pedunculata*, *Salicornia europaea*, *Suaeda maritima* and *Salsola kali*). To the Chenopodiaceae family belong also cultivated species, first of all beetroot (*Beta vulgaris*) and spinach (*Spinacia oleracea*) and also a number of garden plants. In the Polish flora all of the members of the Amaranthaceae family are associated with human sites and activities and virtually all are introduced plants.

Ecology

The members of the Chenopodiaceae occurring in our geographical zone are characterised by similar habitat requirements. Thus the lack of species identifications within this family only partially limits palaeoecological information. The most common species (for example *Chenopodium album* L.) are pioneer plants occurring on bare soils on open sites. Under natural conditions they occupy riverbanks, steep broken slopes and other areas in which soil disturbance and destruction of vegetation have occurred. They can grow under a wide range of soil conditions, from sand and gravel, to compact loam and clay soils; they are also tolerant of drought. Since they both flourish in disturbed conditions and are nitrophiles, they are common components of anthropogenic vegetation. They occur in various ruderal communities and very frequently on cultivated ground, particularly amongst root crops and as garden weeds. Their demographic success is guaranteed by high production of seeds, which maintain their viability for several years (Wójcik 1978).

Pollen production and dispersal

Almost all the species of the Chenopodiaceae family present in our flora flower from July-August to the autumn (Szafer et al. 1969). This family is wind-pollinated; however, generally its pollen does not disperse very effectively. It has been noted that there are considerable differences between species in respect of the amount of pollen production, with the most common species *Chenopodium album* as relatively low pollen producer (Lombardero et al. 1991). According to Huntley and Birks (1983) values >1% of Chenopodiaceae pollen in pollen assemblages indicate their local presence, whereas values >5% show their abundance in the surrounding vegetation. Considering the composition of our flora, as well as the results of aerobiologic research on modern pollen deposition, it can be stated that this estimate is too cautious. Chenopodiaceae pollen values do not exceed 1% in the surface spectra of any of the six lakes located within landscapes in northern Poland (Latałowa & Święta 2002), which have been moderately or greatly transformed by human activity. On the other hand it cannot be excluded that the high Chenopodiaceae pollen values, characteristic of the cold periods of the Late Glacial, result from the presence of other species within this family, which are more efficient pollen producers.

MIGRATION PATTERN IN POLAND (Fig. 83)

14,000 – 10,500 BP

Species of the family Chenopodiaceae must have been components of the Pleistocene steppe-tundra as shown by the significant contribution of Chenopodiaceae pollen in Late Glacial assemblages from the whole of Europe. However, it is not quite clear which of the species could have participated in communities of this kind in Poland. Among the macrofossils found in late Vistulian deposits, the Chenopodiaceae seeds that can be identified to species level are very rare. The occurrence of *Polycnemum arvense* was confirmed by seeds from the Late Glacial at Witów in central Poland (Wasylikowa 1964) and *Chenopodium album* seeds were found in deposits of Older Dryas age at Håkulls Mosse in southern Sweden (Liedberg Jönsson 1988). From the closing stages of the last glaciation derive also the seeds of *Ch. rubrum*, *Atriplex patula*, and *A. glabriuscula* recorded in the British Isles (Godwin 1975).

In the oldest deposits, dated at 14,000 and 13,500 BP and described from sites situated in north-eastern Poland, the rather high Chenopodiaceae pollen values exceeding 1% up to 3.2% have been recorded. They reflect the expansion of pioneer species into areas just abandoned by the ice sheet, and still affected by factors promoting soil instability. Values of Chenopodiaceae pollen remained relatively high in Poland throughout the whole of the late Vistulian. However, the isopollen maps distinctly reflect regional differentiation within Poland, in relation to how important the presence of Chenopodiaceae was within plant communities, and the differences in the role that species of this family played during periods of different climatic conditions. They clearly show lower pollen values of Chenopodiaceae during the warmer period of the Allerød Interstadial (11,500 BP) when forest communities developed, and higher values for the colder periods, particularly the Younger Dryas (10,500 BP). The maps for 11,000 and 10,500 BP show the decline of forest communities, and that this process was spreading from the east.

The isopollen maps illustrate clearly the regional character of plant communities with Chenopodiaceae in the Late Glacial, reflecting probably the climatic differentiation of Polish territories during this time. High Chenopodiaceae pollen values are characteristic mainly of the eastern areas of our country, which also at present show a higher degree of continentality (Matuszkiewicz W. 1999). The high values of Chenopodiaceae pollen particularly in the colder periods of the Late Glacial in the mountainous areas and in their foreland are connected with intensive denudation and erosion processes (Alexandrowicz 1997). These processes caused the development of landslides, which became colonised by pioneer vegetation, as were habitats along the numerous streams and river valleys.

10,000 – 100 BP

At the opening of the Holocene, at around 10,000 BP, the contribution of plant communities typical of open habitats became distinctly restricted in Poland. It appears from the isopollen map that during this time they still played an important role in the Carpathians and in their foreland as well as in the Lublin Upland and the Roztocze. As has been already argued above, such a pattern of Chenopodiaceae isopolls delineates on the one hand the most continental areas, and on the other mountain habitats, where landslide and fluvial processes still played an important role (Gil et al. 1974, Ralska-Jasiewiczowa & Starkel 1988). In these areas, apart from the Bieszczady Mountains, the major stabilization of the environment occurred in the middle of the Preboreal period (9500 BP).

During the course of the Holocene, the contribution of Chenopodiaceae to open vegetational communities was rather restricted because of forest development. Such communities probably remained mainly in habitats along the river valleys, whilst the halophyte species expanded along the low-lying parts of the Baltic Coastal Zone. Small areas with higher values of Chenopodiaceae pollen, visible on the isopollen maps, are associated with the development of human settlements, and in the mountains probably with the increase of denudation, caused either by economic activity or by the development of a wetter climate. The greater abundance of Chenopodiaceae pollen in the Western Carpathians (the 7500 BP map) is a good example; it is a period recognised as a time of intensified landslide phenomena in this area (Alexandrowicz 1997). The 6000 and 4500 BP maps show the appearance of a patch of higher Chenopodiaceae pollen values in the area of Kujawy that can be precisely connected with the development of Neolithic agriculture there. The fertile soils of Kujawy were the areas of the oldest settlements, connected with the Linear Pottery (6500–6000 BP) and Lengyel cultures (ca. 5700–4900 BP) (Grygiel & Bogucki 1997), and then of the younger Neolithic cultures. The archaeobotanical investigations of the Lengyel settlement at Osłonki have revealed a considerable number of *Chenopodium album*-type seeds (Bieniek 2002). This plant has been distributed mainly as a weed of cultivation, and the abundance of its remains in the archaeobotanical material may suggest, according to the author of these investigations, that it was collected as an additional food resource. The absence of sites with higher Chenopodiaceae pollen values in other areas of Early Neolithic settlements (e.g. Pyrzyce Land, or Małopolska) results from the lack of palynological data corresponding to precise time levels used in this book, and the omission of sites falling between them. For instance, in the Małopolska Upland site of the Lengyel culture at Pleszów, percentage values of Chenopodiaceae pollen actually exceed 1% (Wasylikowa et al. 1985).

A significant increase in the amount of Chenopodiaceae pollen appears not earlier than on the map illustrating the present-day period. The highest values form a belt spreading from the north-east and east through the greater part of central Poland to the eastern state frontier. Also they are marked in the south-eastern part of the country. An analysis of this map, against the background of climate and agriculture maps of Poland, indicates that high Chenopodiaceae pollen values are distinctly associated with the areas of lowest precipitation and with relatively light soils on which arable land occupies more than 60% of the area. On the other hand, in the mountain and foothill areas they can reflect a higher abundance of weeds because of less intensive agriculture, and, as in earlier periods, a considerable intensification of processes of denudation and erosion.

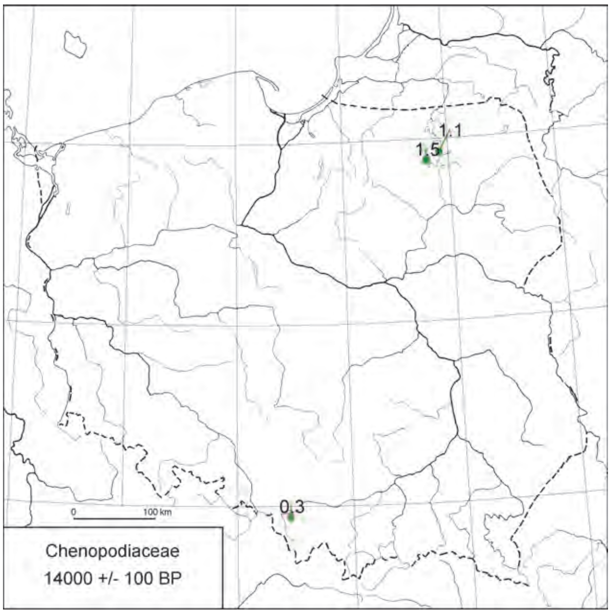
CONCLUSIONS

The isopollen maps for Chenopodiaceae illustrate a pattern of regional differentiation within Poland during the successive periods of the late Vistulian, which may be related to the influence of continentality of climate.

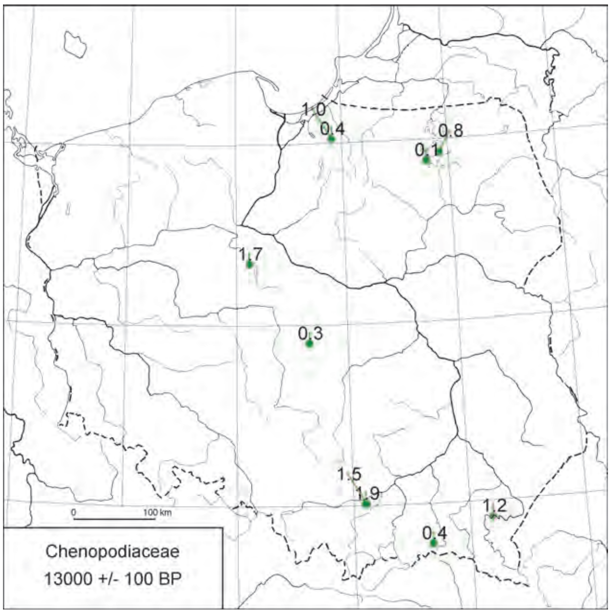
They also reflect periods of both enhanced erosion and denudation in the mountain areas, as well as of anthropogenic transformations of the environment in areas occupied by the oldest Neolithic settlements.

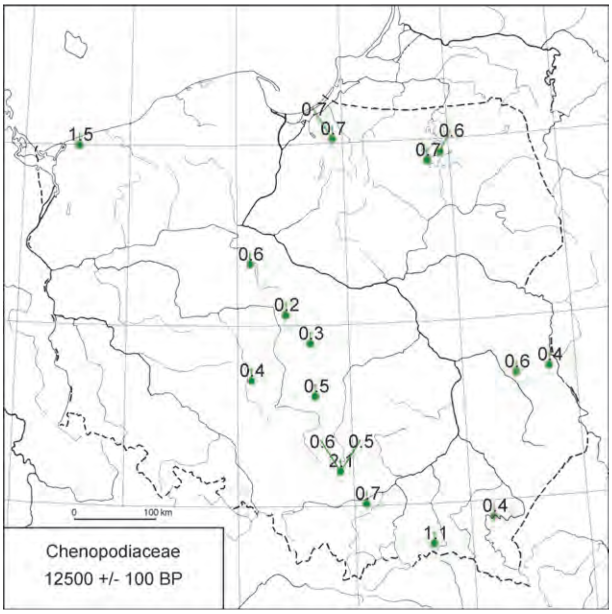
In spite of the relatively low representation of Chenopodiaceae in pollen assemblages and lack of precise taxonomic identifications, the isopollen maps present a very consistent picture, revealing the substantial usefulness of Chenopodiaceae pollen in making palaeoecological and palaeoenvironmental reconstructions.

Fig. 83. Chenopodiaceae: dot and isopollen maps for 14,000–100 ^{14}C yr BP


1.1
1.5
0.3
0
100 km
Chenopodiaceae
14000 +/- 100 BP


3.2
1.3
0.8
0
100 km
Chenopodiaceae
13500 +/- 100 BP

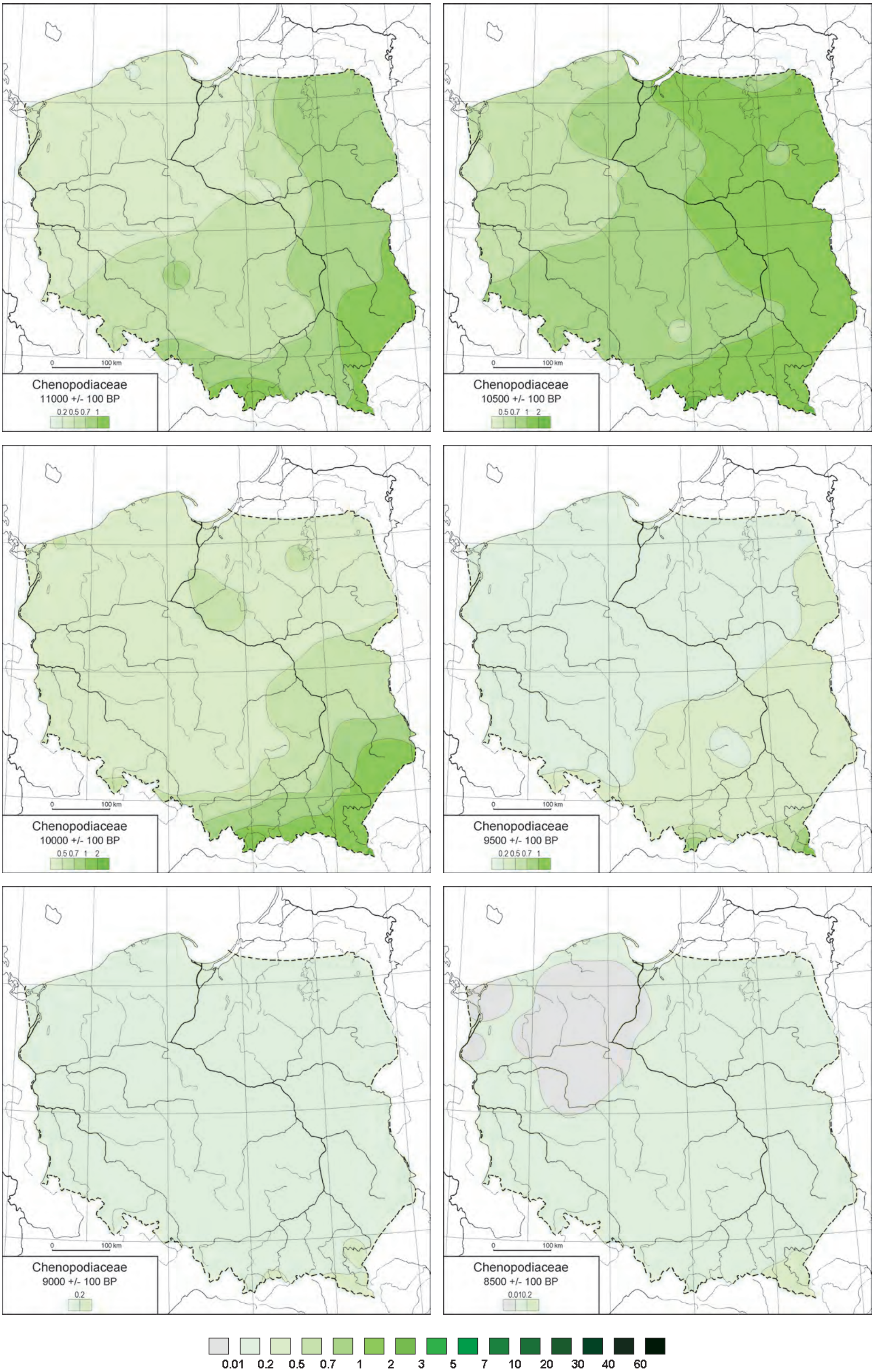

1.0
0.4
0.8
0.1
1.7
0.3
1.5
1.9
1.2
0.4
0
100 km
Chenopodiaceae
13000 +/- 100 BP


0.7
0.7
0.6
1.5
0.7
0.6
0.2
0.3
0.6
0.4
0.4
0.5
0.6
0.5
2.1
0.7
0.4
1.1
0
100 km
Chenopodiaceae
12500 +/- 100 BP


0
100 km
Chenopodiaceae
12000 +/- 100 BP
0.5 0.7 1


0
100 km
Chenopodiaceae
11500 +/- 100 BP
0.2 0.5 0.7


0.01
0.2
0.5
0.7
1
2
3
5
7
10
20
30
40
60


0 100 km
Chenopodiaceae
11000 +/- 100 BP
0.2 0.5 0.7 1
0 100 km
Chenopodiaceae
10500 +/- 100 BP
0.5 0.7 1 2
0 100 km
Chenopodiaceae
10000 +/- 100 BP
0.5 0.7 1 2
0 100 km
Chenopodiaceae
9500 +/- 100 BP
0.2 0.5 0.7 1
0 100 km
Chenopodiaceae
9000 +/- 100 BP
0.2
0 100 km
Chenopodiaceae
8500 +/- 100 BP
0.01 0.2
0.01 0.2 0.5 0.7 1 2 3 5 7 10 20 30 40 60


0
100 km
Chenopodiaceae
8000 +/- 100 BP
0.01


0
100 km
Chenopodiaceae
7500 +/- 100 BP
0.2 0.5

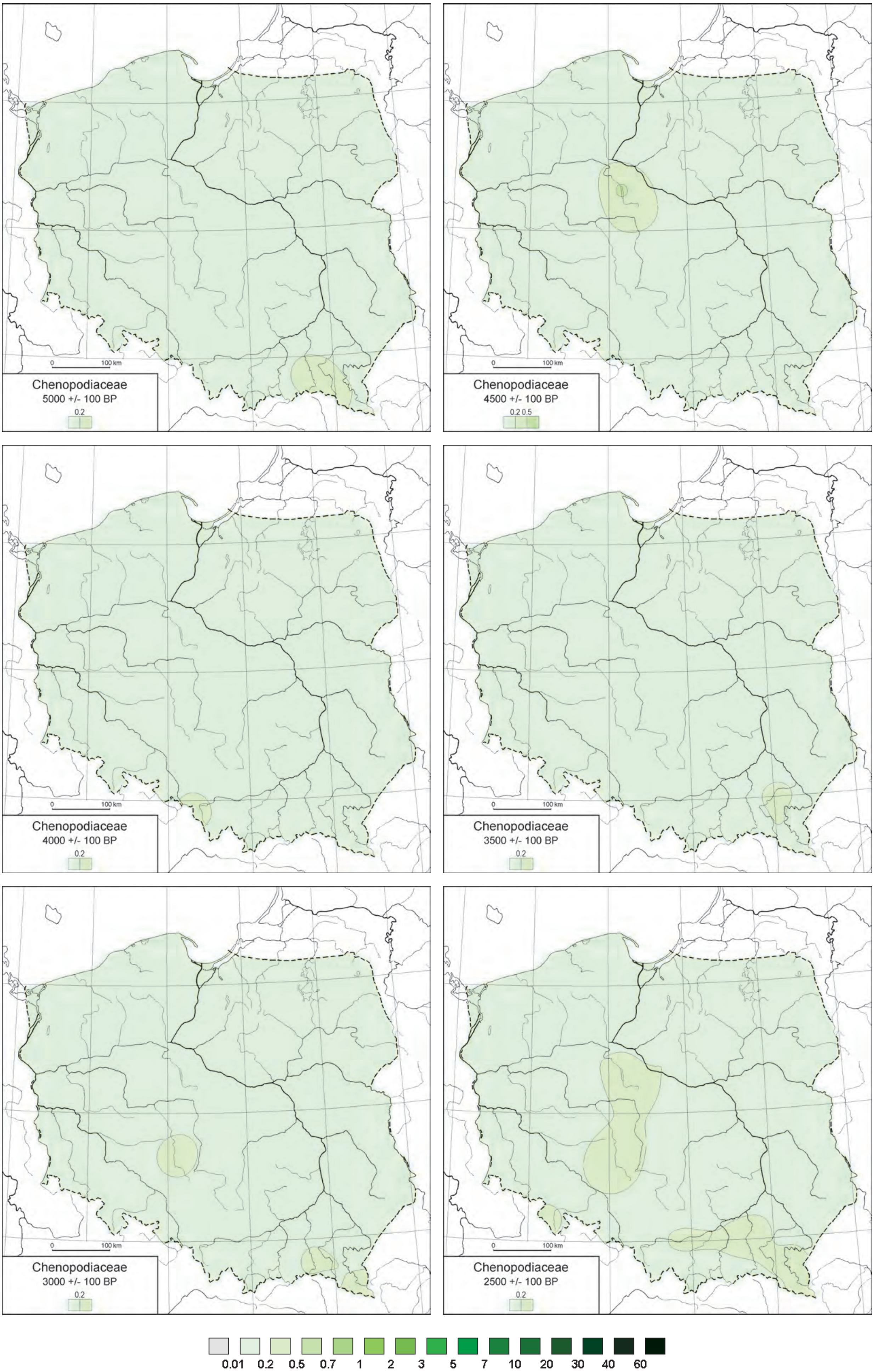

0
100 km
Chenopodiaceae
7000 +/- 100 BP
0.01 0.2

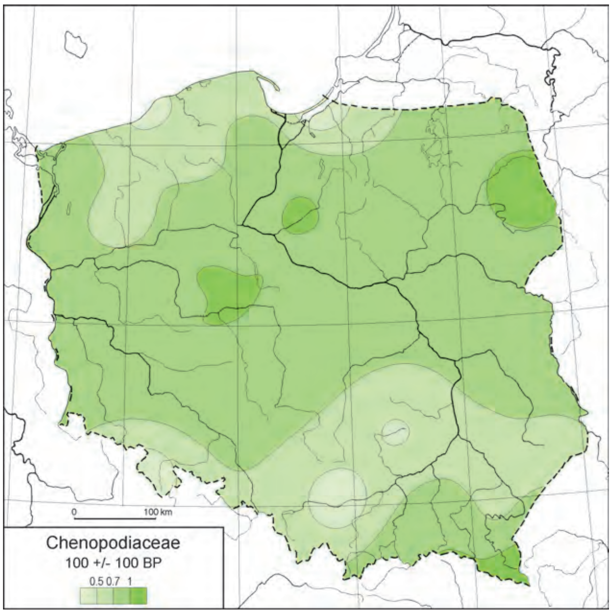

0
100 km
Chenopodiaceae
6500 +/- 100 BP
0.2


0
100 km
Chenopodiaceae
6000 +/- 100 BP
0.2 0.5


0
100 km
Chenopodiaceae
5500 +/- 100 BP
0.2


0.01
0.2
0.5
0.7
1
2
3
5
7
10
20
30
40
60


0
100 km
Chenopodiaceae
5000 +/- 100 BP
0.2
Chenopodiaceae
4500 +/- 100 BP
0.2 0.5
Chenopodiaceae
4000 +/- 100 BP
0.2
Chenopodiaceae
3500 +/- 100 BP
0.2
Chenopodiaceae
3000 +/- 100 BP
0.2
Chenopodiaceae
2500 +/- 100 BP
0.2
0.01 0.2 0.5 0.7 1 2 3 5 7 10 20 30 40 60



⬜	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	⬛
0.01	0.2	0.5	0.7	1	2	3	5	7	10	20	30	40	60

Cyperaceae – Sedge family

Małgorzata Latałowa, Kazimierz Tobolski and Dorota Nalepka

Wherever plants grow throughout the world, members of the family Cyperaceae are common components of the vegetation. In the present flora of Poland it is also one of the families containing a very high number of species, included in 15 genera; in particular, the genus *Carex* L. includes as many as ca. 100 species. The vast majority of the members of this family are marsh and bog plants, although many other species grow on rocks, or in grassland and woodland. Regarding the Polish species of *Carex*, almost 50% are actually not wetland species, but only a few of them are frequent or common, if one considers their occurrence over the whole country (Szafer et al. 1986, Zając A. & Zając M. 2001).

Ecology

Species of the Cyperaceae family are important in the initial development of reedswamps in river valleys, in the successional stages of plant communities that surround and may eventually overgrow lakes, and in different stages in the evolution of peat bogs. Among the reedswamp communities of the *Phragmition* alliance they mainly form those dominated by *Schoenoplectus lacustris* and stands of *Eleocharis palustris*. The tall sedge associations (*Magnocaricion*) are ecologically very diverse marsh and fen communities, which generally play an important role in the colonization of stagnant waters. *Carex rostrata*, *C. pseudocyperus*, *C. elata*, *C. gracilis*, and *C. vulpina* are amongst the commonest species that dominate these types of communities, depending on local conditions. There is an important group of mire communities, with a considerable representation of numerous species of Cyperaceae, for example *Carex nigra*, *C. limosa*, *C. lasiocarpa*, and *C. diandra* in moss mires of the *Scheuchzerio-Caricetea* class. In raised bogs, particularly where the surface is beginning to dry out, patches of cotton-grass (*Eriophorum vaginatum*) and white beak sedge (*Rhynchospora alba*) appear. However, this type of mire is characterized by a smaller number of Cyperaceae species.

From the point of view of analysis of the isopollen maps, the most important contributors must be the reedswamp and mire species. Their remains are generally the main component of fen peats, which results in the local over-representation of Cyperaceae pollen in these types of sediment. Considerable pollen percentages of this family, usually not determined to genus level, are also found in *Eriophorum* peat, more rarely in *Rhynchospora alba* peat.

Pollen production and dispersal

Flowers in the Cyperaceae family are dioecious and wind-pollinated. However, the majority of species produce a moderate amount of pollen, whose dispersal ability can be compared with that of the pollen of grasses (Sugita et al. 1999). Diagnostic features of Cyperaceae pollen grains that might be used for identification to genus or pollen-type level are quite difficult to observe (Faegri & Iversen 1989). The pollen grains are delicate, and they can be relatively easily deformed and damaged, which makes their identification even more difficult. Most palynologists routinely identify the characteristic pollen of *Cladium mariscus*, but not many of them also identify other Cyperaceae pollen taxa (or types).

Migration pattern in Poland (Fig. 84)

Analysing the isopollen maps for the Cyperaceae family, it should be taken into account that the amount of Cyperaceae pollen in a palynological sample is closely dependent upon the role of Cyperaceae within the local vegetation. Thus the isopollen maps for this taxon relate only to a small degree to its history and to its contribution to plant communities in a particular region or in the country, as a whole. They mainly indicate the types of sediments that were the source material studied by a palynologist at a particular site. Moreover, the type of sediment used for pollen analyses depends only partly on its availability or accessibility in a given area. Sometimes it illustrates the personal preferences of particular researchers, some of whom prefer to carry out their investigations on peat bogs (with high or very high values of Cyperaceae pollen in the pollen assemblages), whilst other palynologists take their samples from the bottom sediments of lakes (with low amounts of Cyperaceae pollen).

14,000 – 12,500 BP

The oldest Late Glacial maps display considerable variations in the Cyperaceae pollen values at particular sites, which most likely is an effect of local conditions, especially the contribution of Cyperaceae to the process of colonization and overgrowth of lake basins, as biogenic sediments were accumulating. During this period Cyperaceae formed an important component of marshy tundra. Among the species identified on the basis of the macrofossils obtained from the oldest sediments of the late Vistulian in Poland the following can be mentioned: *Carex aquatilis*, *C. rostrata*, and *C. nigra* (Wasylikowa 1964, Harmata 1987, Tobolski 1988).

12,000 – 10,000 BP

The younger part of the late Vistulian is also characterized by the high amount of Cyperaceae pollen over the whole country, with the highest values occurring mainly in the south. In these areas, situated beyond the limit of the last glaciation, warming of the climate during the Allerød stimulated the development of peat bogs, particularly of moss-type, onto which Cyperaceae encroached (Latałowa & Nalepka 1987). Meanwhile, in the areas that had been within the limits of the last glaciation, there was during that time an intensification of ice-melting processes, which initiated the formation of vast lake districts particularly in northern Poland. The maps for the Allerød (11,500, 11,000 BP) and the opening of the Holocene (10,000 BP) are similar, and their characteristic feature is the occurrence of low Cyperaceae pollen values in the area of the present lake districts. However, it should be emphasized that the area of these low values does not comprise the most northern and eastern areas of the country, where the ice-melting processes were less intensive at that time. These led more often there to the development of mires rather than of water bodies. The maps for the 12,000 BP and the Younger Dryas (10,500 BP) illustrate a partial restriction of the processes leading to the development of lakes and the periodic re-occurrence of communities of wet sedge tundra.

9500 – 6000 BP

The maps for the early and middle Holocene show the widening area of low Cyperaceae pollen values. It is similar, in outline, to the extent of the last glaciation, where for this period the lake sediments are the main objects of palynological studies. This concerns both, sites that have maintained their status as a water body up to the present day and those, which have become overgrown. In southern Poland, particularly in the Carpathians and in the areas of the south Polish uplands, because of the lack of lakes palynological investigations have concentrated on peat bogs. Therefore, much higher Cyperaceae pollen values are recorded from these parts of the country.

5500 – 5000 BP

On the maps for this period the widening of the area of higher Cyperaceae pollen values is marked, which may be connected with the intensified overgrowth and infilling of lakes, and the appearance of new peat bogs. Ralska-Jasiewiczowa and Starkel (1988) as well as Żurek (1996) have already paid some attention to the intensification of these processes during the time period under discussion.

4500 – 1500 BP

The relatively low values of Cyperaceae pollen during the younger Holocene result from transformation of fen and transition peat-bogs into raised bogs, which under favourable conditions of humidity are, as a rule, characterized by a lower abundance of species of Cyperaceae in the flora. Such a changing trend is indicated by regional palaeoecological data for practically the whole area of Poland (Ralska-Jasiewiczowa & Latałowa 1996).

1500 – 100 BP

On the successive maps for this youngest period an increase in Cyperaceae, shown by the isopoll values, spreads, particularly from the western and southern directions. It can be assumed that these maps illustrate the process of overgrowth of lakes and mires due to both, natural causes and as a result of hydrological disturbances caused by the increasing pressure of human activities.

CONCLUSIONS

The isopollen maps for Cyperaceae are strongly affected by the type of sediment used for pollen analysis in particular sites and, as a rule, they illustrate representation of this family in local vegetation. Therefore, the most striking feature of most of the maps are the lower pollen values in the areas covered by extensive lakelands situated within the limit of the last glaciation (Fig. 1, this volume) and the higher ones in S and SE Poland where the main source of the pollen data are different types of mires. However, at least in some periods, due the large number of sites, the regional differentiation of the Cyperaceae pollen contribution reflects some more general trends related to the evolution of wetlands. They might be summarized as follows:

– the large participation of the Cyperaceae pollen in all the time-windows of the late Vistulian illustrates development of shallow mires and tundra vegetation after recession of the ice-sheet and gradual thawing of dead-ice and permafrost;

– in the early Holocene, the contribution of Cyperaceae in the pollen rain diminished due to development of other vegetation types (mainly forests) and in central and northern Poland due to transformation of mires into lakes;

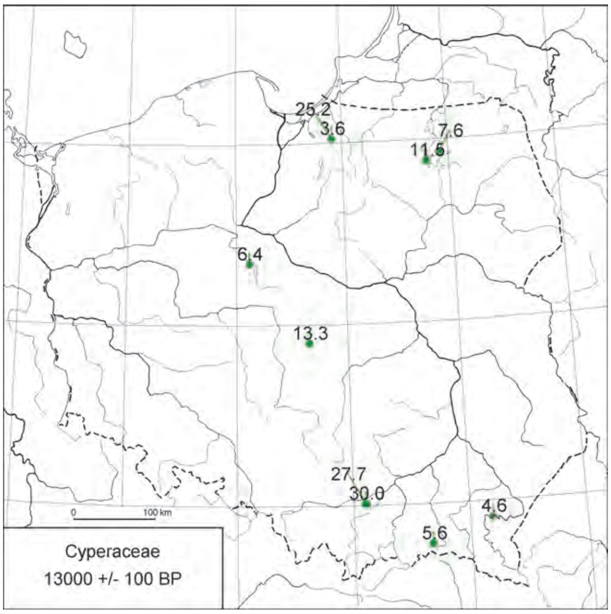
– the opposite trend, i.e. shallowing and overgrowing of lakes as well as increasing tendency of paludification, as observed in the middle of the Holocene, resulted in extension of mires and then, higher Cyperaceae pollen representation;

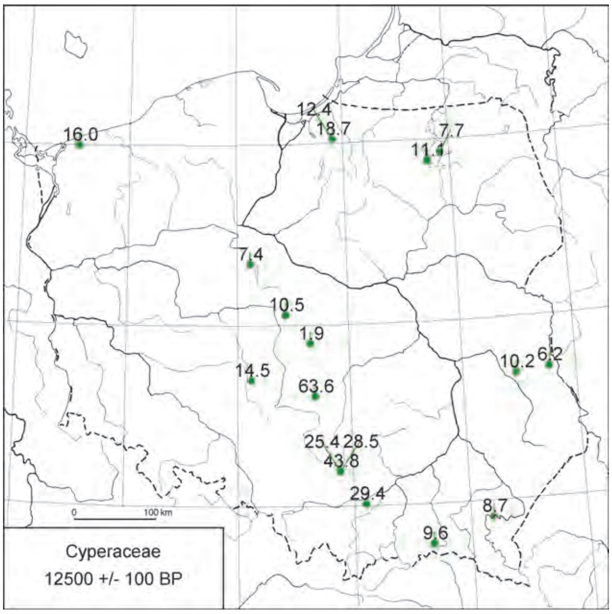
– the most recent map shows very high contribution of Cyperaceae pollen that probably reflects both – the more open landscape resulting in general increase of NAP, and high intensity of contraction of lakes and transformation of raised bogs giving place for different types of Cyperaceae vegetation.

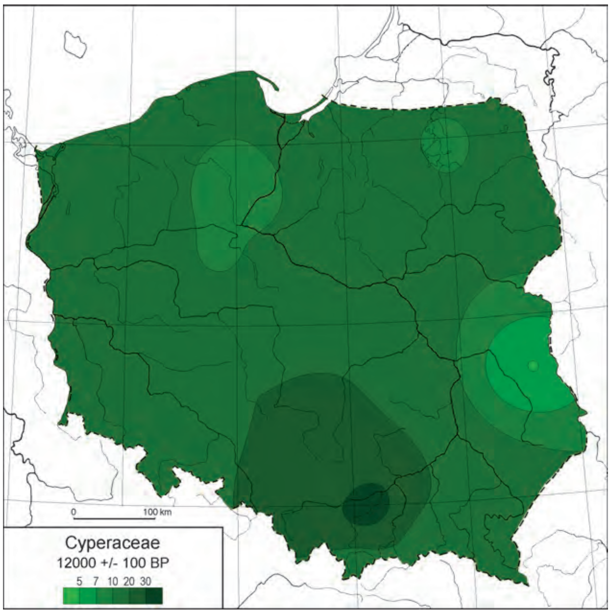
Fig. 84. Cyperaceae: dot and isopollen maps for 14,000–100 ^{14}C yr BP

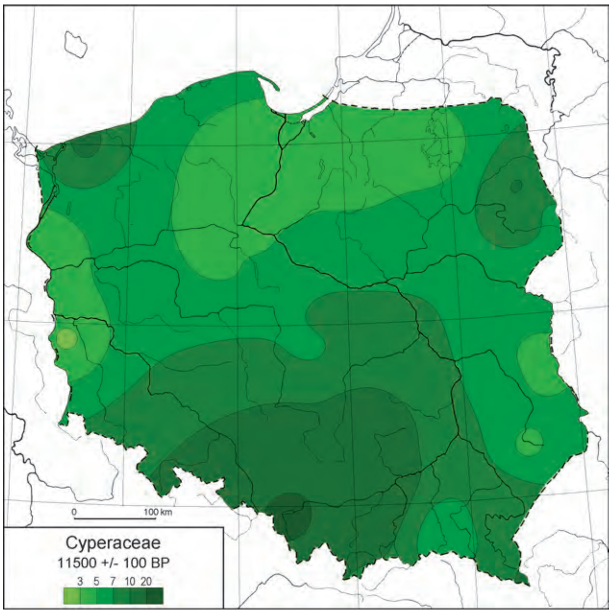

5.3
10.9
60.8
0 100 km
Cyperaceae
14000 +/- 100 BP


47.5
5.2
7.1
0 100 km
Cyperaceae
13500 +/- 100 BP

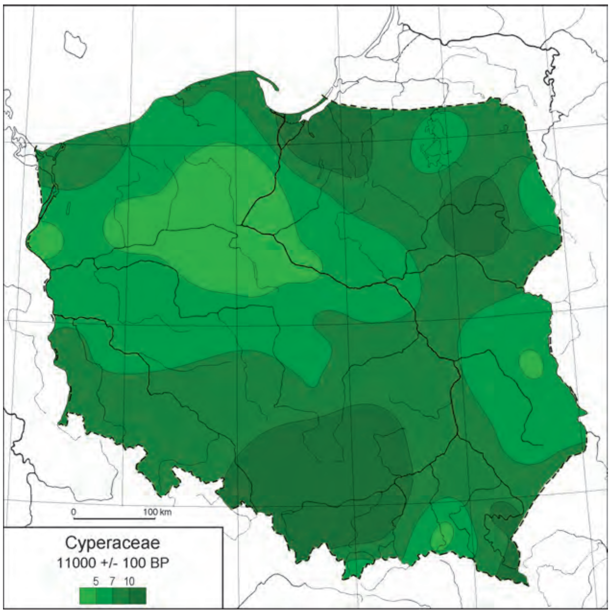

25.2
3.6
7.6
11.5
6.4
13.3
27.7
30.0
4.6
5.6
0 100 km
Cyperaceae
13000 +/- 100 BP

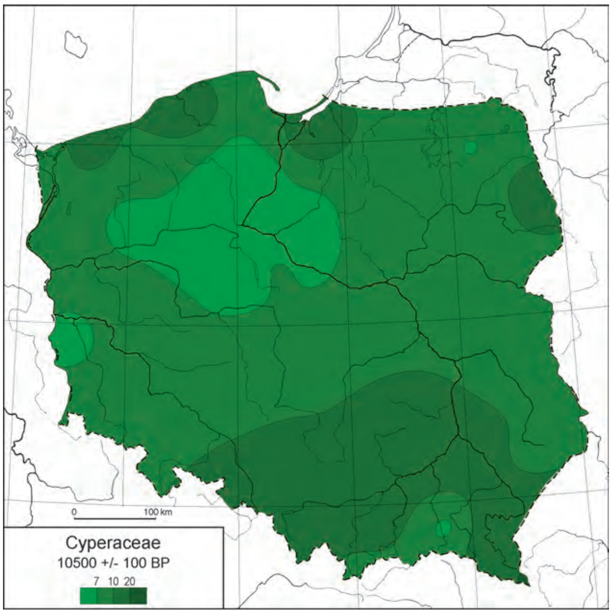

12.4
18.7
7.7
16.0
11.4
7.4
10.5
1.9
10.2
6.2
14.5
63.6
25.4
28.5
43.8
29.4
8.7
9.6
0 100 km
Cyperaceae
12500 +/- 100 BP

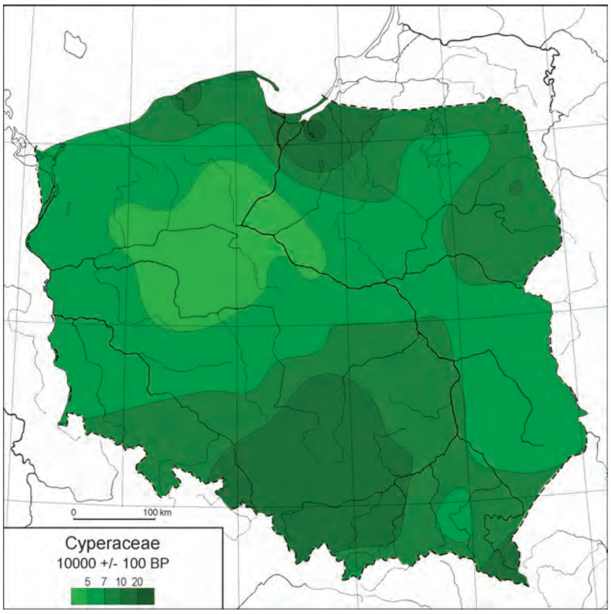

0 100 km
Cyperaceae
12000 +/- 100 BP
5 7 10 20 30

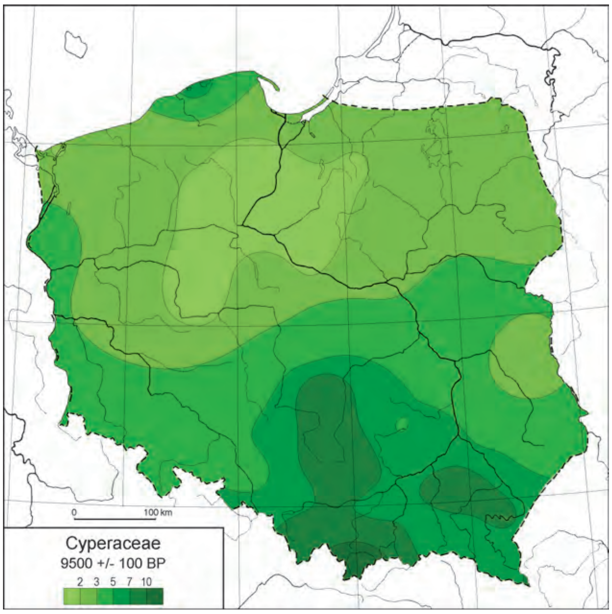

0 100 km
Cyperaceae
11500 +/- 100 BP
3 5 7 10 20

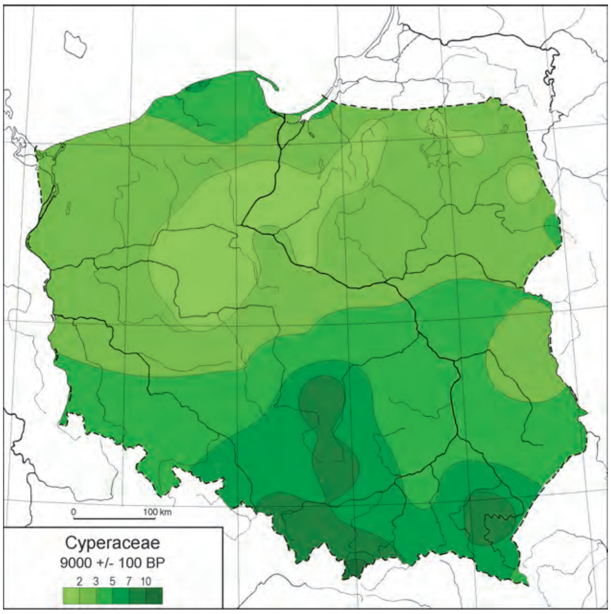

0.01
0.2
0.5
0.7
1
2
3
5
7
10
20
30
40
60

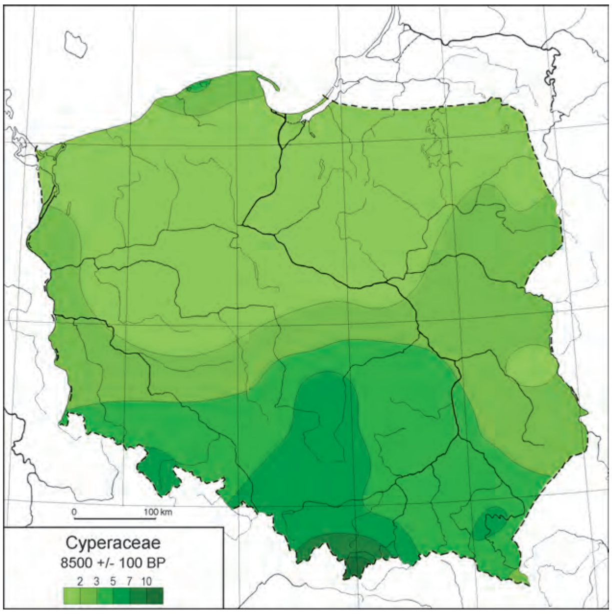




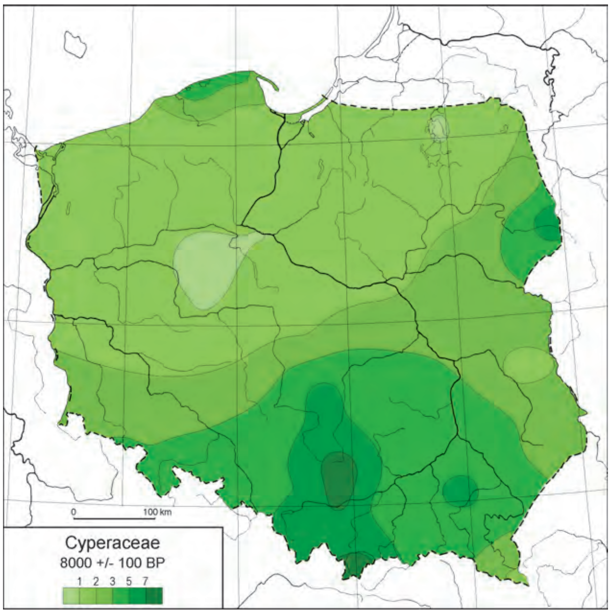


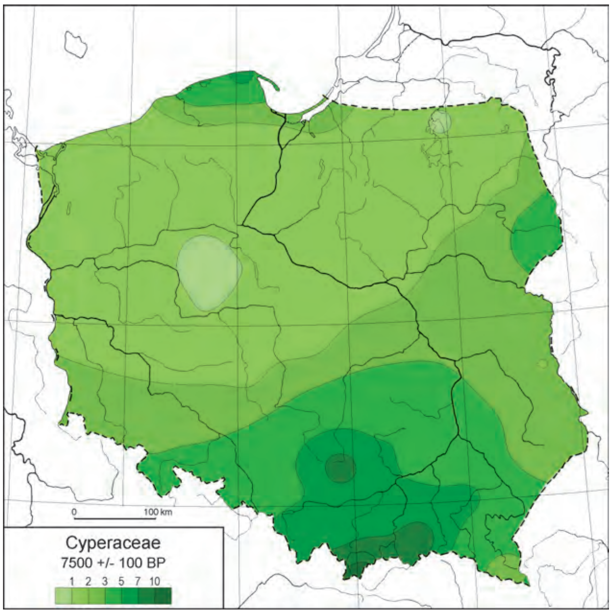


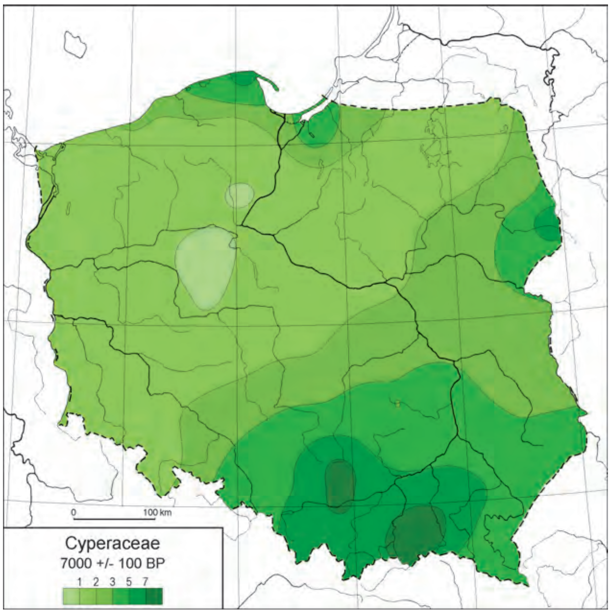


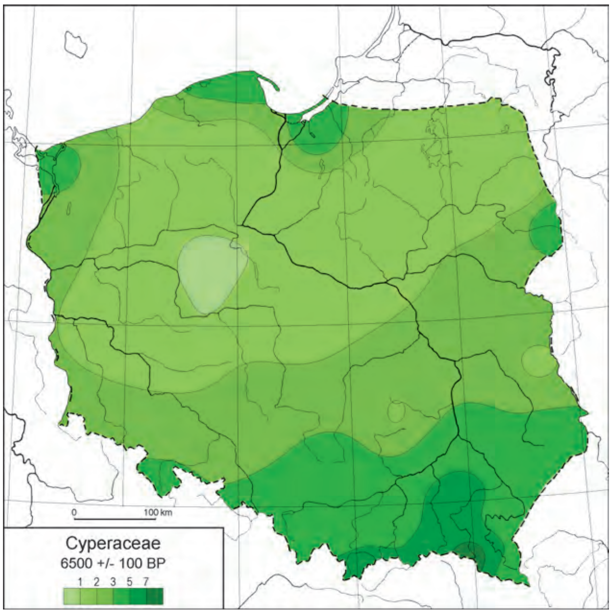


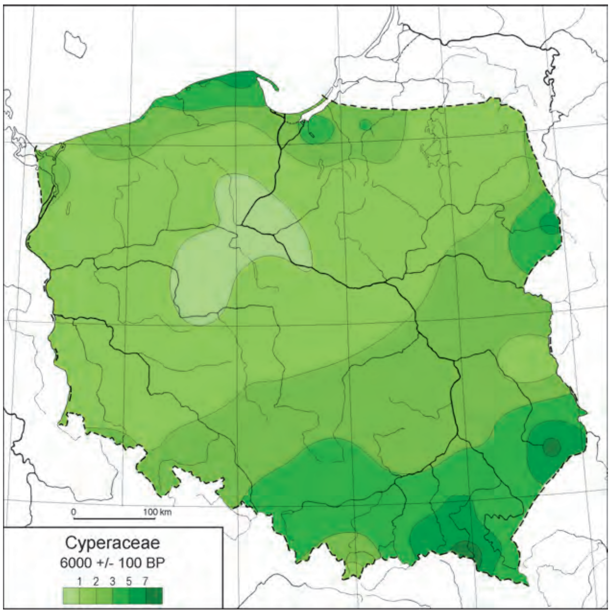
⬜	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	⬛	⬛
0.01	0.2	0.5	0.7	1	2	3	5	7	10	20	30	40	60

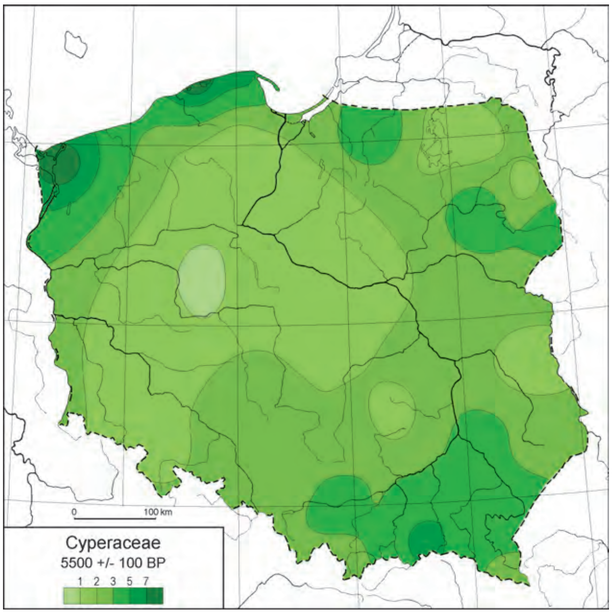

0
100 km
Cyperaceae
8000 +/- 100 BP
1 2 3 5 7


0
100 km
Cyperaceae
7500 +/- 100 BP
1 2 3 5 7 10

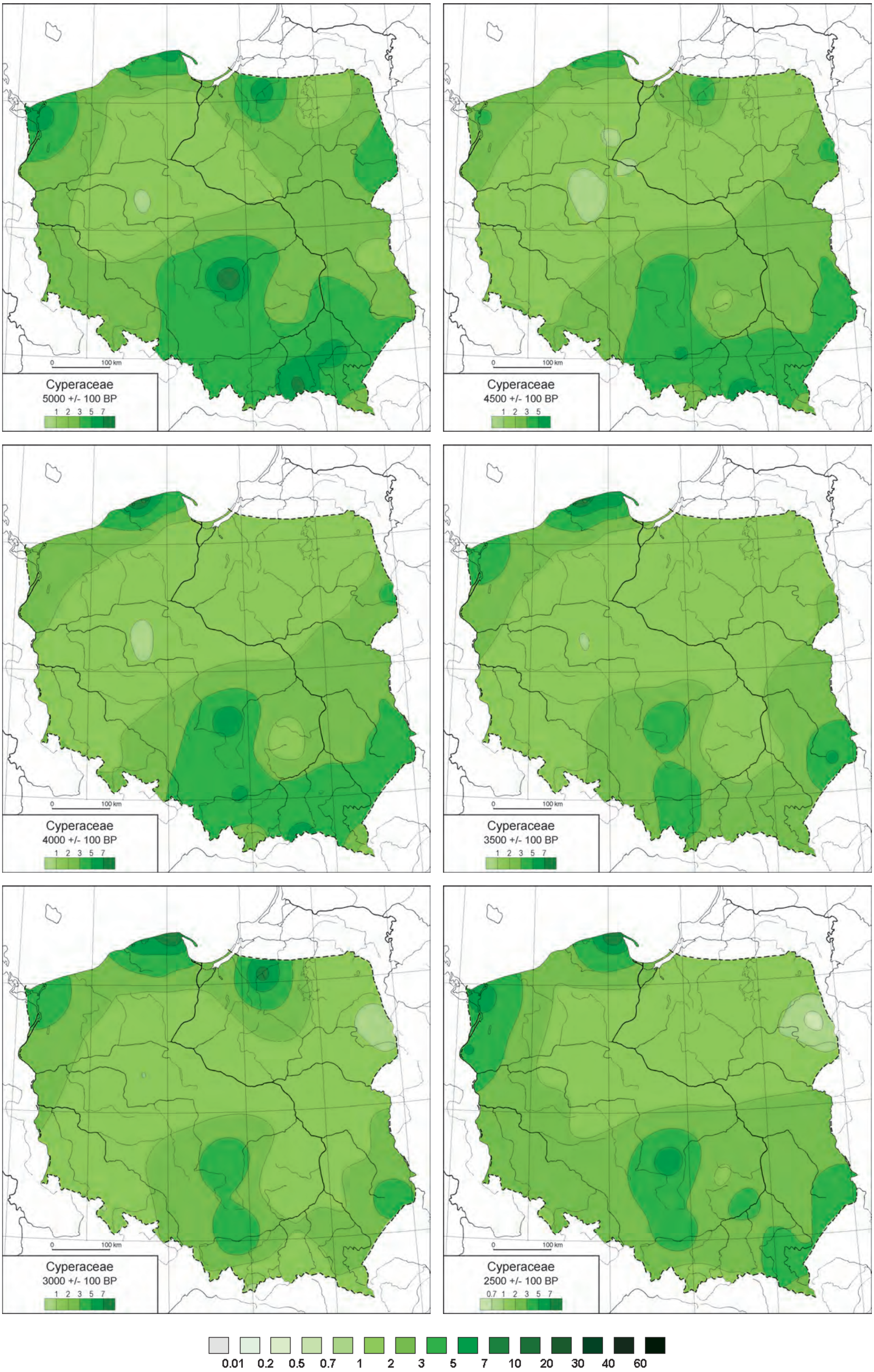

0
100 km
Cyperaceae
7000 +/- 100 BP
1 2 3 5 7

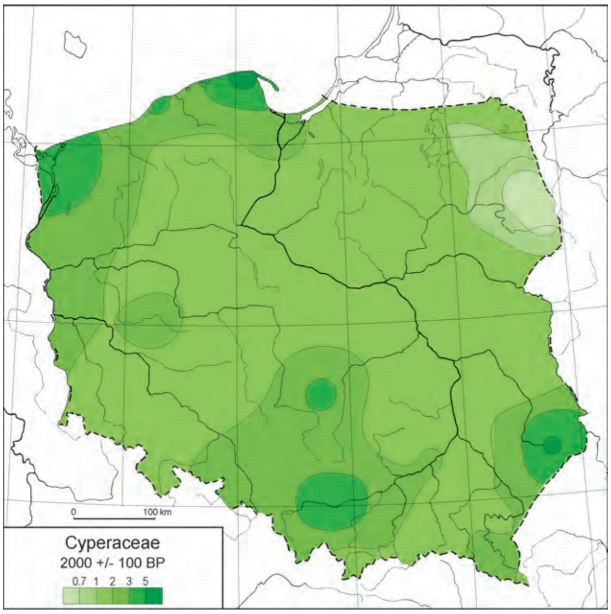

0
100 km
Cyperaceae
6500 +/- 100 BP
1 2 3 5 7

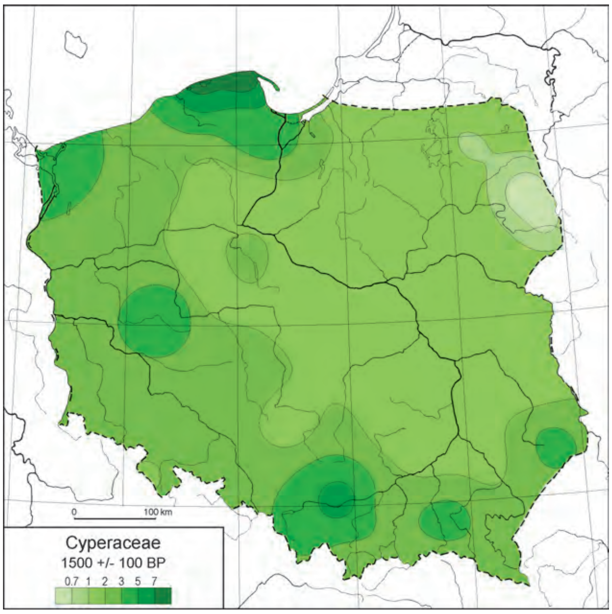

0
100 km
Cyperaceae
6000 +/- 100 BP
1 2 3 5 7

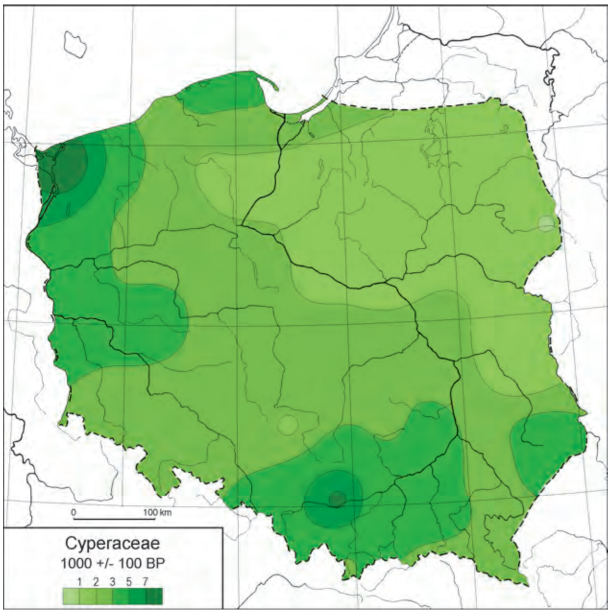

0
100 km
Cyperaceae
5500 +/- 100 BP
1 2 3 5 7

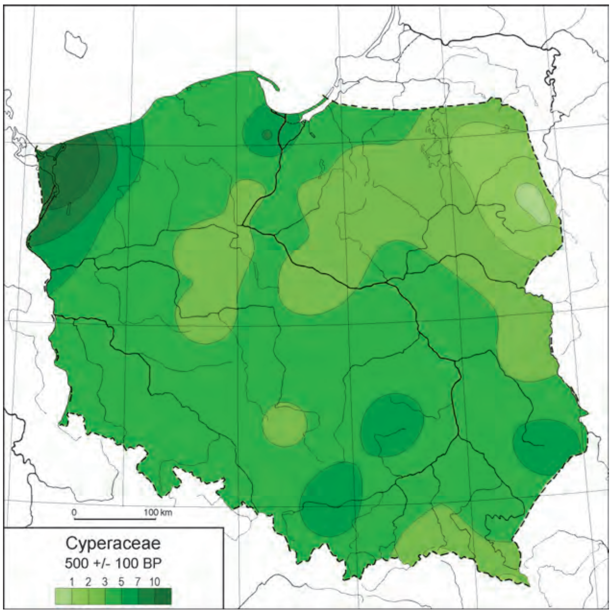

0.01
0.2
0.5
0.7
1
2
3
5
7
10
20
30
40
60

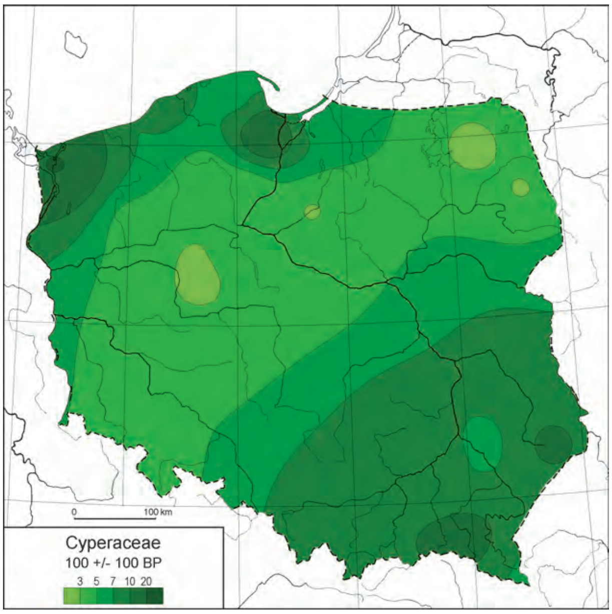

0
100 km
Cyperaceae
5000 +/- 100 BP
1 2 3 5 7
0
100 km
Cyperaceae
4500 +/- 100 BP
1 2 3 5
0
100 km
Cyperaceae
4000 +/- 100 BP
1 2 3 5 7
0
100 km
Cyperaceae
3500 +/- 100 BP
1 2 3 5 7
0
100 km
Cyperaceae
3000 +/- 100 BP
1 2 3 5 7
0
100 km
Cyperaceae
2500 +/- 100 BP
0.7 1 2 3 5 7
0.01 0.2 0.5 0.7 1 2 3 5 7 10 20 30 40 60


0
100 km
Cyperaceae
2000 +/- 100 BP
0.7 1 2 3 5


0
100 km
Cyperaceae
1500 +/- 100 BP
0.7 1 2 3 5 7


0
100 km
Cyperaceae
1000 +/- 100 BP
1 2 3 5 7


0
100 km
Cyperaceae
500 +/- 100 BP
1 2 3 5 7 10


0
100 km
Cyperaceae
100 +/- 100 BP
3 5 7 10 20


0.01 0.2 0.5 0.7 1 2 3 5 7 10 20 30 40 60

Dryas octopetala L. – Mountain avens

Bożena Noryśkiewicz, Anna Filbrandt-Czaja, Agnieszka M. Noryśkiewicz,
and Dorota Nalepka

Present distribution in Europe

Dryas octopetala L. is a species of Arctic origin with a circumpolar distribution. The main centres of its occurrence in Europe are, on the one hand, in northern Scandinavia and along the coast of the Barents Sea, extending down the Atlantic coast to the British Isles, and, on the other, in the mountains of central and southern Europe (the Pyrenees, the Alps, the central Apennines, the Tatras, the Western and Southern Carpathians, the mountains of Yugoslavia and Bulgaria) (Meusel et al. 1978, Kornaś & Medwecka-Kornaś 1986). In the north *Dryas octopetala* grows in the tundra zone, together with numerous species of lichens, low scrubs and dwarf shrubs. In the Scandinavian mountains, *Dryas octopetala* reaches up to 1730 m a.s.l. and in the mountains of central Europe, including the Swiss Alps, even up to 3000 m. In the central European lowlands this species is now found only as fossil remains (Browicz & Gostyńska-Jakuszewska 1970a).

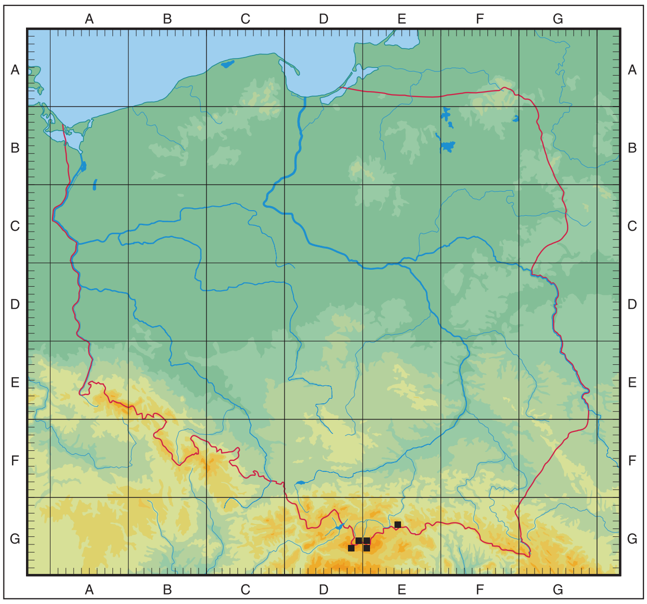


Fig. 85. Present-day distribution of *Dryas octopetala* L. in Poland: ■ – relict site presently existing (after Zając A. & Zając M. 2001)

Present distribution in Poland

In Poland *Dryas octopetala* is a glacial relict of northern origin. In the present plant communities it grows only in the Tatra Mountains and in the Pieniny Mountains (Fig. 85). In the Tatra Mountains it occurs in the subalpine and alpine zones up to 2154 m a.s.l., though along the valleys it descends in some places below 1000 m (Browicz & Gostyńska-Jakuszewska 1970a). In the Pieniny Mountains *Dryas octopetala* has been recorded at 680 m a.s.l. (Kornaś 1958), which is the lowest situated site in Poland.

Ecology

Dryas octopetala occurs on habitats rich in calcium carbonate (Oberdorfer 1982). In general it grows in full light and under severe climatic conditions. In Poland it occurs from the coldest areas (mainly sub-Alpine and subnival zones) through moderately cold (upper montane forest zone) to moderately cool (lower montane forest zone). Its occurrences show no association with continentality of climate. It occupies slightly moist, mesotrophic soils from slightly acid to neutral and alkaline, sandy to loamy and very poor in humus. It occurs on bare rocks, in rock fissures, on stony ground and screes (Zarzycki et al. 2002). Together with *Salix alpina* it forms the association *Firmetum carpaticum* during the first stages of scree colonization (Pawłowski 1959). When screes become overgrown with denser herbaceous vegetation, *Dryas* and *Salix alpina* dwindle in importance and give way to other associations.

Dryas octopetala is a prostrate dwarf shrub, forming relatively loose but extensive clumps 2–10 cm high. One flower at the top of each stem blooms in June, July and even in August. Numerous stamens and pistils stand in the middle of a flower. A mono-seeded, small nut, supplied with a flight-apparatus, is its fruit (Radwańska-Paryska 1961). *D. octopetala* is a characteristic species for the *Elyno-Seslerietea* class and the *Seslerietalia variae* order (Zarzycki et al. 2002).

POLLEN PRODUCTION AND DISPERSAL

Mountain avens is an autogamous and entomophilous species (Oberdorfer 1982), thus it produces a small amount of pollen grains. It may be assumed that the pollen values in diagrams do not reflect its actual occurrence in plant communities. In the Late Glacial deposits, from which *Dryas* pollen was absent, there were often found its macrofossils indicating its presence in tundra communities. Its insignificant pollen production might be the main reason for its small amount in the pollen diagrams, however other factors cannot be excluded such as corrosion of pollen grains or omitting of some pollen during counting a sample. The pollen grains of this species are very differentiated and they can resemble other Rosaceae both in respect to their dimensions and sculpture (Moore et al. 1991). In such situation even the presence of a single, correctly determined pollen grain in fossil material may indicate its occurrence in the Late Glacial communities.

EXPANSION IN EUROPE DURING THE LATE GLACIAL AND HOLOCENE

During the last glaciation *Dryas octopetala* moved from the Arctic towards the south under the influence of glacial climate. Tundra in front of the glacier was a refugial area for mountain avens and other Arctic species. From these places at the time of climate amelioration and the glacier retreat, *Dryas* began its backward migration into the areas of its earlier occurrences. In the mountains it persisted as a species of the northern origin. In some forested areas of northern Europe, for example in central Finland, the relict sites of *Dryas* remained on the exposed limestone rocks (Ralska-Jasiewiczowa, oral information).

MIGRATION PATTERN IN POLAND (Fig. 86)

13,000 – 11,000 BP

Only at one site, from among the eight sites presented, and moreover in the south of Poland, *Dryas octopetala* pollen has been found in the sediment accumulated 13,000 years ago. On the following four maps the number of sites which represent the Late Glacial increases, however, there is no substantial increase in number of the profiles with the presence of *Dryas* pollen. They are situated generally in the lake districts and in the Tatra Mountains. In the profile at Niechorze, in the western part of the Baltic Sea coast (Ralska-Jasiewiczowa & Rzętkowska 1987), a time cut missed the samples with mountain avens from the discussed period. However, abundant leaves of *Dryas octopetala* preserved in the Late Glacial deposits from the Mazurian Lake District (Ralska-Jasiewiczowa 1966), the Wielkopolska (Litt 1988, Kubiak-Martens 1998, Kubiak & Polcyn 1991), and the Pomeranian Lake District (Błaszkiewicz & Krzymińska 1992) indicate that at the end of the Pleistocene mountain avens was an important member of dwarf shrub tundra in central and north Poland. The occurrence of *D. octopetala* pollen in the sections of diagrams from the Pomerania, synchronised with the interstadial complex of Bølling/Allerød suggests that the forests of that time in the mentioned region were characterized by minor density and were probably fragmented by grasslands and swards of a sub-Alpine character.

11,000 – 10,000 BP

On the 11,000 and 10,000 BP maps, in spite of the fact that the numbers of sites with the Late Glacial floras are more numerous, there are no indications of an increase in the amount of mountain avens. From the detailed analysis of pollen tables for these sites, we can see that *Dryas octopetala* was represented by the single pollen grains but the applied time slices caused that some of the data were omitted on the maps. Such situation occurs, for example, in two pollen diagrams from Wolin Island where mountain avens was recorded in the Younger Dryas (Latałowa 1999a).

9500 BP

At the beginning of the Holocene, together with development of the forest cover, habitats favourable for heliophilous plants disappeared. This concerns also *Dryas octopetala*, which on the dot map for 9500 BP is noticed only at one site in the Tuchola Forest. This is its youngest Holocene site found in the lowlands.

CONCLUSIONS

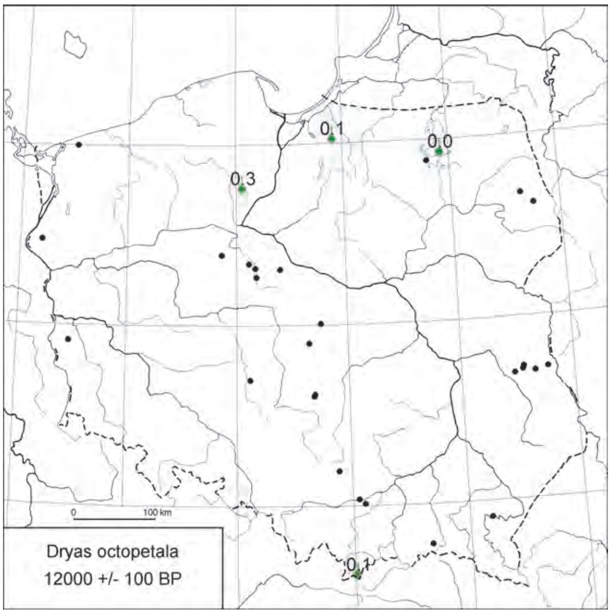
Due to a small prostrate shape of plant, minor pollen production, and varying dimensions and sculpture features of pollen grains impeding species recognition, the amount of *Dryas octopetala* found in the subfossil deposits and indicated on the isopollen maps does not reflect its actual contribution to plant communities. In spite of the low percentage values, fluctuating from 0.1% to 0.5% at the particular sites, it can be concluded that *Dryas octopetala* was an important member of the Late Glacial communities. Its local occurrence is also confirmed by the presence of its macrofossils. In the Holocene, its distribution was limited to the Tatra and Pieniny Mountains, though its representation in the pollen diagrams from the Tatras, due to the reasons mentioned above, is sporadic (Obidowicz 1996).

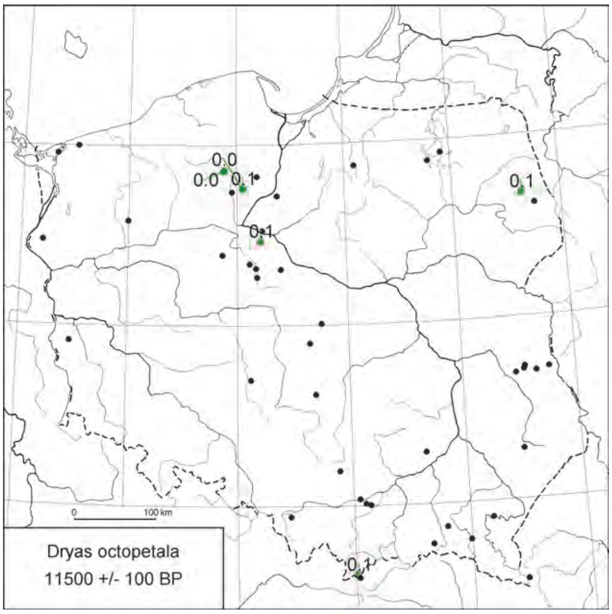
⟶

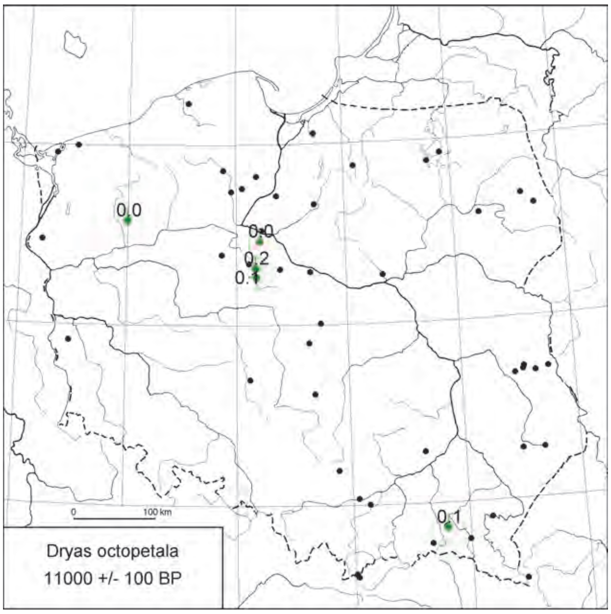
Fig. 86. *Dryas octopetala*: dot maps for 13,000–9500 ^{14}C yr BP

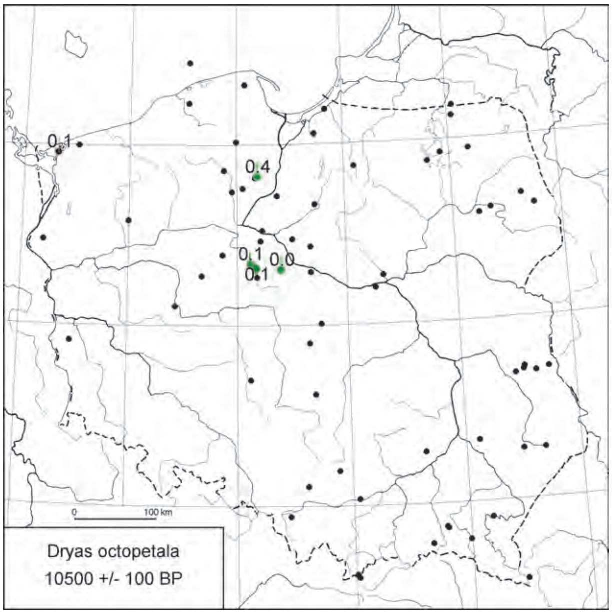

0.1
0 100 km
Dryas octopetala
13000 +/- 100 BP

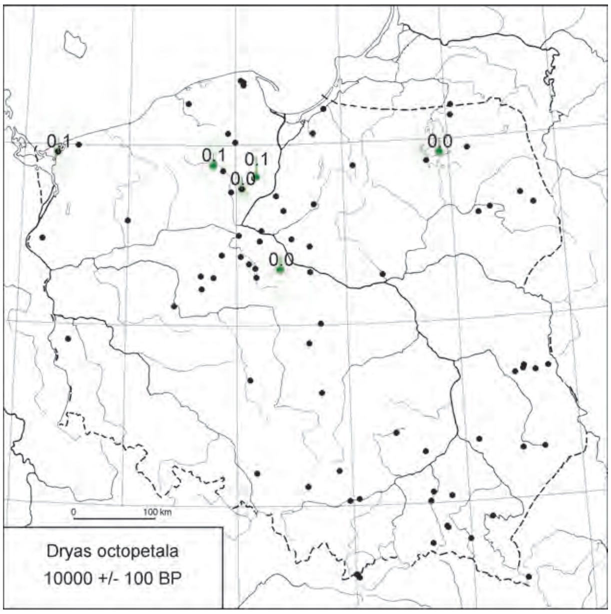

0.1
0.6
0 100 km
Dryas octopetala
12500 +/- 100 BP

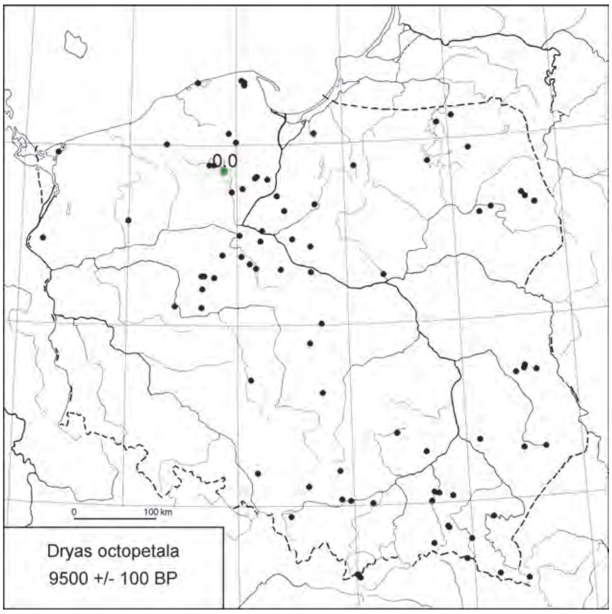

0.1
0.0
0.3
0.1
0 100 km
Dryas octopetala
12000 +/- 100 BP


0.0
0.0
0.1
0.1
0.1
0.1
0 100 km
Dryas octopetala
11500 +/- 100 BP


0.0
0.0
0.2
0.1
0.1
0 100 km
Dryas octopetala
11000 +/- 100 BP


0.1
0.4
0.1
0.0
0.1
0 100 km
Dryas octopetala
10500 +/- 100 BP


0.1
0.1
0.1
0.0
0.0
0.0
0
100 km
Dryas octopetala
10000 +/- 100 BP


0.0
0
100 km
Dryas octopetala
9500 +/- 100 BP

Filipendula Mill. – **Filipendula**

Grażyna Miotk-Szpiganowicz, Kazimierz Tobolski, Joanna Zachowicz,
and Dorota Nalepka

Present distribution in Europe and in Poland

Two species of *Filipendula* grow in Poland: *F. ulmaria* (L.) Maxim. and *F. vulgaris* Moench (= *F. hexapetala* Gilib.) (Szafer et al. 1969). Both species are common in Poland; however, *F. ulmaria* has more localities, whilst *F. vulgaris* is less frequent and has a sparser distribution (Fig. 87). In Europe both species are distributed almost throughout the continent (Hegi 1981).

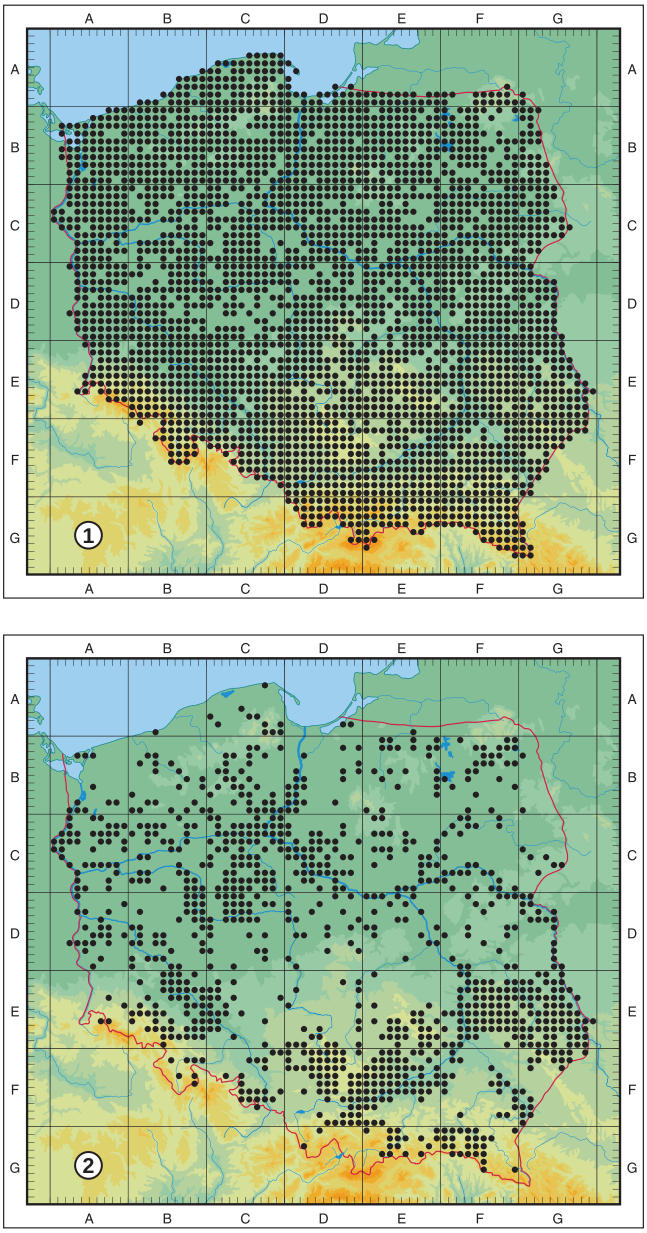


Fig. 87. Present-day distribution of 1 – *Filipendula ulmaria* (L.) Maxim. and 2 – *F. vulgaris* Moench in Poland (after Zając A. & Zając M. 2001)

Ecology

Both species are hemicryptophytes. At present *Filipendula ulmaria* occurs in natural, semi-natural, and anthropogenic forest, brushwood, and meadow communities. Occurrences of its fruits in the fossil record indicate that it grew in similar habitats also during the earlier periods of the Holocene (Marek 1965, Reynaud & Tobolski 1974, Okuniewska & Tobolski 1981, and others). *F. ulmaria* occupies quite a wide variety of habitats within the range of moist to very wet (Ellenberg et al. 1991, Landolt 1977), as well as being able to tolerate periodic changes in soil moisture. It prefers slightly acid or neutral soils rich in nitrogen and in humic substances. These ecological characteristics, and also its preference for growing in partly shaded habitats, contrast strongly with the requirements of *F. vulgaris*. *Filipendula vulgaris* grows in dry habitats, as on moist soils it cannot compete well. It tolerates mesotrophic soils relatively poor in humus. In comparison with *F. ulmaria* it requires full light, grows in open habitats, such as grasslands, also at forest margins, as well as in open, well-lit oak and pine forests.

Considering plant communities, *F. vulgaris* occurs in the *Festuco-Brometea* class, whereas *F. ulmaria* is a species of the order *Molinietalia*, dominant in the *Filipendulion* alliance, which includes tall herb associations growing in the habitats of wet meadows (Matuszkiewicz W. 2001). At the same time it occurs in forests. In central Europe it grows mainly in alder woods (*Alnion glutinosae*), as well as in floodplain woodlands of the

Alno-Padion (=*Alno-Ulmion*) alliance (Matuszkiewicz J.M. 2002).

Falińska (1990, 1996) has emphasized the role of *F. ulmaria* in primary and secondary successions. In the early stages of succession its high competitive ability means that it strongly influences species composition, whereas later it infills gaps in plant cover and tends to exclude new species.

Filipendula ulmaria and *F. vulgaris* differ in their pollen morphology and ecological characteristics. However, species differentiation during routine palynological analysis is impossible. Thus, isopollen maps have been drawn for the genus *Filipendula.* It should be stressed, that, because of the wider distribution of wet habitats in the neighbourhood of the sites investigated, the majority of *Filipendula* pollen grains found in pollen assemblages belong most probably to *F. ulmaria* (Berglund 1966).

Wasylikowa (1964) has stressed the important role played by this plant in Late Glacial vegetation during the Allerød interstadial in Poland. In other areas of Europe, the occurrence of this taxon has also been widely recorded from the Late Glacial (mainly from the Allerød) and during the early Holocene.

POLLEN PRODUCTION AND DISPERSAL

Both species of *Filipendula* are insect-pollinated. *F. ulmaria* produces a great amount of pollen (Danielsen 1970). The rate of pollen production in relation to Gramineae (1) is 2.5 (Sugita et al. 1999). *F. ulmaria* blossoms in June and July, whereas *F. vulgaris* in May and June (Mowszowicz 1983).

MIGRATION PATTERN IN POLAND (Fig. 88)

13,500 – 12,000 BP

In the early stages of the Late Glacial *Filipendula* occurred sparsely (0.1–1.2%) at single sites. It was, most likely, *F. ulmaria*, which found suitable habitats in wet, open places. However, in dry and sunny habitats *F. vulgaris* could also have occurred.

11,500 – 9500 BP

On the 11,500 BP map single sites with higher *Filipendula* values (>2%) are visible in north-western Poland, in Roztocze, and in the Oświęcim Basin. About 10,500 BP a centre of *Filipendula* (values up to 1%) starts to be formed, including the Carpathian foreland, and the southern part of the Małopolska Upland. This centre gradually expands towards the north and west, and by 9500 BP it comprises the whole south and part of central Poland. High values of *Filipendula* pollen may have been associated with the development of tall herb vegetation along the river valleys and at the margins of water bodies (*F. ulmaria*) as well as with the presence of landslides (*F. vulgaris*?). The lowest pollen values of this genus (up to 0.5%) occur in north-western Poland, whereas the highest (>3%) in the Bieszczady Mountains. This may result, to some extent, from the nature of the deposits, lake and bog sediments respectively, that have been subjected to investigation in these rather different regions.

9000 – 1500 BP

Together with an expansion of forest communities a distinct decline of *Filipendula* within the Polish lowlands is observed. In the Carpathians and in the Małopolska Upland its pollen values reach a level of 2–3%, though in the Nowy Targ Basin values up to 7% appear temporarily. During the middle and late Holocene (8000–1500 BP) higher pollen values of *Filipendula* occur only in south-eastern Poland, particularly in the Dukla Pass region (7–10%, possible connection with the landslides). Periodically (about 5000 BP, 4000 BP and 3500 BP), the area of *Filipendula* occurrence expands slightly towards the north-east.

1000 – 100 BP

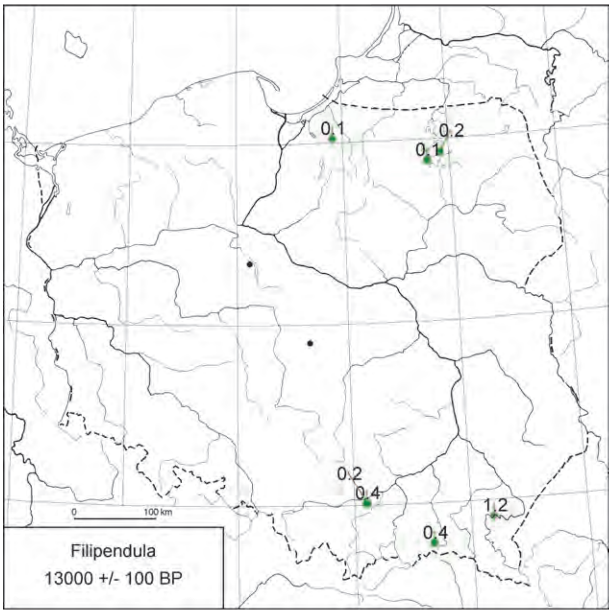
At this time a distinct decline of *Filipendula* pollen values is also indicated in the south-eastern areas. At present in Poland *Filipendula* pollen reaches only values of up to 0.2%, except for the south-east, where they are only slightly higher (up to 0.5%).

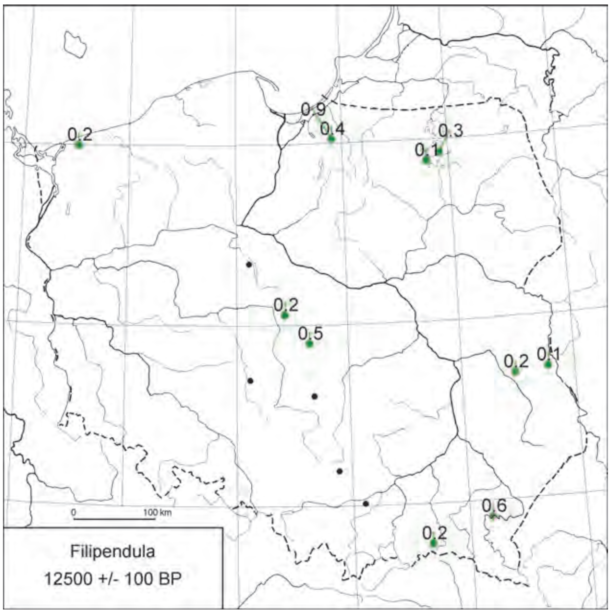
CONCLUSIONS

The greatest amounts of *Filipendula* in the plant communities of Poland occurred at the end of the Late Glacial and at the beginning of the Holocene. In the mountain areas both species could have been present: *F. vulgaris*, a species characteristic of dry grasslands and unstable habitats (for example landslides), and *F. ulmaria*, a species of riverine tall herb communities and of moist meadows. The available data do not show any connections between *Filipendula* distribution and deforestation during prehistoric settlements. Decline to the low present-day *Filipendula* pollen values results probably from the reduction of damp and wet habitats (drainage) and from soil leaching.

Fig. 88. *Filipendula*: dot and isopollen maps for 13,500–100 ^{14}C yr BP


0.5
0.6
0 100 km
Filipendula
13500 +/- 100 BP


0.1
0.2
0.1
0.2
0.4
1.2
0.4
0 100 km
Filipendula
13000 +/- 100 BP

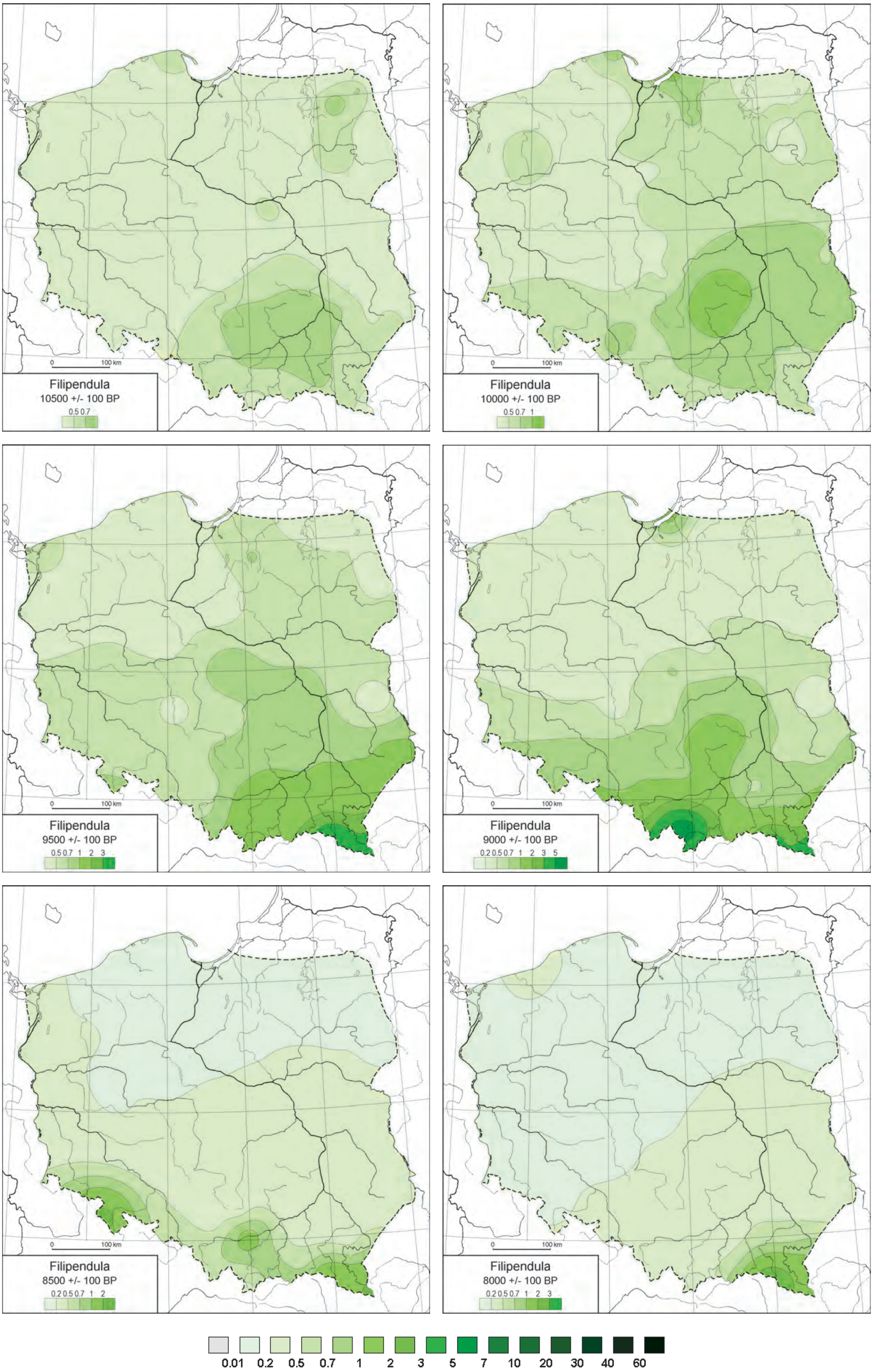

0.9
0.4
0.2
0.3
0.1
0.2
0.5
0.2
0.1
0.6
0.2
0 100 km
Filipendula
12500 +/- 100 BP

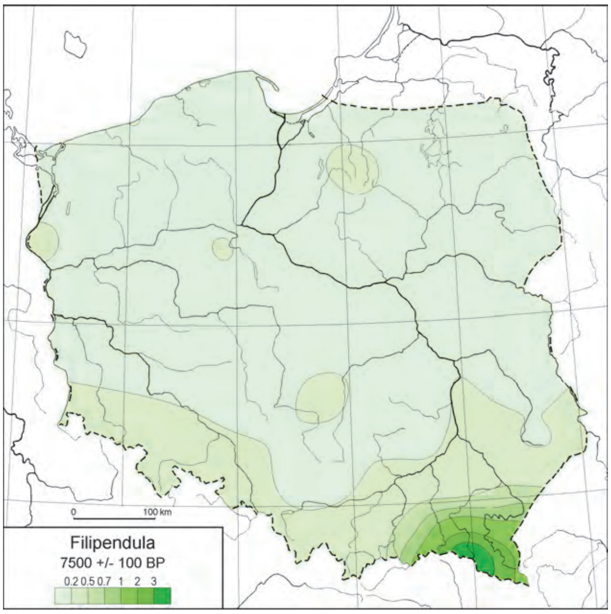

0 100 km
Filipendula
12000 +/- 100 BP
0.2


0 100 km
Filipendula
11500 +/- 100 BP
0.2 0.5 0.7 1 2

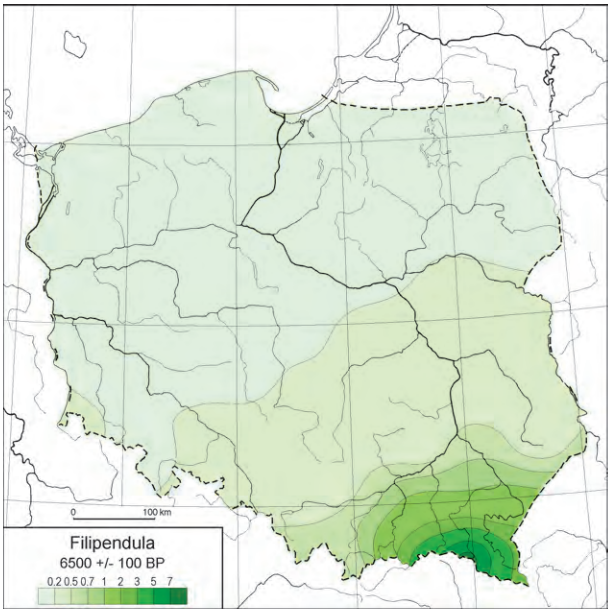

0 100 km
Filipendula
11000 +/- 100 BP
0.2 0.5 0.7

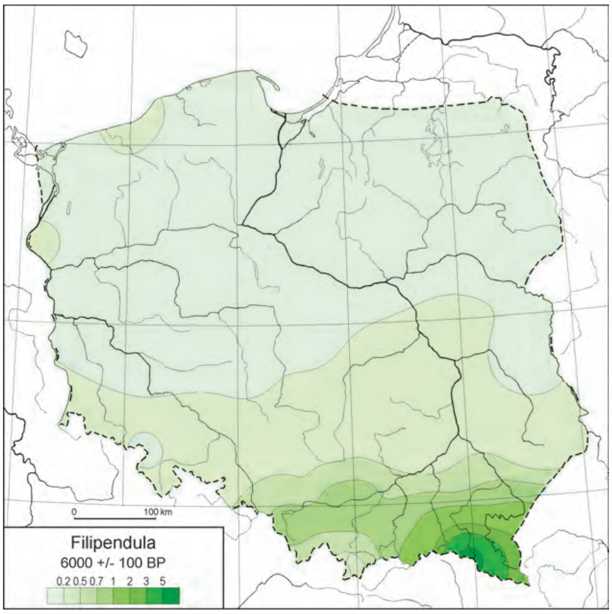

0.01
0.2
0.5
0.7
1
2
3
5
7
10
20
30
40
60

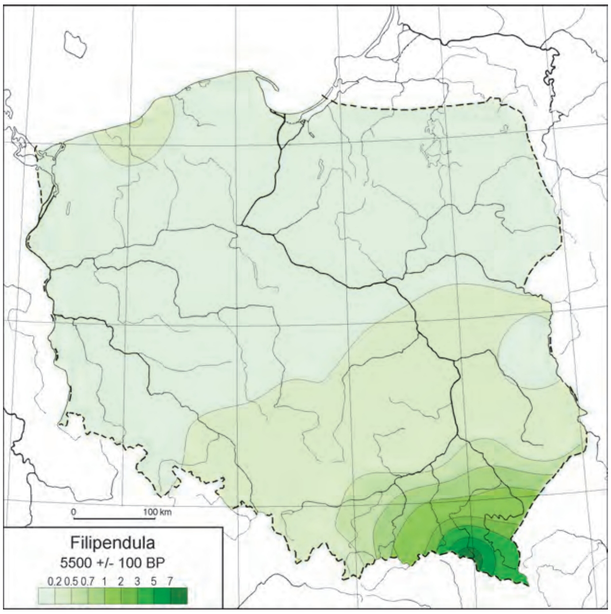

0 100 km
Filipendula
10500 +/- 100 BP
0.5 0.7
0 100 km
Filipendula
10000 +/- 100 BP
0.5 0.7 1
0 100 km
Filipendula
9500 +/- 100 BP
0.5 0.7 1 2 3
0 100 km
Filipendula
9000 +/- 100 BP
0.2 0.5 0.7 1 2 3 5
0 100 km
Filipendula
8500 +/- 100 BP
0.2 0.5 0.7 1 2
0 100 km
Filipendula
8000 +/- 100 BP
0.2 0.5 0.7 1 2 3
0.01 0.2 0.5 0.7 1 2 3 5 7 10 20 30 40 60

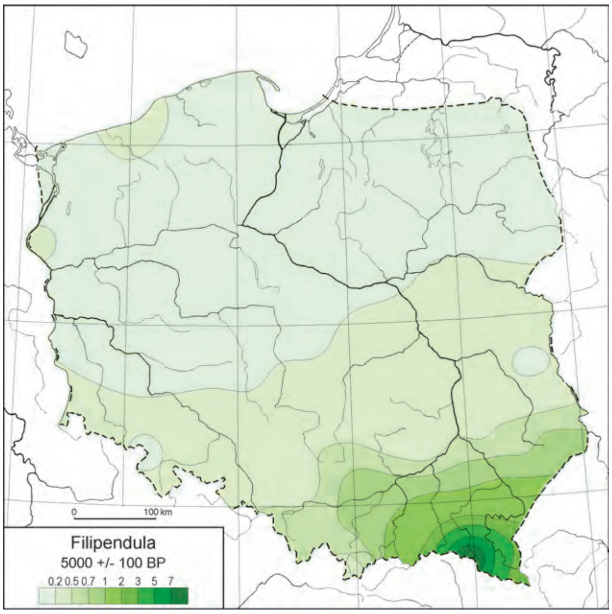

0
100 km
Filipendula
7500 +/- 100 BP
0.2 0.5 0.7 1 2 3


0
100 km
Filipendula
7000 +/- 100 BP
0.2 0.5 0.7 1 2

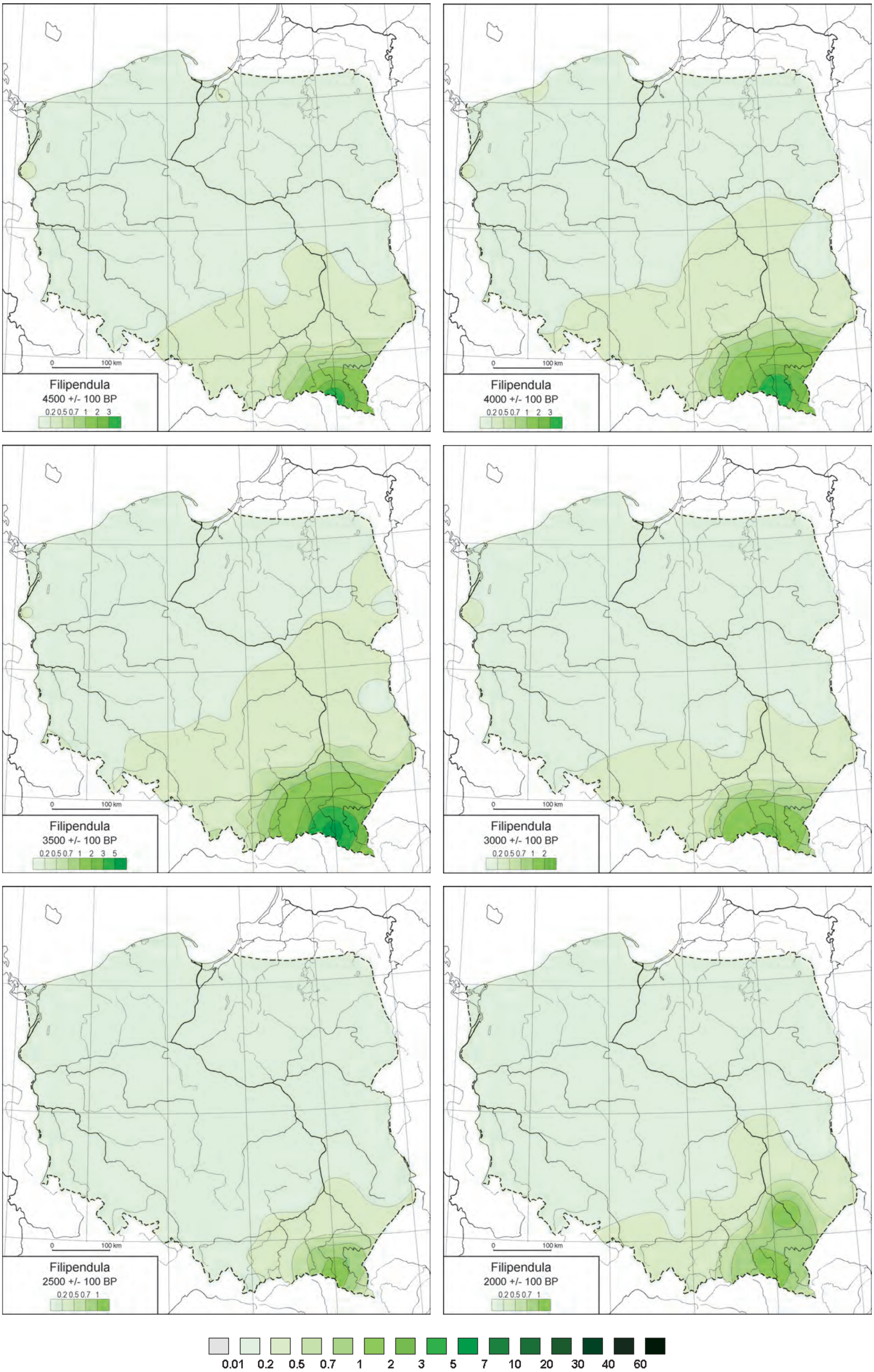

0
100 km
Filipendula
6500 +/- 100 BP
0.2 0.5 0.7 1 2 3 5 7

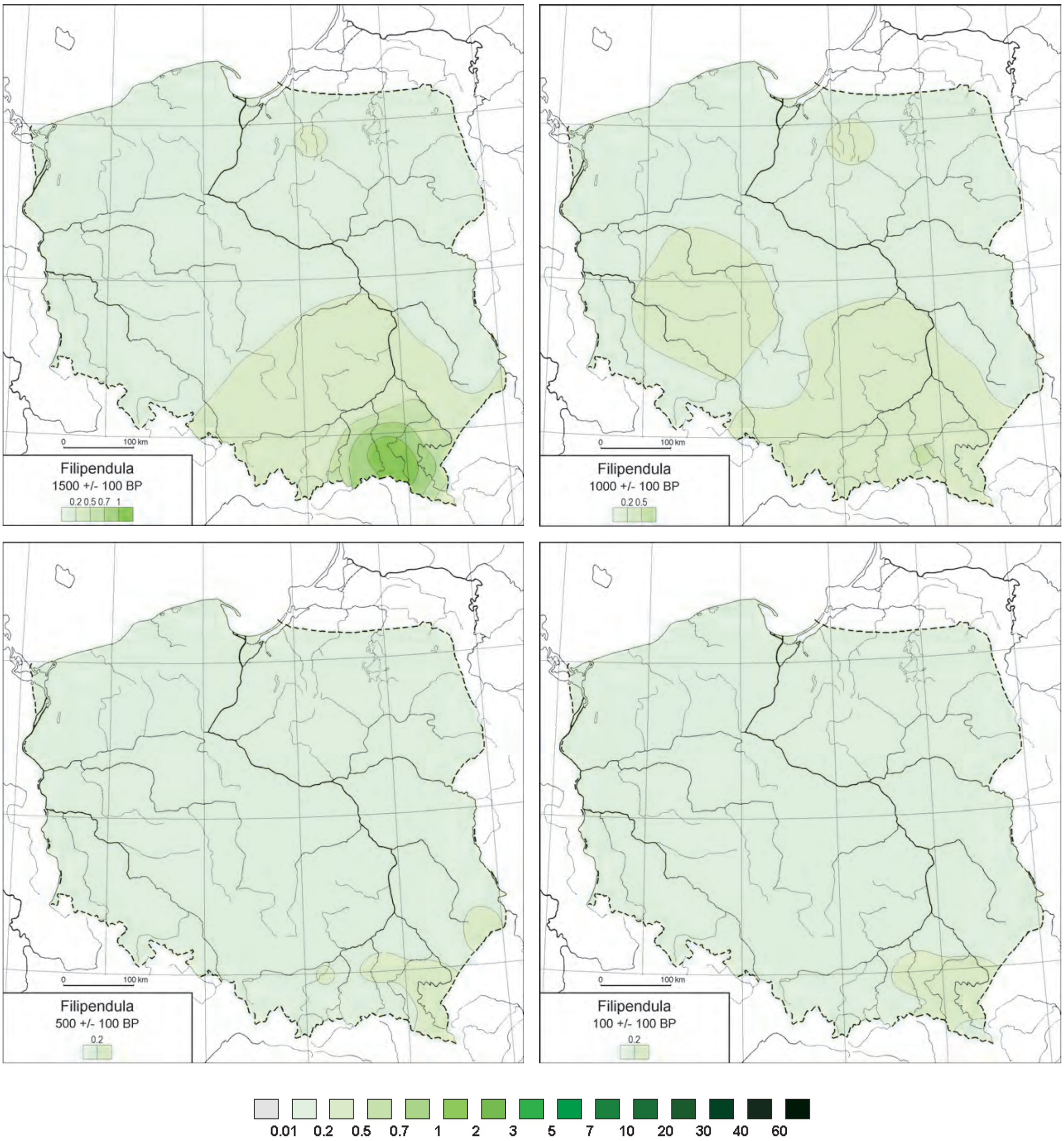

0
100 km
Filipendula
6000 +/- 100 BP
0.2 0.5 0.7 1 2 3 5


0
100 km
Filipendula
5500 +/- 100 BP
0.2 0.5 0.7 1 2 3 5 7


0
100 km
Filipendula
5000 +/- 100 BP
0.2 0.5 0.7 1 2 3 5 7


0.01
0.2
0.5
0.7
1
2
3
5
7
10
20
30
40
60


0 100 km
Filipendula
4500 +/- 100 BP
0.2 0.5 0.7 1 2 3
0 100 km
Filipendula
4000 +/- 100 BP
0.2 0.5 0.7 1 2 3
0 100 km
Filipendula
3500 +/- 100 BP
0.2 0.5 0.7 1 2 3 5
0 100 km
Filipendula
3000 +/- 100 BP
0.2 0.5 0.7 1 2
0 100 km
Filipendula
2500 +/- 100 BP
0.2 0.5 0.7 1
0 100 km
Filipendula
2000 +/- 100 BP
0.2 0.5 0.7 1
0.01 0.2 0.5 0.7 1 2 3 5 7 10 20 30 40 60


0
100 km
Filipendula
1500 +/- 100 BP
0.2 0.5 0.7 1
0
100 km
Filipendula
1000 +/- 100 BP
0.2 0.5
0
100 km
Filipendula
500 +/- 100 BP
0.2
0
100 km
Filipendula
100 +/- 100 BP
0.2
0.01
0.2
0.5
0.7
1
2
3
5
7
10
20
30
40
60

Helianthemum Mill. – **Rock-rose**

BOŻENA NORYŚKIEWICZ, ANNA FILBRANDT-CZAJA, AGNIESZKA M. NORYŚKIEWICZ,
AND DOROTA NALEPKA

PRESENT DISTRIBUTION IN EUROPE

The genus *Helianthemum* Mill. belongs to the family Cistaceae. Its eco-geographic forms are rich and diversified (Meusel et al. 1978). The species of this genus originated in the Mediterranean region (Kornaś & Medwecka-Kornaś 1986). About 80 species and subspecies occur in the Mediterranean region and a smaller number are found in northern and central Europe and in central Asia (Clapham et al. 1962, Hegi 1965). The Iberian Peninsula is the centre of *Helianthemum* occurrence with as many as 27 species of this genus growing there. For example, there are 16 species known in Italy, 10 in Greece, 7 in Armenia and only 2 species in the Far East (Podbielkowski 1991). The ranges of *H. nummularium* and *H. arcticum* extend far towards the north, the first one up to southern Sweden, Finland and southern Russia, and *H. arcticum* even beyond the polar circle (Hegi 1965).

PRESENT DISTRIBUTION IN POLAND

In Poland the genus *Helianthemum* is represented by two species: *H. alpestre* (Jacq.) Dunal with one subspecies, and *H. nummularium* (L.) Mill., including four subspecies. *H. alpestre* subsp. *rupifragum* (A. Kern.) Jáv. grows on rocks and in rocky fissures in the Tatra and the Pieniny Mountains. Its main centre of occurrence, outside the territory of Poland, is situated in Slovakia in the Bielskie Tatra Mountains (Pawłowski 1959). *H. nummularium* subsp. *nummularium* (L.) Mill. grows in the Polish lowlands, it is rare in the south and west of the country and very rare in the Carpathians. It grows on rock outcrops, rocky ground, screes, and gravels (Zarzycki et al. 2002). *H. nummularium* subsp. *obscurum* (Čelak.) Holub occurs throughout the lowland areas and in the mountains up to the lower montane forest zone. It occurs in dry grasslands, thickets, edges of forests and on rocks (Rutkowski 1998). *H. nummularium* subsp. g*labrum* (Koch) Wilczek grows only in the Tatra Mountains (Zając A. & Zając M. 2001). *H. nummularium* subsp. *grandiflorum* (Scop.) Schinz & Thell. is common in grasslands and on calcareous rocks, from the lower montane forest zone up to the alpine grassland zone. In Poland it is known only from the Tatra Mountains (Zając A. & Zając M. 2001, Zarzycki et al. 2002), while in Slovakia it is found in all the higher Carpathian ranges (Piękoś-Mirkowa et al. 1992).

ECOLOGY

Species of the genus *Helianthemum* are mostly dwarf shrubs or less frequently annual herbaceous plants (Tutin et al. 1968). Dwarf shrubs (chamaephytes) are able to survive unfavourable conditions because of the lignified lower part of their stems, where they form regenerating buds (Podbielkowski 1991). In winter their evergreen leaves or buds are better protected in places with snow cover (Remmert 1985). They belong to the group of species, characteristic of protocratic stage vegetation, as defined by Iversen (1958), whose distribution depends on such critical factors as adequate light, basic or neutral soils and slight competition. They are heliophilous species, growing in full sunlight (Zarzycki et al. 2002). However, as their seeds ripen, their pedicels, whilst elongating, display negative phototaxis, and thus protect their fruiting capsules in the shade (Schumacher 1960). They grow both in the cooler parts of the country (*H. nummularium* subsp. *grandiflorum* and *H. nummularium* subsp. *glabrum*), and in the warmest regions (*H. nummularium* subsp. *obscurum*). In Poland they do not show any association with continentality of climate. They grow on soils with different degrees of moisture from dry (*H. nummularium* subsp. *nummularium* and *H. alpestre* subsp. *rupifragum*) to slightly moist. They usually prefer poor (*H. nummularium* subsp. *nummularium*) to moderately poor soils. The majority of rock-rose species and subspecies require neutral and alkaline soils, and only *H. nummularium* subsp. *obscurum* may also be found on acid soils. They all flower from May to September. The fruit is multi-seeded capsule splitting into three valves. The mountain species grow on rocks and in rocky fissures, whilst the species common in the lowlands grow in grasslands, in scrub, along forest margins, and on rock outcrops (Rutkowski 1998).

POLLEN PRODUCTION AND DISPERSAL

The species of *Helianthemum* discussed here are entomophilous or self pollinating (autogamous) (Oberdorfer 1979), therefore producing relatively low amounts of pollen. For this reason *Helianthemum* is usually underrepresented in pollen assemblages.

The structure of pollen grains within the genus *Helianthemum* enables palynologists to distinguish a small number of morphological pollen types (Erdtman et al. 1961). *H. nummularium*-type comprises the following taxa occurring in Poland: *H. nummularium* subsp. *nummularium*, *H. nummularium* subsp. *obscurum*, and *H. nummularium* subsp. *grandiflorum*. *H. oelandicum*-type includes species at present absent from Poland (*H. oelandicum*, *H. canum*, *H. italicum*, and *H. pinegense*). Wasylikowa (1964) has further separated from this group *H. alpestre*-type and *H. canum*-type. However, it is not always possible to distinguish the critical sculptural features of the exine in fossil pollen preparations, and that is why the various *Helianthemum* pollen-types have been treated together here, just as the genus.

EXPANSION IN EUROPE DURING THE LATE GLACIAL AND HOLOCENE

Species of the genus *Helianthemum*, as elements of the protocratic stage of vegetational development (Iversen 1958), spread during the late Vistulian through the unforested areas of Europe. The pollen of this genus is represented during all the Late Glacial subdivisions in southern Scandinavia (Berglund 1966), as well as in central and southern Europe (Meusel et al. 1978, Lang 1994). It can be assumed that the majority of these Late Glacial pollen grains derive from *H. nummularium s.l.* or from *H. alpestre.* Considering pollen morphology, the species *H. oelandicum* (L.) DC. *s.l.* (Meusel et al. 1978) may also be represented in the pollen assemblages. It is quite likely that Late Glacial pollen grains of this morphological type derive from the plants related to *H. oelandicum*, which is the endemic form at present found on the island of Öland (Berglund 1966).

MIGRATION PATTERN IN POLAND (Fig. 89)

14,000 – 13,500 BP

On the dot maps for this period *Helianthemum* is present in north-eastern Poland. The pollen percentage values, reaching 1.4% of the pollen sum, suggest its early migration into these areas. It can be assumed that pollen of *Helianthemum* has originated from *H. oelandicum s.l.* comprising the endemic species *H. oelandicum s.s.*, and/or *H. pinegense*, which occurs at present in northern Russia (Berglund 1966).

13,000 BP

On this map both the number of sites investigated and the number of those at which the *Helianthemum* pollen has been recorded increase. At this time-interval rockrose was present at the northern sites but it appeared also in the south of the country where at the site of Jasło, in the lower central area of the Carpathians, its percentage value reached up to 2.2%. This may indicate a considerable local abundance.

12,500 – 12,000 BP

Helianthemum spread throughout Poland reaching pollen percentage values from 0.1 to 1.7%.

11,500 – 11,000 BP

Species of *Helianthemum* persisted at many sites scattered across the whole country however, the pollen percentage values decrease, generally not exceeding 0.2%, apart from one site in the central area of the Baltic Sea coast where it reached 2.2%. Decline in the pollen percentage values of *Helianthemum* may have resulted from the development of forests during the Allerød. The increase of shaded ground caused a reduction in the frequency of this heliophilous taxon.

10,500 – 10,000 BP

During this period the number of sites where *Helianthemum* was present increased markedly. These maps illustrate the occurrence of *Helianthemum* during the Younger Dryas, up to the transition to the Holocene with maximum distribution shifting from the north-west (10,500 BP) to the south (10,000 BP). A distinct gap in the distribution pattern of *Helianthemum* pollen records at that time includes the areas of Wielkopolska, Lower Silesia and Kielce-Sandomierz Upland. Perhaps the Younger Dryas cooling resulted only in a minor thinning out of tree and shrub communities in these areas, which at present are the warmest regions of the country not greatly subject to continental climatic influences. Thus, these parts of the country would have been less suited to the expansion of grasslands supporting *Helianthemum*.

9500 BP

Helianthemum pollen has been noticed only at five sites. Development of forest cover during the post-glacial restricted habitats suited to the occurrence of grasslands where species of *Helianthemum* could grow.

CONCLUSIONS

Helianthemum pollen was present in Poland during all the subdivisions of the Late Glacial. This taxon was a constituent of dwarf shrub tundra, and it occurred also in unshaded areas within the open Late Glacial forests and parklands. Thus, *Helianthemum* pollen is characteristic of the Late Glacial (Dyakowska 1959). Species of this genus still grow in Poland, but they are distributed thinly; therefore, their pollen may appear sporadically but never plays any significant role in Holocene pollen assemblages.

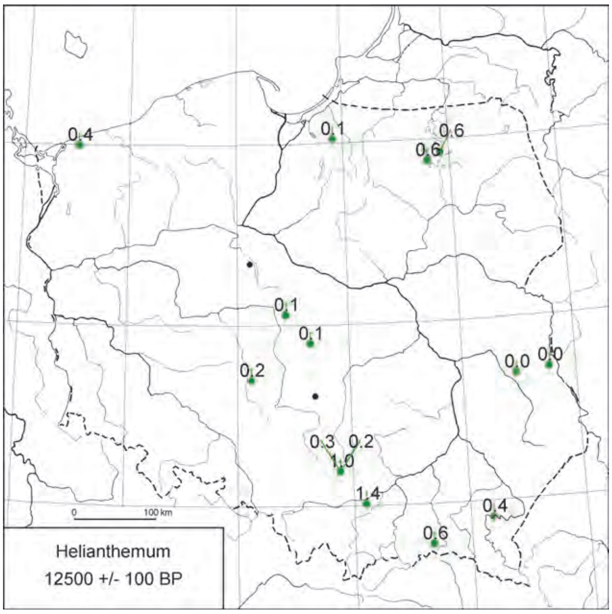
→

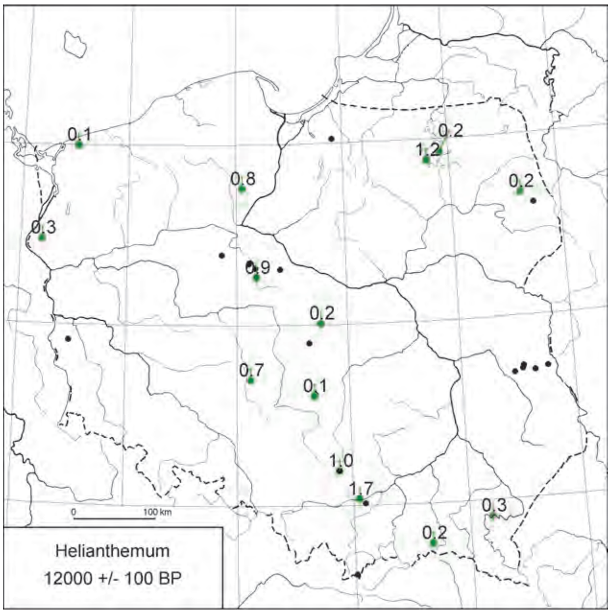
Fig. 89. *Helianthemum*: dot maps for 14,000–9500 ^{14}C yr BP

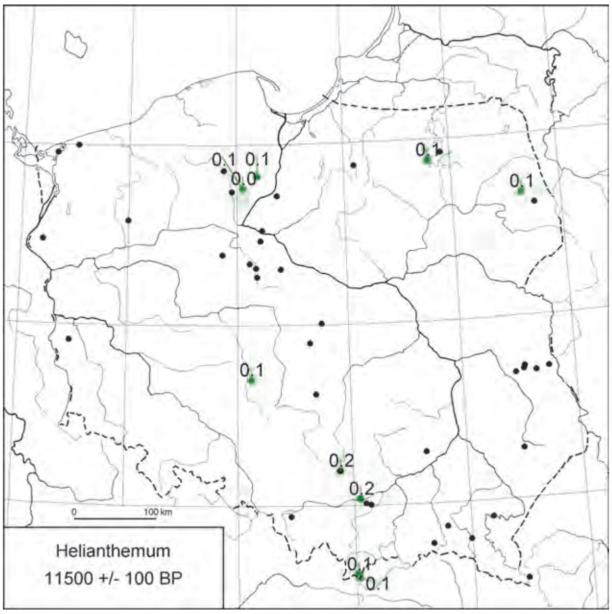

0.8
1.4
0 100 km
Helianthemum
14000 +/- 100 BP

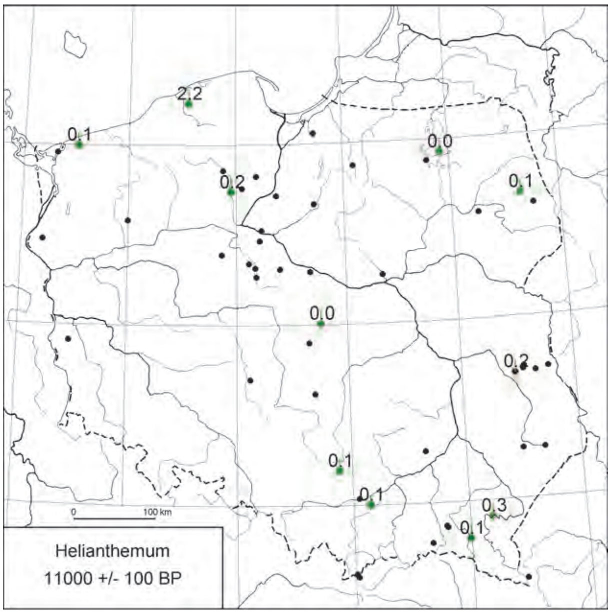

0.4
1.3
0 100 km
Helianthemum
13500 +/- 100 BP

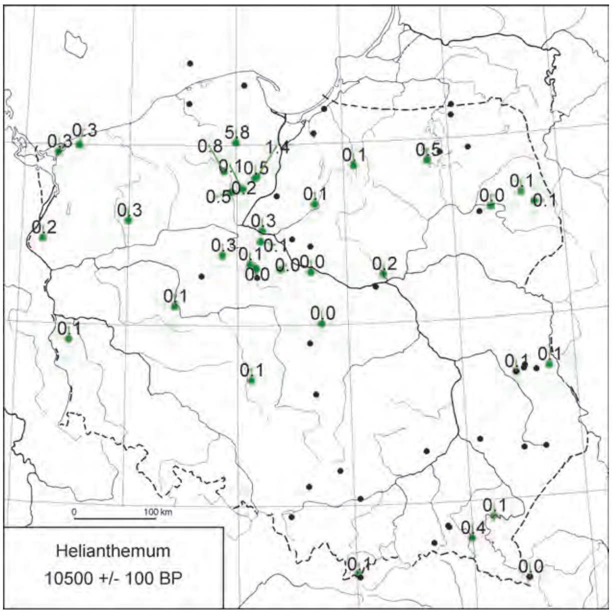

0.9
1.8
1.3
1.2
2.2
0 100 km
Helianthemum
13000 +/- 100 BP

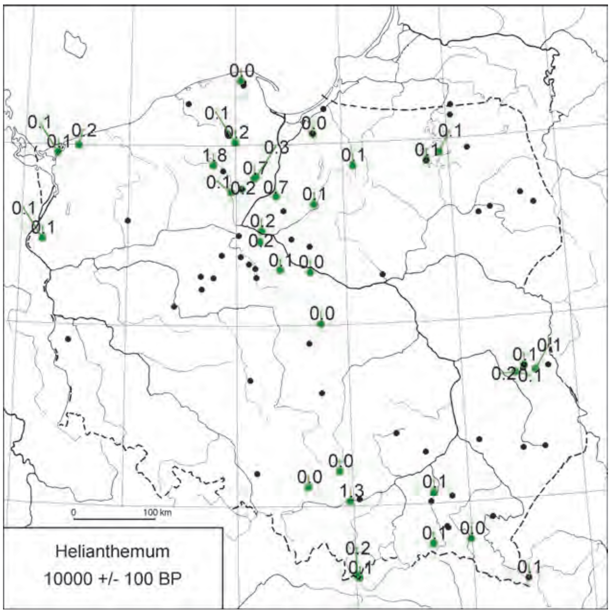

0.4
0.1
0.6
0.6
0.1
0.1
0.2
0.0
0.0
0.3
0.2
1.0
1.4
0.4
0.6
0 100 km
Helianthemum
12500 +/- 100 BP

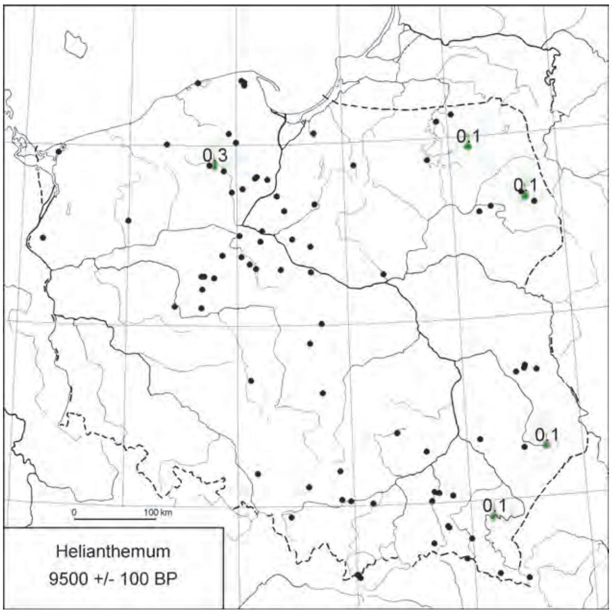

0.1
0.2
1.2
0.8
0.2
0.3
0.9
0.2
0.7
0.1
1.0
1.7
0.3
0.2
0 100 km
Helianthemum
12000 +/- 100 BP


0.1
0.1
0.0
0.1
0.1
0.1
0.2
0.2
0.1
0.1
0 100 km
Helianthemum
11500 +/- 100 BP


2.2
0.1
0.0
0.2
0.1
0.0
0.2
0.1
0.1
0.3
0.1
0
100 km
Helianthemum
11000 +/- 100 BP


0.3
0.3
5.8
0.8
1.4
0.1
0.5
0.1
0.5
0.5
0.2
0.1
0.0
0.1
0.1
0.3
0.2
0.3
0.3
0.1
0.1
0.0
0.0
0.0
0.2
0.1
0.0
0.1
0.1
0.1
0.1
0.1
0.4
0.1
0.0
0
100 km
Helianthemum
10500 +/- 100 BP


0.0
0.1
0.1
0.2
0.1
0.2
0.0
0.1
0.1
1.8
0.3
0.7
0.1
0.1
0.2
0.7
0.1
0.1
0.1
0.2
0.2
0.1
0.0
0.0
0.1
0.1
0.2
0.1
0.0
0.0
1.3
0.1
0.1
0.0
0.2
0.1
0.1
0
100 km
Helianthemum
10000 +/- 100 BP


0.3
0.1
0.1
0.1
0.1
0
100 km
Helianthemum
9500 +/- 100 BP

Plantago lanceolata L. – **Ribwort plantain**

MIROSŁAW MAKOHONIENKO, KRYSTYNA MILECKA, IWONA OKUNIEWSKA-NOWACZYK,
AND DOROTA NALEPKA

Plantago lanceolata L. belongs to a genus including about 260 species of both herbaceous perennial and annual plants and small shrubs inhabiting the temperate zone. About 30 *Plantago* species have a native distribution in Europe. At present, 10 other species of *Plantago*, apart from *Plantago lanceolata*, grow wild in Poland, as native or introduced plants (Mirek et al. 2002).

The morphological features of *Plantago lanceolata* pollen grains, a large number of pores (10 to 14), each surrounded by a thickened, projecting ring, allow fossil material of this species to be readily distinguished from other species of *Plantago* native to northern Europe (Clarke & Jones 1977; Moore et al. 1991). Most palynologists who have investigated sites in Poland have, therefore, recorded *Plantago lanceolata* separately from other *Plantago* species.

PRESENT DISTRIBUTION IN EUROPE AND IN POLAND

Plantago lanceolata occurs almost throughout Europe up to 65°N and at scattered sites right up into the northern regions of Scandinavia (Hultén & Fries 1986). As a plant most commonly associated with and widely introduced by human agencies (synanthropic), it now has an almost cosmopolitan range. In Poland it occurs throughout the country from the Baltic Sea coast to the forest zones in the mountains (Fig. 90).

ECOLOGY

Plantago lanceolata is classified in the Polish flora as an apophyte, i.e. a synanthropic plant of local origin. It occurs at countless sites, usually in populations containing tens to hundreds or thousands of specimens. It is most common in meso- and eutrophic meadow habitats, though it may also occur in ruderal habitats. This species in Poland possesses strong powers of dispersal, appearing in many fresh localities (Zarzycki et al. 2002). Ribwort plantain prefers habitats with full sunlight but will tolerate periodic or temporary shading. It does not spread into areas of more severe climate such as the upper montane forest zone, sub-alpine or alpine zones. It is indifferent to oceanicity or continentality of climate. It occurs on loamy soils with varied amounts of sand, from dry to moist, and moderately to slightly acid (pH 5.5–6.5). It avoids both very dry and very wet soils. It is a characteristic species of the *Molinio-Arrhenatheretea* class including semi-natural and anthropogenic grazed meadow and pasture communities on meso- and eutrophic, sandy and humic-sandy soils, but not in marshes (Matuszkiewicz W. 2001). Communities of this class occur throughout the Euro-Siberian area in the lowlands as well as in the foothills and in montane forest zones.

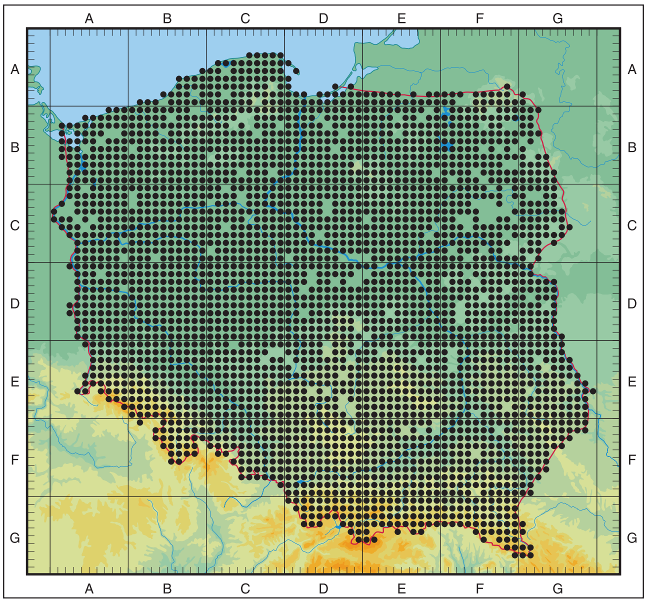


Fig. 90. Present-day distribution of *Plantago lanceolata* L. in Poland (after Zając A. & Zając M. 2001)

POLLEN PRODUCTION AND DISPERSAL

Ribwort plantain is a wind-pollinated species with a very high pollen production. According to Pohl (1937) it produces in one inflorescence about 2 million pollen grains, thus more than the wind-pollinated inflorescences of such trees as ash, hornbeam or beech. However, because of its very low habit (hemicryptophyte) it has much more restricted opportunities for pollen dispersal.

In Poland the flowering period of this plant is long and lasts from May to September (Szafer et al. 1986). In central Europe the period when pollen grains of species of the genus *Plantago* are released into the air is from May to the end of August, with their maximum in July. In the pollen-rain the genus *Plantago* is generally represented in relatively small amounts similar to those of Chenopodiaceae and lower than those of the genera *Rumex*, *Urtica* or *Artemisia* (Spieksma et al. 1993).

EXPANSION IN EUROPE DURING THE LATE GLACIAL AND HOLOCENE

Whereas Huntley and Birks (1983) discussed the history and distribution of the genus *Plantago* during this time, because of taxonomic uncertainties about the identification of earlier pollen records, they treated the genus as a whole and give little specific information about *P. lanceolata*. However, Godwin (1975) discusses the Quaternary history of this species, mainly for the British Isles, but his comments apply to northern Europe in general. It is clear from pollen evidence that *P. lanceolata* was present in the steppe-tundra vegetation of the Vistulian Pleniglacial, albeit at a low frequency, with *P. maritima* being of much commoner occurrence. In western Europe its continued presence during all the subdivisions of the Late Glacial is attested by both pollen and macrofossil remains, when it presumably occupied local areas of naturally disturbed ground. Its pollen record during the early Holocene is extremely sparse, but it seems to have persisted in favourable habitats in coastal areas and exposed areas on river floodplains. Iversen (1941) first recognised the importance of pollen of this plant as an indicator during the Holocene of the arrival and spread of human agricultural and pastoral practices across northern Europe. The earliest 'landnam' clearances of Neolithic times from about 5500 BP, were recorded as brief events characterised by temporary, small peaks in non-tree pollen, including *P. lanceolata* and sometimes cereal pollen. The more widespread and eventually permanent forest clearances expanded from Bronze Age, through Iron Age and Roman eventually to Mediaeval times and resulted in continuous low representation of *P. lanceolata* in most pollen diagrams from lowland areas in northern Europe. By 1000 BP the values higher than 1% are observed in the major part of Europe north of the Mediterranean region up to south Scandinavia and Faroe Islands in the north. The highest values are recorded from west Britain (8%), the Alps (6%) and from the Balkans (6%).

In southern Europe, there are also both Late Glacial and Holocene records for *Plantago* pollen, in some cases identifiable to species. However some Mediterranean species have a similar pollen morphology to *P. lanceolata* (Reille 1992), so the history of that taxon there is quite obscure.

MIGRATION PATTERN IN POLAND (Fig. 91)

7500 – 5500 BP

In the Late Glacial and early Holocene, pollen diagrams from the area of Poland do not record the presence of *P. lanceolata*. The first pollen grains of ribwort plantain appear at just a few (4–5) sites during the Atlantic period when the country had been dominated by stable mixed, species-rich deciduous forests since 7500 BP. Over most of Poland this corresponds with the late Mesolithic Period, so that at that time *P. lanceolata* pollen may have been derived either from natural sites, not connected with human activity, or from the surroundings of small, temporary Mesolithic camps. According to Pawłowska (1965) native origins of *P. lanceolata* are connected with the plant communities of river valleys, open, damp streamsides, gravel banks and riverine alder woods. At a larger number of sites *P. lanceolata* pollen appeared by about 5500 BP, though values of 0.2% were only sporadically exceeded. This horizon corresponds with the decline of settlements of the Lengyel-Polgar culture and the early phase of the Funnel Beaker culture (Kaczanowski & Kozłowski 1998, Kruk & Milisauskas 1999). The increase in pollen values of *P. lanceolata* shows a correlation with an increase in representation of *Artemisia* in the zone of south Polish uplands (see *Artemisia*, Makohonienko et al., this volume). Despite the considerable number of sites analysed, pollen of *P. lanceolata* has not been recorded at that time, either in the Carpathians or in central Wielkopolska.

5000 – 4500 BP

By this time some expansion of ribwort plantain took place, as shown by the pattern of isopolls for 5000 BP, when its pollen was recorded also in the sites from central Wielkopolska. The first so-called elm decline was also recorded then, involving the destruction of elm stands causing some clearings in the forest canopy (see *Ulmus*, Zachowicz et al., this volume). This took place during the middle Neolithic Period, when decline of the Linear Pottery culture took place along with the development of the Funnel Beaker culture (Kośko 1980, Czerniak 1994). Since ca. 4500 BP ribwort plantain has been represented throughout the country. Kujawy and eastern Małopolska, situated within the range of the middle Neolithic settlements of Funnel Beaker and Globular Amphorae cultures, are areas distinguished by slightly higher amounts of *P. lanceolata* pollen values (0.2–0.5%). It should be emphasized that in this case the isopollen maps do not reflect the actual distribution of appearance of this species in the pollen diagrams. At some sites values exceeding 1% were recorded as early as 5000–4800 BP in one or two pollen spectra between the time levels presented on the maps (Latałowa 1992, Ralska-Jasiewiczowa & van Geel 1998). Underestimation of *P. lanceolata* in the isopollen maps results from both the irregular occurrence of its pollen in the diagrams and particularly from its short-lived local peaks.

4000 – 3500 BP

At about 4000 BP, which corresponds to the decline of the Neolithic Period, the distribution and number of sites as well as the pollen percentage values of ribwort plantain in the Wielkopolska-Kujawy Lowland continued to increase, reaching the highest representation in the country. By 3500 BP values of 0.2–0.5% are recorded almost throughout the western part of Poland still with a marked maximum (0.5–0.7%) in the Kujawy area and in a new centre in the north-western margin of Poland, on Wolin Island.

3000 – 2000 BP

The isopolls relating to this period show little variability, reaching 0.2 to 0.5% over most of Poland. The lowest pollen values of *P. lanceolata* (up to 0.2%) persist in the Carpathians, in part of Polesie Lubelskie and in the Lublin and Wołyń Uplands. On the 3000 and 2500 BP maps in the north-western part of the country the isopolls exceed 1%. Also in this case the isopollen maps underestimate considerably the values of *P. lanceolata* pollen in relation to the actual data from the pollen diagrams. Periodic expansion of this species at some of the sites concerned leads to values reaching even 10% (Latałowa 1992) and is a reflection of the changes in settlement and economic activity of the Lusatian culture. At the beginning of the Roman Period (2000 BP) the values of ribwort plantain decrease below 0.5% in the north-western part of Poland, whereas higher values are observed in the central part of Wielkopolska, in the uplands of southern Poland and in the Mazurian Lake District.

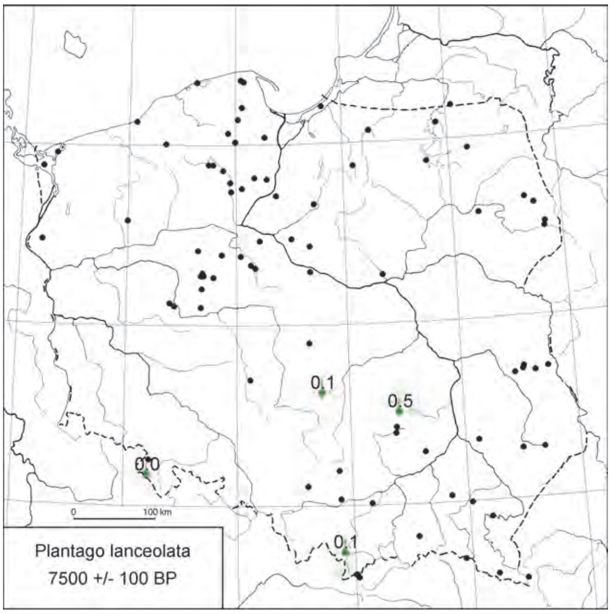
1500 – 100 BP

During the Migration Period (1500 BP), in many areas of Poland, the pollen values of ribwort plantain fall to minimal values. Its pollen values only rise again in the Early Middle Ages (1000 BP) when the widest distribution of this species is recorded. The high isopollen values recur in north-western Poland (Wolin Island) exceeding 1%. In the central part of Wielkopolska, in the areas of incipient organisation of the early state of the Piasts dynasty, mean values of *P. lanceolata* isopolls reach >1%, as in southern Poland, in the Kraków region. Smaller values of ribwort plantain (0.2–0.5%) occur along the Baltic Sea coast in the vicinity of Gdańsk, in north-eastern Poland in the areas inhabited by the tribes of the Bałts, as well as in the eastern part of the country in Mazovian Lowland, Podlasie, the Lublin Upland, and in the Carpathian foreland. By 500 BP, the mean pollen values of ribwort plantain in the majority of Polish territories increase further to 0.5–1% and in times close to the present (100 BP) reach up to 2%.

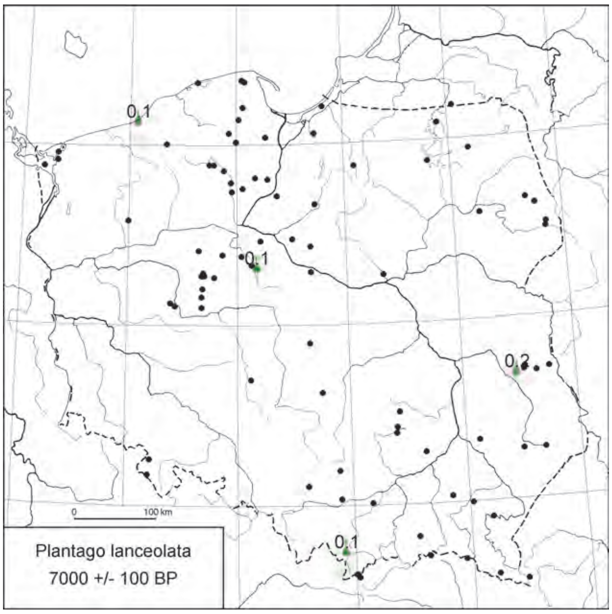
Conclusions

Pollen of *Plantago lanceolata* appears in the fossil record in Poland during the Atlantic period about 7500 BP, when the Mesolithic hunter-gatherer mode of life was dominant. The single ribwort plantain pollen grains recorded at that time may reflect its local presence in natural plant communities. Its distribution, influenced by anthropogenic activity, increased during the period of the development of the Neolithic cultures. It appeared at more numerous sites by 5500–5000 BP. Its values increased during the Bronze Age, after 3500–3000 BP. At some sites its maximum values appear at levels reflecting development of the Lusatian culture. However, the main spread in Poland of plant communities with *P. lanceolata* took place as a result of the development of Early Medieval settlements.

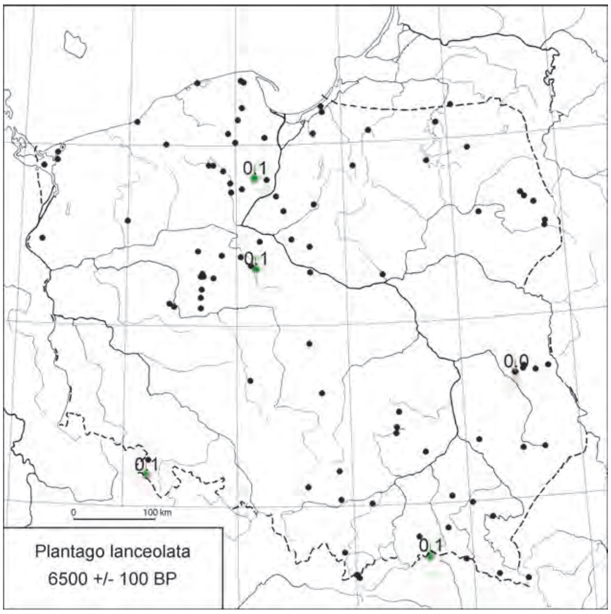
Fig. 91. *Plantago lanceolata*: dot and isopollen maps for 7500–100 ^{14}C yr BP



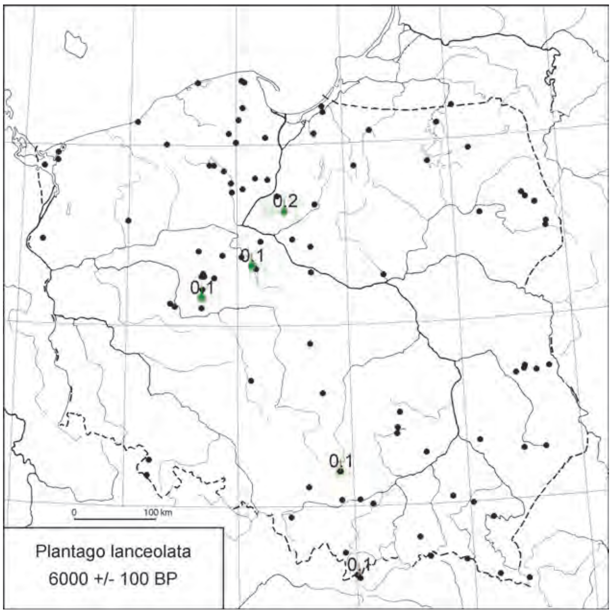
Plantago lanceolata
7500 +/- 100 BP



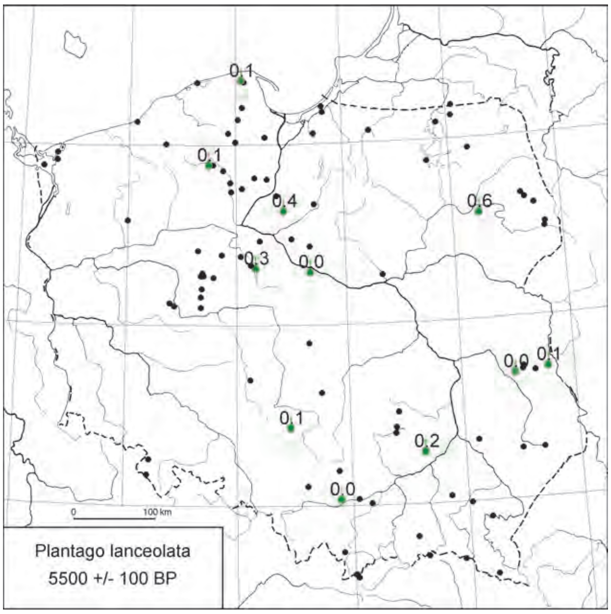
Plantago lanceolata
7000 +/- 100 BP



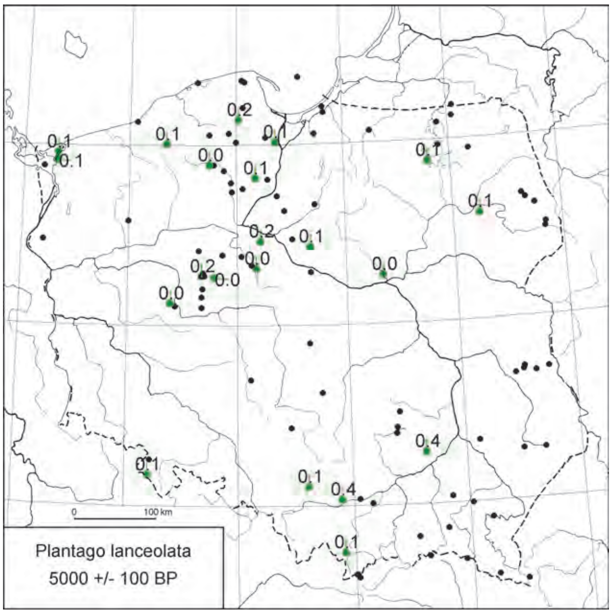
Plantago lanceolata
6500 +/- 100 BP



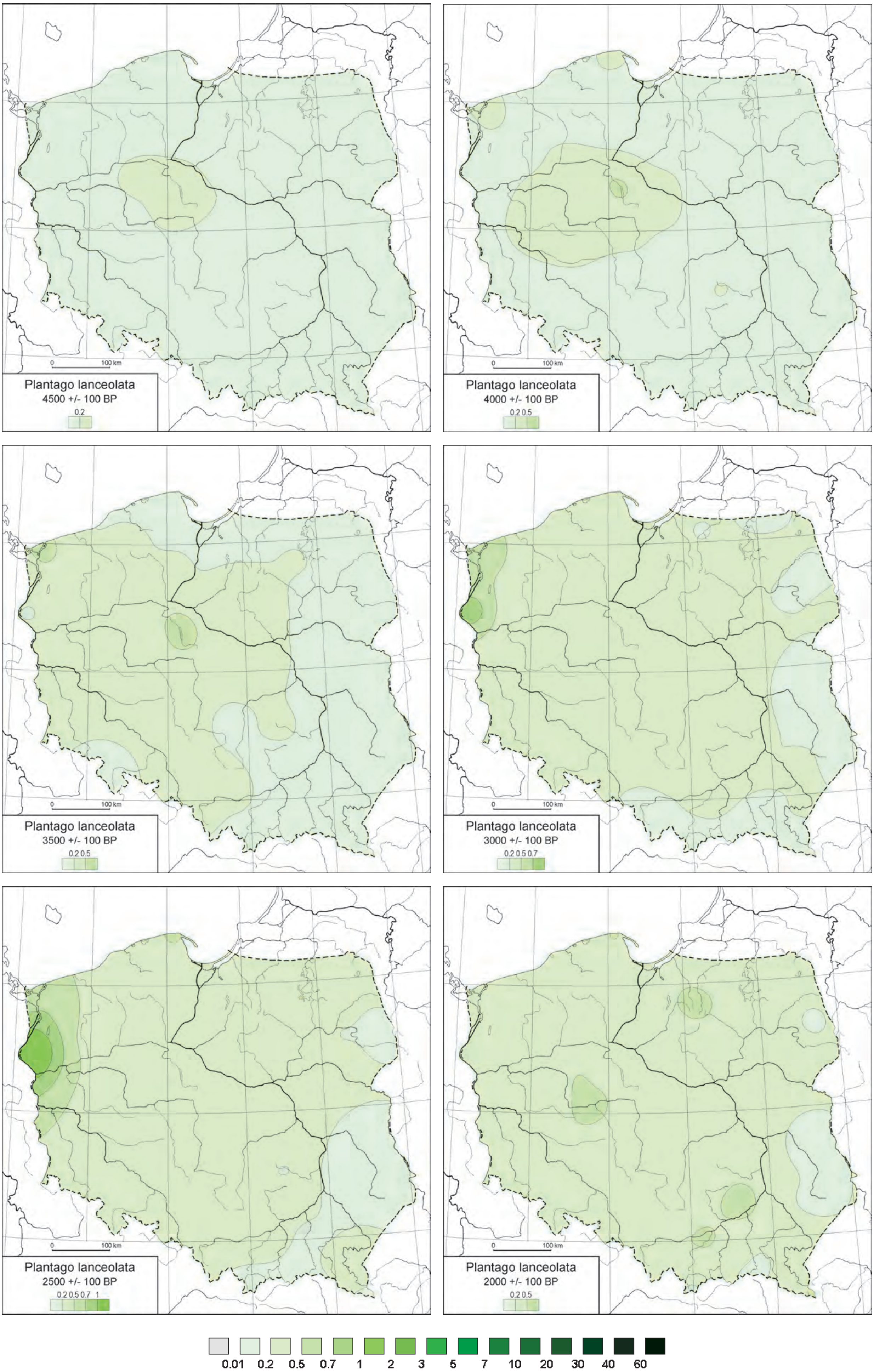
Plantago lanceolata
6000 +/- 100 BP

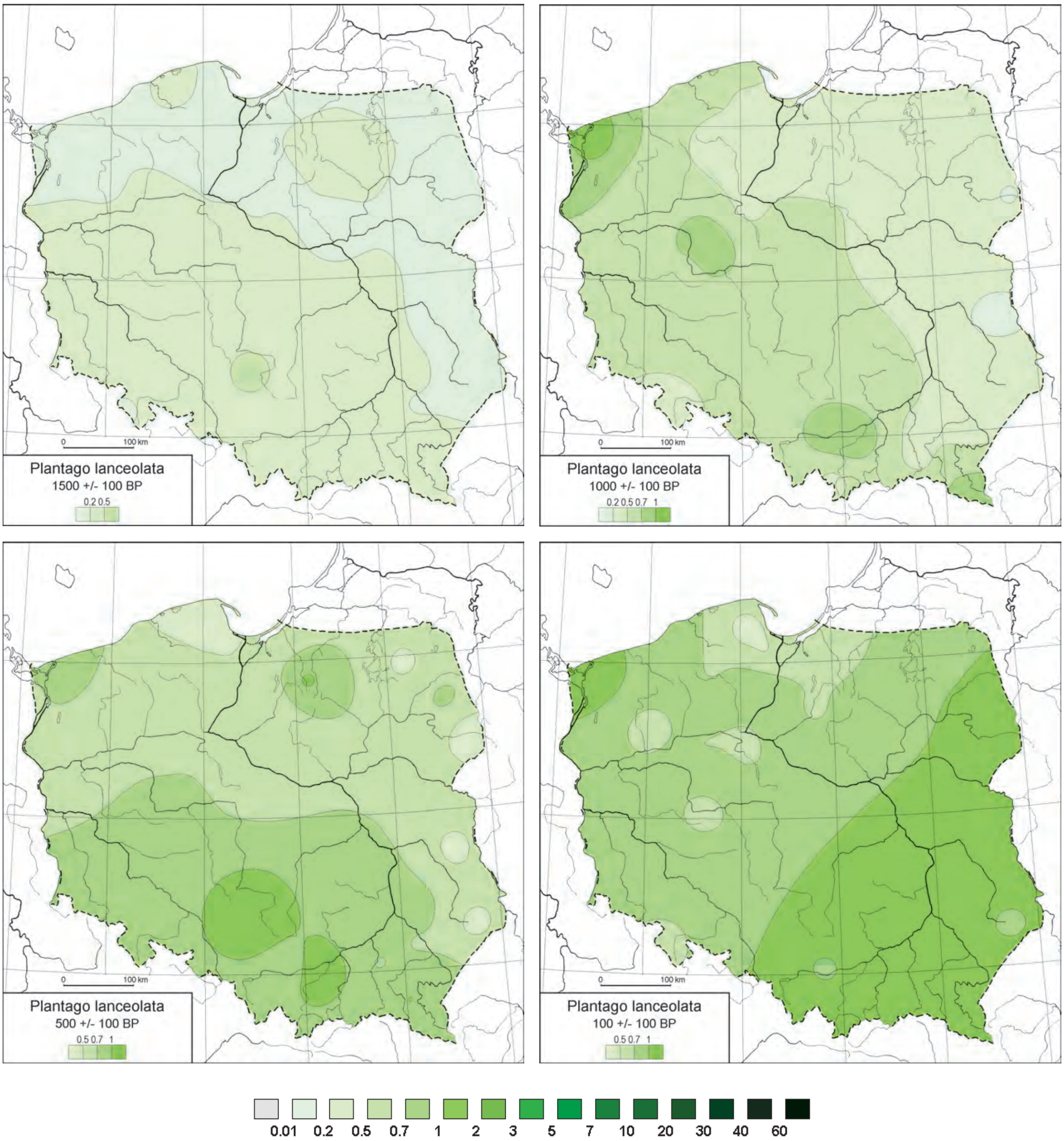


Plantago lanceolata
5500 +/- 100 BP



Plantago lanceolata
5000 +/- 100 BP


0
100 km
Plantago lanceolata
4500 +/- 100 BP
0.2
0
100 km
Plantago lanceolata
4000 +/- 100 BP
0.2 0.5
0
100 km
Plantago lanceolata
3500 +/- 100 BP
0.2 0.5
0
100 km
Plantago lanceolata
3000 +/- 100 BP
0.2 0.5 0.7
0
100 km
Plantago lanceolata
2500 +/- 100 BP
0.2 0.5 0.7 1
0
100 km
Plantago lanceolata
2000 +/- 100 BP
0.2 0.5
0.01
0.2
0.5
0.7
1
2
3
5
7
10
20
30
40
60


0
100 km
Plantago lanceolata
1500 +/- 100 BP
0.2 0.5
0
100 km
Plantago lanceolata
1000 +/- 100 BP
0.2 0.5 0.7 1
0
100 km
Plantago lanceolata
500 +/- 100 BP
0.5 0.7 1
0
100 km
Plantago lanceolata
100 +/- 100 BP
0.5 0.7 1
0.01
0.2
0.5
0.7
1
2
3
5
7
10
20
30
40
60

Poaceae (Gramineae) – **Grass family**

KRYSTYNA HARMATA, JACEK MADEJA, IWONA OKUNIEWSKA-NOWACZYK,
AND DOROTA NALEPKA

GEOGRAPHICAL DISTRIBUTION AND ECOLOGY

Grasses belong to one of the most abundant families in the world. From among more than 300 species of grasses known from Poland, there are 160 species permanently established in natural habitats. They include 130 species native to Poland and more than 30 alien species (Mirek et al. 2002). The remaining ones represent widely treated casuals or cultivated species, sometimes temporarily running wild. Grasses occur in almost all kinds of habitats; however, they are primarily components of non-forest communities, such as meadows, grasslands, and marshes.

When trying to unravel the Late Glacial and Holocene history of our flora, analysis of the broad distribution ranges of particular species makes it possible to recognise groups of plants that can be regarded as elements of the Polish flora with common or similar histories (Zając M. & Zając A. 2002). Amongst the grasses these historical elements include mountain, mainly Alpine, species that are common to many European mountain ranges. In particular, species showing an Arctic-Alpine disjunct distribution must be an ancient, at least Pleistocene element.

Species of grasses having wide, circum-boreal or European-Siberian ranges, and growing mainly in the communities of the *Phragmitetea* or *Scheuchzerio-Caricetea* classes can be considered as an element from the Late Glacial or from the Preboreal period. Many species of grasses growing in Poland have distribution ranges that extend far to the north, indicating their tolerance of severe arctic climate. Those species could have occurred in Poland during the glacial period. Among them there are present common meadow species, such as *Anthoxanthum odoratum*, *Nardus stricta*, *Phleum pratense*, *Poa pratensis*, *Alopecurus pratensis*, or *Deschampsia caespitosa*.

Some species of xerothermic grasslands, showing links with an Irano-Turanian distribution pattern, are at present confined to the uplands of southern Poland, where they probably immigrated during the climatic optimum (Zając M. & Zając A. 2002). On the other hand, many species of forest grasses, associated with the *Querco-Fagetea* class of deciduous forests, may have appeared together with deciduous trees during the Boreal period.

Among the species that are permanent components of our flora, as many as 143 are diagnostic species for the classification and systematic description of plant communities in Poland, with 134 of these species being strictly characteristic (Balcerkiewicz 2002). This indicates that many species of grasses have narrow ecological requirements. These are species of both extremely poor habitats and rich or very rich ones. Heliophilous species are in the majority, and they contribute to communities of meadows, grasslands, pastures, and agricultural land. Some grass species constitute a shade-tolerant element in forest communities.

Grasses and grass communities can be used as an indicator of human modification. Excessive development of grasses within the herb layer of forest communities, caused by external factors results in creation of a grassy type of subcontinental oak-hornbeam forests with lime or beech forests with dominant *Poa nemoralis* as well as grassy types of conifer forests with *Festuca ovina* or *F. trachyphylla* (Olaczek 1974). In mesophilous forests which have been thinned out by felling, *Milium effusum* may form dense stands in opened clearings, similarly as *Avenella flexuosa* in conifer forests (Balcerkiewicz 2002).

POLLEN PRODUCTION AND DISPERSAL

Grasses are typical wind-pollinated plants. They form small, inconspicuous flowers that are reduced to bracts (glumes, palea and lemma) and delicate scales (lodicules) that open out to reveal the stigmas and stamens. The stamens have long, thin filaments and large anthers (Szafer & Wojtusiakowa 1969). Grass pollen is fragile, with a simple morphological structure, and produced in great quantities. The period of grass pollen production, because of the large number of species involved, lasts from May to August. In periods of maximum pollen production there are about 200 pollen grains in 1 m^3 of air. Not all species of grasses are wind-pollinated; some taxa are autogamous such as *Cynosurus*, *Bromus*, *Phalaris*, *Aira*, *Avena*, and *Triticum* (Szafer & Wojtusiakowa 1969), whereas *Secale* and many other grasses have self-sterile flowers.

In the case of a family so rich in species it is not possible to interpret its abundance and/or mode of taxon occurrence in plant communities using its percentage values in a pollen diagram. Huntley and Birks (1983) have stated that presently forested areas are characterized by Poaceae (Gramineae) values up to 10%. Higher values indicate deforested areas, whereas values >25% may point to the presence of treeless areas. Investigations of surface pollen assemblages show a positive correlation between amount of grasses and cultivation, thus changes in their frequency can be one of the pieces of evidence that allow one to distinguish settlement stages (Broström et al. 1998).

EXPANSION IN EUROPE DURING THE LATE GLACIAL AND HOLOCENE

In Europe, isopollen maps for 12,000 BP (Huntley & Birks 1983) indicate widespread pollen values of >10%, and of >25% throughout much of western Europe. In the Younger Dryas (10,500 BP) frequencies of grasses exceeding 25% are recorded both in south-eastern and western Europe. The early Holocene is marked by rapidly declining Poaceae (Gramineae) pollen frequencies, and by 9000 BP values higher than 10% are recorded only in western and south-eastern Europe, whereas values of >25% occur mainly in the Arctic. The 7000 BP map shows minor changes in the distribution of values of >10%, while there is a significant decline of higher values in the Arctic. Poaceae (Gramineae) pollen values increase at about 5000 BP, at first in western Europe and since ca. 3000 BP also in extensive areas of the south-eastern part of the continent. On the 1000 BP map vast areas of south and western Europe lie within the range of >10%, with maximum values in the west.

MIGRATION PATTERN IN POLAND (Fig. 92)

14,000 – 10,500 BP

The oldest maps for Poaceae (Gramineae), which are dot maps because of the small number of sites involved (14,000–13,000 BP), indicate quite high percentage values of >10%. However they display a variation in the abundance within the limits of ca. 6–22%. On the 12,500 BP map, the amounts of grasses show similar values of >10% in most of Poland; on the 12,000 BP map (presenting already the isolines) the area of lower values (below 10%) extends through most of eastern and northern Poland. Development of forests during the Allerød warming (11,500–11,000 BP) caused a reduction in the role of Poaceae (Gramineae), except in the Eastern Carpathians. The 10,500 BP map indicates an increase in pollen percentage values in the north of the country, which may have resulted from a considerable decline of forests in this area due to cooling during the Younger Dryas.

10,000 – 7000 BP

The subsequent maps (10,000 and 9500 BP) record a gradual decline in Poaceae (Gramineae) pollen frequencies, particularly in the northern and the north-eastern parts of Poland, where they fall below 5%. The 9000 and 8500 BP maps display similarly low values for the entire west and central-north of Poland, a trend connected with the expansion of deciduous trees and shrubs such as *Corylus* or *Quercus*. However, isopolls in the southern part of the country indicate higher values (5–20%), being gradually reduced on subsequent maps (8000–7000 BP). Locally, in the Sudetes and in north-eastern Poland, grass pollen values fall below 2%. It is unquestionably the result of the dominance of forests during this period.

6500 – 1500 BP

Since 6500 BP local increases in pollen frequencies of grasses have been observed. This is particularly well visible on the 5500 BP map in the northern and southern parts of Poland. The maps from 5000 to 3500 BP display low, unequally distributed values. This mosaic pattern may be connected with human activity. A distinct increase in pollen values throughout the country is seen on the 3000 BP and 2500 BP maps, which undoubtedly results from deforestation caused by the settlements of the Lusatian culture. However, on the 2000 BP map there is no distinct increase in Poaceae (Gramineae) pollen values that would result from settlement activities during the period of Roman influences. Nor does the 1500 BP map reflect any reduction in treeless areas during the Migration Period, unlike the isopollen maps for many other taxa.

1000 – 100 BP

On the maps relating to the last thousand years a radical increase in Poaceae (Gramineae) pollen values can be seen, indicating progressive deforestation throughout the country.

CONCLUSIONS

To sum up, it can be stated that, because of such a wide ecological spectrum of particular species within the family Poaceae (Gramineae), it is very difficult to draw detailed conclusions concerning the factors responsible for changes in abundance of grass pollen. Difficulties in this interpretation are enhanced, among others, because it has not been possible, whilst producing these maps, to separate out *Phragmites australis* pollen from that of other taxa of Poaceae (Gramineae).

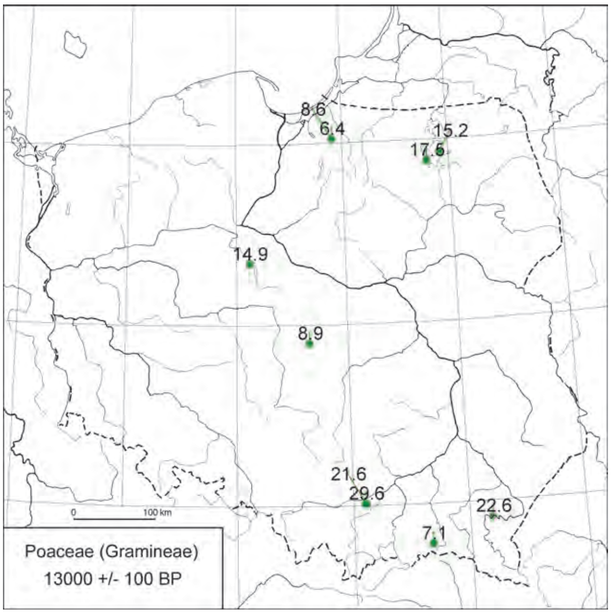
The Poaceae (Gramineae) family is one of the most important constituents of the majority of treeless plant communities. Therefore the abundance of its pollen mainly reflects how open or forested, or perhaps deforested, an area may be. At the end of the Vistulian the processes of spread and contraction of treeless plant communities were conditioned by the climate, whilst during the Holocene they resulted mainly from human activity. The gradual decline of treeless communities is distinctly marked at the beginning and during an early phase of the Holocene. Their later renewed expansion, particularly in the southern part of the country, was connected with the development of agrarian cultures. Increasing pollen values of Poaceae (Gramineae), observed since 6500 BP at sites along the Baltic Sea coast, have resulted from the expansion of reedswamp communities with *Phragmites australis* at the margins of water bodies originating from the Littorina transgression of the southern Baltic Sea (Zachowicz et al. 1982, Tobolski 1987, Latałowa 1992).

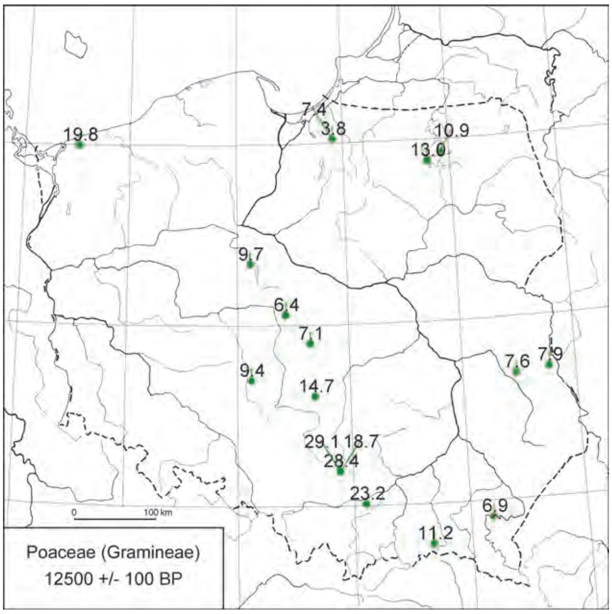
An attempt was made to show the Poaceae (Gramineae) maps calculated with Cyperaceae included into the pollen sum, compared with the basic series calculated without Cyperaceae. Those maps demonstrate in the Late Glacial section restriction of higher grass pollen values, particularly in the south-western part of Poland, however the general pattern does not reveal differences substantial enough to be presented in print. The significant differences do not exceed the beginning of the Holocene (10,000 BP map), and appear again on the three youngest maps (1000–100 BP) in form of more advanced fragmentation of high grass pollen values not suitable for any sober interpretation.

Fig. 92. Poaceae (Gramineae): dot and isopollen maps for 14,000–100 ^{14}C yr BP


13.2
15.6
31.4
0
100 km
Poaceae (Gramineae)
14000 +/- 100 BP


22.6
20.8
9.9
0
100 km
Poaceae (Gramineae)
13500 +/- 100 BP

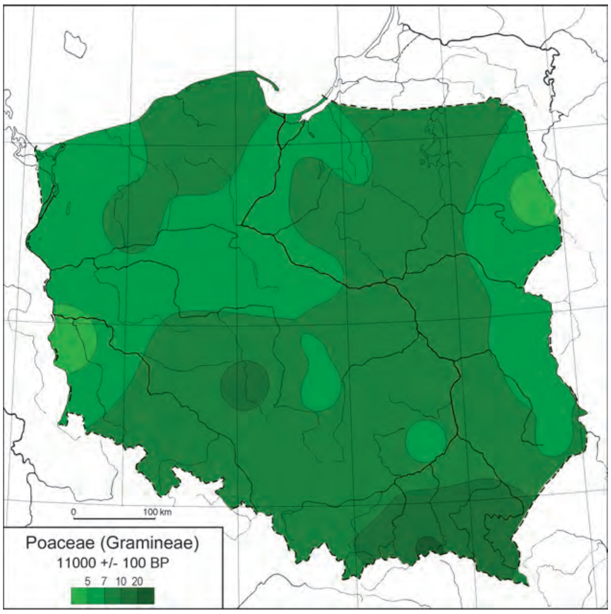

8.6
6.4
15.2
17.6
14.9
8.9
21.6
29.6
22.6
7.1
0
100 km
Poaceae (Gramineae)
13000 +/- 100 BP

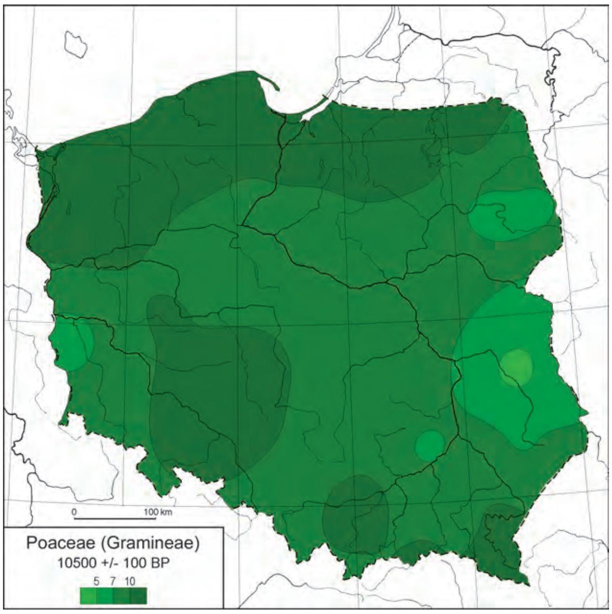

7.4
3.8
19.8
10.9
13.0
9.7
6.4
7.1
7.6
7.9
9.4
14.7
29.1
18.7
28.4
23.2
6.9
11.2
0
100 km
Poaceae (Gramineae)
12500 +/- 100 BP

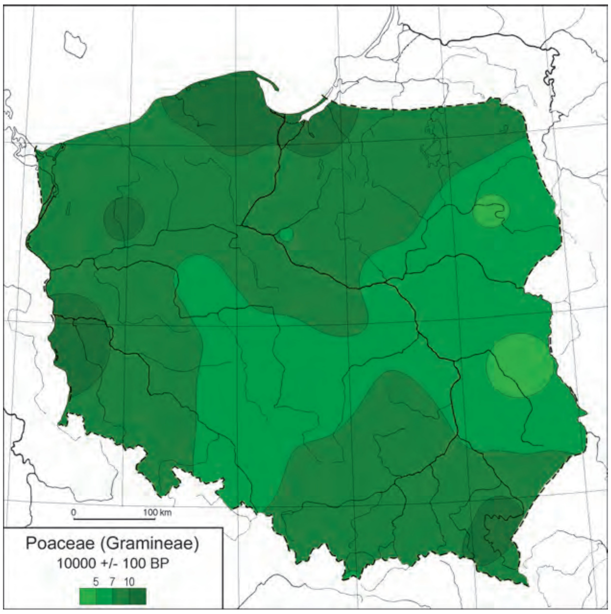

0
100 km
Poaceae (Gramineae)
12000 +/- 100 BP
7
10
20

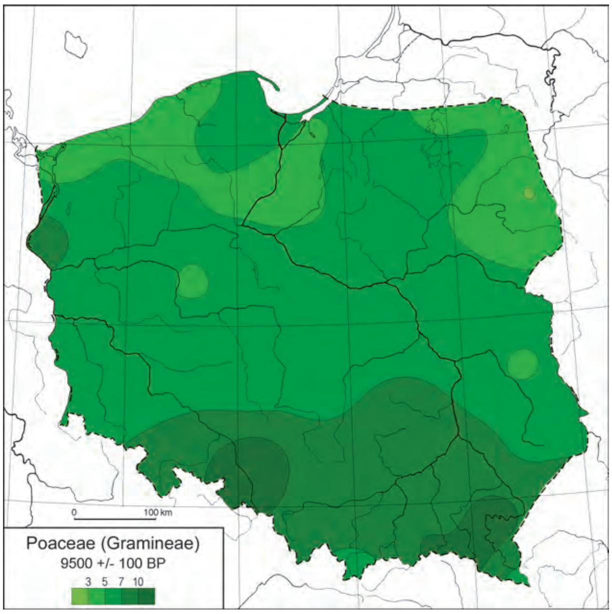

0
100 km
Poaceae (Gramineae)
11500 +/- 100 BP
5
7
10

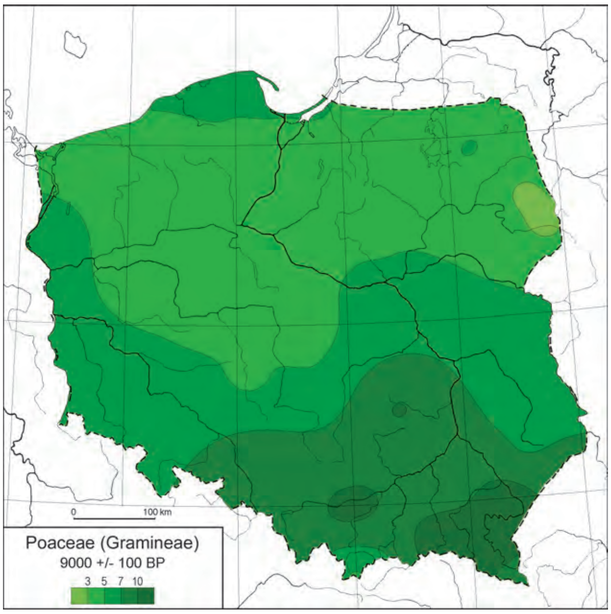

0.01
0.2
0.5
0.7
1
2
3
5
7
10
20
30
40
60


0
100 km
Poaceae (Gramineae)
11000 +/- 100 BP
5 7 10 20


0
100 km
Poaceae (Gramineae)
10500 +/- 100 BP
5 7 10


0
100 km
Poaceae (Gramineae)
10000 +/- 100 BP
5 7 10


0
100 km
Poaceae (Gramineae)
9500 +/- 100 BP
3 5 7 10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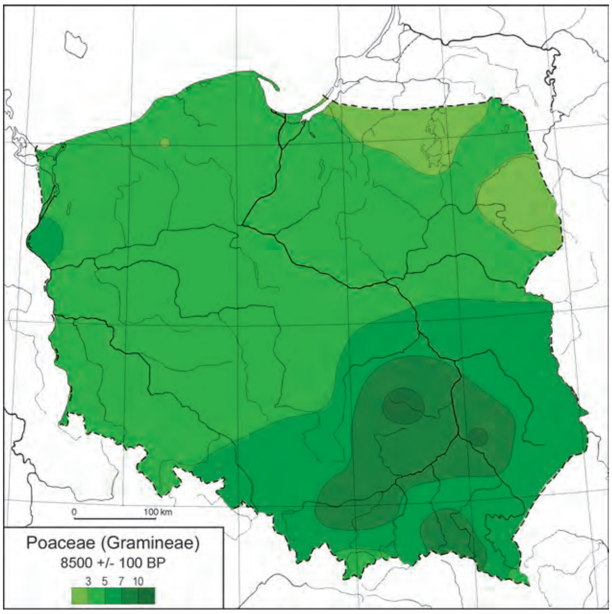
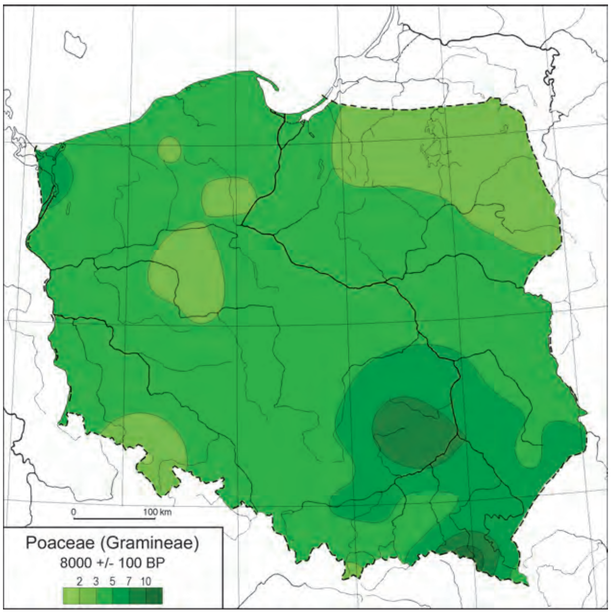
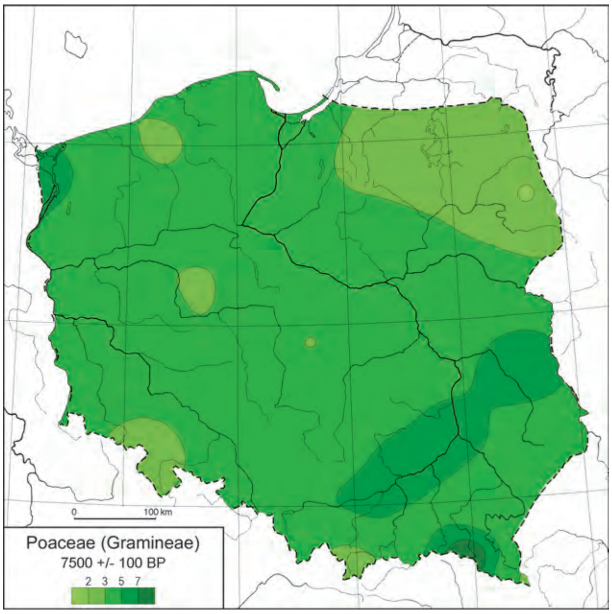
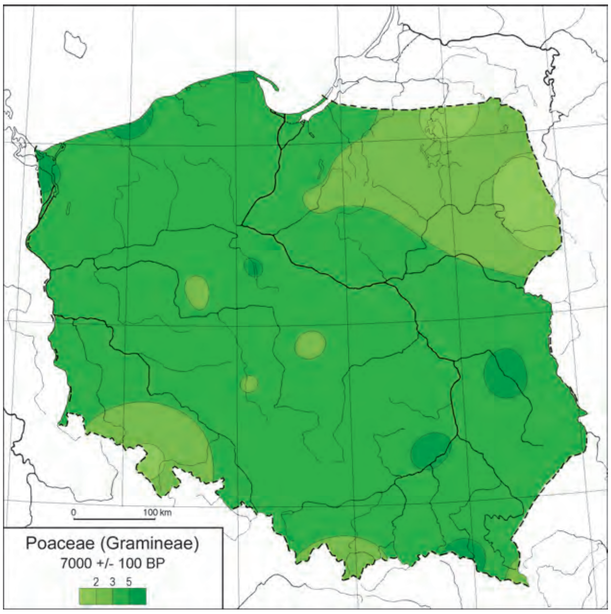
100 km
Poaceae (Gramineae)
9000 +/- 100 BP
3 5 7 10

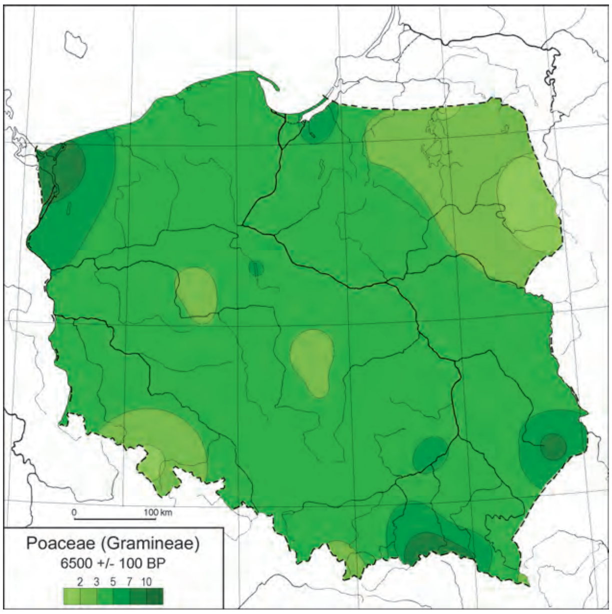

0
100 km
Poaceae (Gramineae)
8500 +/- 100 BP
3 5 7 10

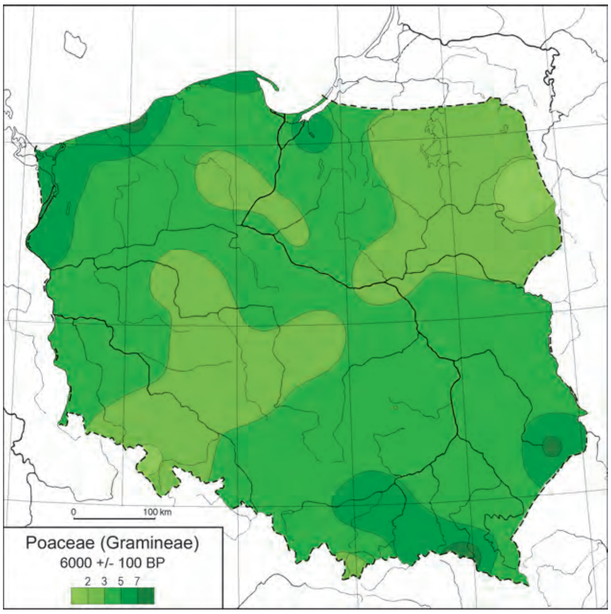

0.01
0.2
0.5
0.7
1
2
3
5
7
10
20
30
40
60

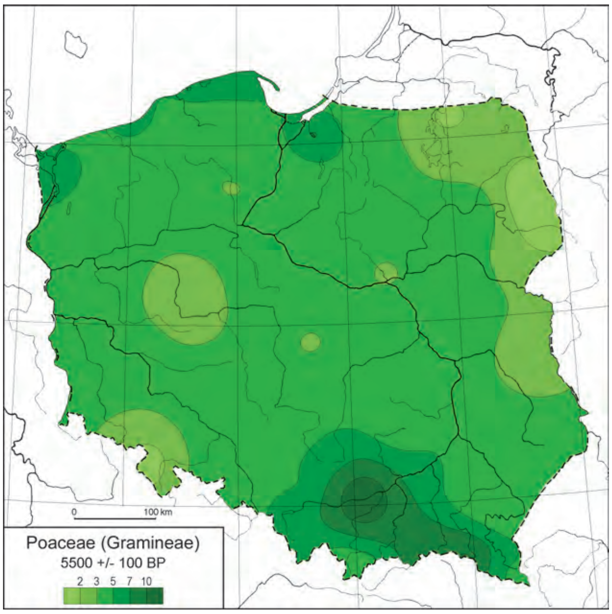

Poaceae (Gramineae)
8000 +/- 100 BP

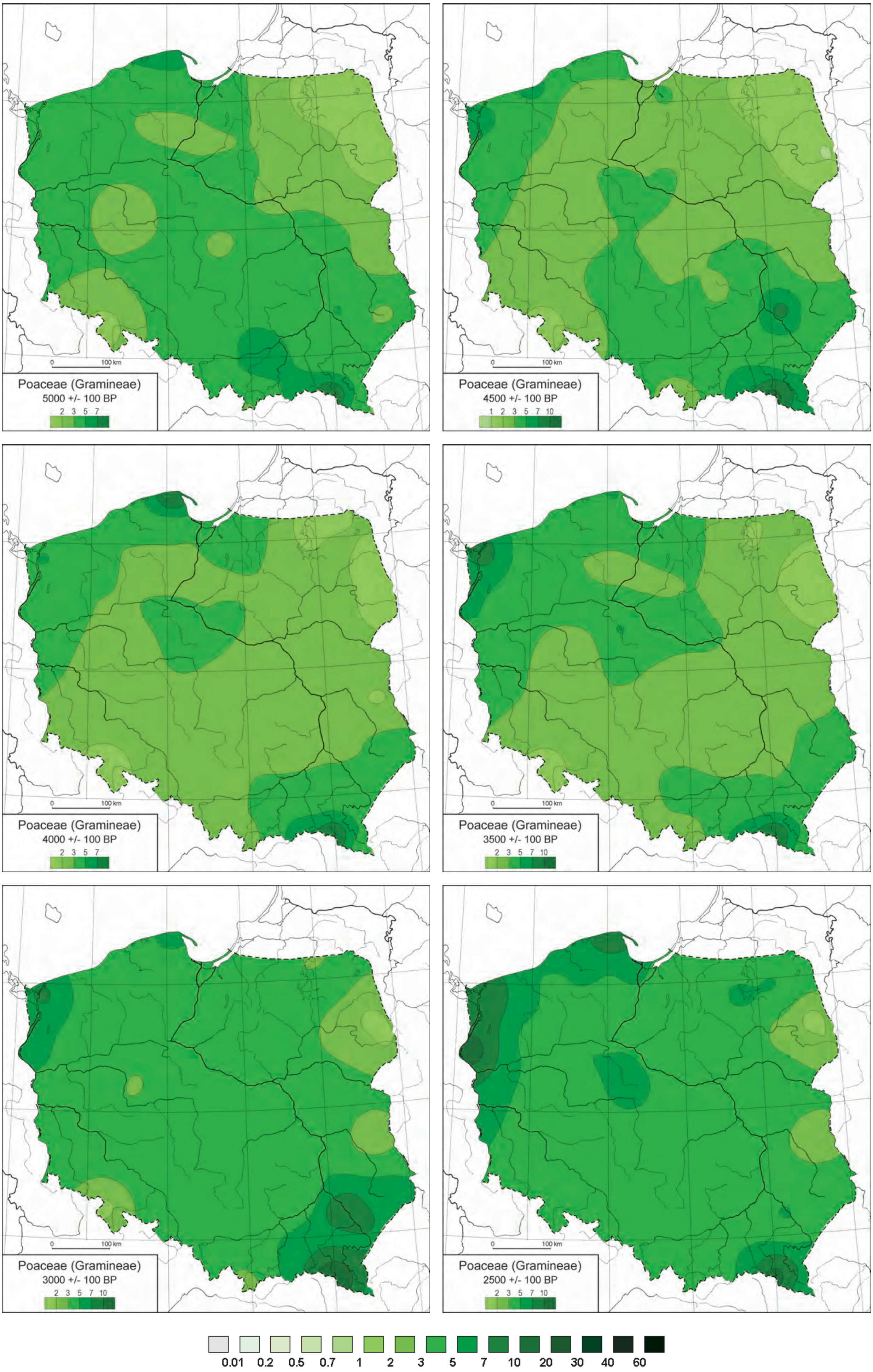

Poaceae (Gramineae)
7500 +/- 100 BP


Poaceae (Gramineae)
7000 +/- 100 BP


Poaceae (Gramineae)
6500 +/- 100 BP


Poaceae (Gramineae)
6000 +/- 100 BP


Poaceae (Gramineae)
5500 +/- 100 BP


0
100 km
Poaceae (Gramineae)
5000 +/- 100 BP
2 3 5 7
Poaceae (Gramineae)
4500 +/- 100 BP
1 2 3 5 7 10
Poaceae (Gramineae)
4000 +/- 100 BP
2 3 5 7
Poaceae (Gramineae)
3500 +/- 100 BP
2 3 5 7 10
Poaceae (Gramineae)
3000 +/- 100 BP
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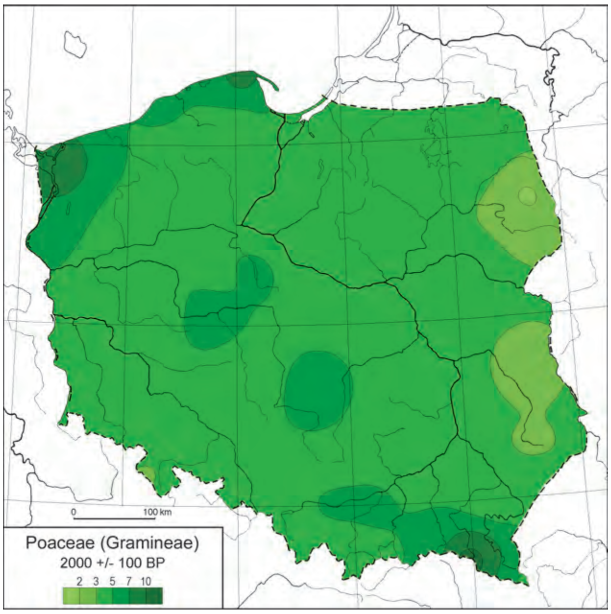
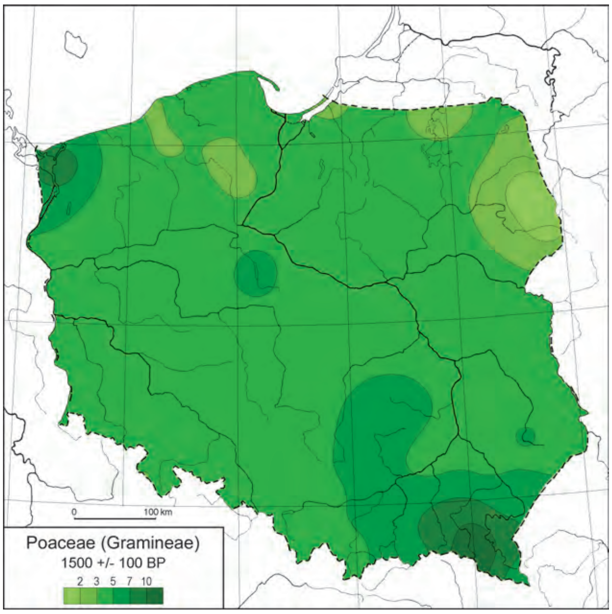
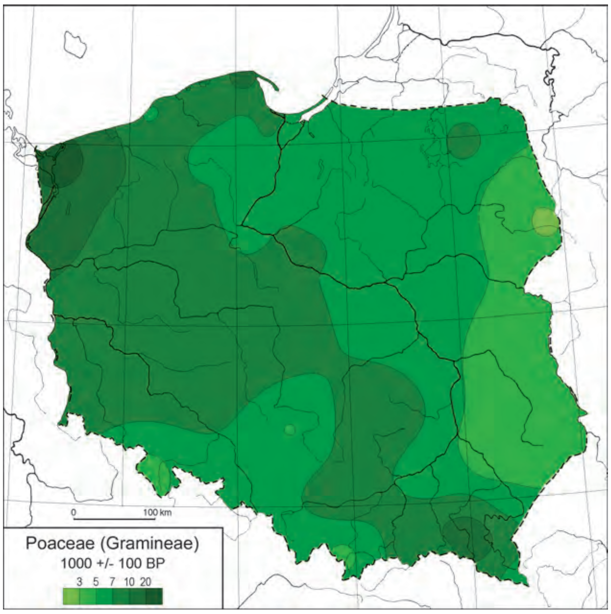
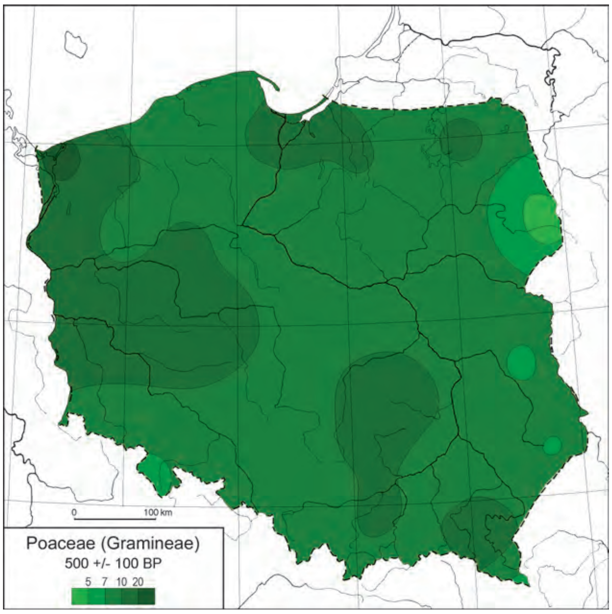
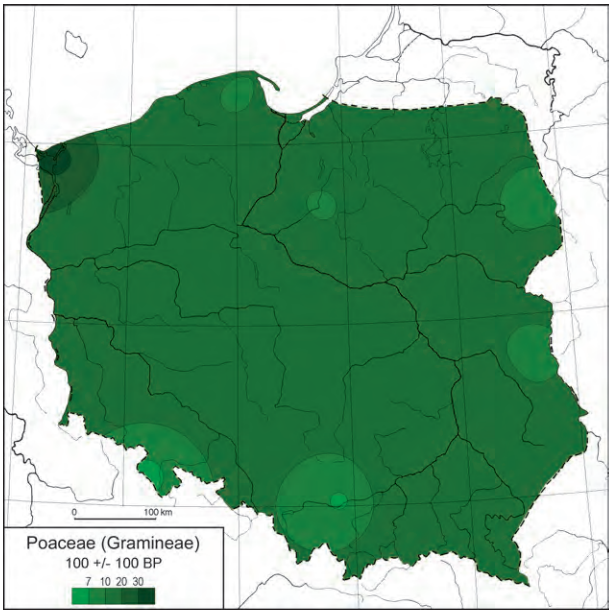
Poaceae (Gramineae)
2500 +/- 100 BP
2 3 5 7 10
0.01 0.2 0.5 0.7 1 2 3 5 7 10 20 30 40 60











🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩
0.01	0.2	0.5	0.7	1	2	3	5	7	10	20	30	40	60	

Pteridium aquilinum (L.) Kuhn – **Bracken**

JACEK MADEJA, KRYSTYNA BAŁAGA, KRYSTYNA HARMATA, AND DOROTA NALEPKA

PRESENT DISTRIBUTION IN POLAND, EUROPE AND IN THE WORLD

Pteridium aquilinum (L.) Kuhn is a cosmopolitan species occurring almost throughout the world, apart from the hot and cold deserts. *P. aquilinum* subsp. *aquilinum* occurs mainly in the Northern Hemisphere, whereas *P. aquilinum* subsp. *caudatum* in the southern one. In Europe bracken is absent from higher altitudes in the mountains, from the sub-Arctic and Arctic regions as well as from a part of the Mediterranean region (Hultén 1962, Meusel et al. 1964). The distribution map of *Pteridium aquilinum* in Poland (Zając A. & Zając M. 2001) shows that this is a common taxon almost throughout the country; it is absent only from the high mountains (Fig. 93).

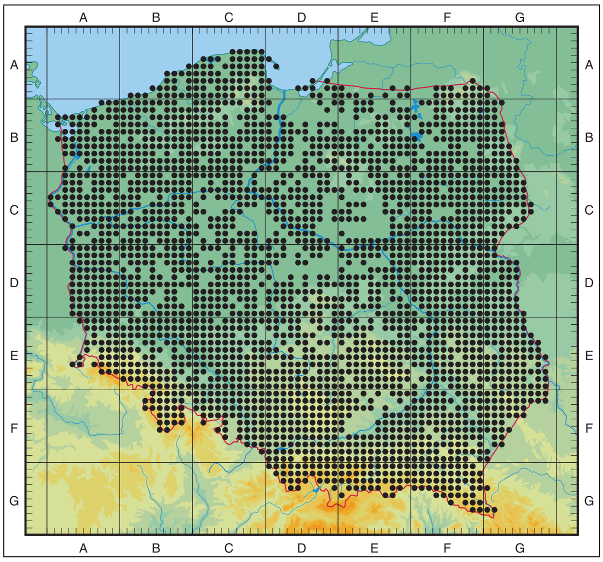


Fig. 93. Present-day distribution of *Pteridium aquilinum* (L.) Kuhn in Poland (after Zając A. & Zając M. 2001)

ECOLOGY

Pteridium aquilinum is a pioneer plant intolerant of shade. According to Emmingham (1972) bracken is an indicator of high light intensity. This author observed that at 60–100% of sunlight the density of bracken cover was 75% and it decreased to 50% when insolation was 25–60%, and when the insolation decreased below 25% of the full sunlight, *Pteridium* covered less than 5% of the area.

According to Zarzycki et al. (2002) bracken spreads on sandy and clayey-sandy soils, mineral-humic to organic, and poor to moderately poor soils. It avoids both shallow soils and rocky habitats as well as peat or fen soils, which are too wet for this taxon. It occurs in acid to moderately acid habitats.

The leaves of *Pteridium* are sensitive to frost. In the cold climate of northern areas they shrivel in winter, and the new leaves grow again in spring. Under temperate climatic conditions individual leaves can grow for 2–3 years and then they are replaced (Paysen et al. 1980). Dead leaves form a mat that protects rhizomes against frost, particularly when there is no snow cover. Early spring frosts occurring during the Late Glacial and the beginning of the Holocene may have been a factor restricting the occurrence of *Pteridium* (Huntley & Birks 1983).

Bracken is a species favoured by burning. After fire, because its rhizomes grow deep in the ground, this plant regenerates before other species appear to compete with it (Chapman & Crow 1981, Flinn & Pringle 1983, Stickney 1986, Taylor 1986). Fire contributes to acidification of the soil and such conditions facilitate germination of spores (Page 1986). That is why its young individuals appear abundantly on soil enriched by ash (Oberdorfer 1990).

Bracken reproduces mainly vegetatively. Rhizomes of *Pteridium* are well adapted for vegetative reproduction because of the numerous dormant buds along their surface. It is estimated that some of the clones may be several hundred or even more than one thousand years old (Oinonen 1967, Page 1986, Sheffield et al. 1989). Young plants are ready to produce spores in the second season of growth. However, they usually do not produce them before the third or fourth season (Conway 1957, Haeussler & Coates 1986). Generally, the number of young plants developing from spores is very low (Oinonen 1967, Stickney 1986).

Bracken is a plant that occupies disturbed or ecologically unstable areas (Frye 1956, Jackson 1981). It occurs in clearings and along the margins of forests. It encroaches on heaths and dried up mires and appears in cultivated fields. It is a species that competes efficiently for water and mineral nutrients with other vegetation. Its rhizomes grow beneath the roots of herbs or germinating seedlings, and when the leaves of *Pteridium* expand, they overshadow smaller plants. However, under certain conditions such overshadowing of young seedlings of trees may protect them by increasing their chances of survival. Marrs and Hicks (1986) have observed the efficiency of *Pinus sylvestris* in competition with abundant *Pteridium*, whereas Markowski (1971) and Rackham (1980) have recorded the restraining influence of expanses of bracken on the regeneration of pine. In wintertime dead leaves of *Pteridium* may press down other plants into the soil (Levy 1970, Crouch 1974, Hines & Land 1974). Its ability to form allelopathic phytotoxins is one of the important factors that fosters its domination over other plants (Gliessman & Muller 1972, 1978, Coffman et al. 1980, Brown 1986).

P. aquilinum is regarded as one of the plant resources exploited by humans. Its rhizomes and young shoots may have been used for consumption in Mesolithic times (Göransson 1986). In the Middle Ages, in some regions, *Pteridium* was used as a means of payment (Rymer 1976). Its leaves were also used for thatching roofs. In Wales it is still used as litter for animal bedding during wintertime (Frankland 1976).

SPORE PRODUCTION AND DISPERSAL

A single fertile leaf can produce about 300,000,000 spores per year (Conway 1952, 1957). However, in aerobiological samples from Warsaw, analysed during 1995 and 1996, only a few spores of *Pteridium* were found (Harmata, unpubl.). The production of spores, varying from year to year, depends on the age of plant, the stage of development of its leaves, weather conditions, and accessibility to light. The higher the degree of shade, the lower is the production of spores (Conway 1957).

EXPANSION IN EUROPE DURING THE LATE GLACIAL AND HOLOCENE

In pollen assemblages from European sites, dating from the Late Glacial and the beginning of the Holocene, spores of *Pteridium* occur sporadically and rarely exceed 1%. It is very likely that bracken survived at that time in local scattered sites of a refugial character, from which it expanded in northern and eastern directions at the beginning of the Holocene (Huntley & Birks 1983). Higher frequencies of spores appeared in south-western Europe at about 8500 BP. This could have been associated with amelioration of climate. At about 7000 BP it expanded around the Alps and, next, in the middle Holocene, it was already present across the major part of Europe. This process may have resulted from the gradual alteration of soils, for example the progressive accumulation of humus. Since 3000 BP, because of climatic cooling, and since 2500 BP because of increasing wetness of climate, as demonstrated by the growth of peat-bogs, the pollen diagrams record the disappearance of bracken from previously occupied sites, particularly in the north (Huntley & Birks 1983). Values of *Pteridium* spores do not exceed 1% during this period.

MIGRATION PATTERN IN POLAND (Fig. 94)

11,500 – 8500 BP

The dot maps for the Late Glacial since 11,500 BP and for early Holocene (10,000–9000 BP) record the presence of *P. aquilinum* in Poland at scattered sites, with spore values much lower than 1%. The 8500 BP map is the first one that shows sparse sites with higher values of bracken spores (up to 1.8%).

8000 – 7500 BP

On the 8000 BP map at some sites (Wolin Island, the Mazurian Lake District, Sandomierz Depression with Staszów District) these values exceed even 1%.

Some of the highest amounts of *P. aquilinum* recorded from Poland are found in the pollen diagrams from the Baltic Sea coast (Latałowa 1994), where, as at other sites, they are correlated with an increase in frequencies of charcoal and probably reflect the use of fire by the Mesolithic tribes. The other rises of *Pteridium* values on the 8000 BP map might have already had similar reasons. The isopollen maps show the lowest percentage values of *Pteridium* in the mountainous regions and in the north-eastern part of Poland. Regarding the mountainous regions, such a distribution can be explained by the plant's tendency to avoid shallow, rocky soils, while the reasons for lower values in the north-eastern part of Poland are less clear.

7000 – 5000 BP

This is a period of maximum spread of *Pteridium aquilinum* in Poland. All this time bracken occurs in irregular islands, the biggest ones appearing in central-north and south Poland (7000 BP map), and later also in north-west Poland (6500–5000 BP maps). They most probably originate from overgrowing by bracken local forest gaps burned out during the activities at first of Mesolithic, and next of Neolithic populations. As mentioned before, *Pteridium* expands effectively on soils enriched in ash, which highly improves its spore production (Latałowa 1992, Ralska-Jasiewiczowa & van Geel 1998).

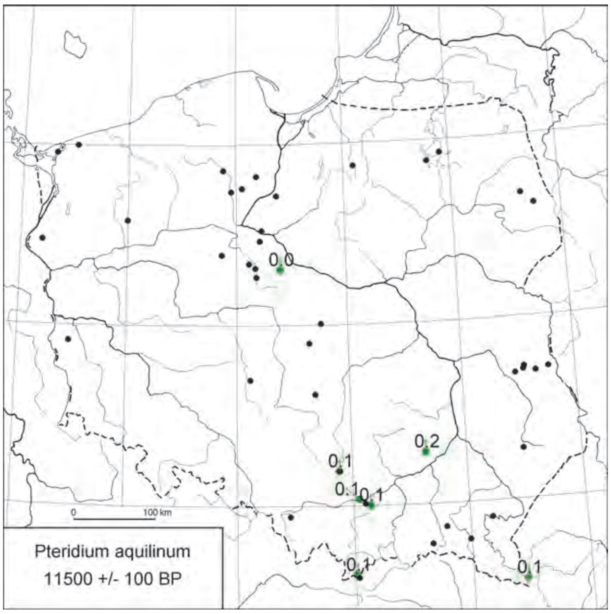
4500 – 100 BP

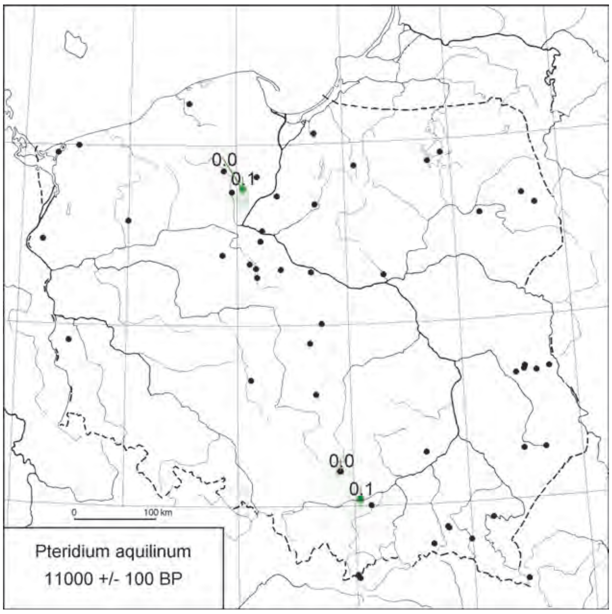
The amount of spores of *P. aquilinum* on the isopollen maps decreases rapidly after 4500 BP, and these low values have persisted up to the present time. This phenomenon must be related to economic changes, particularly to the way forests were managed. The analysis of individual pollen diagrams shows that, locally, *P. aquilinum* still played an important role accompanying the phases of settlement. This is proved for example by its high values in the diagram from Czajków at Staszów District (ca. 2000 BP, Szczepanek 1971a) as recorded on the isopollen map.

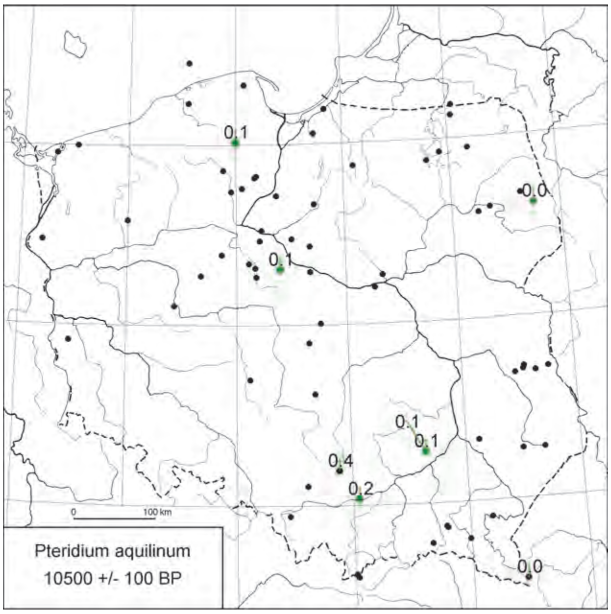
CONCLUSIONS

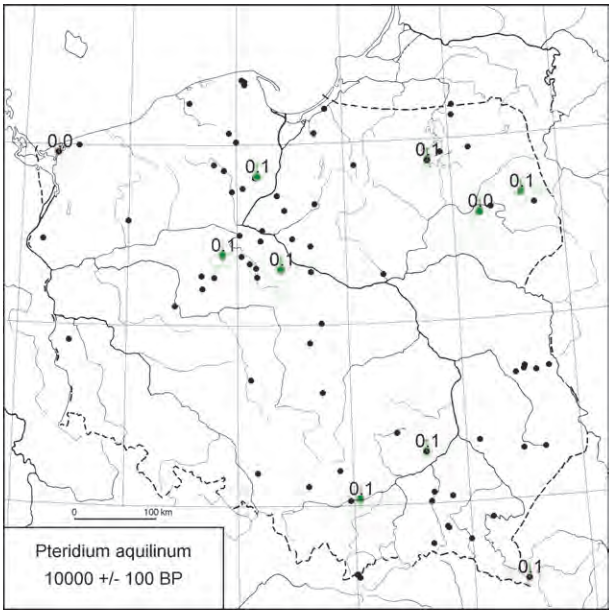
Spores of *Pteridium aquilinum* appear for the first time in the palynological record of the Late Glacial, but its expansion took place not earlier than the development of mixed oak forests. The period between 8000 and 5000 BP saw the optimum for the occurrence of bracken in Poland. At this time it was an important element of the mixed deciduous and pine forests that were utilised first by Mesolithic and then by Neolithic tribes. The decline in importance of *P. aquilinum* since 4500 BP may have been connected with the changing methods of forest exploitation, resulting in changes in the structure of forest communities and in the expansion of light-demanding species. The gradual reduction in the use of slash-and-burn methods may have been the basic factor in this decline. *P. aquilinum* belongs to those taxa which, because of their irregular pattern of occurrence in pollen diagrams (higher values most often form relatively short peaks associated with phases of settlement), are underrepresented on the isopollen maps.

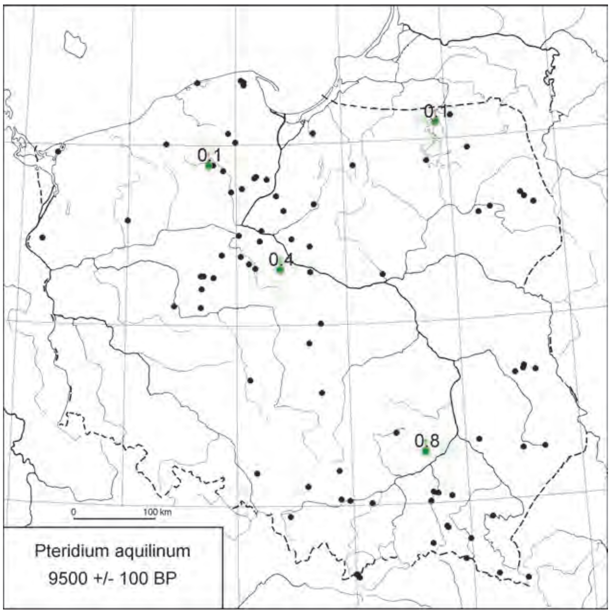
Fig. 94. *Pteridium aquilinum*: dot and isopollen maps for 11,500–100 ^{14}C yr BP

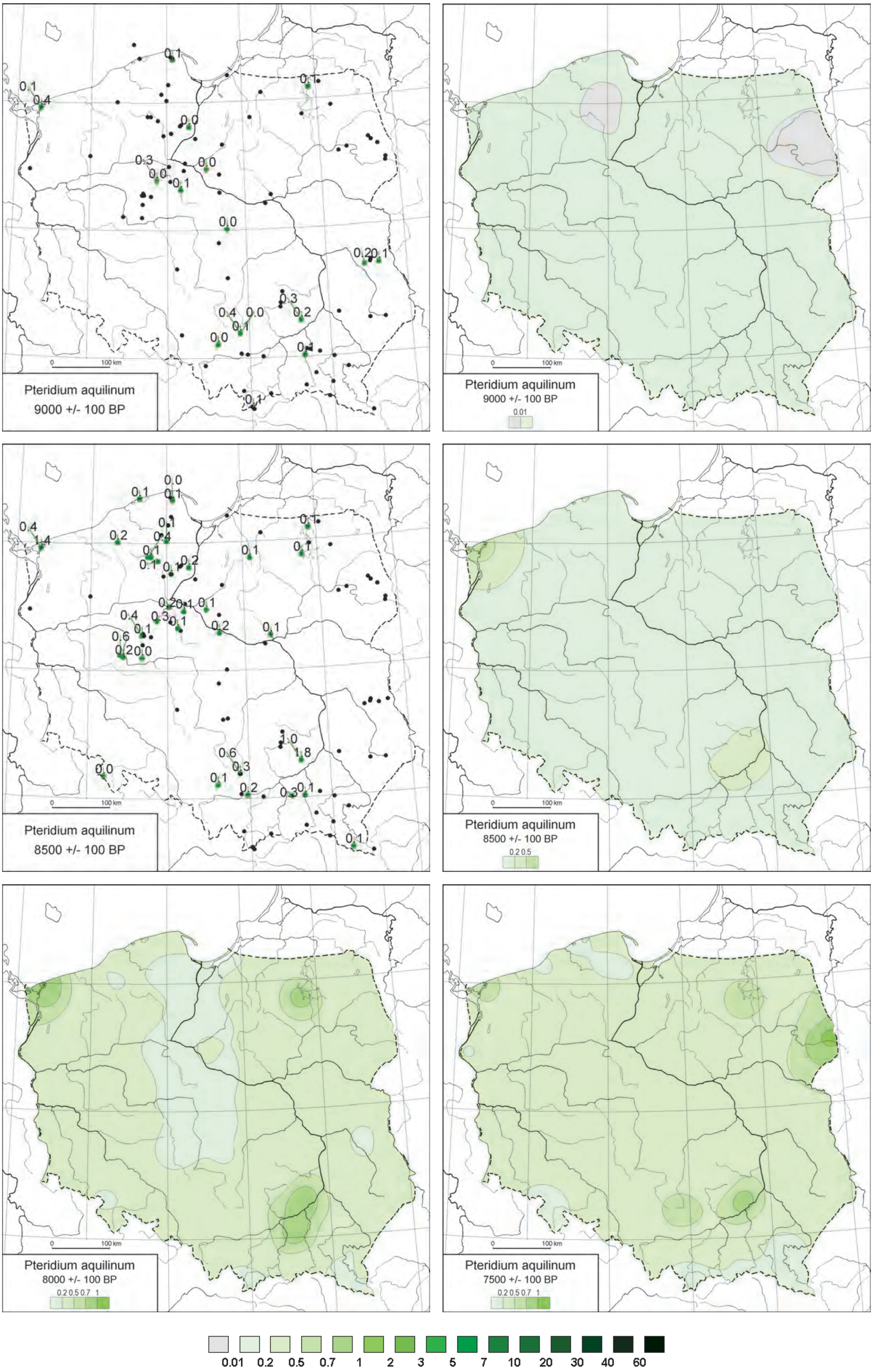

Pteridium aquilinum
11500 +/- 100 BP

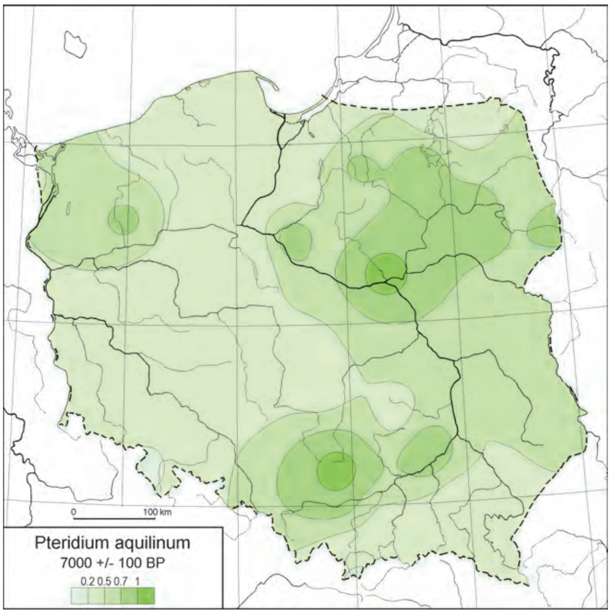

Pteridium aquilinum
11000 +/- 100 BP

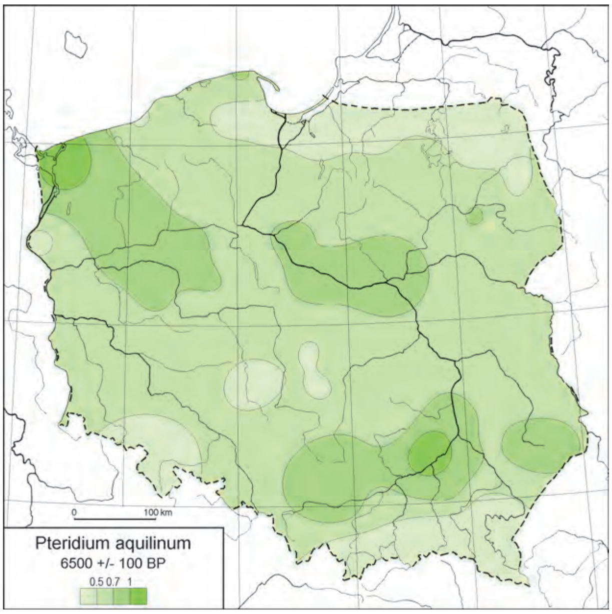

Pteridium aquilinum
10500 +/- 100 BP

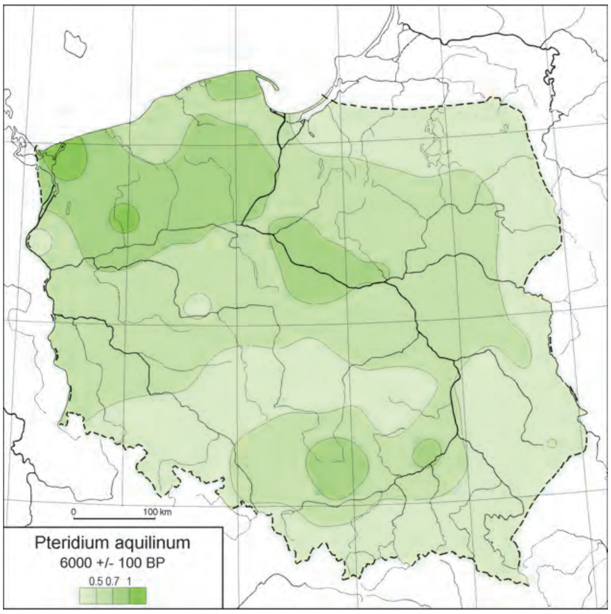

Pteridium aquilinum
10000 +/- 100 BP


Pteridium aquilinum
9500 +/- 100 BP


Pteridium aquilinum
9000 +/- 100 BP
0 100 km
Pteridium aquilinum
9000 +/- 100 BP
0.01
Pteridium aquilinum
8500 +/- 100 BP
Pteridium aquilinum
8500 +/- 100 BP
0.2 0.5
Pteridium aquilinum
8000 +/- 100 BP
0.2 0.5 0.7 1
Pteridium aquilinum
7500 +/- 100 BP
0.2 0.5 0.7 1
0.01 0.2 0.5 0.7 1 2 3 5 7 10 20 30 40 60


0
100 km
Pteridium aquilinum
7000 +/- 100 BP
0.2 0.5 0.7 1


0
100 km
Pteridium aquilinum
6500 +/- 100 BP
0.5 0.7 1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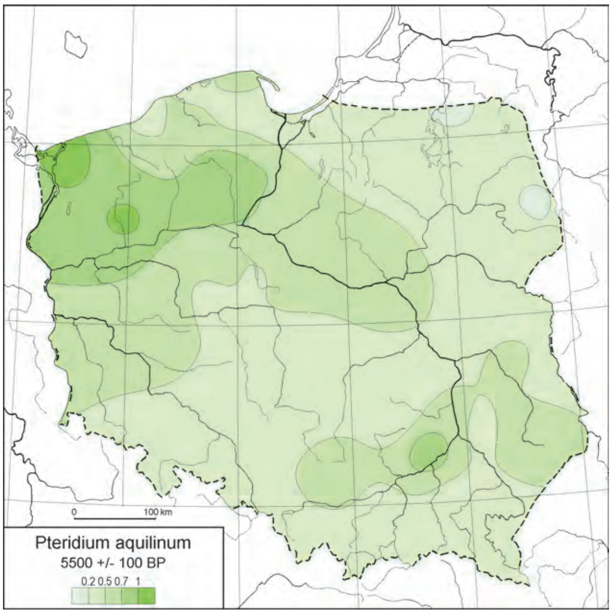
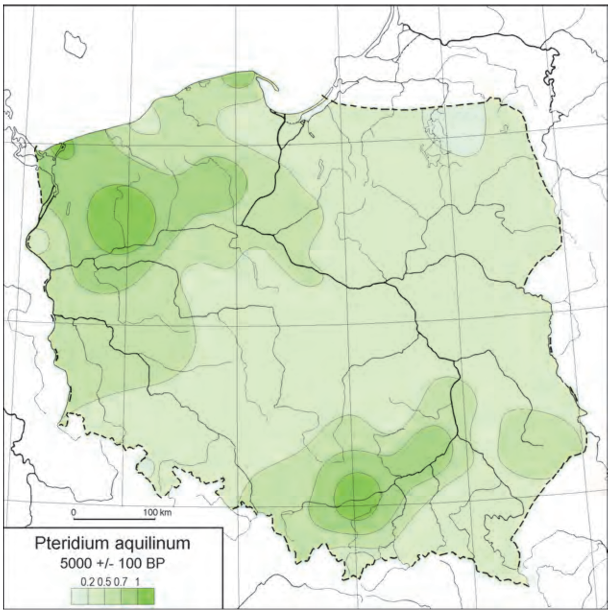
100 km
Pteridium aquilinum
6000 +/- 100 BP
0.5 0.7 1


0
100 km
Pteridium aquilinum
5500 +/- 100 BP
0.2 0.5 0.7 1


0
100 km
Pteridium aquilinum
5000 +/- 100 BP
0.2 0.5 0.7 1


0
100 km
Pteridium aquilinum
4500 +/- 100 BP
0.2 0.5


0.01
0.2
0.5
0.7
1
2
3
5
7
10
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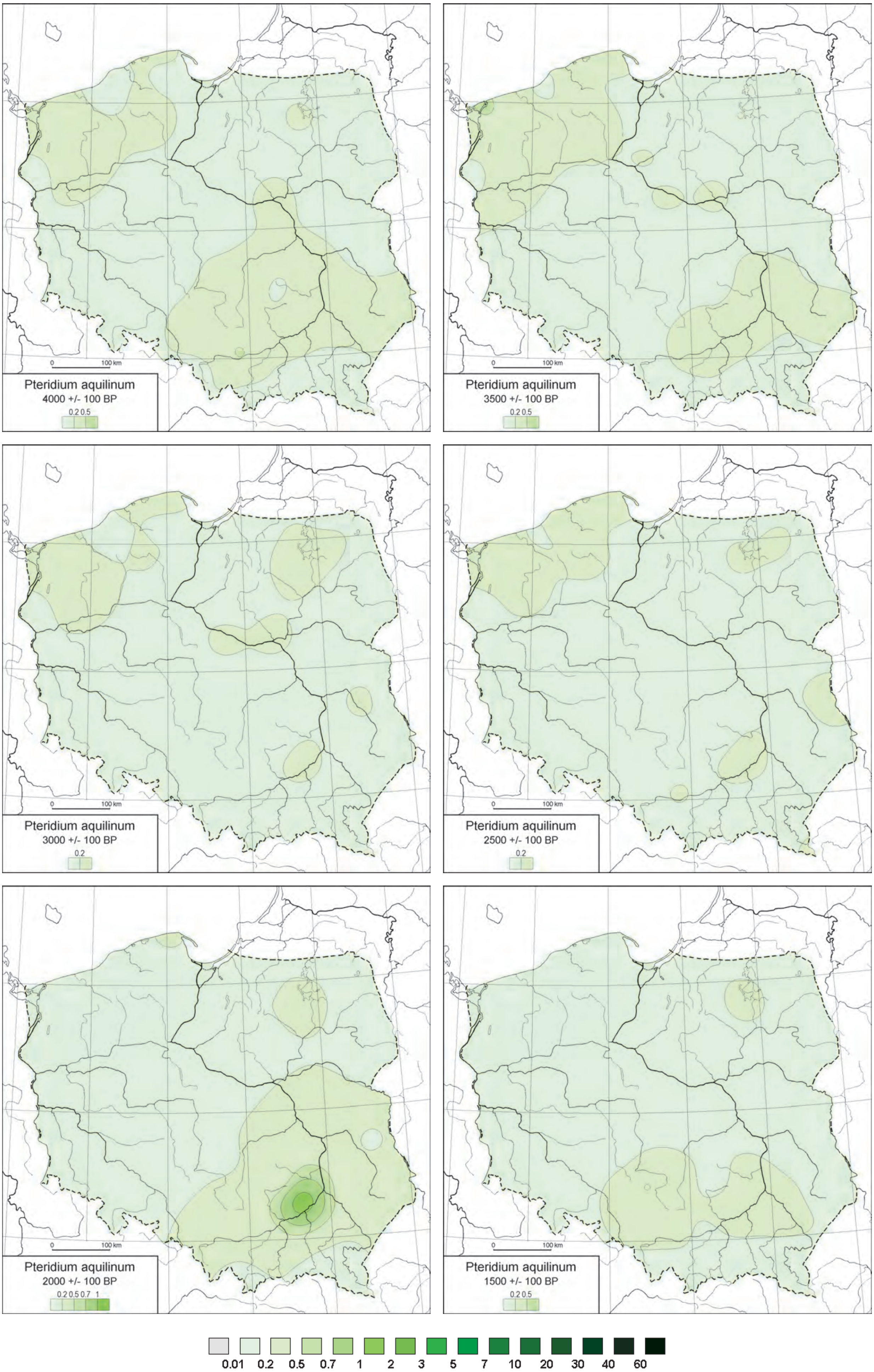
30
40
60


0 100 km
Pteridium aquilinum
4000 +/- 100 BP
0.2 0.5
Pteridium aquilinum
3500 +/- 100 BP
0.2 0.5
Pteridium aquilinum
3000 +/- 100 BP
0.2
Pteridium aquilinum
2500 +/- 100 BP
0.2
Pteridium aquilinum
2000 +/- 100 BP
0.2 0.5 0.7 1
Pteridium aquilinum
1500 +/- 100 BP
0.2 0.5
0.01 0.2 0.5 0.7 1 2 3 5 7 10 20 30 40 60

⬜	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	⬛
0.01	0.2	0.5	0.7	1	2	3	5	7	10	20	30	40	60

Rumex L. – Sorrels and docks

GRAŻYNA MIOTK-SZPIGANOWICZ, JOANNA ZACHOWICZ, KRYSTYNA HARMATA, JACEK MADEJA,
AND DOROTA NALEPKA

A small number of morphological types of *Rumex* pollen can be distinguished (van Leeuwen et al. 1988), but only a few palynologists try to determine these. Consequently, in the present paper, the data for all terrestrial *Rumex* species are treated together, the local *R. aquaticus* L. and *R. hydrolapathum* Hudson being excluded. It should be emphasized that *Rumex acetosella* L. and *R. acetosa* L., as well as a type including both species, are the most commonly distinguished *Rumex* types in pollen assemblages.

PRESENT DISTRIBUTION IN EUROPE

More than 40 species of *Rumex* are known from Europe (Hegi 1981). They grow in different habitats such as dunes, pastures, moorlands, meadows, forests, and watersides. They occur most commonly in open, unshaded communities and often on disturbed soils. Many species are common weeds or plants that grow in grazed and mown meadows or in cleared woodland. Some species, such as *R. acetosella*, most frequently prefer cultivated fields, others, for example *R. maritimus*, occupy moist habitats with oscillating water levels. Other taxa, such as *R. alpinu*s, which have high nitrogen requirements, are associated with anthropogenic ruderal associations of tall herbs (Zarzycki et al. 2002). Among the most common species are *Rumex acetosella*, occurring in the northern and temperate zones of Eurasia, and *R. acetosa*, occurring frequently from the Arctic areas and Greenland down into southern Eurasia.

PRESENT DISTRIBUTION IN POLAND

18 species of *Rumex*, including both sorrels (subgenus *Acetosa*) and docks (subgenus *Rumex*) growing in various habitats, occur in Poland (Mirek et al. 2002). For instance *Rumex aquaticus* and *R. hydrolapathum* grow in wet ditches and on river and pond banks, *R. sanguineus* and *R. obtusifolius* in shade and damp forests, whilst *R. confertus* occurs on dry slopes and riverbanks. Some of the dock species are widespread throughout Poland, for example *R. conglomeratus* and *R. crispus*, whilst the distribution of *R. palustris* and *R. maritimus* is restricted to the lowlands. *R. alpinus*, *R. alpestris*, and *R. scutatus* are restricted to mountain meadows and pastures rich in nitrogen or calcium carbonate. Turning to the common sorrels, *R. acetosa* occurs over the whole area up to the lower montane forest zone, and *R. acetosella*, associated with cultivated fields, fallow ground, sandy meadows and pastures, is found over the whole country up to the zone of dwarf mountain pine. These are the most widespread species of *Rumex* in Poland (Zając A. & Zając M. 2001).

ECOLOGY

Rumex acetosella is a hemicryptophyte characterized by considerable dispersal capacities. It occurs in sunny habitats, on dry, poor, strongly acid (pH 3.5–4.5) to acid (pH 4.5–5.5) soils, sandy-loamy and poor in humic compounds. According to Wójcik (1978) and Podbielkowski and Podbielkowska (1992) *R. acetosella* is an indicator species of acid soils. It is a typical species of dry, poor, and sandy grasslands of the order *Corynephoretalia*, growing also in dry pine forests and on heaths. It spreads in anthropogenic habitats such as: field banks, roadsides, fallow ground, and cultivated fields. It grows in fields of cereals, particularly of winter (autumn-sown) varieties, and in root crops (Wójcik 1978, Matuszkiewicz W. 2001, Zarzycki et al. 2002). It is an indicator of grazing on poor soils. A rise in its pollen curve often occurs simultaneously with the rising content of mineral matter in sediment, indicating erosion of sandy soils (Behre 1986).

Rumex acetosa is also a hemicryptophyte. Its dispersal capacity is reasonably efficient. It occurs in strongly insolated places, only temporarily shaded. It tolerates a wide range of soils from slightly moist to moist, from moderately acid to weakly acid (pH 5.5–6.5), from mineral-humic to peaty with a considerable amount of mineral particles, rich in nitrogen. It is associated with communities of mown, slightly moist or periodically wet meadows of the *Molinio-Arrhenatheretea* class and with pastures (Behre 1986, Zarzycki et al. 2002).

POLLEN PRODUCTION AND DISPERSAL

Rumex acetosella and *R. acetosa* are both wind-pollinated species (Danielsen 1970); however their pollen secretes sticky substances suggesting that wind-pollination in the sorrels may be a secondary phenomenon (Szafer & Wojtusiakowa 1969). According to Meeuse & Morris (1984) an inflorescence of *R. acetosa* may produce 400 million of pollen grains. A fall rate in air of *R. acetosa* pollen is 0.019 m/s and its production rate in relation to Gramineae (1) is 3.9 (Sugita et al. 1999). The period of *Rumex* pollen production starts at the end of May and lasts to the end of August or the beginning of September. Seasonal pollen concentration values show a marked negative correlation with the number of rainy days. The highest values occur during days of high mean temperature and low rainfall (Latałowa & Góra 1996, Aerobiologic Database, Gdańsk 1994–2002).

DISTRIBUTION IN EUROPE DURING THE LATE GLACIAL AND HOLOCENE

Rumex pollen values on the maps for the Late Glacial reach 1% in western Europe, from the south of Spain up to the north of Norway and in the Alps. The highest values have been recorded in the north-western part of the British Isles and in Fennoscandia. On the 9000 BP map, values >1% are confined to the Alps, the western part of the British Isles and the Arctic. At that time a new area with values >1% also appears in south-east Europe. The highest values within this area are found in the south-east (12%) and in the north (30%). Since 7000 BP values >1% have occurred only locally, apart from the higher values, exceeding even 10% and known from more numerous sites in Iceland, Greenland, Spitsbergen, and the north of Norway. By 5000 BP a renewed rise of *Rumex* pollen is seen in south-eastern Europe and in the Arctic, and, from 3000 BP, also in the south-western part of the British Isles. By 1000 BP high amounts of *Rumex* pollen occur in the majority of European lowland areas (Huntley & Birks 1983).

MIGRATION PATTERN IN POLAND (Fig. 95)

14,000 – 12,500 BP

Rumex pollen appears in small amounts in the oldest deposits, particularly in the Mazurian Lake Districts (0.1–0.6%), and in Kujawy (0.3, 0.4%). The highest values have been recorded at 12,500 BP from the Małopolska Upland (1.2 to 2.1%).

12,000 – 10,500 BP

The number of sites with *Rumex* pollen present increase. They are situated throughout Poland. In general, *Rumex* pollen values rarely exceed 0.5%. However, on the 12,000 BP map a small *Rumex* centre reaching above 1% appears in the western corner of Sandomierz Depression. At about 10,500 BP, in north-west Poland, a centre of considerably higher values (1.4–2.3%) developed in Pomerania. This area saw the most significant regression of forest communities during the Younger Dryas.

10,000 – 5500 BP

At this time, species of *Rumex* were not very significant in the vegetation of Poland. Most likely they did not find suitable habitats for their growth due to the development of forest communities, since most species prefer sunny, unshaded habitats. Values exceeding 1% appear only on the 7500–6000 BP maps in the Małopolska area (Wolbrom). Values of *Rumex* pollen in north-east Poland (Lake Maliszewskie) exceeding 1% on the 5500 BP map may result from contamination of the sediments (Balwierz & Żurek 1987).

5000 – 4500 BP

Rumex still occurs in small quantity (<0.5%) throughout Poland. On the 5000 BP isopollen map a local area in south-east Poland with values exceeding 1% appears in the Sandomierz Depression. It may be connected with an increase in the intensity of human settlement in that area. An almost insignificant rise in *Rumex* values, probably linked to the development of human settlement, is also observed on both maps in north-west Poland, in the uplands of south Poland, and in the Sandomierz Depression.

4000 – 2000 BP

Since 4000 BP a distinct rise in significant pollen values of *Rumex* has been observed, particularly in north-west Poland. A similar phenomenon can be observed in pollen diagrams from north-east Germany (Jahns 2000, 2001). At the end of this period, *Rumex* values are close to or slightly exceeding 1% over almost the entire area of Poland, apart from the mountains and the eastern part of the country. An increase in *Rumex* pollen values is connected with the development of settlements and increased deforestation.

1500 BP

This isopollen map reflects a distinct regression of *Rumex* as a result of the regeneration of forest communities during the Migration Period. Pollen values of this genus remained higher only in central Poland, in Wielkopolska, Kujawy, the central part of the lake districts and in Małopolska. The extent of these areas coincides with the regions where, at present, plants associated with human activities and disturbance of the landscape have almost entirely replaced the natural vegetation. In those territories degradation of habitats due to human activity is most pronounced (Kozłowski 1994).

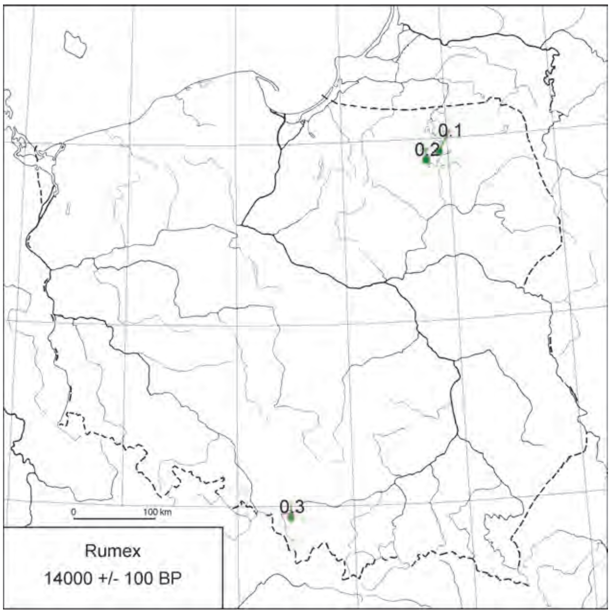
1000 – 100 BP

This period saw very intensive *Rumex* re-expansion across the whole area of Poland. At 1000 BP, the lowest *Rumex* values were observed in south-east Poland, while the highest were in Wielkopolska. It may be assumed that the distribution of docks and sorrels in Wielkopolska was connected with the intensive Mediaeval settlements at the time of the founding of the Polish State. At present, *Rumex* values of 5–7% occur throughout Poland, and locally they have reached 10% as a result both of progressive deforestation and of widespread acidification of habitats.

CONCLUSIONS

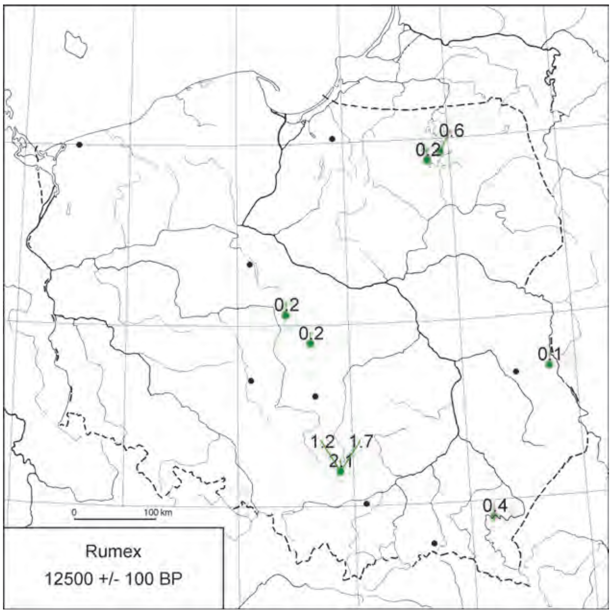
Spread of the genus *Rumex* in the Late Glacial was possible due to the presence of open and sandy habitats. In the early Holocene, as forest communities developed, there was a decline in significance of the representatives of this genus. Local, short-lived spread of *Rumex* during the younger part of Holocene resulted probably from intensification of human agriculture and pastoralism. The Holocene expansion of species of this genus, particularly of *R. acetosella*, in the area of Poland began at about 4000 BP and displayed a gradual extension of its range up to the time of the Migration Period (the 1500 BP map). Acceleration of this process has increased during the last millennium.

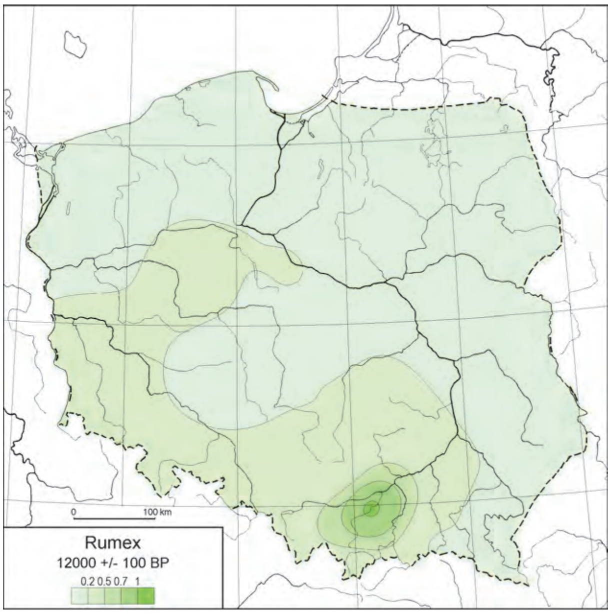
Fig. 95. *Rumex*: dot and isopollen maps for 14,000–100 ^{14}C yr BP


0.1
0.2
0.3
0
100 km
Rumex
14000 +/- 100 BP


0.2
0
100 km
Rumex
13500 +/- 100 BP


0.4
0.2
0.1
0
100 km
Rumex
13000 +/- 100 BP


0.6
0.2
0.2
0.2
0.1
1.2
1.7
2.1
0.4
0
100 km
Rumex
12500 +/- 100 BP


0
100 km
Rumex
12000 +/- 100 BP
0.2 0.5 0.7 1


0
100 km
Rumex
11500 +/- 100 BP
0.01 0.2


0.01
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1
2
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5
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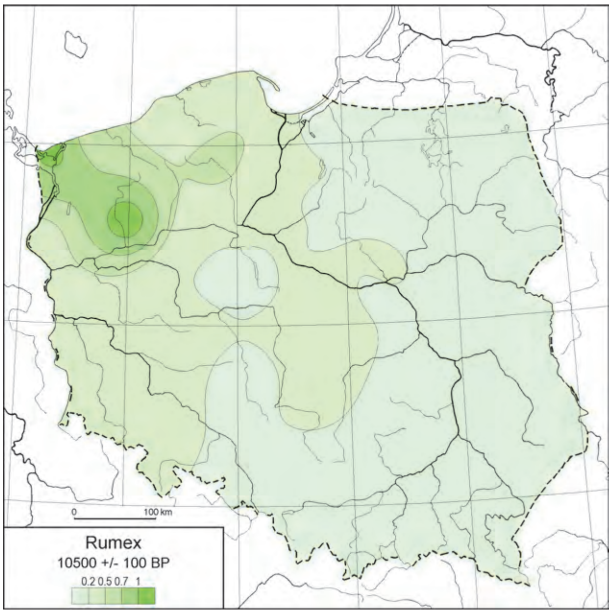
10
20
30
40
60



⬜ 0.01 🟩 0.2 🟩 0.5 🟩 0.7 🟩 1 🟩 2 🟩 3 🟩 5 🟩 7 🟩 10 🟩 20 🟩 30 🟩 40 ⬛ 60


0
100 km
Rumex
8000 +/- 100 BP
0.2


0
100 km
Rumex
7500 +/- 100 BP
0.2 0.5 0.7


0
100 km
Rumex
7000 +/- 100 BP
0.2 0.5 0.7


0
100 km
Rumex
6500 +/- 100 BP
0.2 0.5 0.7 1


0
100 km
Rumex
6000 +/- 100 BP
0.2 0.5 0.7 1


0
100 km
Rumex
5500 +/- 100 BP
0.2 0.5 0.7 1


0.01
0.2
0.5
0.7
1
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7
10
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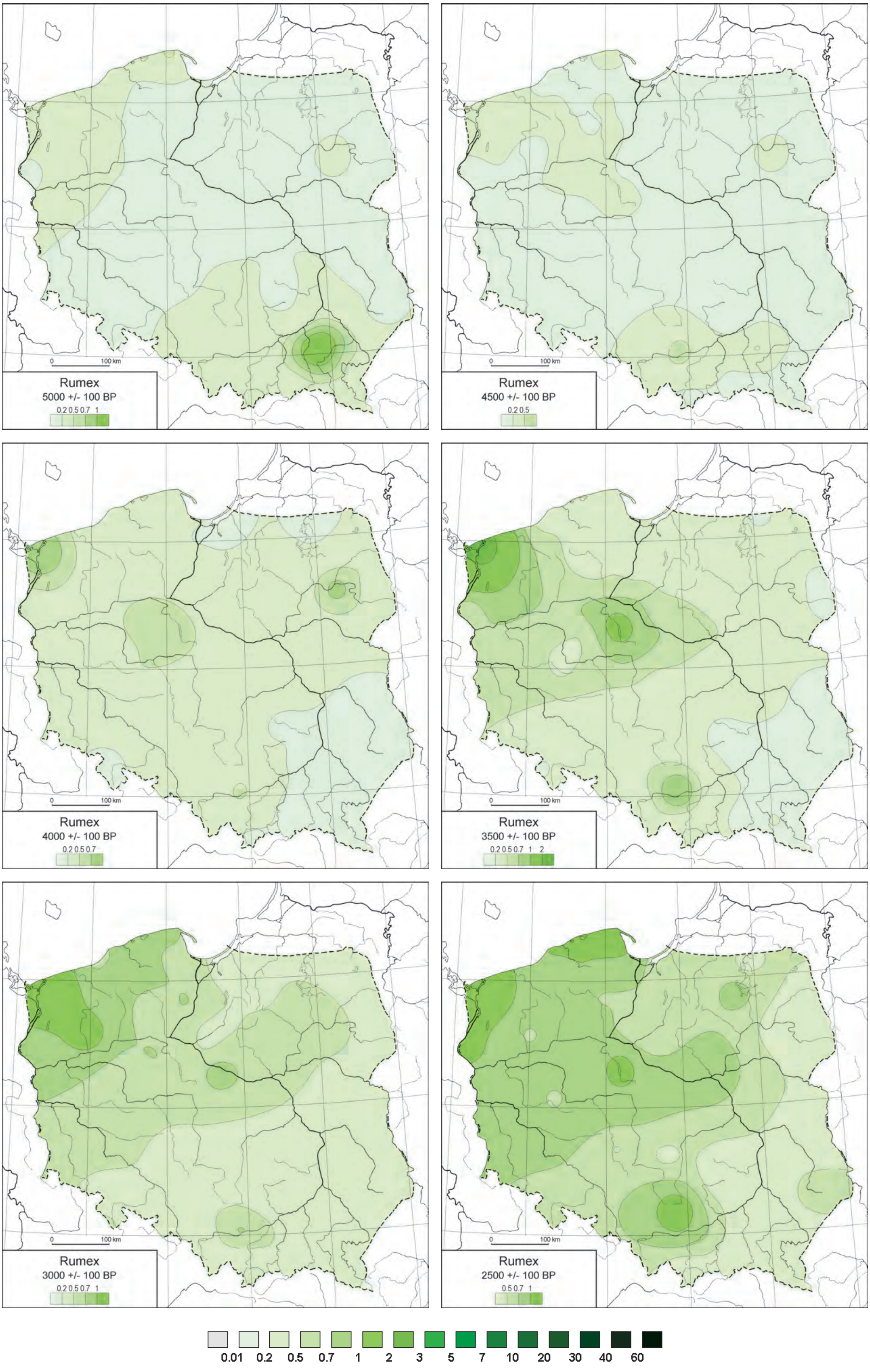
30
40
60


0
100 km
Rumex
5000 +/- 100 BP
0.2 0.5 0.7 1
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Rumex
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Rumex
4000 +/- 100 BP
0.2 0.5 0.7
0
100 km
Rumex
3500 +/- 100 BP
0.2 0.5 0.7 1 2
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100 km
Rumex
3000 +/- 100 BP
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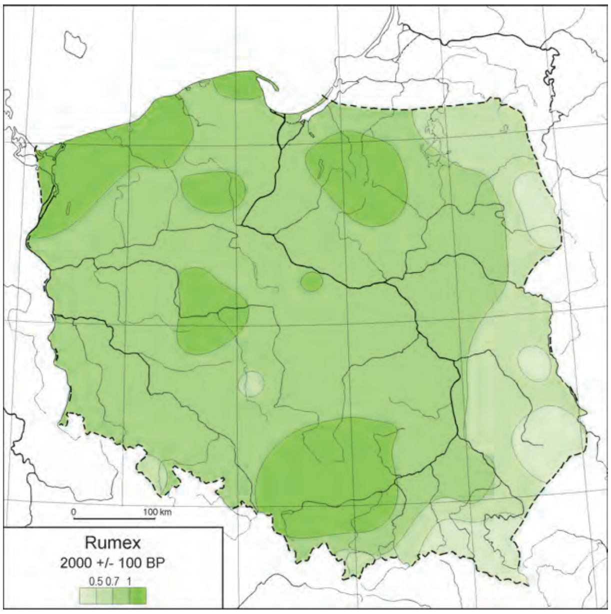
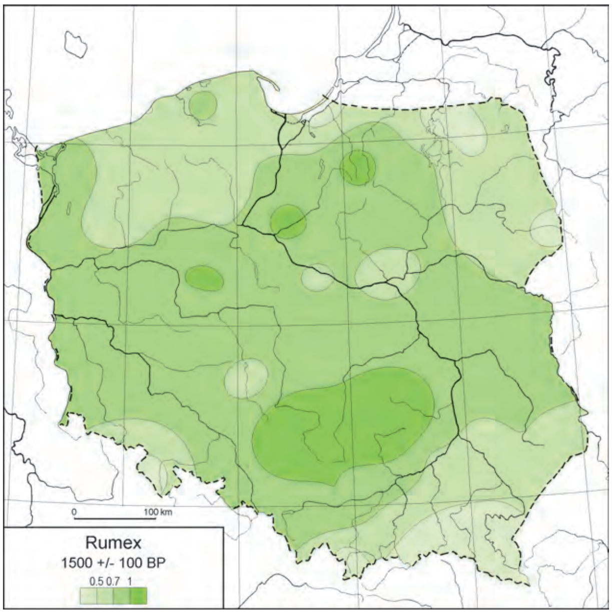
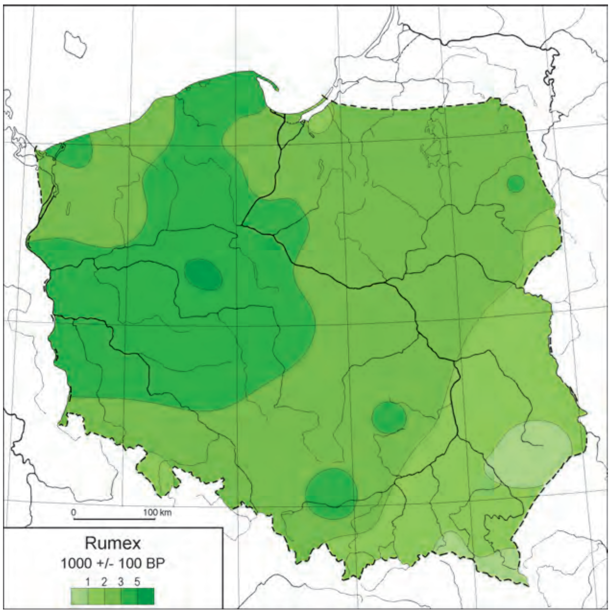
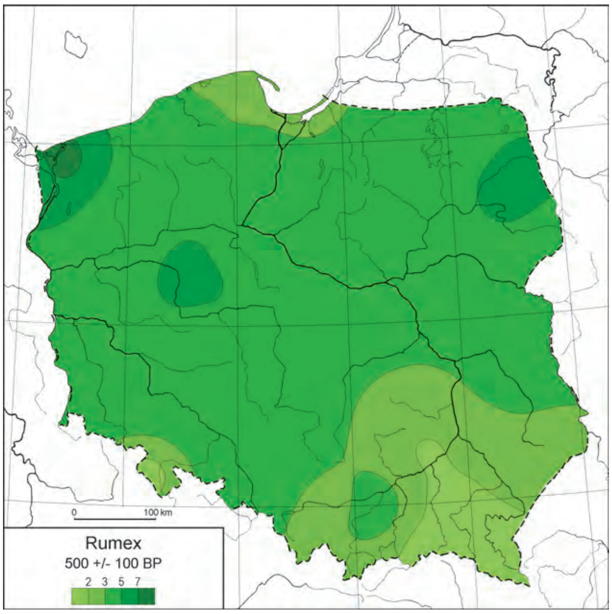
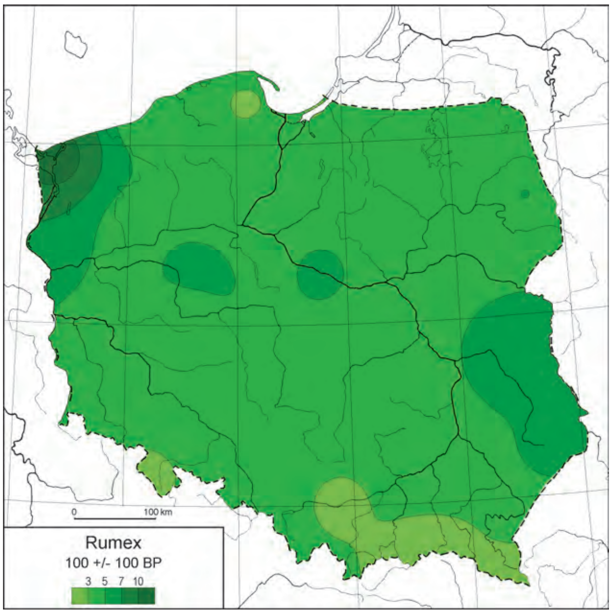










0.01 0.2 0.5 0.7 1 2 3 5 7 10 20 30 40 60

Secale cereale L. – **Rye**

IWONA OKUNIEWSKA-NOWACZYK, KRYSTYNA MILECKA, MIROSŁAW MAKOHONIENKO,
KRYSTYNA HARMATA, JACEK MADEJA, AND DOROTA NALEPKA

The genus *Secale* comprises several species of annual, biennial and perennial plants. *Secale cereale* L. – rye is regarded, by the majority of taxonomists, as an aggregate species encompassing several annual, allogamous (out-pollinating) subspecies that can interbreed giving fertile hybrids (Lityńska-Zając & Wasylikowa, in press). These forms have been described as separate species, and at present they are still often treated in this way. Within the aggregate biological species *Secale cereale* belong: 1. cultivated common rye *Secale cereale* L. subsp. *cereale*, 2. abundant forms of wild rye, growing within cultivated cereals as obligatory or facultative weeds, for instance *S. segetale* (Zhuk.) Roshev., *S. afghanicum* (Vav.) Roshev., which occur in the Middle East and in the Balkans, and 3. two forms of wild rye *S. ancestrale* (Zhuk.) Zhuk., discovered in Turkey and *S. vavilovii* Grossh., occurring in Armenia and in eastern Turkey. However, it is most likely that *S. ancestrale* is a secondary form that originated from cultivated rye (Zohary & Hopf 2000, after Lityńska-Zając & Wasylikowa, in press). Fodder rye, *Secale montanum* Guss., should be mentioned among other species of *Secale*, which may have contributed to the origin of cultivated rye. In its native localities it occurs in communities of a steppe character in the mountainous areas of the Mediterranean countries and in the Middle East as far north as the Caucasus and Iran. It is a perennial, allogamous form, crossing with *S. cereale* to give partially fertile hybrids. *S. sylvestre* is the second wild species, which occurs in south-eastern Europe. It is an annual rye, growing on sandy soils.

PRESENT DISTRIBUTION IN EUROPE

Rye is cultivated in 50 countries of the world but is largely limited to Europe (according to FAO Yearbooks, after Grzebisz & Szramka 1998), where it is concentrated mainly in the central, eastern and northern parts. These are the western areas of the former Soviet Union, Poland, Germany and the mountainous regions of eastern and southern Europe. According to the statistical data about 94% of all the world’s rye production comes from the European continent (Herse 1976). Since the 1960s its role in cereal cultivation has gradually declined.

PRESENT DISTRIBUTION IN POLAND

In Poland, according to Herse (1976), of all cultivated plants *Secale cereale* covers the most extensive area of arable land – Podbielkowski (1992) suggest 25% of all arable land there. The second cultivated species is fodder rye (*Secale montanum*), but its importance is insignificant.

ECOLOGY

The majority of wild species of rye are the xerothermic perennial plants occupying dry, well-insolated, rocky slope habitats, whilst the wild annual varieties occur mainly on sands and on other light soils. The ecological requirements of this cereal, lower than those of wheat or even barley, favour its cultivation mainly in the cool temperate zone. Rye is resistant to winter frosts, and it can withstand a severe mountain climate. This cereal needs daily temperatures higher than 10°C for just 3.5 months, whereas wheat requires as long as 6 months (Nowiński 1970). *Secale cereale* is a winter or spring grass. According to Herse (1976) the growth period from germination to the full maturity lasts 295–300 days in Poland; Nowiński (1957) suggests about 280–320 days for winter crops, but 110–140 days for spring crops. Rye is a long-day plant, with characteristics similar to those of xerophilous plants. It flowers at the end of May and the beginning of June (Falkowski 1982). *Secale* tolerates lower temperatures compared to the other species of winter cereals, and it can already germinate at a temperature of 1–2°C. It usually germinates in the autumn. It tolerates winters without snow with temperatures down to –25°C (Falkowski 1982) or even down to –35°C (Herse 1976). It is the most tolerant of low temperatures in comparison with other winter cereals. Much more dangerous for rye are winters with moderately low temperatures but with thick and long-lasting snow cover and thaws with renewed snow falls following them (Herse 1976). It also shows a considerable sensitivity to changes in the weather during flowering. Seed setting is much lower if it is cold and rainy during the flowering period, but again, too high a temperature during flowering and the ripening of its seeds diminishes the grain yield (Herse 1976). On dry soils and under cold conditions *Secale cereale* seeds may remain viable for up to 10 years (Podbielkowski 1995). Rye can be grown on a variety of soil types; it tolerates light, less fertile and even acid soils (Nowiński 1970). Falkowski (1982) quotes values of soil pH for rye from 4.5 to 6.0. Rye, in comparison with other cereals, has a well developed, fine root system and can send down roots to a depth of 120 (250) cm, but 60% of the root system reaches a depth of 25 cm (Falkowski 1982). Such a root structure enables water and nutrients to be garnered from deeper less exploited layers. This feature favours rye cultivation on light, sandy, permeable soils with a poor water retention capacity. It enables rye to withstand even conditions of longish periods of drought (Herse 1976). Rye is much less demanding and more resistant than wheat. Repeated sowing of the same mixture of wheat and rye, in a proportion of 1:1, results in the growth of almost pure crops of rye after a period of a few years (Nowiński 1970).

POLLEN PRODUCTION AND DISPERSAL

Cultivated rye starts to flower 7–12 days after development of the flowering spike. Pollen is shed from the anthers successively as the spikelets mature. This process begins before the full protrusion of the anthers, and, later, the stamens, opening in succession, impact on one another, stimulating the dispersal of pollen. A special structural adaptation of the stamens in rye prevents its pollen falling to the ground; the end of the mature anther rolls up, and pollen can be trapped and dispersed by the wind (Piotrowska 1999). Rye is an allogamous, wind pollinated plant, and produces large numbers of pollen grains – up to 6000 in each flower (Herse 1976) or even 19,000 and 13,200 grains per anther according to other authors (Pohl 1937, Agnihorti & Singh 1975, after Subba Reddi & Reddi 1986). During flowering clouds of rye pollen, consisting of millions of grains released from the relatively large anthers, float over the cereal fields (Szafer & Wojtusiakowa 1969). The period of flowering lasts 8 to 10 days but it may be longer when atmospheric conditions are unfavourable. Such a situation may also result in distorted caryopses and irregular ripening. Both kinds of weather, hot and dry as well as cold, with significant amounts of rain, are unfavourable for pollination. Then, a considerable number of flowers may be left unpollinated. Self-pollination does not usually lead to fertilisation. If that happens, a distinctly smaller grain with much lower viability may exceptionally be formed (Herse 1976).

EXPANSION IN EUROPE DURING THE HOLOCENE

The oldest finds of cultivated rye from the Early Neolithic Period were discovered in Anatolia (Behre 1992). Most likely it was a weed within the wheat and barley crops. During harvesting it was gathered together with corn and then sown together with it. At this stage unconscious selection happened favouring rye mutants with spikelets no longer disarticulating from the rachis. This led to the development of 'weed-rye' displaying features of the domesticated cereal, though it was still essentially a weed and not yet cultivated as a separate crop. As agriculture moved into areas, where climatic conditions were less favourable for wheat and barley, the amount of rye in crops gradually increased. Because of this process rye has become a separately cultivated cereal. Winter rye was probably derived from a form that was a weed of winter wheat and barley. The less frequently cultivated spring rye may have originated from a weed-rye growing in fields of spring wheat and barley. From evidence of caryopses dated by the AMS (accelerator) method it is believed that since about 11,000–10,500 BP varieties of rye displaying features of domestication have appeared in the Middle East. They may have migrated from there to Europe through the Balkan Peninsula (Behre 1992) during Neolithic times.

In Europe, the presence of rye in the Neolithic has been documented rarely in sites from Germany, Austria, Czech Republic, Ukraine, and from Poland. More numerous European sites with rye macrofossils (from Ukraine, Moldavia, south Germany, Austria, Czech Republic, and Slovakia) are assigned to the Bronze Age. In pollen diagrams, rye appears sporadically in profiles corresponding to the Neolithic and Bronze Age in various parts of Europe. During the Hallstatt Period the number of sites with macroscopic remains of rye increased, but it still formed only a minor component with other cereals (Lityńska-Zając & Wasylikowa, in press). Only at a few sites in Germany is it proposed that rye was cultivated separately. Quite considerable amounts have been found at a few Scythian sites from the period 2600–2500 BP, reflecting its cultivation in the Ukraine (Yanushevich 1986, after Lityńska-Zając & Wasylikowa, in press). According to Behre (1992) a centre of early cultivation of rye existed around the Black Sea. A considerable increase of sites number, where rye was present, occurred in Europe in pre-Roman time (La Tène, from about the turn of the 5th to 4th century BP).

Roman times (from ca. 2000 BP) saw the spread of rye cultivation across the whole of Europe, its remains occurring either as an admixture with other cereals or as concentrations simply of rye, indicating deliberate cultivation. A further extension of rye cultivation took place in the Scandinavian countries during the Migration Period and over the whole of Europe in the Early Middle Ages (Lityńska-Zając & Wasylikowa, in press). The exceptions were the Mediterranean countries where rye cultivation has always been of minor importance because of unfavourable climatic conditions. Numerous pollen diagrams and finds of macroscopic remains from the Middle Ages demonstrate the increasing economic importance of rye (Behre 1992). It was cultivated both by the Germans and Slavs, though in earlier papers *Secale* was considered to be a Slavonic or even pre-Slavonic cereal. The Celts and particularly the Germans, conquering the Slavonic territories, were said to have adopted it from the Slavs (Becker-Dilingen 1927, after Nowiński 1970). According to Behre (1992) the distribution of rye was influenced more by natural conditions favouring its cultivation than by any ethnic factor.

SPREAD OF *SECALE CEREALE* CULTIVATION IN POLAND (Fig. 96)

Finds of macrofossils, particularly those from archaeological sites, have provided a lot of information about the occurrence of rye. The isopollen maps present the data for the selected time levels only. Rye appeared in Poland probably as a weed of wheat. Its presence in the southern part of the country has been recorded in association with the Neolithic Linear Pottery and Radial Pottery cultures (Giżbert 1958). It is not known whether rye was already cultivated at that time, but it is assumed that some attempts were made to exploit it (Nowiński 1970).

5500 – 3000 BP

The dot map showing the oldest finds of *Secale* has been drawn for the 5500 BP time level. Pollen grains of rye have been found at only four sites. On the maps from 4500 BP the number of sites with the finds of rye increases, however, the investigations do not cover the whole country evenly thus it is difficult to discuss its migration patterns. The 3000 BP map shows the highest amounts of *Secale* pollen in the Małopolska Upland and in the area of the Świętokrzyskie Mountains.

2500 – 1500 BP

Slightly higher values of rye pollen appear in pollen assemblages at about 2500 BP, but their really significant rise takes place not earlier than 2000 BP. In Poland relatively high amounts of charred rye grains have been recorded from the Roman Period (Moldenhaver 1959, Giżbert 1960, Klichowska 1975, Lityńska-Zając 1997). The 2000 BP time horizon illustrates the beginning of real rye cultivation during the period of Roman influence, though *Secale* pollen percentage values in the diagrams are still not very high. This level, as well as the next one for 1500 BP, does not cover the period of most intensive economic activity at this stage of human settlement. According to Lityńska-Zając (1997, 1999) rye was connected with different cultures in different parts of the country. To record basic changes in cereal cultivation it would be necessary to draw maps at a time interval of 200 years.

1000 – 100 BP

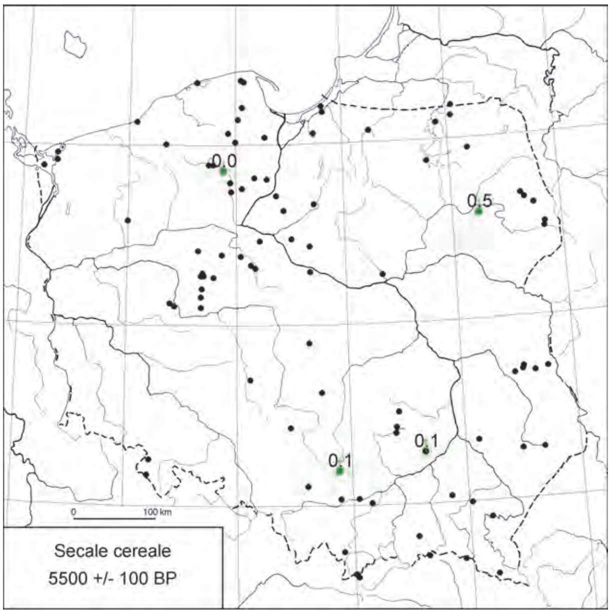
The 1000 BP map illustrates a distinct rise in rye pollen percentage values almost across the whole country, with the highest values in the Małopolska Upland (>3%) and with the lowest amounts in south-eastern Poland. Winter cereals, particularly rye, were known to the Slav peoples already in the 10th century. At first this cereal was common only along the western boundary of Poland and from this area its cultivation spread eastwards. In the second half of the 10th century cultivation of rye was already widespread (Godłowski 1960, after Nowiński 1970).

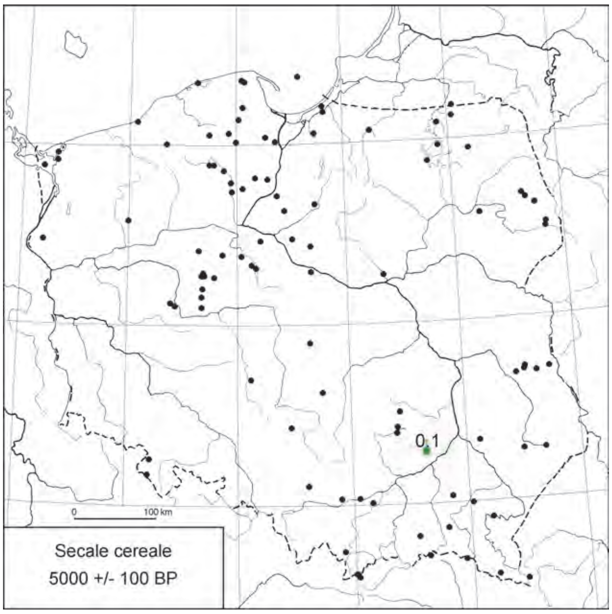
The 500 BP map indicates a further increase in the frequency of rye pollen particularly in the lowland areas of central Poland, apart from the higher values in the Małopolska Upland. The lower values are recorded in the marginal areas. The present-day map shows high *Secale* percentage pollen values for the whole country, locally reaching over 5%.

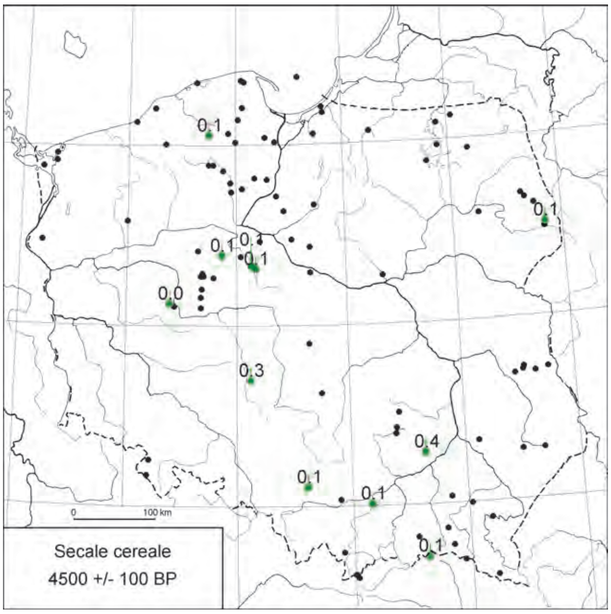
CONCLUSIONS

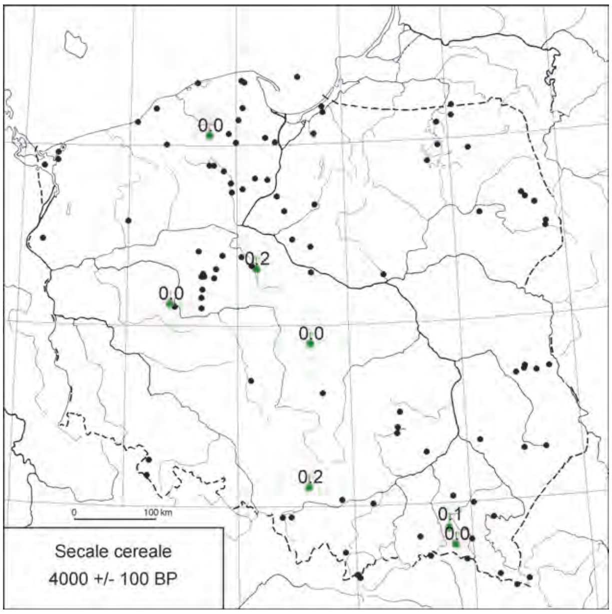
The isopollen maps reflecting the amount of *Secale* in the pollen spectra for the period of 5500–2500 BP demonstrate a low presence of rye in the Polish territories during the Neolithic and Bronze Age. Since the Roman Period rye has been cultivated on a larger scale in the areas that have become the Polish state. The isopollen maps for the last 1000 years show an increased amount of *Secale* in pollen assemblages and a gradual extension of the acreage of rye cultivation. However, it is not possible to describe the direction of spread and increase in the economic use of rye on the basis of its variable percentage values. To trace changes in the economic exploitation of cereal crops, it would be necessary to construct maps with a 200-year time resolution.

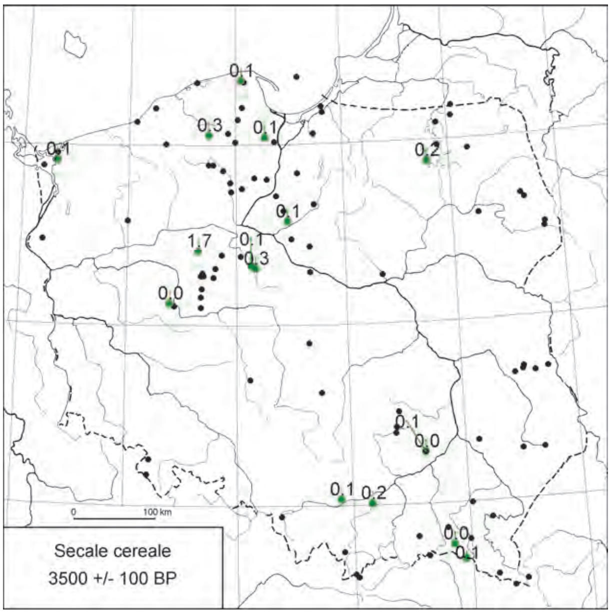
Fig. 96. *Secale cereale*: dot and isopollen maps for 5500–100 ^{14}C yr BP

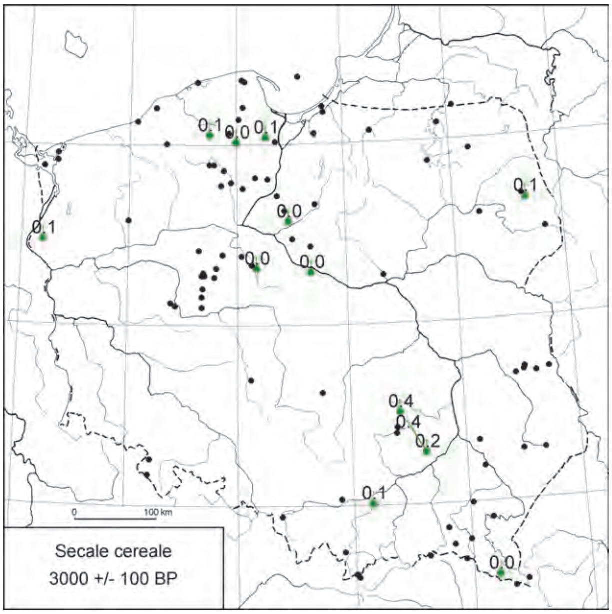

0.0
0.5
0.1
0.1
0
100 km
Secale cereale
5500 +/- 100 BP

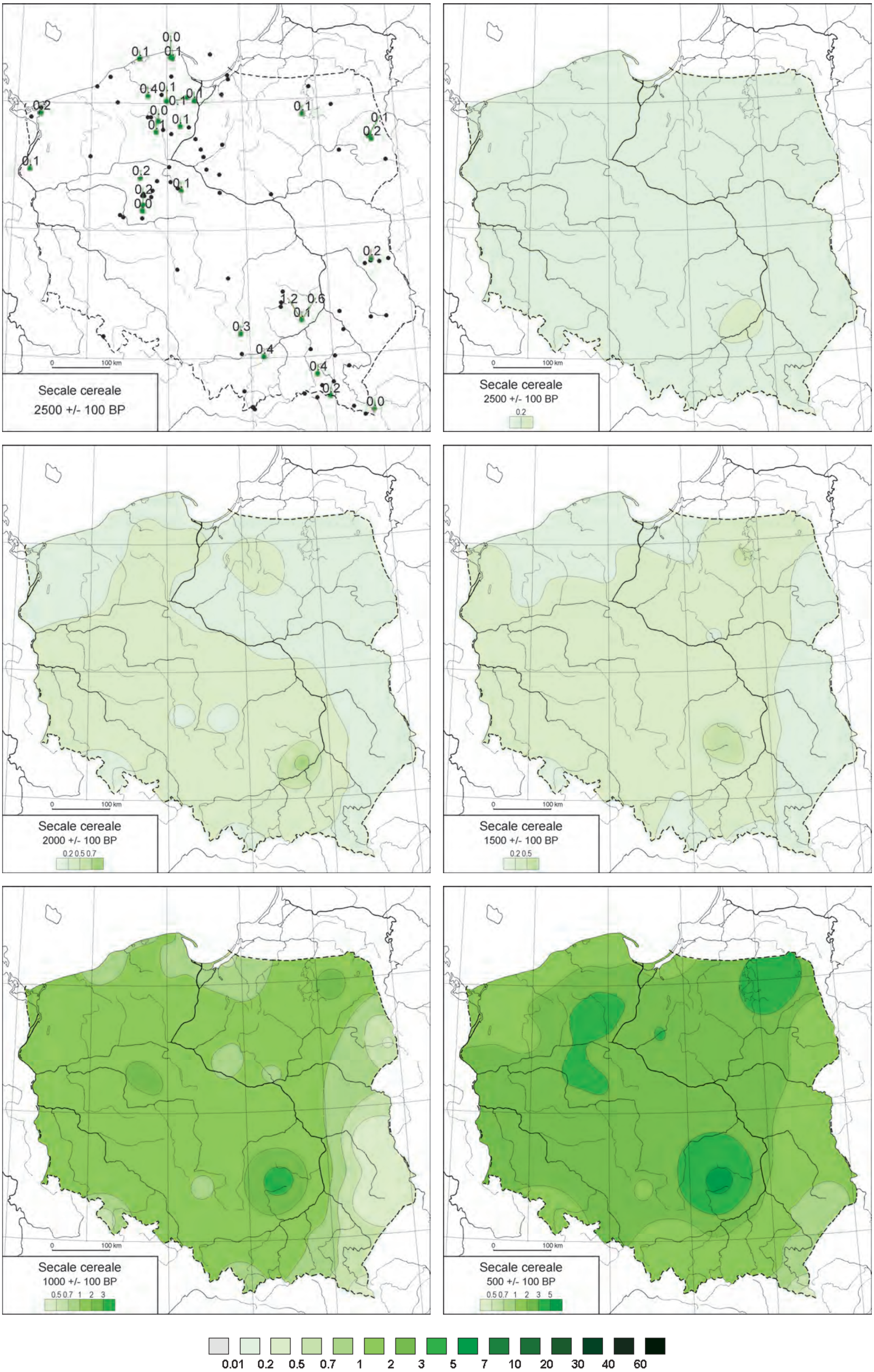

0.1
0
100 km
Secale cereale
5000 +/- 100 BP

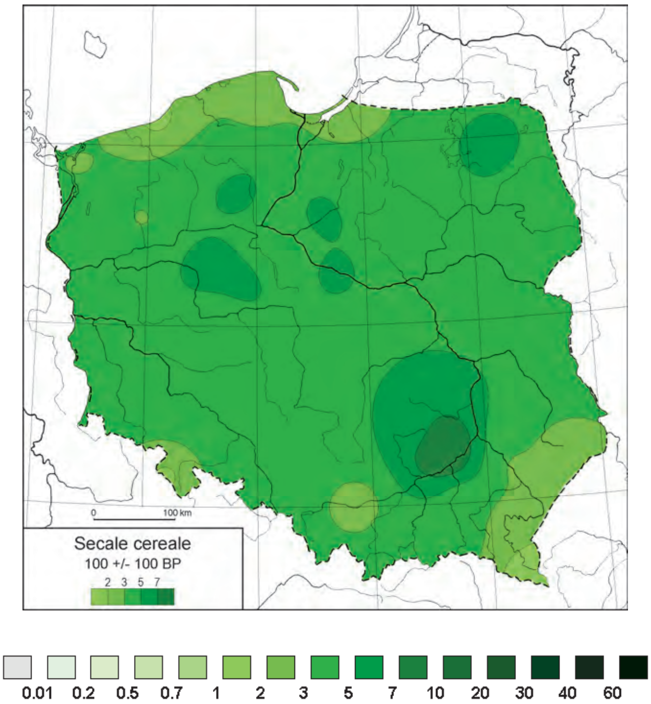

0.1
0.1
0.1
0.1
0.1
0.0
0.3
0.4
0.1
0.1
0.1
0
100 km
Secale cereale
4500 +/- 100 BP


0.0
0.2
0.0
0.0
0.2
0.1
0.0
0
100 km
Secale cereale
4000 +/- 100 BP


0.1
0.3
0.1
0.1
0.2
0.1
1.7
0.1
0.3
0.0
0.1
0.0
0.1
0.2
0.0
0.1
0
100 km
Secale cereale
3500 +/- 100 BP


0.1
0.0
0.1
0.1
0.1
0.0
0.0
0.0
0.4
0.4
0.2
0.1
0.0
0
100 km
Secale cereale
3000 +/- 100 BP


Secale cereale
2500 +/- 100 BP
0 100 km
0.0
0.1
0.1
0.2
0.4
0.1
0.1
0.1
0.0
0.1
0.1
0.1
0.1
0.2
0.1
0.2
0.2
0.1
0.0
0.2
1.2
0.6
0.1
0.3
0.4
0.4
0.2
0.0
Secale cereale
2500 +/- 100 BP
0.2
Secale cereale
2000 +/- 100 BP
0.2 0.5 0.7
Secale cereale
1500 +/- 100 BP
0.2 0.5
Secale cereale
1000 +/- 100 BP
0.5 0.7 1 2 3
Secale cereale
500 +/- 100 BP
0.5 0.7 1 2 3 5
0.01
0.2
0.5
0.7
1
2
3
5
7
10
20
30
40
60


0
100 km
Secale cereale
100 +/- 100 BP
2 3 5 7
0.01
0.2
0.5
0.7
1
2
3
5
7
10
20
30
40
60

Selaginella selaginoides (L.) P. Beauv. ex Schrank & Mart. – Lesser clubmoss

Wojciech Granoszewski, Małgorzata Nita and Dorota Nalepka

Present distribution in Europe and in Poland

Selaginella selaginoides (L.) P. Beauv. ex Schrank & Mart. is an Arctic-Alpine species found throughout northern Europe, Iceland, Greenland, the Alps, the Carpathians, the Rhodope Mountains, the Dinaric Alps and the Pyrenees (Hultén & Fries 1986). In Poland (Fig. 97) it is found in the Western Carpathians and the highest part of Sudetes (Karkonosze).

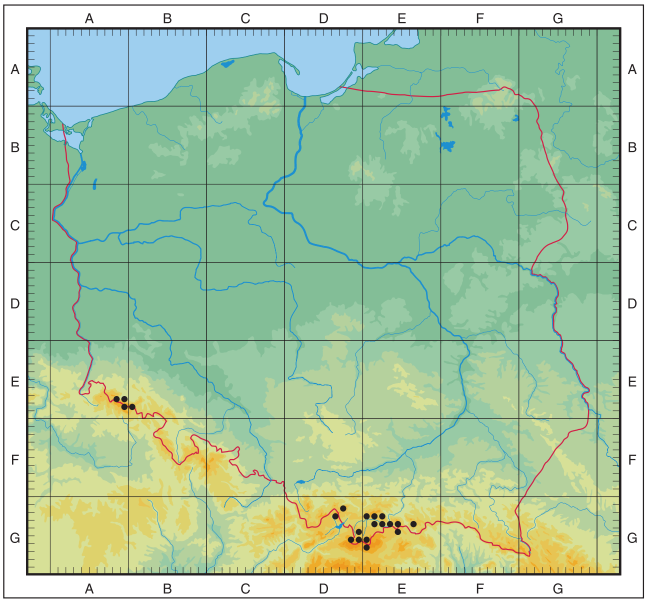


Fig. 97. Present-day distribution of *Selaginella selaginoides* (L.) P. Beauv. ex Schrank & Mart. in Poland (after Zając A. & Zając M. 2001)

Ecology

In Poland lesser clubmoss grows in regions with the coldest climate (alpine and subnival montane zones) and in cold temperate and cool temperate regions (subalpine and upper and lower montane forests zones) (Zarzycki et al. 2002). It grows on slightly moist and moist soils and prefers soils rich in calcium carbonate (Pawłowski 1956), in full light or temporary shade. It is indifferent to continentality of climate. It is a characteristic species of the association *Festuco versicoloris-Seslerietum Tatrae* assigned to the order *Seslerietalia variae*, but it also grows in the associations of the order *Caricetalia davallianae*.

Spore production and dispersal

Selaginella selaginoides is a heterosporous pteridophyte. It produces spores in July and August (Szafer et al. 1953). *Selaginella* spores generally constitute a minor component of pollen assemblages (<1%), though in some Late Glacial sites, where it may have been locally present, its contribution to pollen assemblages can exceed 10%.

Expansion in Europe during the Late Glacial and Holocene

Selaginella selaginoides spores are very frequently found in floras of the different glacial periods, including the last glaciation, in areas which lie today beyond its range of occurrence, e.g. the European lowlands (Hultén & Fries 1986). During the course of the climatic warming and the expansion of forest communities, *Selaginella* became confined to the areas of its present-day range.

Migration pattern in Poland (Fig. 98)

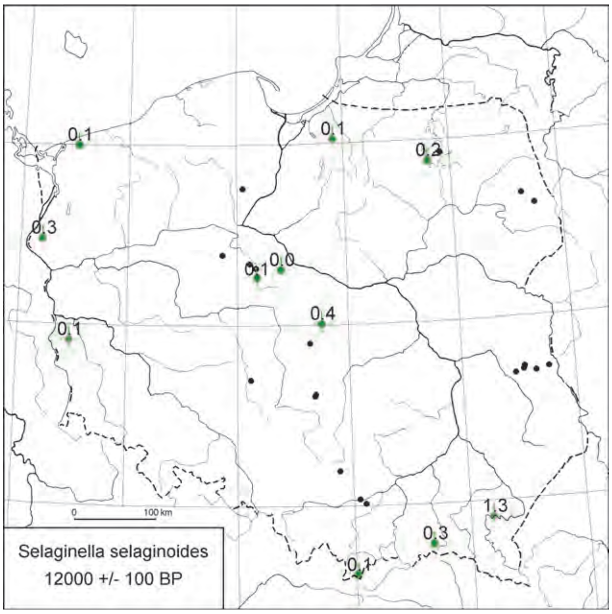
Selaginella spores appear on the earliest isopollen map at 14,000 BP in north-eastern Poland. At 12,000 BP lesser clubmoss was present throughout the territory of Poland. This situation prevailed until the beginning of the Holocene (10,000 BP). The highest values in pollen assemblages were recorded in the Bieszczady Mountains at 11,000 BP (11.6%), at the Małopolska Upland at about 10,000 BP (16.7%), and up to 15% between 12,500 and 12,000 BP at the western Baltic Sea coast (Ralska-Jasiewiczowa & Rzętkowska 1987), not recorded on the maps. Between 10,000 and 9500 BP *Selaginella* became restricted to the mountain regions, and its present-day range was finally determined.

Fig. 98. *Selaginella selaginoides*: dot maps for 14,000–9500 ^{14}C yr BP


0.1
0 100 km
Selaginella selaginoides
14000 +/- 100 BP


0.1
0.1
0.9
0 100 km
Selaginella selaginoides
13000 +/- 100 BP


0.6
0.1
0.7
0.1
0 100 km
Selaginella selaginoides
12500 +/- 100 BP


0.1
0.1
0.2
0.3
0.1
0.0
0.1
0.4
1.3
0.3
0.1
0 100 km
Selaginella selaginoides
12000 +/- 100 BP


0.0
0.3
0.1
0.1
16.3
0 100 km
Selaginella selaginoides
11500 +/- 100 BP


0.1
0.0
0.1
0.0
0.0
0.1
0.1
11.6
0 100 km
Selaginella selaginoides
11000 +/- 100 BP


0.1
0.1
0.0
0.1
0.1
0.0
0.1
0.2
2.5
3.0
0
100 km
Selaginella selaginoides
10500 +/- 100 BP


0.5
0.0
0.1
0.3
0.2
0.0
0.2
0.0
16.7
1.3
1.5
0
100 km
Selaginella selaginoides
10000 +/- 100 BP


0.1
0.3
0.4
0
100 km
Selaginella selaginoides
9500 +/- 100 BP

Typha latifolia L. – Bulrush, cat-tail

MAGDALENA RALSKA-JASIEWICZOWA, KAZIMIERZ TOBOLSKI AND DOROTA NALEPKA

PRESENT DISTRIBUTION IN EUROPE AND IN POLAND

Typha latifolia L. is a Eurasian-North American species (Lauber & Wagner 2001), widespread and common in the temperate zone. It reaches the boreal zone and is abundant in the Mediterranean zone. It occurs as far north as Scotland, southern Norway and the Gulf of Bothnia; in Siberia it reaches about 57°N, and in the river-basin of the Lena river 65°N (Casper & Krausch 1980). Its southern boundary runs across the Mediterranean Basin (including the northern margins of Africa), Asia Minor, the Caucasus, Iraq to Japan and Kamchatka; further afield, it is found in North America and Mexico, Australia and Polynesia.

Since *Typha latifolia* pollen forms flat tetrads, it is easily identified in pollen assemblages. However, it is more difficult to distinguish the small thin fruits of *T. latifolia* and *T. angustifolia* L. where the epidermal cell pattern must be examined under a high-power microscope. Since hybridisation occurs there is some variability. In the flora of central Europe there are two species of bulrush, not found in Poland, whose pollen remains in tetrads (Casper & Krausch 1980). One of them – *T. shuttleworthii* Koch et Sonder (= *T. transsilvanica* Schur) is distributed in the southern part of central Europe and the eastern Pyrenees, the Alps and their forelands, and in the Balkan Peninsula. The other species with tetrad pollen – *T. minima* Funck in Hoppe (Reille 1992) is found in the Alps and their forelands, Italy, the Balkan Peninsula, and the region of the Caucasus (Casper & Krausch 1980, Krausch 1996).

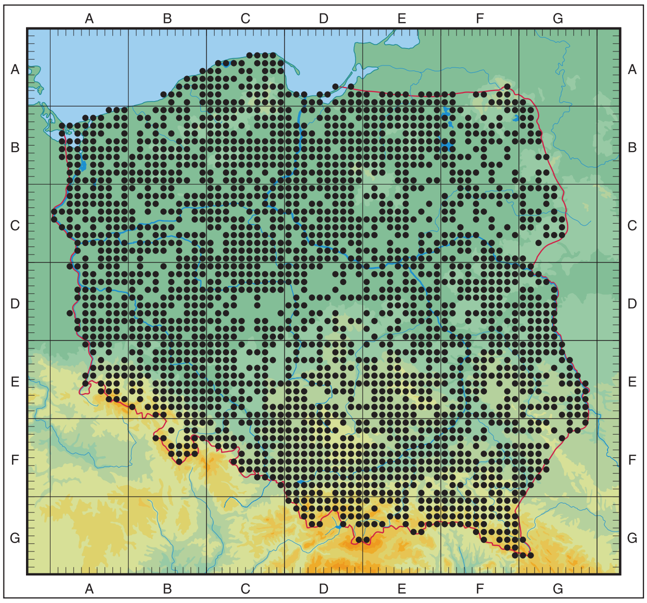


Fig. 99. Present-day distribution of *Typha latifolia* L. in Poland (after Zając A. & Zając M. 2001)

In Poland *Typha latifolia* is one of the common plants present almost throughout the country (Fig. 99), but it is less common in lower montane regions, and does not occur in the higher mountains.

ECOLOGY

The three bulrush species producing pollen in tetrads are indicators of different climates: *T. shuttleworthii* favours a cool climate, *T. minima* has a wide thermic amplitude, whereas *T. latifolia* is an indicator of warm temperate climate (Ellenberg et al. 1991).

Typha latifolia is considered by Iversen (1954, 1973), and many other authors, to be the Late Glacial indicator of minimum July temperatures of +14°C. Isarin and Bohncke (1999) assume that July temperatures of +13°C are sufficient for its occurrence. However, it seems that *Typha latifolia* is better as an indicator of habitat rather than of climate. It can grow in water up to 1 m deep, both standing and slowly flowing, but it can also colonise waterlogged areas that may dry up for long periods. Therefore, Landolt (1977) considers this species as one of the indicators of fluctuating water level. It is a eutrophic species (Zarzycki et al. 2002), an indicator of fertile conditions, and, according to Ellenberg et al. (1991) is also an indicator of high levels of nitrogen. It grows on soils with an average humus content but rarely occurs on acid peat-bogs (Landolt 1977), yet in Poland, together with *T. angustifolia* it belongs to eutrophic peat-forming species (Tobolski 2000). It favours weakly acid soils, neutral or slightly alkaline (pH 4.5–7.5). It can also grow on poorly aerated soils, deficient in oxygen. It is one of the pioneer plants of marshy areas binding the damp ground with its tough, vigorous rhizomes (formerly used as a food resource).

It is a component of communities belonging to the class *Phragmitetea* and forms a separate association (not unanimously approved, cf. Pott 1995), *Typhetum latifoliae* (Matuszkiewicz W. 2001).

MIGRATION PATTERN IN POLAND (Fig. 100)

12,500 – 12,000 BP

At 14,000 and 13,500 BP maps *Typha latifolia* has been found a one site in NE Poland. More frequently it occurs only in sediments of the Bølling interstadial on the 12,500 BP map in Polesie Lubelskie (0.9%, 0.4%), and as single tetrads in Warmia and the Łódź Upland. In the later part of the Bølling (12,000 BP) it is found in more numerous sites in Polesie Lubelskie, central Poland, the Mazurian Lake District, and on the eastern coast of the Baltic Sea. In the south it is found in the eastern mountain foothills. Its presence in the Bølling, especially in eastern and central Poland is obvious. Therefore, it must be assumed that, if this species is really a good temperature indicator, then July temperatures not lower that +13°C (Isarin & Bohncke 1999) must have prevailed in those regions of Poland during the full and declining phases of the Bølling interstadial.

11,500 – 11,000 BP

The map covering the mid-Allerød, when interstadial conditions were well developed, shows the presence of *Typha latifolia* throughout the country, which is consistent with the temperature conditions assumed for this period.

During the transition from the Allerød to the much cooler Younger Dryas stadial, a reduction in the number and distribution of sites with *Typha latifolia* pollen is marked. The species disappears from Polesie Lubelskie and the uplands of central Poland, but is still present in Kujawy and to the south in the Carpathian foreland. There are sparse records from the lake districts (with an abundant site – 1.8% – in the Mazurian Lake District), the Tuchola Forest and the north-western margins of the country.

10,500 BP

Typha is still absent from the uplands of central Poland, but present in Kujawy and in the foreland of the Carpathians. It has single sites in the lake districts and marshes of Polesie Lubelskie, at the junction of the Narew and Biebrza rivers, and still occurs on the west coast of the Baltic Sea.

Isarin & Bohncke (1999) constructed a map with isotherms for the period 10,950–10,550 BP in Europe. It shows the line of the +13°C isotherm running across the north-eastern lake districts of Poland (Mazurian lakes), then south-westwards crossing Wielkopolska, where the Nysa Łużycka river joins the Odra river. The pattern of sites with bulrush on the 11,000 and 10,500 BP maps moves this isotherm in the north-western Poland towards the Baltic coastline. Bulrush has more sites on this than on the 11,000 BP map, both in south-eastern Poland and the eastern lake districts, and in the region of the middle and lower course of the Vistula river. The occurrence of bulrush might suggest that, even during the older part of the Younger Dryas with its more severe climate, those regions still enjoyed favourable enough conditions for bulrush to grow and flower (Ralska-Jasiewiczowa et al. 1998).

10,000 – 100 BP

With the rapid warming at the onset of the Holocene *Typha* appears at almost all the sites investigated. Although it is wind-pollinated, it is rare to find its pollen in large quantities in sediments (except in the case of inflorescences falling into the water *in situ*). Its pollen values do not exceed 0.5%, and are only exceptionally higher than 1%. Further maps cannot be interpreted, because higher values occur only irregularly at single sites. Attention can be drawn, however, to the 8500 and 8000 BP maps, where increased *Typha latifolia* values in the upland region of southern Poland might be related to the occurrence of extreme hydrological phenomena at that time, periods of sudden rainfall, floods, etc. (Starkel 1999). As a consequence, additional habitats favouring the development of reedswamps may have been created. The 500 BP map shows a local, extremely abundant occurrence of bulrush pollen at Woryty in the Olsztyn Lake District, where the lake had become overgrown and a fen has been formed.

CONCLUSIONS

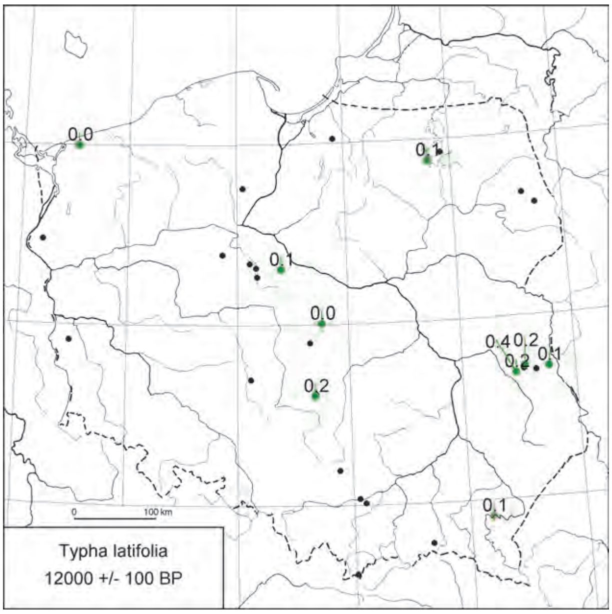
Typha latifolia appeared in Poland most probably during the Bølling interstadial (12,500–12,000 BP). If this species is a reliable climatic indicator, its appearance defines July temperatures, at least in central and northern Poland, during the full and declining phases of the Bølling interstadial at a minimum of +13°C. During the Allerød interstadial *Typha* occurred over the whole of Poland. The Younger Dryas cooling restricted its distribution. However, considering the isotherm map of Europe for the time interval 10,950–10,550 BP constructed by Isarin & Bohncke (1999), its surviving sites suggest that the +13°C isotherm run by then further to the north-west, following the Baltic Sea coast.

From the beginning of Holocene *Typha* appears at nearly all sites in Poland. Its higher values at 8500–8000 BP in south Poland may document a phase of intensified extreme climatic events (storms, floods) creating many suitable habitats for this species.

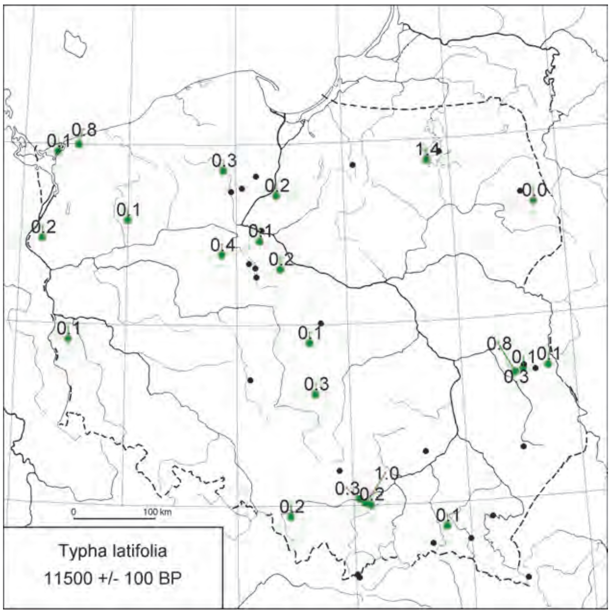
The isopollen maps of *Typha latifolia* reveal some shortages of statistical methods used for drawing the maps. On the majority of maps (from 7500 BP on), the southern part of Poland which has no sites with *Typha* because there are no lakes there and the pollen data come exclusively from mires is, however, included into the impact area from the Nida Basin and Roztocze regions and shows presence of low *Typha* values. Also the irregularly distributed single sites with higher *Typha* values cover with their impact too wide surrounding areas.

Fig. 100. *Typha latifolia*: dot and isopollen maps for 12,500–100 ^{14}C yr BP

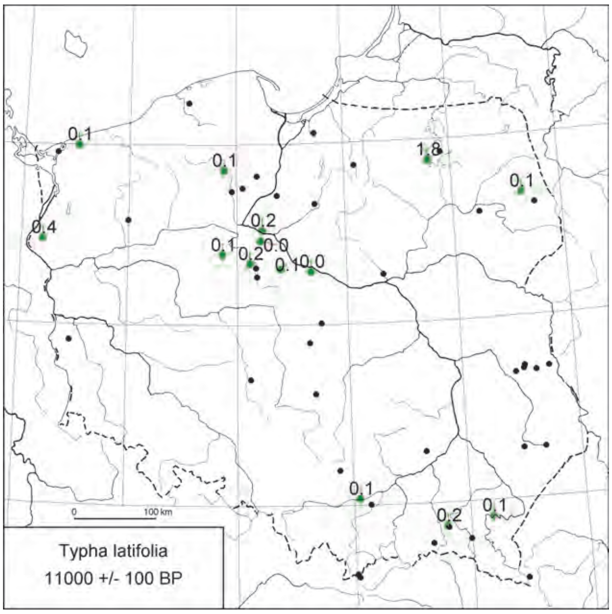
Typha latifolia
12500 +/- 100 BP



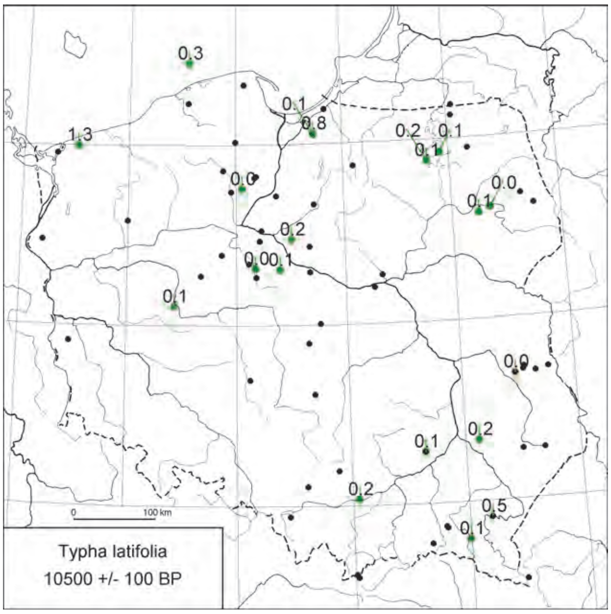
Typha latifolia
12000 +/- 100 BP



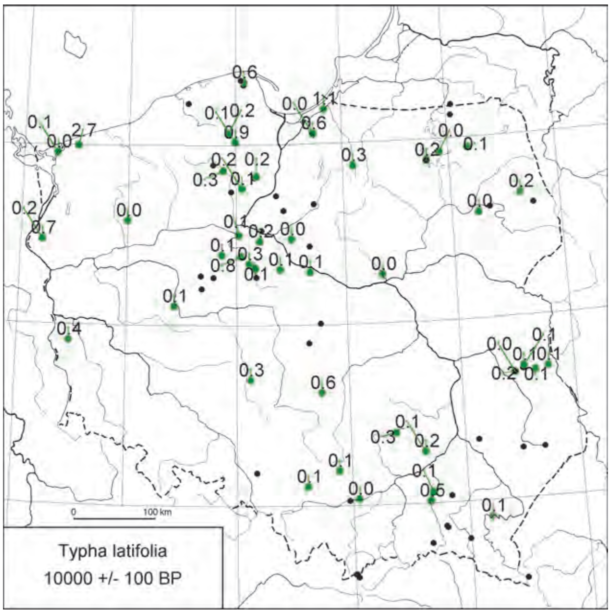
Typha latifolia
11500 +/- 100 BP



Typha latifolia
11000 +/- 100 BP



Typha latifolia
10500 +/- 100 BP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0.0 1.1
0.1
0.0
2.7
0.9
0.6
0.0
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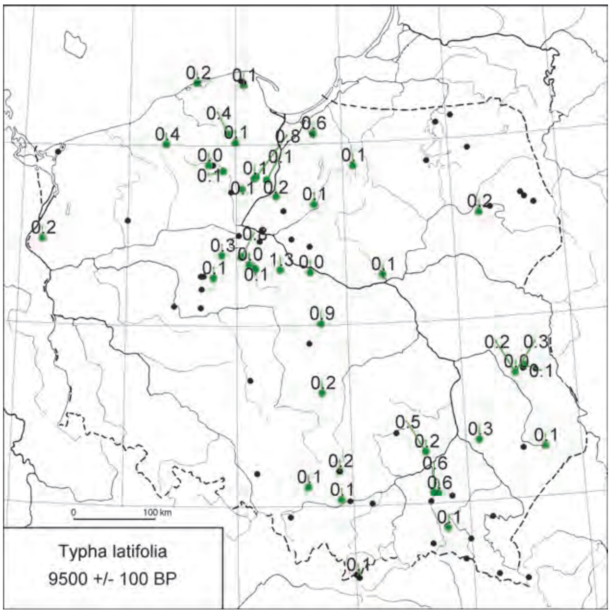
0.3
0.2
0.2 0.2
0.3 0.1
0.2
0.0
0.2
0.7
0.0
0.1
0.2 0.0
0.1
0.3
0.8
0.1
0.1 0.1
0.0
0.1
0.4
0.1
0.0 0.1 0.1
0.2 0.1
0.3
0.6
0.1
0.3
0.2
0.1
0.1
0.1
0.0
0.5
0.1
0 100 km
Typha latifolia
10000 +/- 100 BP


0 100 km
Typha latifolia
10000 +/- 100 BP
0.2 0.5 0.7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0.1 0.2
0.1
0.2
0.2
0.3
0.5
0.0 0.0
1.3 0.0
0.1
0.1
0.1
0.9
0.2 0.3
0.0
0.1
0.2
0.5
0.2
0.3
0.1
0.6
0.2
0.1
0.6
0.1
0.1
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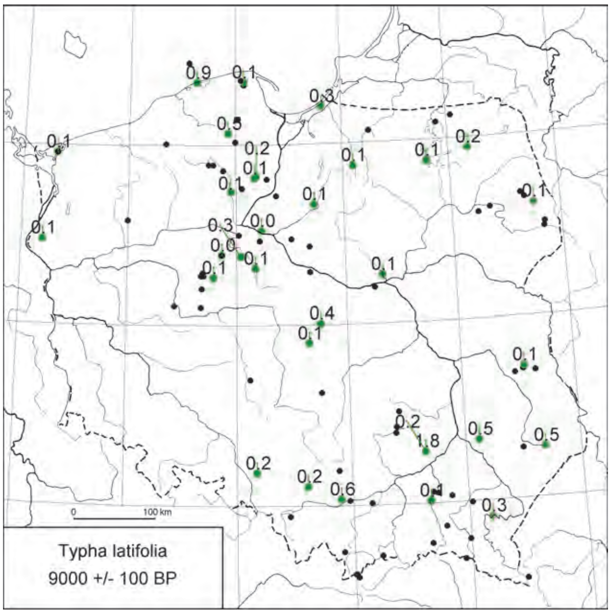
0 100 km
Typha latifolia
9500 +/- 100 BP


0 100 km
Typha latifolia
9500 +/- 100 BP
0.2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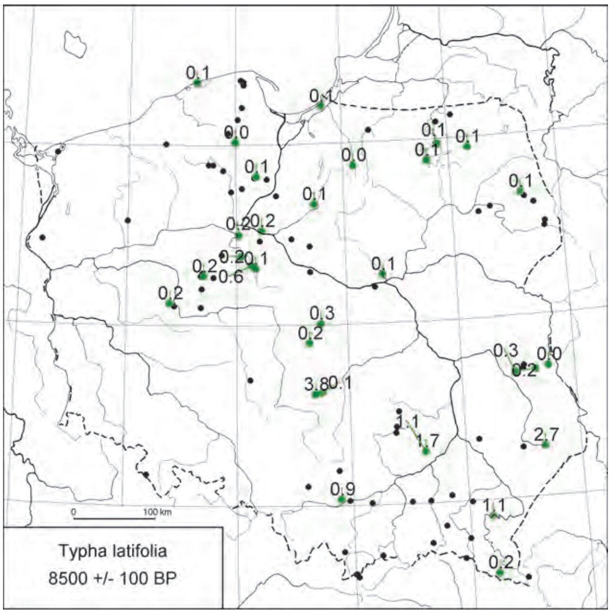
0.1
0.3
0.0
0.0
0.1
0.1
0.1
0.4
0.1
0.1
0.2
1.8
0.5
0.5
0.2
0.2
0.6
0.1
0.3
0 100 km
Typha latifolia
9000 +/- 100 BP


0 100 km
Typha latifolia
9000 +/- 100 BP
0.2


0.01
0.2
0.5
0.7
1
2
3
5
7
10
20
30
40
60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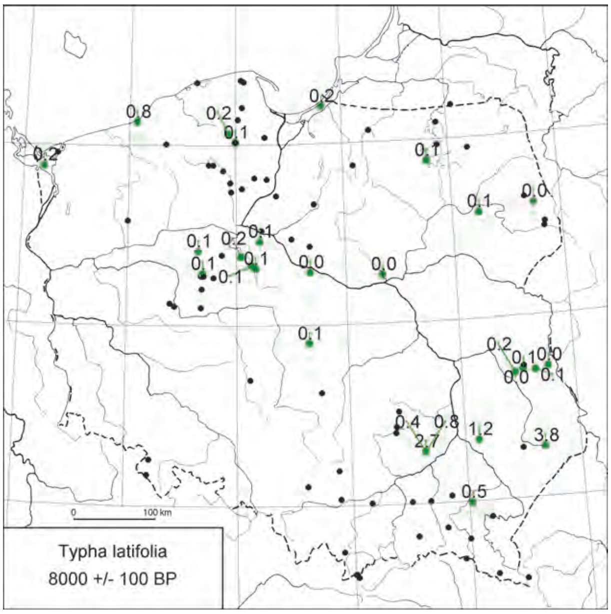
0.0
0.1
0.1
0.2
0.2
0.2
0.2
0.1
0.6
0.2
0.1
0.3
0.2
0.3
0.0
0.2
3.8
0.1
1.1
1.7
2.7
0.9
1.1
0.2
0
100 km
Typha latifolia
8500 +/- 100 BP


0
100 km
Typha latifolia
8500 +/- 100 BP
0.2 0.5 0.7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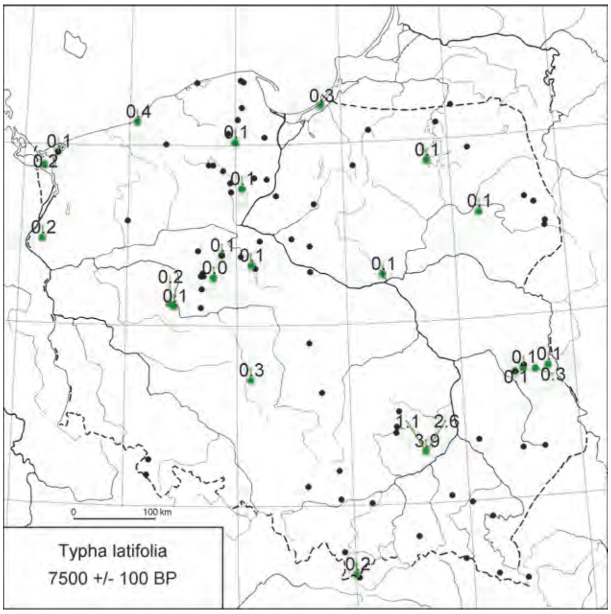
0.1
0.1
0.0
0.0
0.1
0.2
0.1
10.0
0.0
0.1
0.4
0.8
1.2
2.7
3.8
0.5
0
100 km
Typha latifolia
8000 +/- 100 BP


0
100 km
Typha latifolia
8000 +/- 100 BP
0.2 0.5 0.7 1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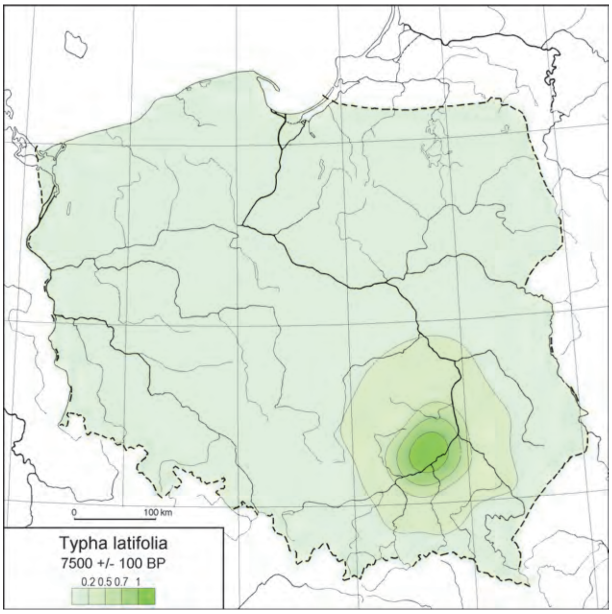
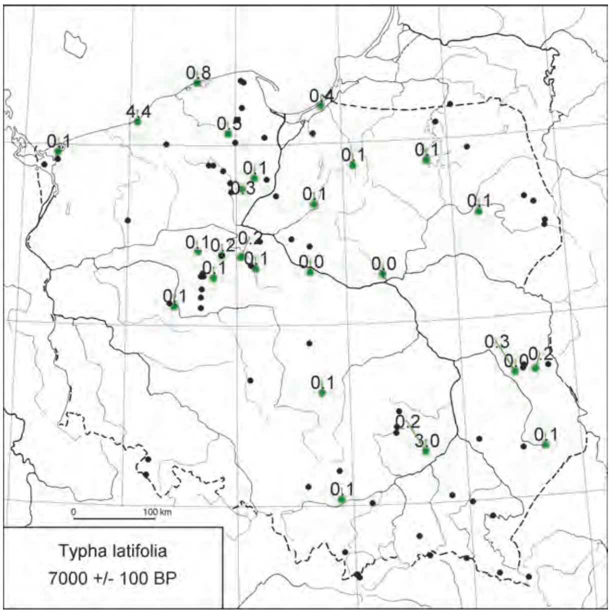
0.1
0.2
0.1
0.1
0.3
0.1
10.1
0.1
0.3
1.1
2.6
3.9
0.2
0
100 km
Typha latifolia
7500 +/- 100 BP


0
100 km
Typha latifolia
7500 +/- 100 BP
0.2 0.5 0.7 1


0.01
0.2
0.5
0.7
1
2
3
5
7
10
20
30
40
60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0.1
0.5
0.1
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0.1
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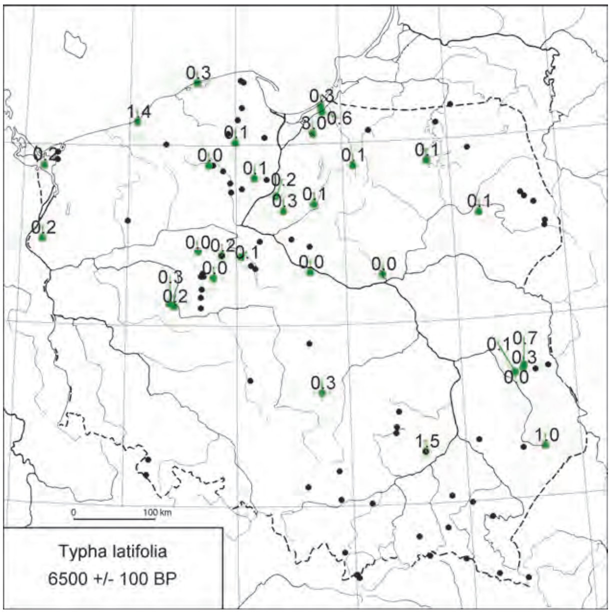
0.2
0.2
0.1
0.0
0.0
0.1
0.1
0.3
0.0
0.2
0.1
0.2
3.0
0.1
0.1
0 100 km
Typha latifolia
7000 +/- 100 BP


0 100 km
Typha latifolia
7000 +/- 100 BP
0.2 0.5 0.7 1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0.6
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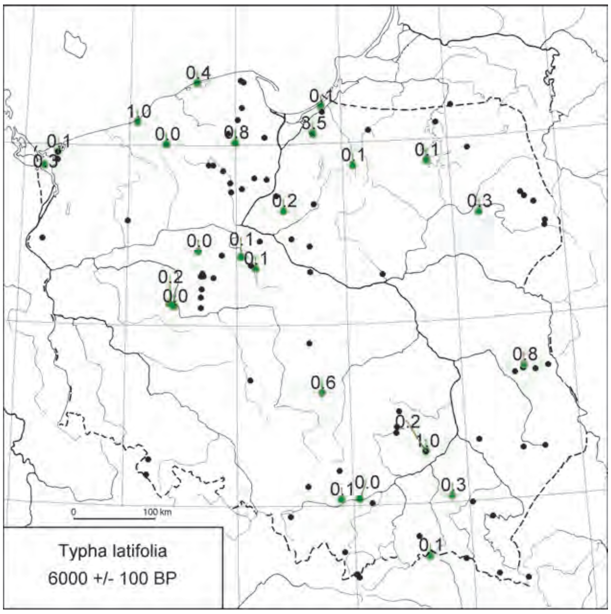
0.3
0.1
0.1
0.2
0.0
0.2
0.1
0.0
0.0
0.0
0.3
0.2
0.1
0.7
0.3
0.0
0.3
1.5
1.0
0 100 km
Typha latifolia
6500 +/- 100 BP


0 100 km
Typha latifolia
6500 +/- 100 BP
0.2 0.5 0.7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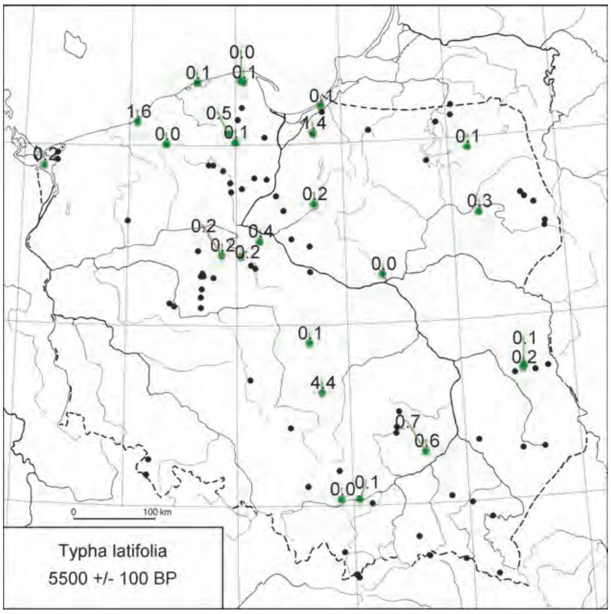
0.0
0.1
0.1
0.2
0.0
0.8
0.6
0.2
1.0
0.1
0.0
0.3
0.1
0 100 km
Typha latifolia
6000 +/- 100 BP


0 100 km
Typha latifolia
6000 +/- 100 BP
0.2 0.5 0.7


0.01
0.2
0.5
0.7
1
2
3
5
7
10
20
30
40
60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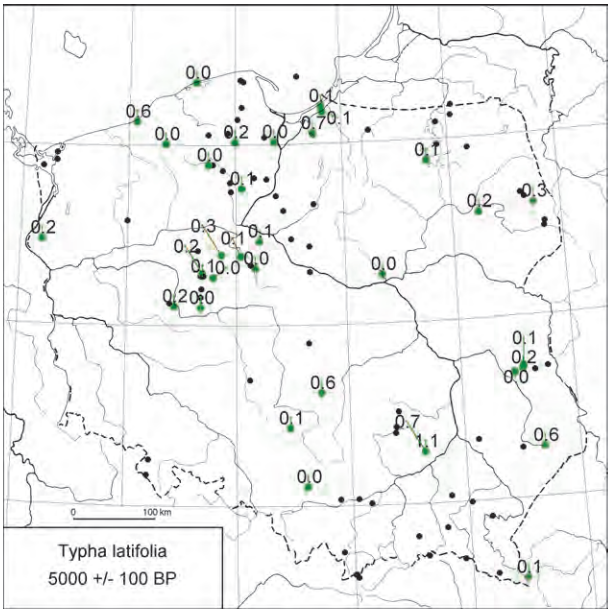
0.3
0.2
0.4
0.2
0.2
0.0
0.1
0.2
0.1
4.4
0.7
0.6
0.0
0.1
0
100 km
Typha latifolia
5500 +/- 100 BP


0
100 km
Typha latifolia
5500 +/- 100 BP
0.2 0.5 0.7 1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0.2
0.3
0.2
0.1
0.1
0.1
0.0
0.0
0.0
0.2
0.0
0.1
0.2
0.0
0.6
0.1
0.7
1.1
0.6
0.0
0.1
0
100 km
Typha latifolia
5000 +/- 100 BP


0
100 km
Typha latifolia
5000 +/- 100 BP
0.2


0
100 km
Typha latifolia
4500 +/- 100 BP
0.2 0.5


0
100 km
Typha latifolia
4000 +/- 100 BP
0.2


0.01
0.2
0.5
0.7
1
2
3
5
7
10
20
30
40
60


0 100 km
Typha latifolia
3500 +/- 100 BP
0.2


0 100 km
Typha latifolia
3000 +/- 100 BP
0.2


0 100 km
Typha latifolia
2500 +/- 100 BP
0.2


0 100 km
Typha latifolia
2000 +/- 100 BP
0.2


0 100 km
Typha latifolia
1500 +/- 100 BP
0.01


0 100 km
Typha latifolia
1000 +/- 100 BP
0.01
0.2


0.01
0.2
0.5
0.7
1
2
3
5
7
10
20
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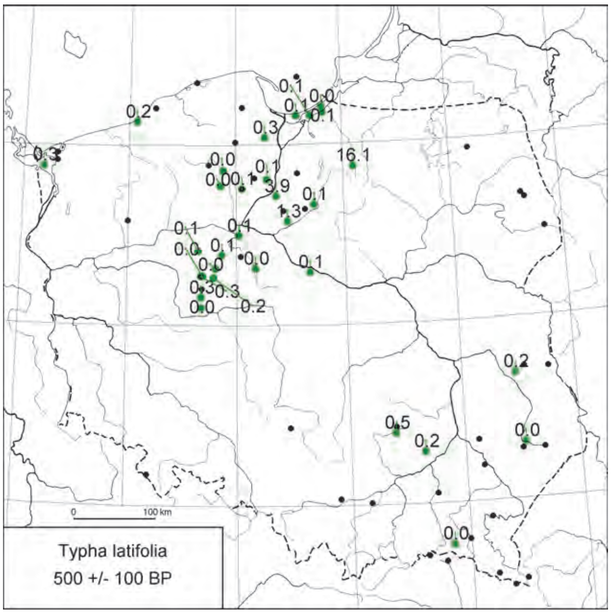
40
60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0.1
0.0
0.0
0.1
0.3
0.3
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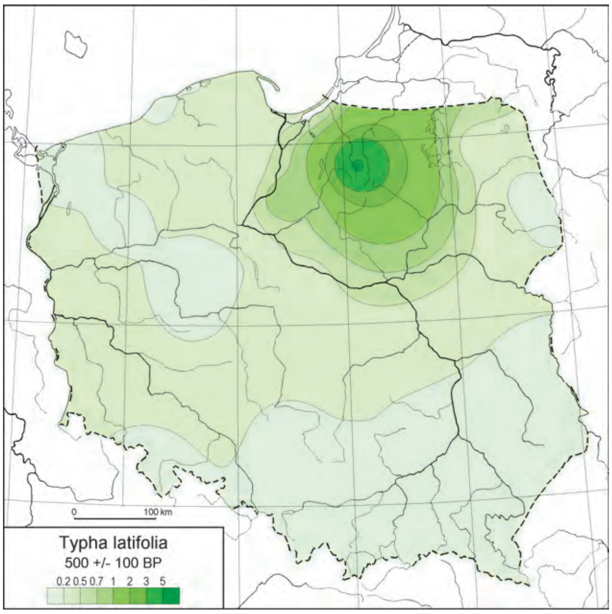
0.2
0.5
0.2
0.0
0.0
0
100 km
Typha latifolia
500 +/- 100 BP


0
100 km
Typha latifolia
500 +/- 100 BP
0.2 0.5 0.7 1 2 3 5


0
100 km
Typha latifolia
100 +/- 100 BP
0.2 0.5


0.01
0.2
0.5
0.7
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7
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40
60

SUM OF HERB POLLEN (NAP)

KRYSTYNA HARMATA, MAŁGORZATA LATAŁOWA, JACEK MADEJA, AND DOROTA NALEPKA

The pollen sum of all herbaceous plants, excluding the pollen of open-water and marginal aquatic plants (limnophytes and telmatophytes), Cyperaceae as local element mostly, and the spores of pteridophytes and bryophytes, is described as the sum of the NAP (non arboreal pollen), and is calculated in all pollen assemblages. It comprises pollen of taxa that possess different ecological requirements, can occupy various habitats, contribute to many plant communities, and develop under different climatic conditions. Thus, fluctuations in the total NAP curve generally have no single ecological cause or interpretation but rather they reflect the influence of a variety of factors. These factors might include the presence or absence of plants growing *in situ* (and maybe actually contributing to peat formation), the size of any open, unforested areas in the vicinity of the sedimentary basin being studied, and whether these were supporting natural vegetation or anthropogenic plant communities (e.g. cultivated fields), the possibility of pollen transport to the basin from these areas, or alternatively the size and nature of such sedimentary basins (e.g. whether they are or were supporting a peat bog or lake). Because of factors of this kind, when interpreting changes in NAP, note should be taken of which taxa have been dominant, which palaeoecological indicator species or species indicating human exploitation were present, and whether changes in the NAP curve are accompanied by specific changes in the tree pollen curves.

MIGRATION PATTERN IN POLAND (Fig. 101)

14,000 – 10,500 BP

The very high percentage values of NAP on the maps representing the older part of the Late Glacial (14,000–12,000 BP) indicate absolute dominance of open communities during this stage of vegetation development. NAP values >50% reflect the presence of an entirely treeless landscape. A gradual decrease in NAP values is seen between 12,500 BP (Bølling) and 11,500 BP (Allerød), then they increase again during the Younger Dryas (11,000–10,500 BP) when almost the whole of Poland is covered by NAP pollen values of 20–30%. At the south-eastern and north-western margins of the country they reach 30–40%.

Changes in NAP values on these maps illustrate the gradual development of forests during interstadial periods, as well as the gradual disappearance of trees from those communities during the Younger Dryas.

10,000 – 100 BP

From the beginning of the Holocene up to 7500 BP the frequencies of NAP show lower values (locally they fall below 5%), particularly over the greater part of central and northern Poland. In the southern part, NAP values are higher, which may be the result of over-representation of local plant pollen in peats that form the main type of deposits, whereas in northern Poland, the majority of the profiles analysed derive from lake sediments.

The 7000–6000 BP maps reflect local and minor increase in pollen values of herbaceous plants, particularly in the north-western and the south-eastern parts of Poland. At sites situated along the Baltic Sea coast this is mainly a result of the development of reedswamp and its deposits resulting from the Littorina transgression of the southern Baltic Sea (Zachowicz et al. 1982, Tobolski 1987, Latałowa 1992, as well as comments on Poaceae (Gramineae) by Harmata et al., this volume). Higher NAP values in the south may have resulted from the development of Neolithic cultures; the same reason of higher NAP concerns the ‘island’ appearing in central Poland (Kujawy). On the 5500 BP map the extent of these changes expands considerably, particularly with regard to pollen assemblages from southern Poland.

The subsequent maps from 5000 BP to 4000 BP do not show any decrease in NAP, although this covers a period when various human tribes were actively occupied with animal husbandry and agriculture. This may perhaps result from forest management in the form of coppicing at that time (Latałowa 1992). In such cases evidence for human management may be provided rather by the presence of indicator taxa than by any increase in NAP values. Not earlier than on the 3500 BP map is it possible to see higher NAP values illustrating a greater degree of deforestation, particularly in central and north-western

Poland. The 2000 BP map reflects the very beginning of the period of Roman influence. The changes that occurred then were rather of a qualitative than a quantitative character; a distinct spread of the higher NAP values is present in southern Poland only. Beyond that, it can be accepted with a considerable degree of certainty, that the fall in pollen values of herbaceous plants visible on the 1500 BP map, especially in northern Poland, is a result of regeneration of forests during the Migration Period, as recorded also in other parts of Europe.

The maps for the last millennium with Cyperaceae excluded illustrate the rapidly progressing devastation of forest communities. The NAP values, on the 100 BP map, are so high, that only those representing the older part of the Late Glacial are similar.

Isopolls calculated with Cyperaceae included into pollen sum (Fig. 101)

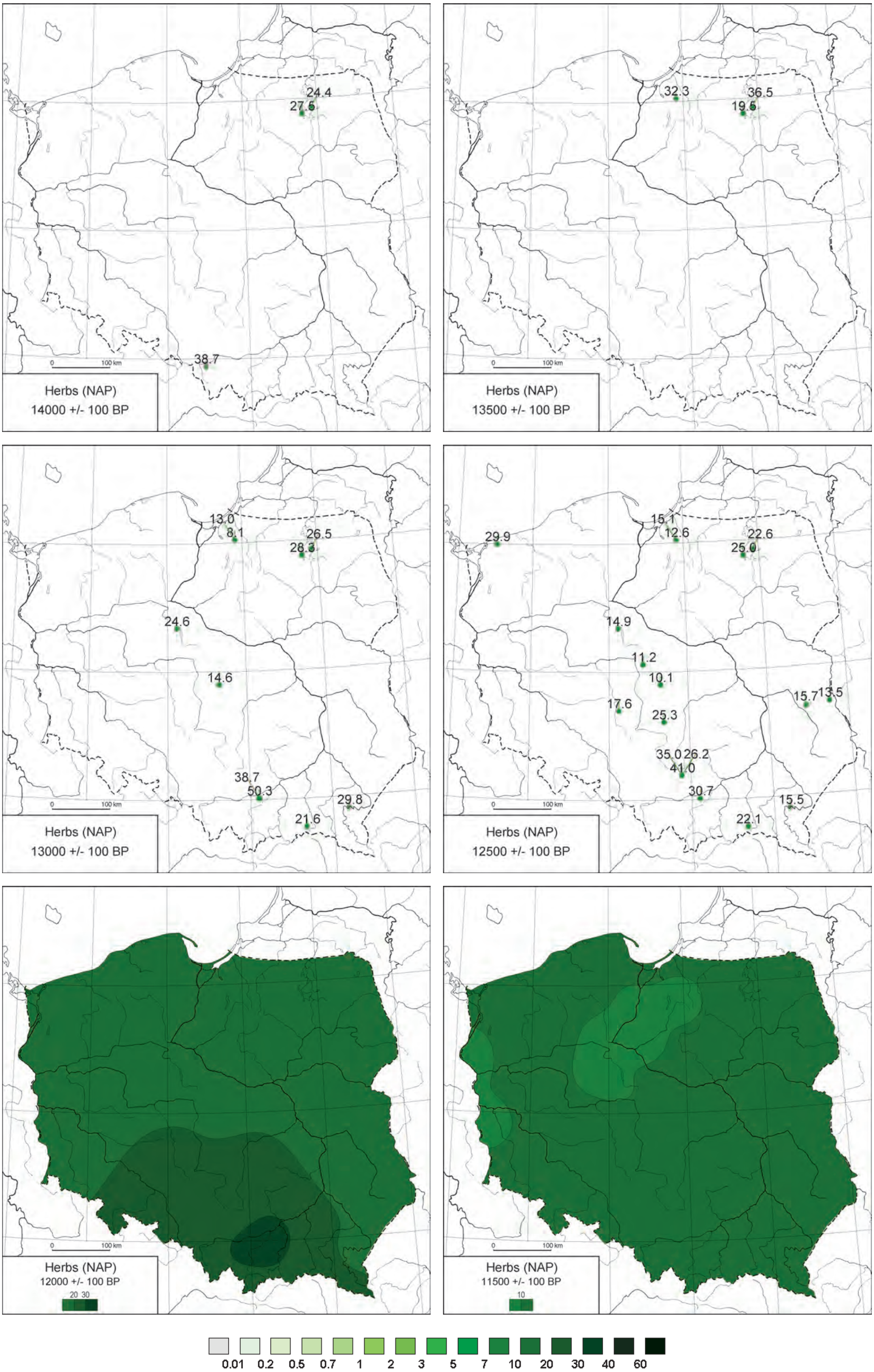
The main set of maps in the NAP chapter is based on the pollen sums calculated without Cyperaceae. Pollen of Cyperaceae represents mostly the elements of local vegetation and because of abundant presence in many pollen spectra, it restricts proper interpretation of contribution of other taxa. However, pollen of Cyperaceae cannot be treated uniformly regardless the period of the vegetation development. While in the Holocene pollen spectra it originates mostly from the strictly local flora, in the Late Glacial samples several species typical of tundra or steppe-tundra could contribute the pollen record of this family. Therefore, it can be assumed, that for the Late Glacial, at least partly, the Cyperaceae pollen reflects openness of the landscape and for that reason should be included into the NAP sum.

The comparison of both types of maps (calculated with and without Cyperaceae) shows not only the higher NAP values when Cyperaceae are included, but also may reveal different patterns of isopolls. In this case any interpretation of the NAP maps should involve an extra analysis of the Cyperaceae isopollen maps (see chapter on Cyperaceae, this volume). For instance, a rather false picture has been obtained for the Allerød and the beginning of the Holocene. The maps with Cyperaceae included indicate higher proportions of NAP (more open landscape) in southern part of the country than in the north, what is in contradiction with the data on the forest development in these periods. In this case, the higher NAP results from a fact that the most common type of sites investigated in southern Poland are different mires. This set of maps shows also a not adequately diversified picture of changes in the openness of the landscape throughout the whole Holocene, with the exception of the last 1000 years.

CONCLUSIONS

In general, high NAP values are connected with treeless or unforested landscapes, and an increasing pollen sum of herbaceous plants is a result of reduction in forested areas. Deforestation may be of local or regional extent, and its character and causes can be determined from the taxonomic composition of pollen assemblages. For example, the period of the Late Glacial is characterised by high percentage pollen values of herbaceous plants. Pioneer and heliophilous plants play an important role with some characteristic Arctic-Alpine plants among them. In the early and middle Holocene minor, short rises in NAP values may indicate the moderate interference of hunters-gatherers or populations practising farming. In the younger Holocene, there are repeated and significant rises in NAP values, with cultivated and synanthropic species being represented among them. These changes are accompanied by a fall in tree pollen values, which is the basis for distinguishing phases of settlement and gauging the intensity of economic change.

Fig. 101. Sum of herb pollen (NAP): dot and isopollen maps for 14,000–100 ^{14}C yr BP (Cyperaceae excluded); dot and isopollen maps of Herbs (NAP) for 14,000–100 ^{14}C yr BP calculated with Cyperaceae included into pollen sum are added and distinguished by green background of map legend


24.4
27.6
38.7
0
100 km
Herbs (NAP)
14000 +/- 100 BP
32.3
36.5
19.6
0
100 km
Herbs (NAP)
13500 +/- 100 BP
13.0
8.1
26.5
28.3
24.6
14.6
38.7
50.3
29.8
21.6
0
100 km
Herbs (NAP)
13000 +/- 100 BP
15.1
12.6
22.6
29.9
25.0
14.9
11.2
10.1
15.7
13.5
17.6
25.3
35.0
26.2
41.0
30.7
15.5
22.1
0
100 km
Herbs (NAP)
12500 +/- 100 BP
0
100 km
Herbs (NAP)
12000 +/- 100 BP
20 30
0
100 km
Herbs (NAP)
11500 +/- 100 BP
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0.01
0.2
0.5
0.7
1
2
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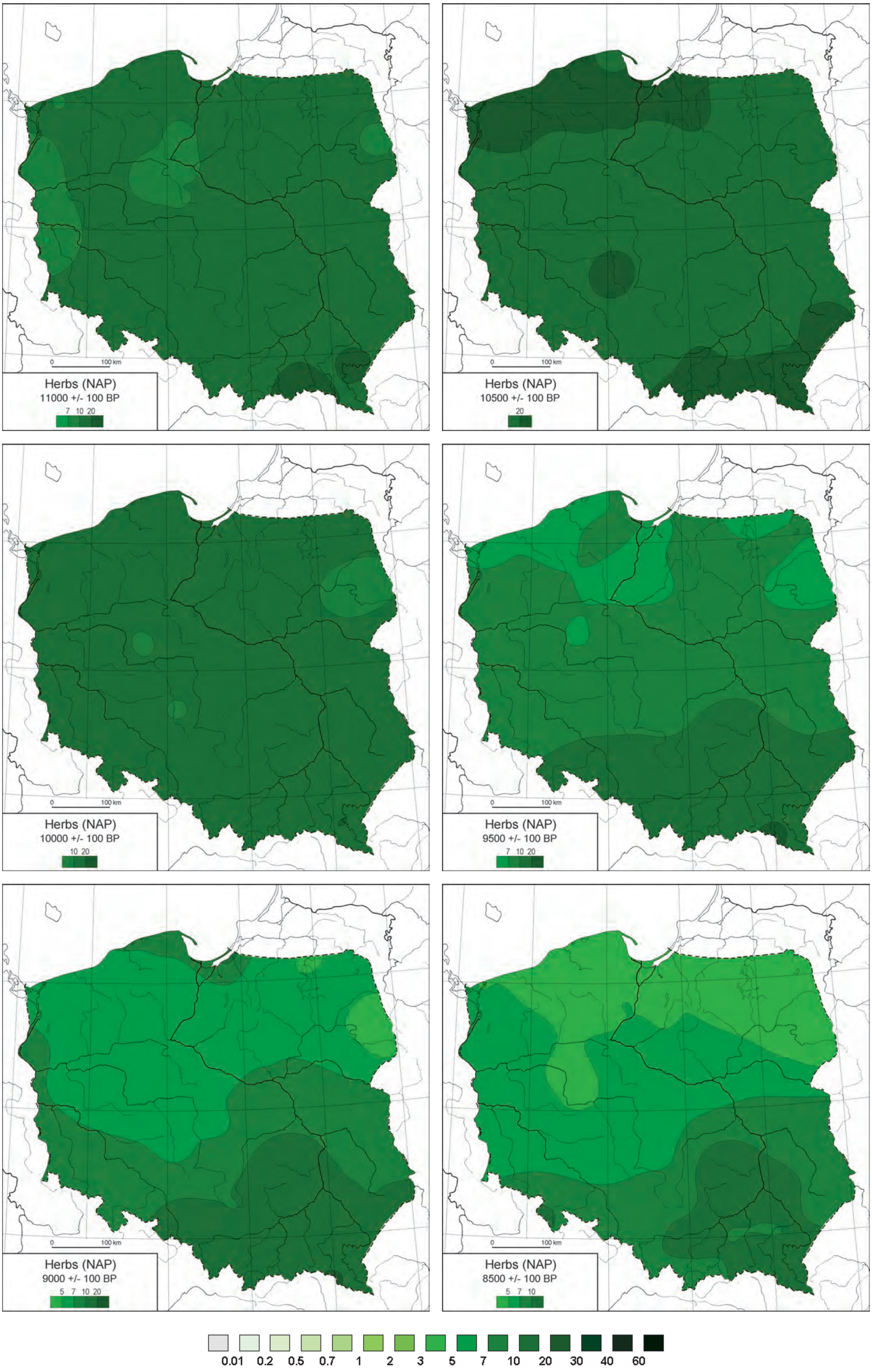
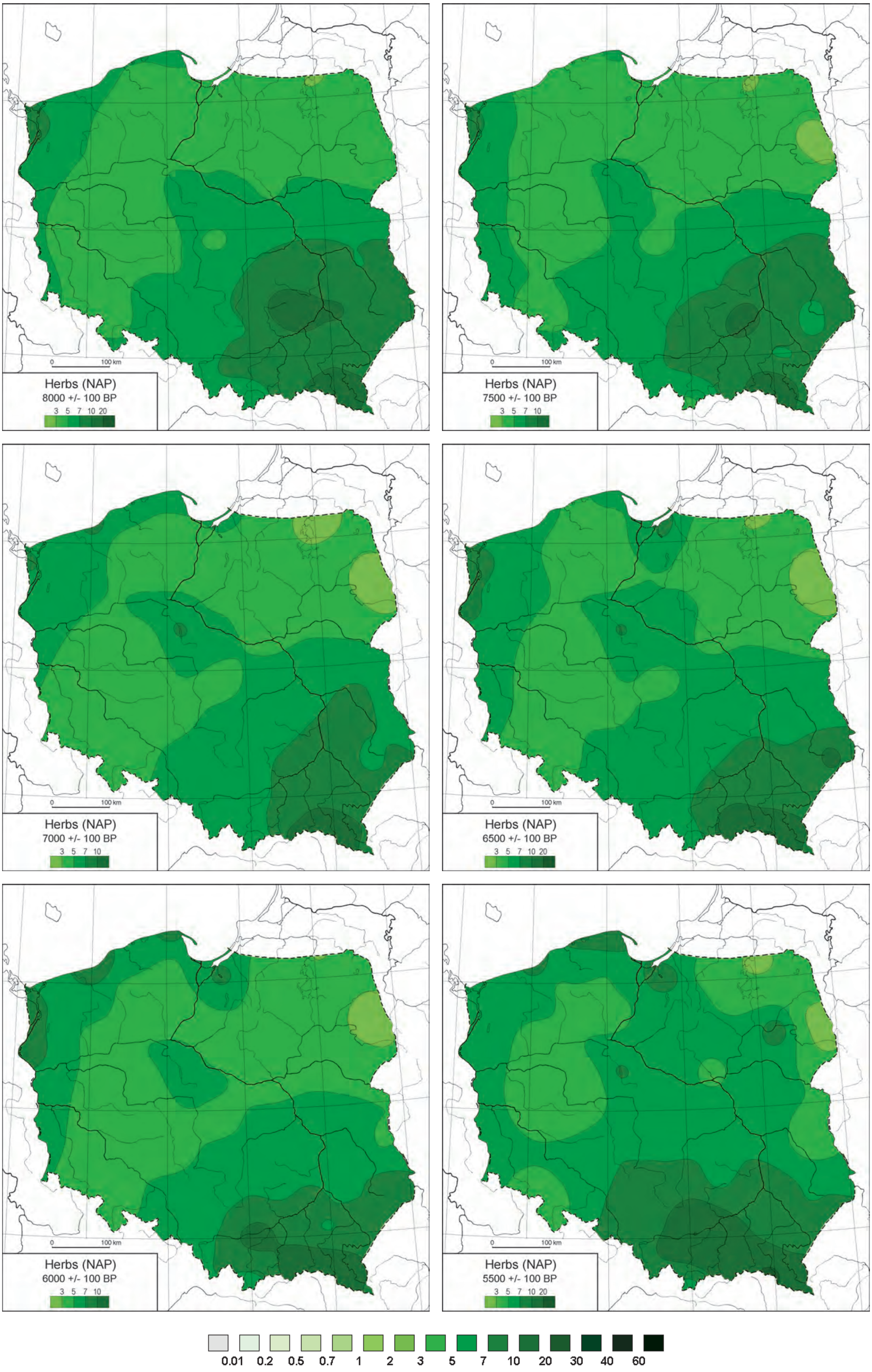
7
10
20
30
40
60


0 100 km
Herbs (NAP)
11000 +/- 100 BP
7 10 20
0 100 km
Herbs (NAP)
10500 +/- 100 BP
20
0 100 km
Herbs (NAP)
10000 +/- 100 BP
10 20
0 100 km
Herbs (NAP)
9500 +/- 100 BP
7 10 20
0 100 km
Herbs (NAP)
9000 +/- 100 BP
5 7 10 20
0 100 km
Herbs (NAP)
8500 +/- 100 BP
5 7 10
0.01 0.2 0.5 0.7 1 2 3 5 7 10 20 30 40 60


0
100 km
Herbs (NAP)
8000 +/- 100 BP
3 5 7 10 20
0
100 km
Herbs (NAP)
7500 +/- 100 BP
3 5 7 10
0
100 km
Herbs (NAP)
7000 +/- 100 BP
3 5 7 10
0
100 km
Herbs (NAP)
6500 +/- 100 BP
3 5 7 10 20
0
100 km
Herbs (NAP)
6000 +/- 100 BP
3 5 7 10
0
100 km
Herbs (NAP)
5500 +/- 100 BP
3 5 7 10 20
0.01
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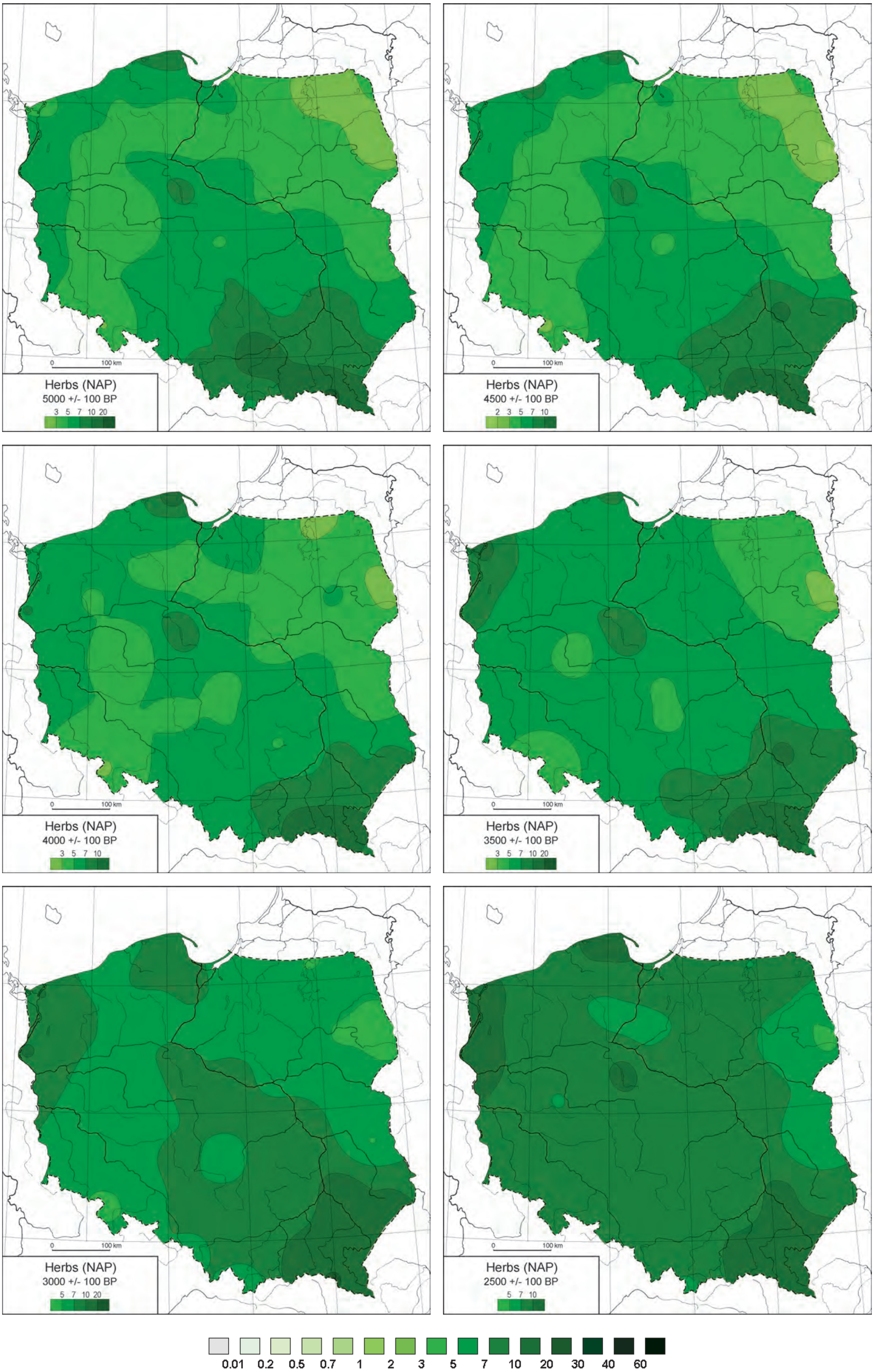
0 100 km
Herbs (NAP)
5000 +/- 100 BP
3 5 7 10 20
0 100 km
Herbs (NAP)
4500 +/- 100 BP
2 3 5 7 10
0 100 km
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4000 +/- 100 BP
3 5 7 10
0 100 km
Herbs (NAP)
3500 +/- 100 BP
3 5 7 10 20
0 100 km
Herbs (NAP)
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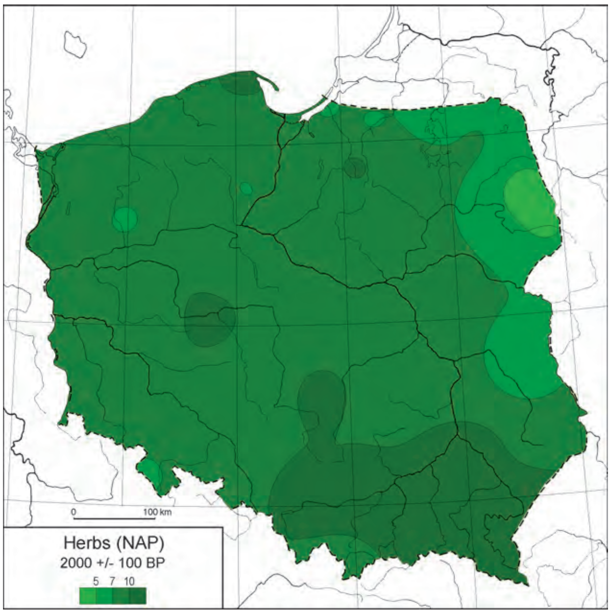
0
100 km
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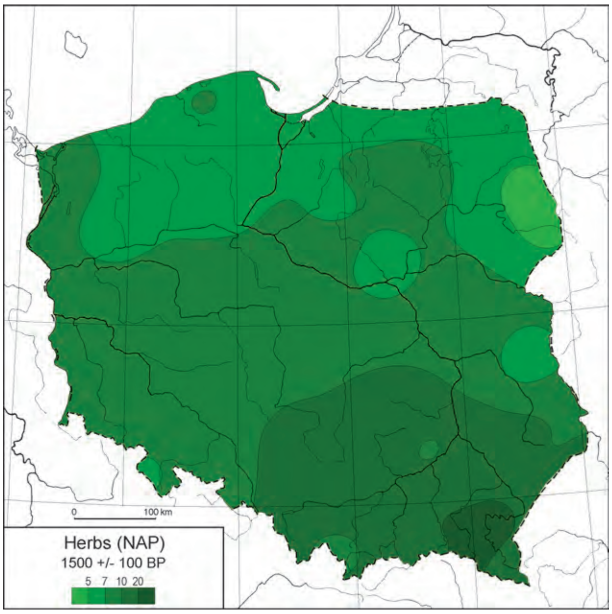
2000 +/- 100 BP
5 7 10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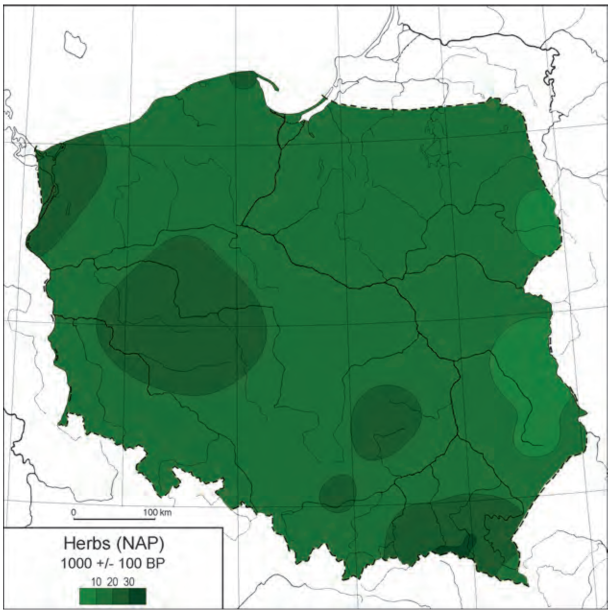
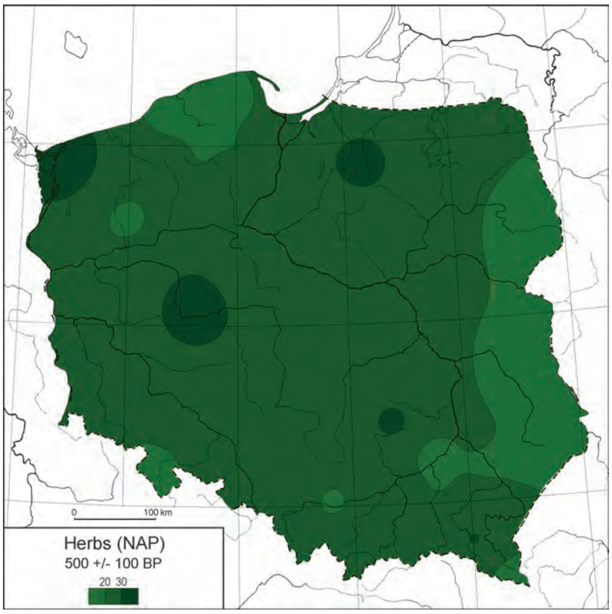
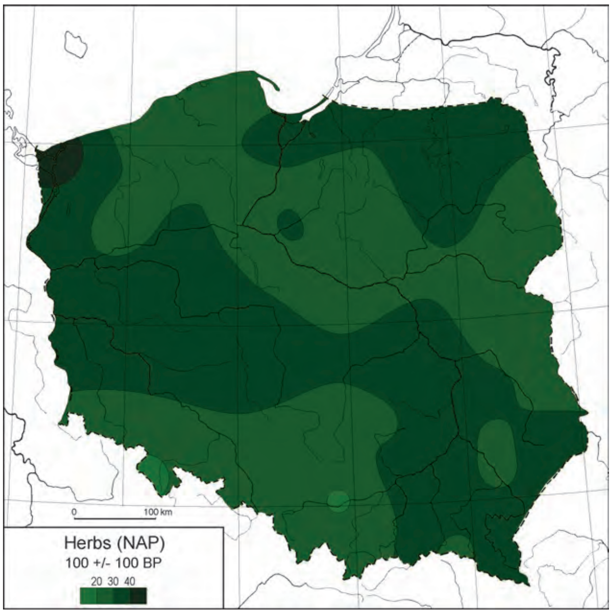
5 7 10 20


0
100 km
Herbs (NAP)
1000 +/- 100 BP
10 20 30


0
100 km
Herbs (NAP)
500 +/- 100 BP
20 30


0
100 km
Herbs (NAP)
100 +/- 100 BP
20 30 40


0.01
0.2
0.5
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1
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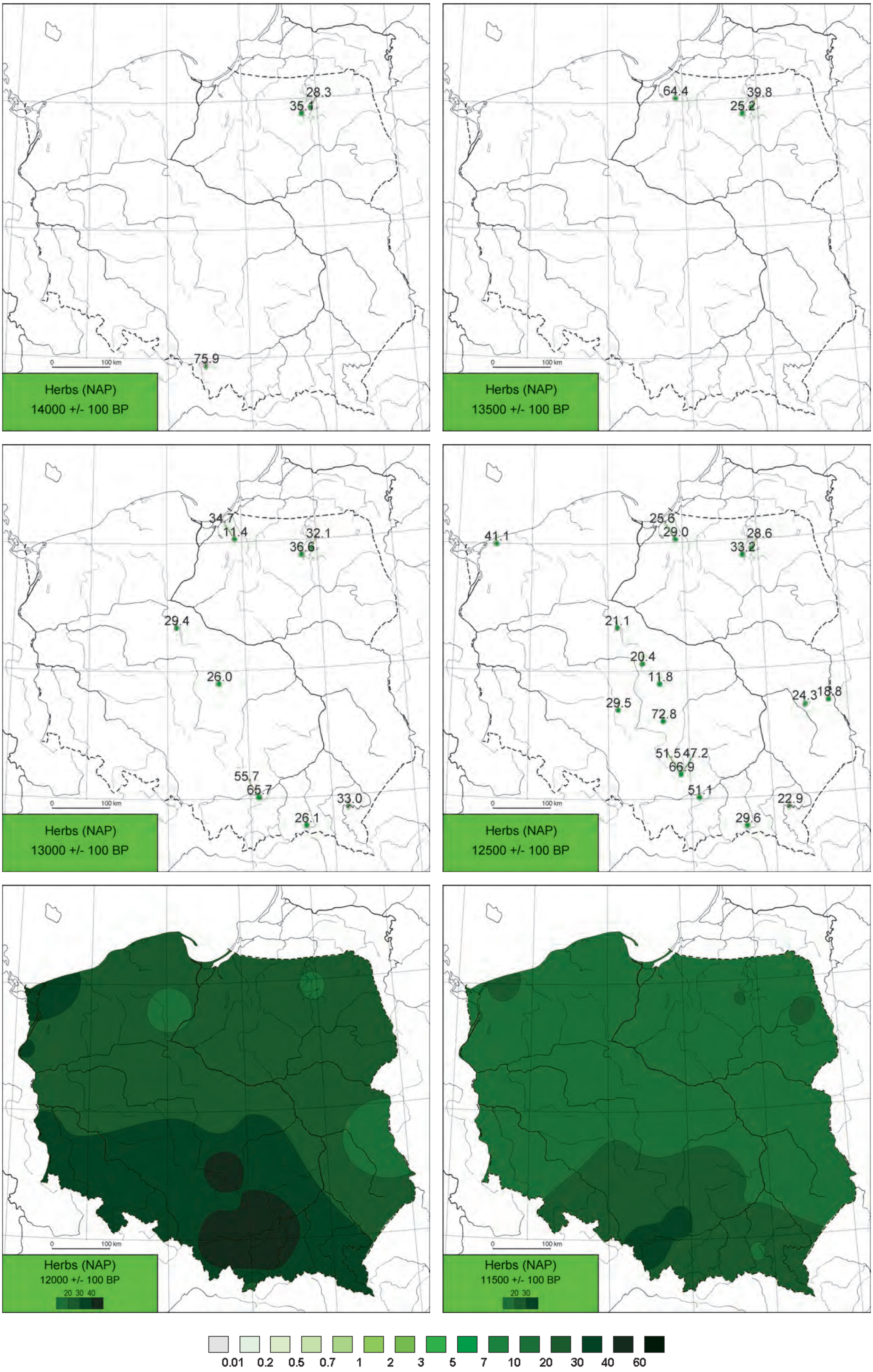


Herbs (NAP)
14000 +/- 100 BP

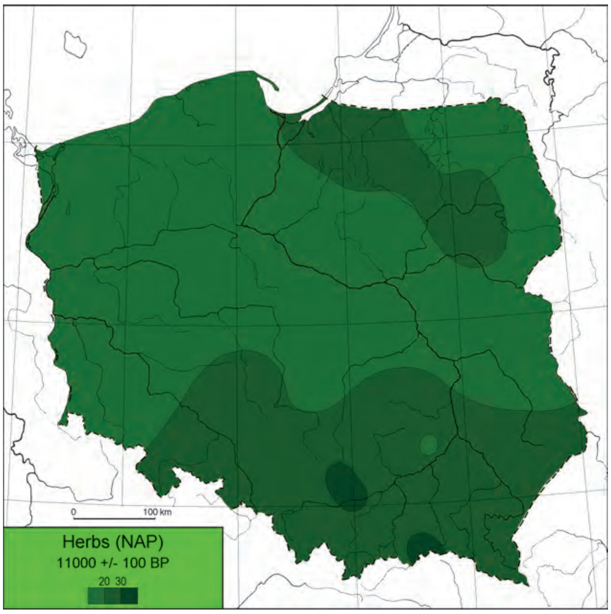
Herbs (NAP)
13500 +/- 100 BP

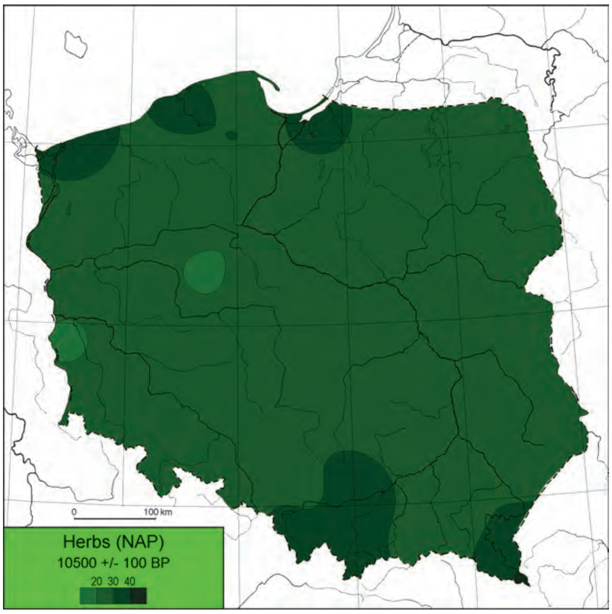
Herbs (NAP)
13000 +/- 100 BP

Herbs (NAP)
12500 +/- 100 BP

Herbs (NAP)
12000 +/- 100 BP

Herbs (NAP)
11500 +/- 100 BP


0
100 km
Herbs (NAP)
11000 +/- 100 BP
20 30


0
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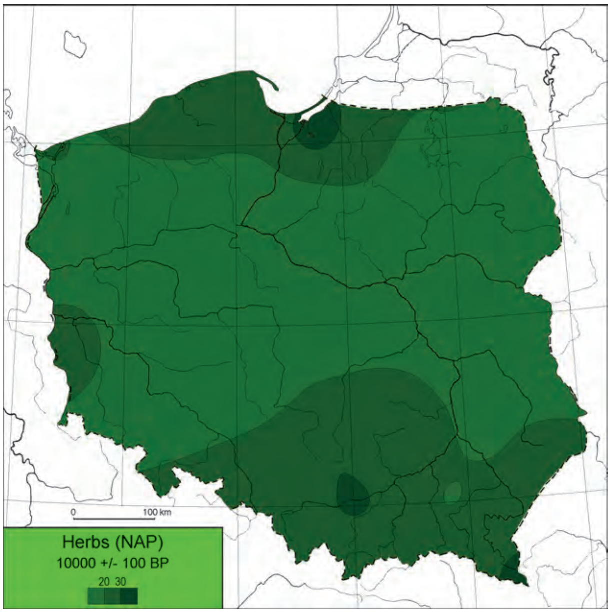
Herbs (NAP)
10500 +/- 100 BP
20 30 40


0
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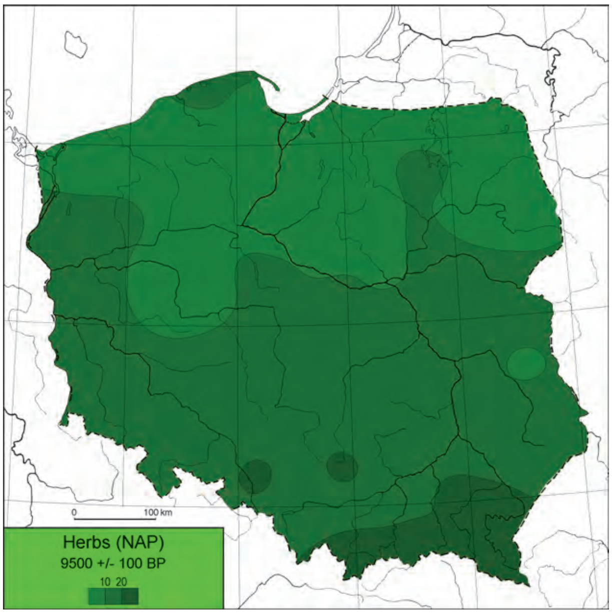
Herbs (NAP)
10000 +/- 100 BP
20 30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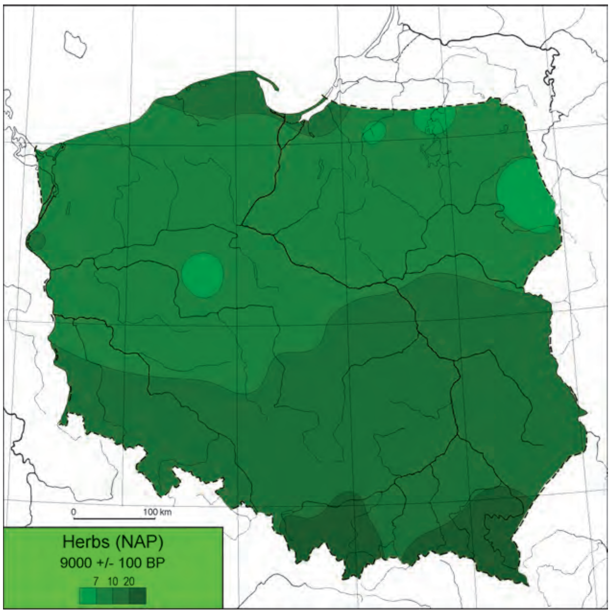
Herbs (NAP)
9500 +/- 100 BP
10 20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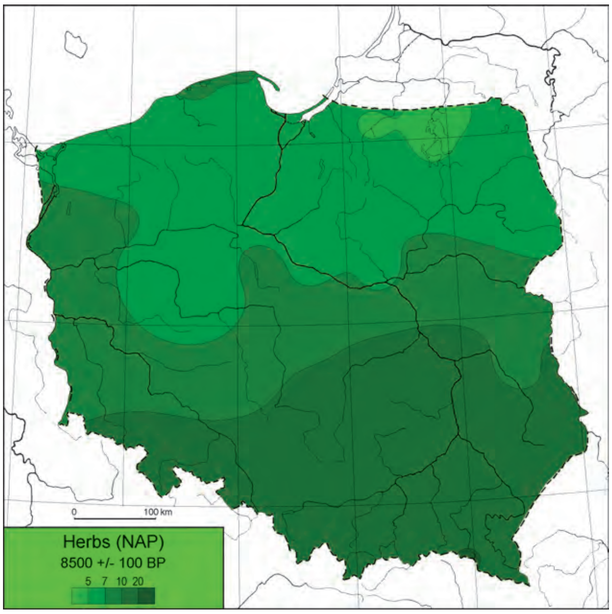
9000 +/- 100 BP
7 10 20


0
100 km
Herbs (NAP)
8500 +/- 100 BP
5 7 10 20


0.01
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0
100 km
Herbs (NAP)
8000 +/- 100 BP
5 7 10 20
Herbs (NAP)
7500 +/- 100 BP
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Herbs (NAP)
7000 +/- 100 BP
5 7 10 20
Herbs (NAP)
6500 +/- 100 BP
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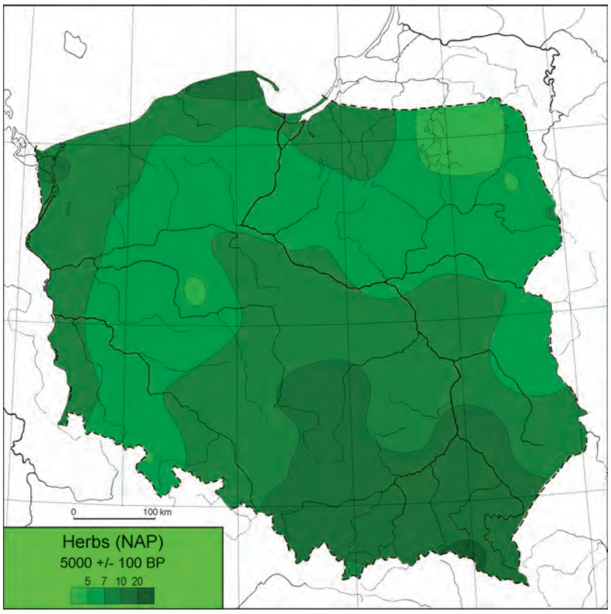
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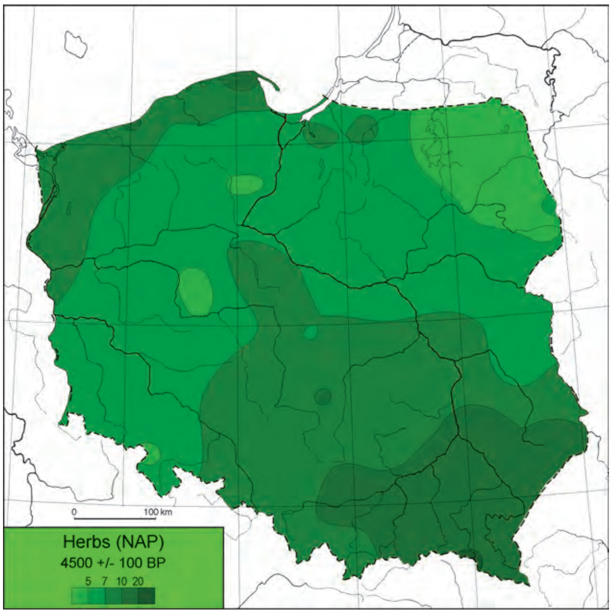
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Herbs (NAP)
4500 +/- 100 BP
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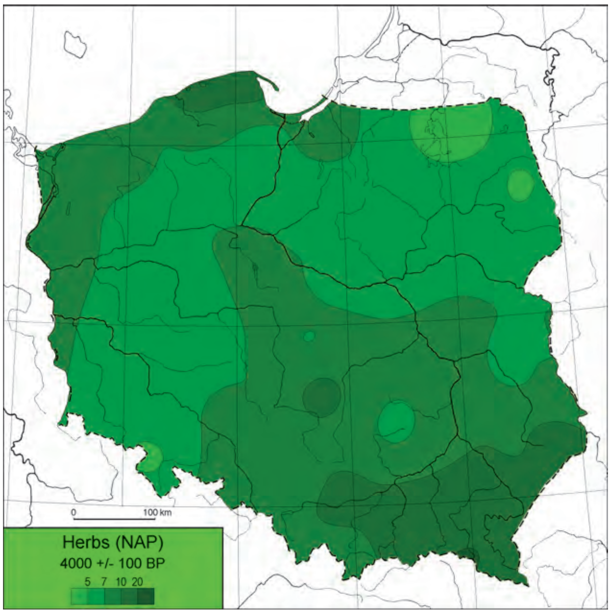
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4000 +/- 100 BP
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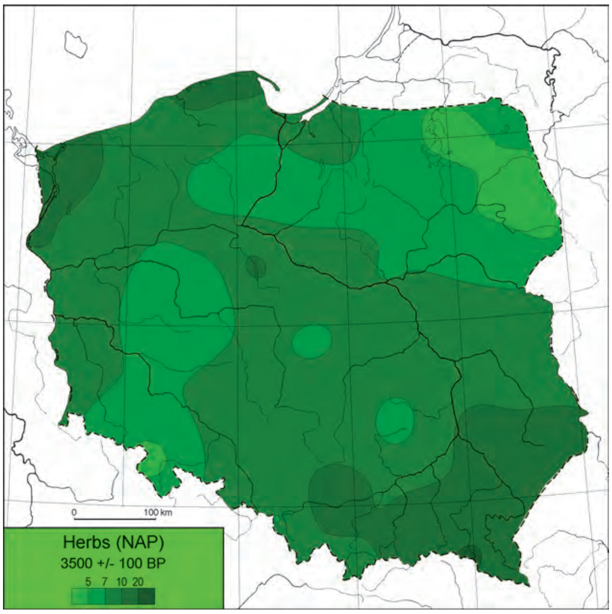
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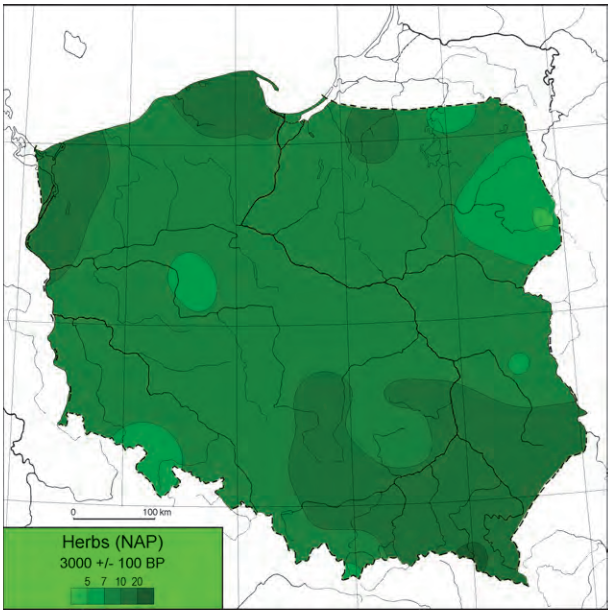
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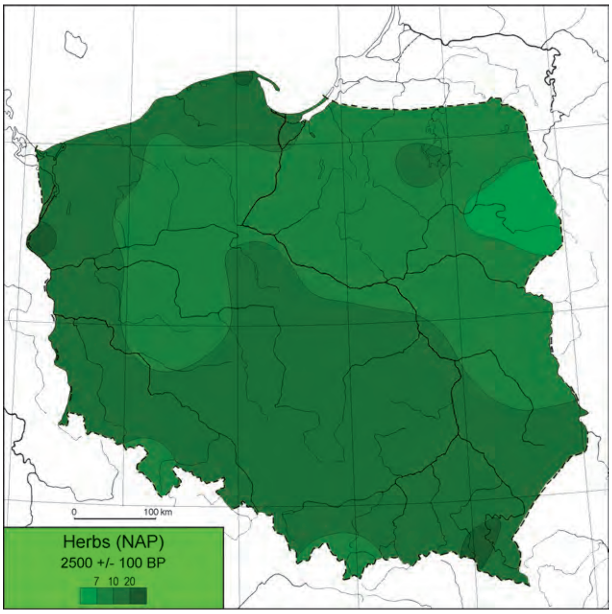
3000 +/- 100 BP
5 7 10 20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100 km
Herbs (NAP)
2500 +/- 100 BP
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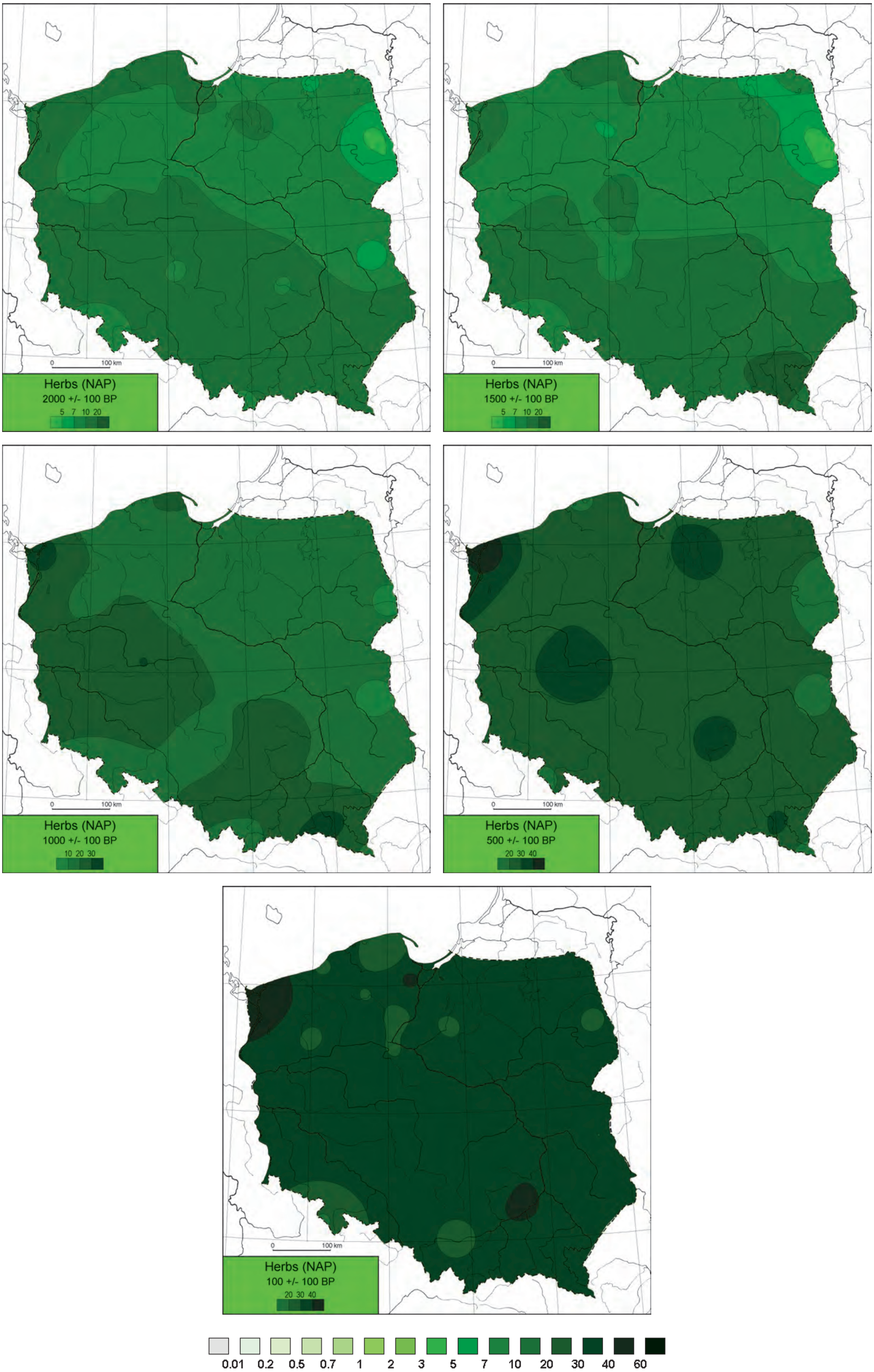
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Herbs (NAP)
2000 +/- 100 BP
5 7 10 20
0 100 km
Herbs (NAP)
1500 +/- 100 BP
5 7 10 20
0 100 km
Herbs (NAP)
1000 +/- 100 BP
10 20 30
0 100 km
Herbs (NAP)
500 +/- 100 BP
20 30 40
0 100 km
Herbs (NAP)
100 +/- 100 BP
20 30 40
0.01 0.2 0.5 0.7 1 2 3 5 7 10 20 30 40 60

Main pattern of palaeoecological events in the Late Glacial and Holocene

LATE GLACIAL

14,000–10,000 ^{14}C yr BP (ca. 15,500 (16,000)–11,500 cal yr BP)

MAŁGORZATA LATAŁOWA

ISOPOLLEN MAPS AS A BASE FOR RECONSTRUCTING VEGETATION HISTORY IN THE LATE GLACIAL – POSSIBILITIES AND LIMITATIONS

Reconstructing changes in vegetation based on the palynological data from Late Glacial sediments requires particular caution concerning both the interpretation of pollen diagrams and the isopollen maps based on these data. More than in the case of Holocene profiles, the pollen composition of these sediments and determination of their age depend on factors that render difficult their unequivocal interpretation. The most important problems regarding the composition of the pollen spectra are as follows:

1. Possibilities of taxonomic identification based on pollen morphology. Identification of pollen grains to the species level is relatively limited considering the variety of forms. In the case of rich pollen floras, and the long list of taxa, pollen types (even of higher taxonomic rank) generally provide sufficient palaeoecological information for reconstruction of the most important plant communities. This information is more complete when a pollen type includes species of the same life form and of similar ecological requirements. In the case of the late Vistulian, lack of precise identification within the most common genera (*Pinus*: *P. sylvestris* (*diploxylon*-type), and *P. cembra* (*haploxylon*-type); *Betula*: *B. nana*-type (dwarf shrubs), and *B. alba*-type (trees); *Salix*: *S. herbacea*-type and *S. polaris*-type (dwarf shrubs) and *S. pentandra*-type (shrubs and trees)) may lead to completely wrong interpretation even at the level of reconstruction of plant formations (compare chapters concerning particular taxa, this volume).

2. Contribution of pollen from long-distance transport. Pollen spectra always contain some admixture of pollen brought from a considerable distance. However, in woodless areas covered with poor vegetation, the amount of pollen from long-distance transport may be several times higher than that produced by local vegetation (Aario 1940, Tipping 1989). Such regularities must have also occurred in the Late Glacial in Poland.

3. Contamination of sediments with redeposited pollen. Activity of the ice-sheet and its meltwaters uncovered older substrate, exposing it to erosion. In the Late Glacial conditions with poorly developed vegetation the stabilization of the surface was very slight, so lake and peat sediments were all enriched with the allochthonous material brought to the basins by water and wind. Apart from the mineral particles, pollen occurring in the older geological deposits was thus also eroded and then redeposited. This pollen originated not only from exotic species, which are easy to be distinguished, but also from the taxa of the most common tree genera occurring in the late Quaternary. The contribution of reworked pollen to the sediments of the cold periods of the Late Glacial may reach from a few to tens of percent. In reconstruction of the isopollen maps only highly contaminated samples were excluded, so it can be assumed that the values may to some extent record also the presence of the older material.

The uncertainty in age determination of the Late Glacial sediments and the pollen spectra results mostly from the following reasons:

1. Frequent discontinuity of sediments (presence of unconformities) resulting from intensive erosion.

2. Low content of organic matter in the sediments and the risk of natural contamination with older or younger geological material. The Late Glacial deposits in general are characterized by material eroded from older strata. These are both the mineral particles and material containing organic carbon, which may cause radiocarbon dates that are too old. On the other hand, because of melting and degradation of permafrost mixing of sediments may have occurred, resulting in inversion of radiocarbon dates (Latałowa & Nalepka 1987). Abundant supply of mineral material results also in decreasing amount of organic matter in sediments. When the classical ^{14}C method of dating is applied it is necessary to use large samples, i.e. sections of profiles several centimetres long; in such cases the age determination cannot be precise. This last problem has been recently eliminated by

applying the method of AMS (Accelerator Mass Spectrometry) radiocarbon dating, which permits dating of an individual seed. Unfortunately, among the materials used for the isopollen maps only a few profiles have AMS dates (for example Lake Gościąż, Ralska-Jasiewiczowa et al. 1998, Lake Perespilno, Goslar et al. 1999).

3. Reservoir effect. Most organic matter deposited in lake sediments is derived from decomposition of remains of aquatic organisms. These organisms use in their physiologic processes not only atmospheric carbon but also carbon in the water, often much older, derived either from the sediments accumulated earlier or from the material eroded from older geological formations occurring in the vicinity of the reservoir. This makes the radiocarbon ages older.

4. Occurrence of so called 'radiocarbon plateaux'. At the decline of the last glaciation 'a radiocarbon clock' stopped a few times, and for this reason the ^{14}C dates of samples from successive layers display the same or very similar age in spite of passing time and sediment accumulation (Ammann & Lotter 1989, Stuiver et al. 1998). Radiocarbon plateaux cover a part of the Bølling and the Younger Dryas/Holocene transition. In such cases more precise age determination has to be based on methods other than radiocarbon dating. The presence of sediments built of annual lamination permits the most valuable dating (Ralska-Jasiewiczowa et al. 1998, Brauer et al. 1999, Litt et al. 2001), but occurrence of such sediments is very rare (in Poland only 3 sites with Late Glacial lamination have been studied so far). For these periods the age estimation is based on the sequence of events recorded in the pollen diagram by comparison with the established bio- and chronostratigraphic schemes (palynological dating).

These factors limit interpretation of pollen diagrams from the Late Glacial and thus the information contained in the isopollen maps. However, other factors, which may deform to some extent the history of a particular taxon and of vegetation changes that we try to read from the analysis of series of isopollen maps, are also included in the methods for preparation of the maps. The most important are as follows:

1. Accepted time horizons. In the work presented the equal time intervals of 500±100 years are applied. This may not fully reflect the chronology of palaeoecological events occurring during the period in question.

2. The number and distribution of sites over the area and the accepted model for drawing the isopollen maps. The maps for the period of 14,000–12,000 ^{14}C BP are based on a small number of unevenly distributed sites. Data are sparse for the Sudetes and the greater part of western Poland, and this situation improves only slightly during the succeeding periods. That is why the description of vegetation development takes into account the specific character of these areas only to a small degree. The method accepted for drawing of the isopollen maps (Nalepka & Walanus, this volume) assumes adequate models of interactions of values among the sites. Special attention is required for interpretation of the isopollen patterns in the areas of sparse network of sites, and when the sites of strongly contrasting pollen percentage values appear on the maps.

The above mentioned remarks concerning the natural and methodological limitations of the palynological data for the Late Glacial sediments, and particularly of the isopollen maps, should facilitate the understanding of necessary simplifications, which are accepted in description of the vegetation history for this period. On the other hand, the isopollen maps offer a unique possibility of reconstructing the migration routes of particular taxa as well as changes in vegetation on regional and supraregional scales. Indirectly, while analysing the isopollen patterns of particular taxa and groups of taxa displaying specified bioindication features with respect to thermic and/or moisture conditions, we get a basis for past climatic regionalization of an area studied as well as data for reconstruction of the changes in palaeoclimate.

HISTORY OF VEGETATION (Fig. 102)

The dot maps for the older part of the Late Vistulian are based on a number of sites too small to draw the more comprehensive conclusions for a regional differentiation of vegetation in Poland during this period. The description presented below is complemented with the information given by original pollen diagrams.

On the 14,000–13,000 yr BP maps, which correspond with the Oldest Dryas and maybe with the preceding Meiendorf phase (Litt 1988, Litt et al. 2001) the most important component of the pollen spectra is pollen of herbs. High contributions of Cyperaceae, Poaceae (Gramineae), and several heliophytes (*Artemisia*, Chenopodiaceae, *Helianthemum*, and *Dryas octopetala*) indicate the presence of the Late Glacial steppe-tundra. Willows were an important component of vegetation. Their pollen is not always determined precisely, however, at some sites the occurrence of dwarf willows was recorded (*Salix herbacea*-type and *S. polaris*-type). Dwarf birch (*Betula nana*) is a species that has not been presented separately on the isopollen maps because it has been determined only at a few sites. However, even from this incomplete data we may conclude that it played an important role in the plant communities, and its macroremains are known from some sites (Wasylikowa 1964, Ralska-Jasiewiczowa 1966, Latałowa & Nalepka 1987, Litt 1988). *Juniperus* (*communis*) and *Hippophaë rhamnoides* belong to the oldest elements of vegetation in the whole country. Their role increased during succeeding periods of the Late Glacial. Sea-buckthorn was then a component of vegetation mainly in those areas that earlier were within the range of the last glaciation.

Migrations of particular tree species and formation of forest communities belong to the most interesting research problems concerning the succession of vegetation in the Late Glacial. Considerable contribution of *Pinus* and *Betula* pollen occur in the oldest sections of profiles located particularly in north-eastern Poland. This pollen most likely comes from the long-distance transport but partly also from the contamination of sediments with the older geological material. It can only be assumed that some *Betula alba*-type pollen represents *B. pubescens* subsp. *tortuosa*, whose present geographical range reaches the Arctic today. The only site from which macrofossils of this subspecies have been determined is Lake Mikołajki (Ralska-Jasiewiczowa 1966). Other species of trees that probably survived the last glaciation in the Carpathian valleys of Poland are: *Populus tremula*, *Pinus sylvestris*, *P. cembra*, *Picea abies*, and *Larix decidua*. This is documented by the very early presence of their pollen in the Late Vistulian sediments in the area of the Carpathians and their piedmont, often confirmed by macroscopic finds (Koperowa 1970, Ralska-Jasiewiczowa 1980, Harmata 1987, Obidowicz 1996). Moreover, numerous sites of their occurrence are known from various phases of the Pleni-Vistulian (Mamakowa 1968, Środoń 1968, Mamakowa & Starkel 1974, Ralska-Jasiewiczowa 1980). It is thought that in the period discussed here a cold, arctic or sub-arctic climate with the mean temperatures of June about 10°C (Ralska-Jasiewiczowa et al. 1998) or even 13°C (Wasylikowa 1964) prevailed in central Poland.

Data for the time horizons 12,500–12,000 yr BP are also based on a relatively small number of sites. Taking into account the generalized picture presented on the isopollen maps and the accepted time intervals, it can be assumed that these maps represent the Bølling interstadial. It has been impossible to find evidence of the Older Dryas cooling (12,000–11,800 yr BP), which should have been recorded on the 12,000 yr BP map. This short episode, lasting only about 200 years, connected with the recurrence of cold and continental climate, is not always identified in the palynological profiles in Europe and Poland (Tobolski 1998). This may be caused by the presence of unconformities in the sediments, too great distance between analysed samples, and poor palynological record resulting from local features of climate and plant communities (Latałowa 1988a). This brief change of climate influenced mainly the vegetation developing on unstable habitats (dune and loess areas), as well as plant communities occurring at the geographical distribution limits of particular tree species. Thus in Poland the picture of the Older Dryas in pollen diagrams is fragmentary, probably one of the reasons that it has not been recorded on the isopollen maps.

During the Bølling there was mainly the expansion of the tree birches. Open birch forests with willows, aspen, and in some areas also pine spread mainly in central and eastern Poland. High values of *Hippophaë rhamnoides* in the Wielkopolska and in some parts of northern Poland suggest that the northern limit of birch forests may have extended there at this time. Northwards, park tundra with juniper developed. Larch was a component of forest-tundra in the Mazurian Lake District as well as of the parkland communities in other regions of lowland and upland areas. In the south, particularly in the Carpathian slopes and in their piedmont birch had a less significant role, whereas *Pinus sylvestris*, *P. cembra*, *Picea abies*, and *Larix decidua* were important components of the forests. The steppe vegetation (*Artemisia*, Chenopodiaceae) was widespread, particularly in the eastern regions of the country. Stands of humid tundra with the representatives of Arctic-Alpine and Arctic-Boreal elements such as *Selaginella selaginoides*, *Betula nana*, and others were common in the whole country. Pollen of aquatic and mire species considered to be climate indicators include *Typha latifolia*, presented on the isopollen maps, indicating amelioration of climate during this period (Wasylikowa 1964, Tobolski 1988, 1998). The climate of the Bølling in central Poland is described as boreal or even temperate, with the mean temperature of July reaching 15–16°C (Wasylikowa 1964, Tobolski 1998).

The time range of the maps 11,500–11,000 yr BP includes the Allerød (11,800–10,700 ^{14}C yr BP). This period was climatically differentiated (Björck et al. 1998, Litt et al. 2001). In Poland it is traditionally divided into two phases: in the older phase has forests dominated by birch (birch phase), whereas in the younger phase the role of pine increased (pine phase). This type of succession is marked in the pollen diagrams from the sites in the lowland areas of Poland, where a more nearly complete sediment record of this period has been found (Wasylikowa 1964, Litt 1988). The isopollen maps reflect the above process known from the pollen diagrams. At the decline of the Allerød (map 11,000 BP), the proportion of *Pinus* pollen reaches the highest values as recorded for the whole Late Glacial – Holocene period. Also the isopollen maps for *Betula* illustrate gradual reduction in birch occurrence due to the expansion of pine, and in the uplands and mountains also of larch. In the Carpathians the proportions of *Pinus cembra* increased, and expansion of spruce proceeded from the eastern Carpathians. Small admixture of spruce and possibly also of alder may have occurred in the upland areas of Małopolska. The forests of northern and central Poland were poorer in the number of species. Aspen occurred there together with birch and pine, and a looser structure of woodlands provided favourable light conditions for juniper growth. On the 11,500 yr BP maps the contribution of open-land vegetation is the lowest in the whole Late Glacial period. The isoline pattern for the steppe components (*Artemisia* and Chenopodiaceae) suggests regional differentiation of the country concerning climate – higher contribution of steppe elements was characteristic of the eastern areas with more continental climate. The 11,000 yr BP maps represent the close of the Allerød, which was characterised by the cooling of climate, forecasting the approach of the Younger Dryas (Schwander et al. 2000). Once more there was westward expansion of steppe communities resulting from continentality of climate progressing in this direction. The isolines still show the same pattern of previous division of the country into the eastern and western parts.

In the Allerød the climatic conditions not only favoured development of forests but also enabled further spread of the species of higher thermic requirements, particularly of aquatic and telmatic types. The number of sites at which the presence of *Typha latifolia* has been noted increased at this time. According to the estimations made so far the mean July temperatures fluctuated in central Poland between 13° and 16°C (Wasylikowa 1964, Ralska-Jasiewiczowa et al. 1998). Development of the forests, lasting for a few hundred years, contributed to stabilization of substrate and development of incipient soils (Borówka et al. 1986, Latałowa 2001).

The 10,500 yr BP maps illustrate changes caused by the cooling of climate in the Younger Dryas (10,700–10,000 yr BP). An analysis of these maps implies that the reaction of vegetation to the cooling of climate was not the same in the whole country. Two types of gradient changes are observed: from east to west (steppe elements) and from north to south (forest species).

Transformation of forest vegetation proceeded throughout the country. It had the most drastic course in areas previously occupied by the ice sheet, where the succession of the forest communities was less advanced during the Allerød (Latałowa 1999a). It was also very distinct in the mountains (Ralska-Jasiewiczowa 1980) and in sandy areas, where dune-forming processes were activated (Wasylikowa 1964, 2001). Reduction in birch and aspen proportions, and in Western Pomerania particularly in pine, enabled the spread of heliophilous communities, with considerable contribution of juniper. The elements of cold steppe (*Artemisia*, Chenopodiaceae, *Helianthemum*) spread in drier habitats, and the species typical of tundra (*Dryas octopetala*, *Betula nana*, *Selaginella selaginoides*, and many others) in more humid places.

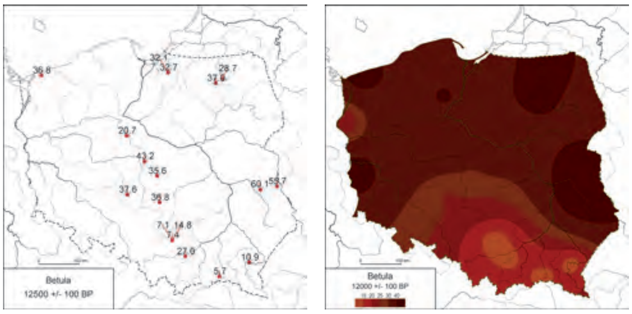
In the north the dominating type of plant formations was forest-tundra, with not only abundant juniper and dwarf birch (*Betula nana*) but also *B. humilis*, *B. pendula*, *B. pubescens*, *B. pubescens* subsp. *tortuosa*, and *Pinus sylvestris*, all documented by finds of macrofossils (Latałowa 1999a). Birch-pine forests with juniper in a parkland character prevailed in the lowland landscape of central Poland (Wasylikowa 1964, Litt 1988, Ralska-Jasiewiczowa et al. 1998). These communities were characterized by higher proportions of pine and lower contribution of juniper than in northern Poland. Species typical of tundra and steppe played a less significant role in this area. The eastern regions of Poland were characterized by a high contribution of steppe elements with *Artemisia* and representatives of the Chenopodiaceae family. The open forests dominating in the uplands and in the Carpathian foothill zone contained a considerable contribution of *Larix decidua*, *Pinus sylvestris*, *Betula*, with an admixture of *Picea abies*. Open-land communities present in these areas were of relatively minor importance in comparison with the areas discussed above. The Carpathian forests with *Pinus sylvestris*, *P. cembra*, *Larix*, and *Picea abies* were more open. The role of grasslands and landslide vegetation increased in these areas, and at the same time the timber line lowered (Ralska-Jasiewiczowa 1980, Obidowicz 1996).

At the end of the Younger Dryas several short climatic fluctuations occurred that generally were characterized by higher temperatures but showed different level and seasonal variability of precipitation (Ralska-Jasiewiczowa et al. 2003a). Amelioration of climate enabled consolidation of the forest communities, particularly the fast spread of birch and pine and at the same time disappearance of steppe-tundra and forest-tundra elements. Spruce continued further migration. The beginning of these processes, which proceeded in the Holocene, is illustrated by the isopollen maps for the 10,000 yr BP time-horizon.

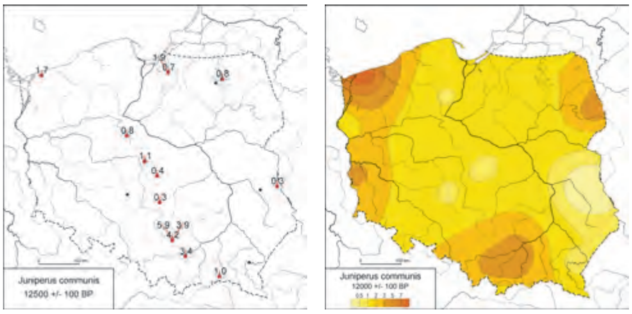
It is estimated that during the cooler phase of the Younger Dryas the mean July temperatures in central and northern Poland may have dropped down to 10°C, whereas during the warmer phase they were not lower than 12°C (Wasylikowa 1964, Tobolski 1998, Latałowa 1999a).

Fig. 102 (p. 390–391). Isopollen maps of selected tree and herb taxa illustrating vegetation changes during the period 12,500–10,000 yr BP

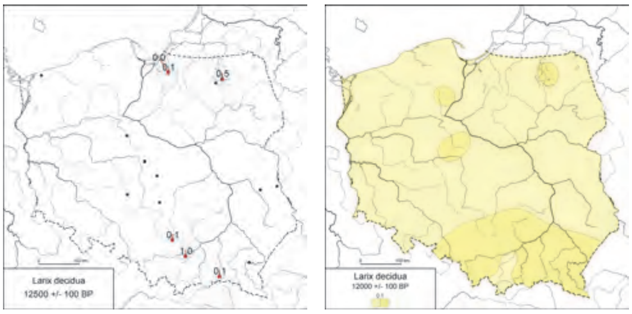
Betula



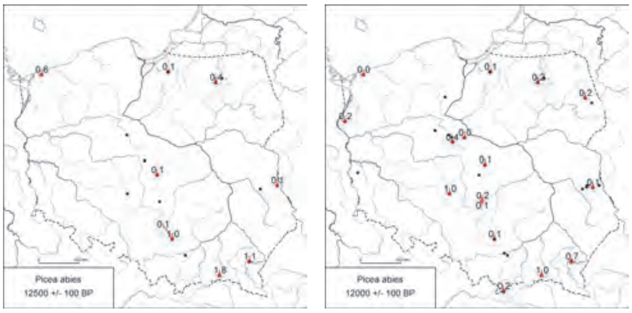
Juniperus communis



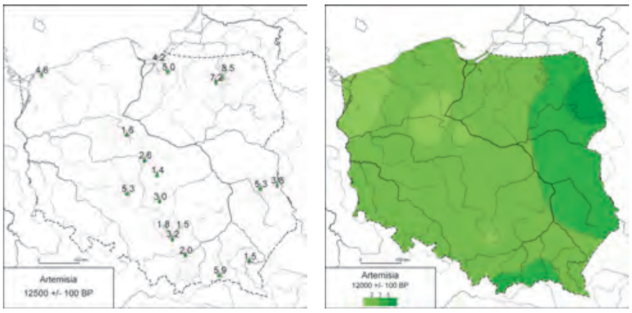
Larix decidua



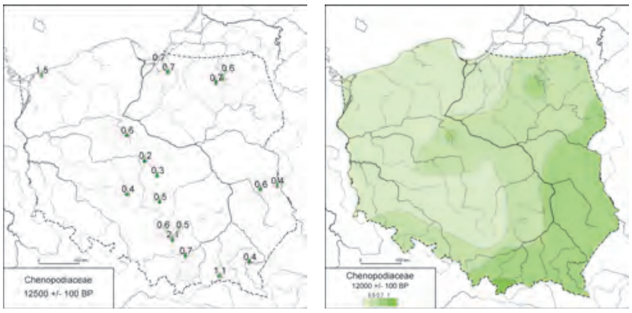
Picea abies

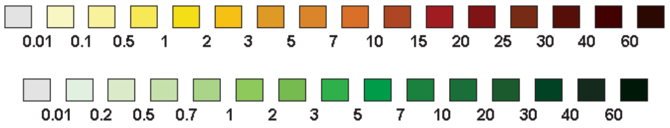


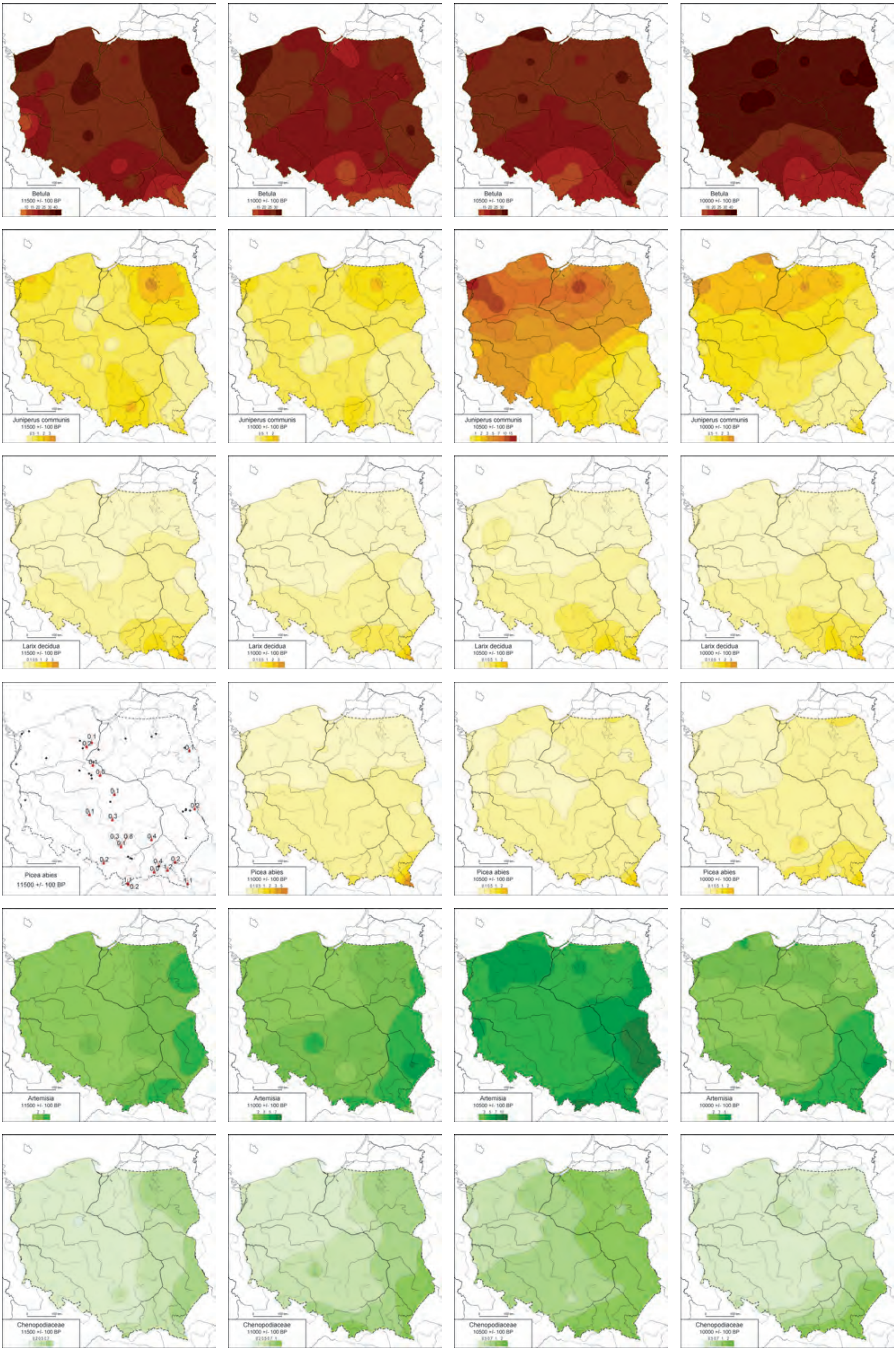
Artemisia



Chenopodiaceae






Betula
11500 +/- 100 BP
Betula
11000 +/- 100 BP
Betula
10500 +/- 100 BP
Betula
10000 +/- 100 BP
Juniperus communis
11500 +/- 100 BP
Juniperus communis
11000 +/- 100 BP
Juniperus communis
10500 +/- 100 BP
Juniperus communis
10000 +/- 100 BP
Larix decidua
11500 +/- 100 BP
Larix decidua
11000 +/- 100 BP
Larix decidua
10500 +/- 100 BP
Larix decidua
10000 +/- 100 BP
Picea abies
11500 +/- 100 BP
Picea abies
11000 +/- 100 BP
Picea abies
10500 +/- 100 BP
Picea abies
10000 +/- 100 BP
Artemisia
11500 +/- 100 BP
Artemisia
11000 +/- 100 BP
Artemisia
10500 +/- 100 BP
Artemisia
10000 +/- 100 BP
Chenopodiaceae
11500 +/- 100 BP
Chenopodiaceae
11000 +/- 100 BP
Chenopodiaceae
10500 +/- 100 BP
Chenopodiaceae
10000 +/- 100 BP

EARLY HOLOCENE

10,000–7500 ^{14}C yr BP (ca. 11,500–8300 cal yr BP)

MAGDALENA RALSKA-JASIEWICZOWA

Rapid warming of climate at ca. 10,000 BP opened the climatic cycle of the Holocene interglacial, which has lasted up to the present. The temperatures were similar to the modern ones, but the insolation and the continentality were higher, and seasonality was marked by shorter transition periods between summer and winter (Birks 1986).

This caused initially (10,000–9500 yr BP) the expansion of trees that had survived the cooling of the Younger Dryas *in situ*. These were mainly birches and pine. *Betula* was shown by pollen amounts up to 50% in north-eastern, mid-eastern (Polesie Lubelskie) and mid-western (Wielkopolska) Poland, and up to 40% throughout other parts of the lowland (Fig. 103). In the mountains and their piedmonts the contribution of *Betula* was much lower. The abundance of *Pinus* in the lowlands was similar or greater, dominating distinctly over *Betula* in the uplands and mountains. In the mountainous regions and their foothills the other coniferous trees expanded from local refugia. These were *Larix*, *Pinus cembra*, and also some *Picea excelsa*, and the trees reaching today the highest montane forest zone, *Populus tremula* and *Sorbus aucuparia*, grew in the lower tree layer of those forests.

The forests of that time were more open and well lighted, particularly in the mountains and in the southern uplands, as indicated by values of herb pollen sum reaching (without Cyperaceae) up to 30% at ca. 9500 yr BP. In south-eastern Poland considerable amounts of *Artemisia* and Chenopodiaceae still occurred. These remnants of steppe-like communities decreased distinctly towards 9500 yr BP. In the lake districts of northern Poland *Juniperus* played yet an important role in the open places and forest undergrowth. At the same time in the southern, central, and partly in the north-eastern part of the country the tall-herb communities with *Filipendula* (*ulmaria*?) and grasses started to spread. The development of *Pinus-Betula* forests continued, and *Betula* reached its maximum to the east of the Vistula river, while *Pinus* became common in the whole country. At this time *Corylus* appeared in Poland, at first scattered throughout the country, but locally – in the lake districts and in the Bieszczady Mountains – it had already occurred more abundantly.

After 9500 yr BP the role of *Betula* in the woodlands gradually diminished. By 9000 yr BP its highest representation persisted in north-eastern Poland as far west and south as the Vistula and Narew river valleys, in the Wielkopolska area, and in the marshes of Polesie Lubelskie. It gradually became reduced southwards in the upper Vistula river catchment area, and in the Beskid Niski range and its foreland. At ca. 8000 yr BP the participation of *Betula* in the forests still decreased throughout the country, especially in the lowlands, with higher amounts persisting only in the Polesie Lubelskie. In southern Poland the pattern of *Betula* representation appeared rather stable. The occurrence of *Pinus* persisted still at a high level throughout the country, showing no increase. It seems that *Betula* was ousted from the mountains and foothills not by *Pinus*, but at first by *Ulmus* and then, between 8500–8000 yr BP, also by *Corylus*.

Ulmus started its migration through the mountains from the south and south-east before 9500 yr BP. Its refugia must have been not far away, as its presence was recorded by a pollen curve of a few percent in the Carpathian range in north-western Romania as early as the Allerød (Björkman et al. 2002). It was most probably *Ulmus scabra* – mountain elm. The later appearance of *Ulmus* in north-eastern Poland (at 9000 yr BP) could have been connected with another species (*U. laevis*?), whose refugia, as supposed by Huntley & Birks (1983), may have been located in Russia (the southern Ural?). *U. minor* may have migrated from southern Europe. The existence of other 'crypto-refugia' of deciduous trees, including *Ulmus*, in different regions of Europe also cannot be excluded (Kullman 1998, Stewart & Lister 2001). Later, the mountain centre of *Ulmus* extended north-eastwards and combined with the north-eastern centre (8500 yr BP), resulting finally (8000, 7500 yr BP) in covering the remaining parts of the country with scattered, but substantial distribution.

Assumption of ‘crypto-refugia’ concerns also *Corylus* (Stewart & Lister 2001), the distinct expansion of which into Poland from the north-west took place at about 9000 yr BP. Its simultaneous entrance from the south-west and the north is also recorded at that time. By 8500 yr BP *Corylus* expanded in north-western Poland and later (8000 yr BP) migrated towards the south, reaching its maximum Holocene coverage of the country during the next millenium.

Quercus was the next genus reaching Poland. Unfortunately we can say nothing about the distribution of its species, not determinable in pollen analysis. Directions of *Quercus* migrations are not clear enough. The palynological data (Bennett et al. 1991), as well as molecular studies (Taberlet et al. 1998, Hewitt 1999, Mátyás & Sperisen 2001) suggest the occurrence of a few southern refugia of *Quercus* between the Iberian Peninsula and the Balkans. Huntley and Birks (1983) consider the existence for another refugium in the Caucasus. A possible occurrence of crypto-refugium of *Quercus* in Belgium has also been suggested (Otte 1994, Stewart & Lister 2001). This might explain its migration into Poland from the north-west, which is reflected in the isopollen maps. However, the beginnings of *Quercus* expansion recorded in the diagrams from Holland (van Geel et al. 1980/81) or from north-western Germany (Kubitz 2000) do not differ with respect to age from those in Poland.

At ca. 9000 yr BP very low *Quercus* pollen values appear in south-eastern Poland and in the area of the Moravian Gate, locally occurring also in the Nida Basin. At the same time *Quercus* pollen percentages in central Poland do not exceed 1%. However, the trunk of black oak from Lublinek (Łódź Upland), dated to 9200±70 BP (Goslar & Pazdur 1985), proves that locally growing *Quercus* may be recorded by quite low pollen values of this taxon. So, the limit of 2% accepted by Huntley and Birks (1983) for local presence of *Quercus* seems to be too cautious. Another *Quercus* trunk, dated to 8390±100 yr BP, has been found in the Oświęcim Depression (Krąpiec 1992), where *Quercus* pollen values are 2–3% on the 8500 yr BP map. By about 8000 yr BP a steady increase in *Quercus* pollen values in almost the whole country apart from the Baltic Coastal Zone, the Podlasie Lowland in the north-east, and the Bieszczady Mountains, indicates its widespread significant contribution to the forests. At ca. 7500 yr BP a distinct expansion wave of *Quercus* from the north-west is marked, as its approach could be foreseen from the two preceding maps.

Between 9000 and 8500 yr BP *Tilia* appeared in southern Poland (*Tilia cordata* and/or *T. platyphyllos*). It shows a distinct migration route through the central, low part of the Carpathians recorded at ca. 8000 yr BP. The other smaller centre appears also in north-eastern Poland. The glacial refugia of *Tilia* were probably located not only in the Balkan and Apennine Peninsulas, but also in the southern and south-eastern margins of the Alps (Lang 2003). *Tilia* pollen was also found in the Late Glacial sediments from the foothills of the Southern Carpathians (Farcas et al. 1999).

The first evidence of a local scattered appearance of *Fraxinus exelsior*, spreading from the Western Carpathians north-eastwards, may be seen about 8500 yr BP, and this tendency can be traced on the 8000 and 7500 yr BP maps. On the 8500 BP map another migration route from the east is indicated. The new molecular investigations recognized the refugial sources of common ash occurring today in Europe (Heuertz et al. 2004). Out of 12 haplotypes found, only two, most common ones, have been stated in Poland. The haplotype widespread over central Europe is supposed to come from the east-Alpine refugium, from where it might begin its expansion at ca. 9500 BP as suggested by fossil pollen data (Huntley & Birks 1983). This one has been found at the south-western extremes of Poland and in Pomerania. The other, east-European-Scandinavian haplotype, widely distributed in Romania, Moldova, Bulgaria and Macedonia, had possibly its refugial area in southern Romanian Carpathians. This haplotype occurs abundantly in south-eastern Poland up to Podlasie Upland, and in western Pomerania. *Fraxinus* is a poor pollen producer, and the picture of its expansion is poor on the isopollen maps however, the quoted data seem to be in accordance with the isopolls pattern.

Picea had its glacial refugia very close, in the different parts of the Carpathians (*Picea*, this volume). The East-Carpathian spruce, expanding in the north-west Romania and appearing in the Polish part of the Bieszczady Mountains already during the Allerød, spread there from before 9500 BP, occupying mostly the cool and humid valley floors, and entering even the mires. In the West Carpathians spruce started to expand from 9000 BP. Here, and later (8000 BP) also in the Sudetes, it occupied the higher montane forest zone, causing the shift in the upper tree limit to the higher altitudes.

It is estonishing that the spruce from the most part of the Western Carpathians reveals the same centre-Carpathian haplotype as the spruce from the Bieszczady Mountains and from the adjoining ranges of Eastern Carpathians (Bucci & Vendramin 2000). The studies on the morphological types of cones (Staszkiewicz 1977) have shown very distinct differences between the East-Carpathian (including the Bieszczady), and the West-Carpathian (including also partly the Sudetes) types. This allowed to distinguish those types of spruce as the different varieties: East-Carpathian var. *acuminata*,West-Carpathian var. *abies*, occurring also partly in the Sudetes, and the third one var. *alpestris*, occurring in minority in the West Carpathians, but more abundant in the higher altitudes of the Sudetes. It seems that the West-Carpathian spruce genetic zone of Bucci & Vendramin (2000) could correspond roughly with the var. *alpestris* of Staszkiewicz (1977), however centre-Carpathian zone would include two, very strongly differing varieties – western var. *abies* and eastern var. *acuminata*.

Between 8500 and 8000 yr BP, all the most important trees encroached on the territories of Poland and the development of mesophilous mixed deciduous forests could begin.

The existence of favourable climatic conditions is shown by the appearance of *Viscum* and *Hedera helix*. Mistletoe is assumed to be a climatic indicator of warm summers and autumns, with mean temperature of the warmest month above 16°C, and ivy not exceeds the isotherm of –2°C in the coldest winter month (Iversen 1944). *Viscum* appears already at ca. 9000 and 8500 yr BP in the very warm regions of Kujawy and Wielkopolska, spreading its range on the succeeding maps. *Hedera* occurs from 8500 yr BP in southern Poland, and later appears in central lake districts at the north. It is very rarely recorded from other parts of Poland, and does not appear in the early Holocene in the eastern regions of the country.

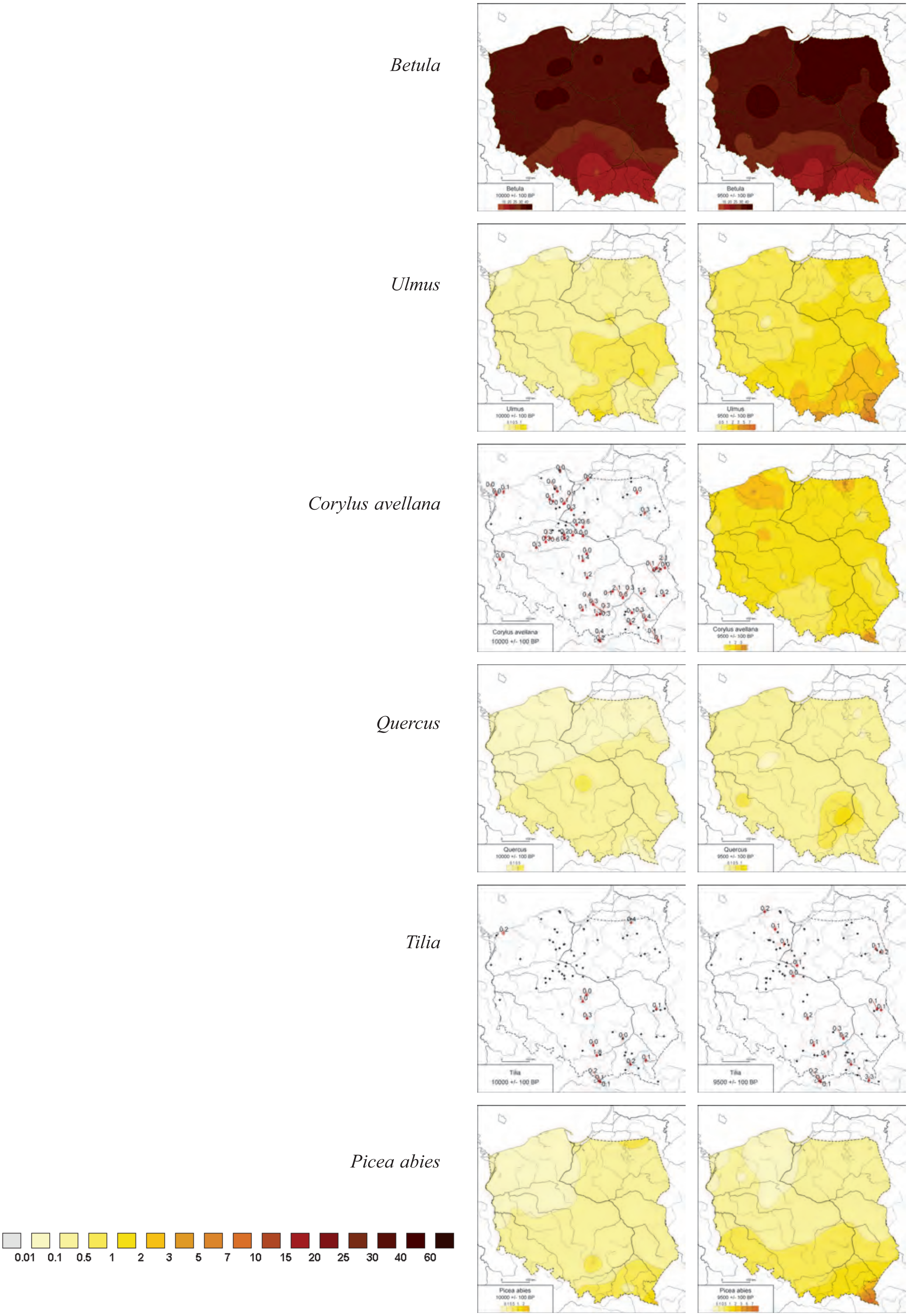
Between 9000 and 8500 yr BP both *Alnus glutinosa* and *A. incana* immigrated from the south through the low central part of the Carpathians. The studies on *Alnus glutinosa* DNA suggested location of its refugia within the Carpathians (King & Ferris 1998). *Alnus glutinosa* settled in various low wet areas, *Alnus incana* together with *Ulmus* and *Fraxinus* formed riparian forests along the rivers and streams in mountains and mountain foothills. *Alnus* species migrated along the Vistula river basin northwards, and by about 8000 yr BP they spread into the lowlands, where they occupied habitats similar to those they colonized in the south.

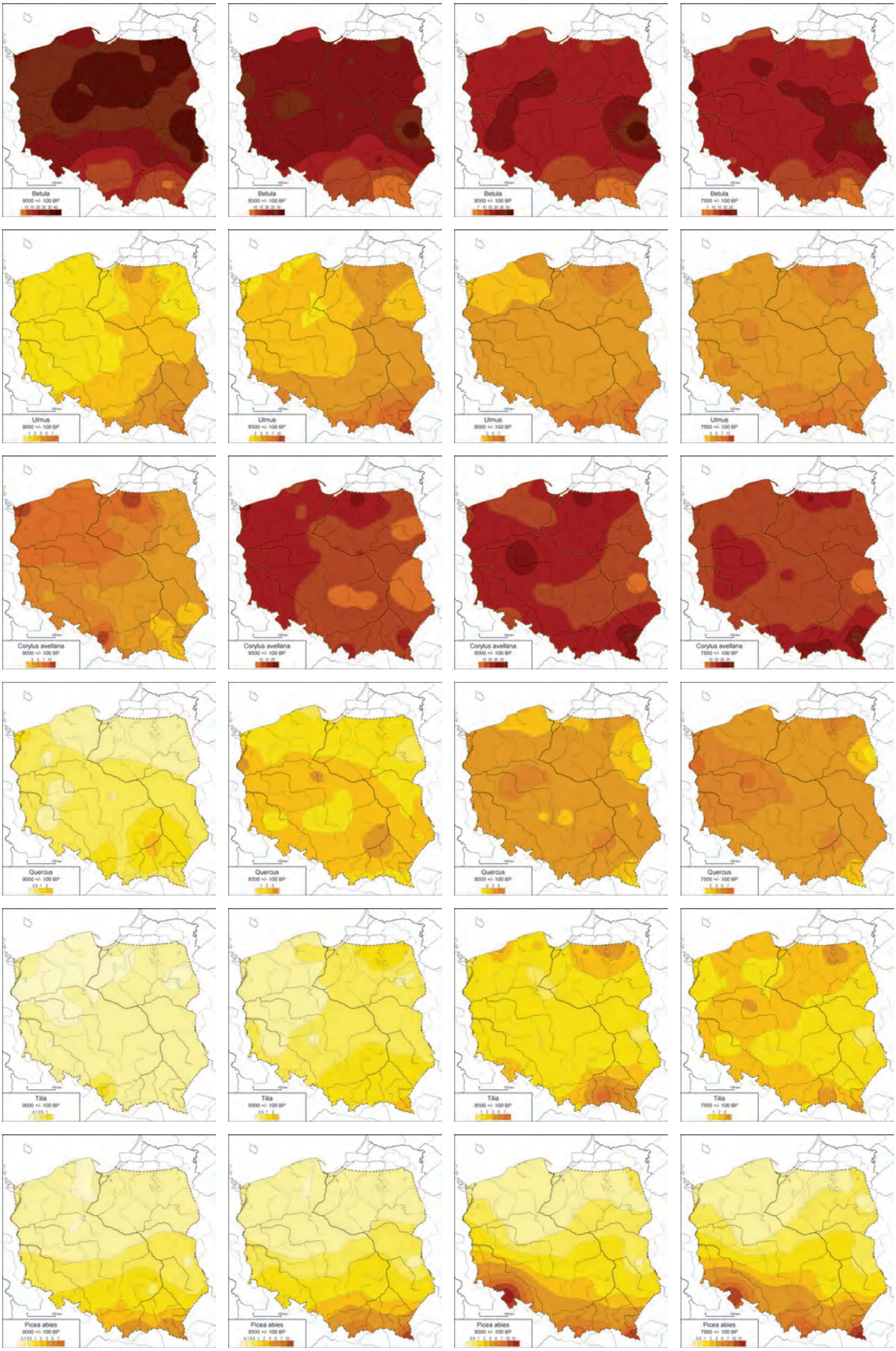
Summarizing, we can say that the directions from the south and south-east were very important routes of arrival for new tree species, as the Carpathians appear to have been one of the main refugial areas for the forest trees during the Vistulian glaciation. The most important routes led along the Bieszczady Mountains, through the low middle part of Polish Carpathians, and also via the Moravian Gate. For *Ulmus*, *Tilia*, *Fraxinus*, *Alnus* those passages were the main routes, and for *Corylus* and *Quercus* they were probably the additional migration tracks only. In the lowlands the direction from the north-west seems to mark an important way of migration as both *Corylus* and *Quercus* developed their main expansion front along this route, though at different times. Moreover, additional less distinct migration routes from the north-east are marked on the maps of *Ulmus*, *Quercus*, *Tilia*, and *Alnus*. However, their importance is difficult to estimate. They may have been connected with the crypto-refugial areas of the tree species mentioned above.

Thus the period discussed was the time of continuous plant migrations and vegetation changes on the territory of Poland, connected with the formation of new types of forest communities, caused by the immigration of mesophilous deciduous trees. *Pinus* still played an important role in some types of forests, particularly on poor sandy soils as well as on waterlogged habitats, even mires. On light soils grew also *Betula pendula*, while *B. pubescens* preferred wetter, often peaty substrates. As the higher herb pollen values recorded at this time in southern Poland were distinctly connected with a type of sites that contained mostly Cyperaceae, this pollen taxon has been excluded from the NAP sum.

While analysing the progressive formation of new vegetation types we are inclined to compare them with the composition of the modern forest communities. However, it should be borne in mind that the Preboreal/Boreal forests were at the very early phases of their development. Species were in the course of migration, the competition was at the initial stage. In the early Holocene the migration processes were the main factor influencing dynamics of the forest communities, as proven by simulation models (Keller et al. 2002). Only the succeeding millennia brought some stabilization of the newly-formed communities based on a balance between habitat, ecological demands of particular species, and competition among different plants.

Fig. 103 (p. 396–397). Isopollen maps of selected tree taxa illustrating vegetation changes during the period 10,000–7500 yr BP


Betula
Betula 10000 +/- 100 BP
Betula 9500 +/- 100 BP
Ulmus
Ulmus 10000 +/- 100 BP
Ulmus 9500 +/- 100 BP
Corylus avellana
Corylus avellana 10000 +/- 100 BP
Corylus avellana 9500 +/- 100 BP
Quercus
Quercus 10000 +/- 100 BP
Quercus 9500 +/- 100 BP
Tilia
Tilia 10000 +/- 100 BP
Tilia 9500 +/- 100 BP
Picea abies
Picea abies 10000 +/- 100 BP
Picea abies 9500 +/- 100 BP
0.01
0.1
0.5
1
2
3
5
7
10
15
20
25
30
40
60


Betula
9000 +/- 100 BP
10 15 20 25 30 40
Betula
8500 +/- 100 BP
10 15 20 25 30
Betula
8000 +/- 100 BP
7 10 15 20 25 30
Betula
7500 +/- 100 BP
7 10 15 20 25
Ulmus
9000 +/- 100 BP
1 2 3 5 7
Ulmus
8500 +/- 100 BP
2 3 5 7 10
Ulmus
8000 +/- 100 BP
3 5 7
Ulmus
7500 +/- 100 BP
3 5 7 10
Corylus avellana
9000 +/- 100 BP
3 5 7 10
Corylus avellana
8500 +/- 100 BP
10 15 20
Corylus avellana
8000 +/- 100 BP
10 15 20 25
Corylus avellana
7500 +/- 100 BP
10 15 20 25
Quercus
9000 +/- 100 BP
0.5 1 2
Quercus
8500 +/- 100 BP
1 2 3
Quercus
8000 +/- 100 BP
2 3 5
Quercus
7500 +/- 100 BP
2 3 5 7
Tilia
9000 +/- 100 BP
0.1 0.5 1
Tilia
8500 +/- 100 BP
0.5 1 2
Tilia
8000 +/- 100 BP
1 2 3 5 7
Tilia
7500 +/- 100 BP
1 2 3
Picea abies
9000 +/- 100 BP
0.1 0.5 1 2 3 5 7
Picea abies
8500 +/- 100 BP
0.1 0.5 1 2 3 5 7 10
Picea abies
8000 +/- 100 BP
0.5 1 2 3 5 7 10 15
Picea abies
7500 +/- 100 BP
0.5 1 2 3 5 7 10 15

MIDDLE HOLOCENE

7500–5000 ^{14}C yr BP (ca. 8300–5700/5800 cal yr BP)

KAZIMIERZ TOBOLSKI

In the radiocarbon chronostratigraphy of uncalibrated (conventional) dates, the time sequence between 7500 and 5000 yr BP belongs to the Atlantic period (Mangerud et al. 1974, Starkel 1991). In the scale of varve calendar years of the Lake Gościąż sediments (Ralska-Jasiewiczowa et al. 1998), this period includes solar years from about 8300 to 5700 BP, and the whole Atlantic period extends from about 8950 to 5800 BP (Starkel et al. 1998). In the scheme of postglacial ecological succession, the Atlantic period was the time of specific climatic and edaphic phenomena, typical for the main part of the mesocratic stage (Berglund 1966, Tobolski 1976, Birks 1986). Plant cover was dominated by components of mediocratic vegetation characterised by higher climate and soil requirements as compared to terminocratic vegetation, which comprises a larger number of less demanding taxa, tolerating a wider range of climatic and pedological conditions. Therefore the mesocratic phase between the initial progressive protocratic stage and the regressive telocratic stage is characterised by a considerable stabilisation. A stage of climax equilibrium, often located in the course of postglacial succession in this period concurs with the Holocene climatic optimum (Iversen 1964). This climax equilibrium, however, did not last long because it was in the Atlantic period in Poland that an anthropogenic factor intensified its impact on the ecological, geological, and pedological conditions of natural environment. In the mid-Atlantic period, several areas in Poland were within the limits of expansion of the Neolithic societies. For example, by the end of the 6th millennium BP the Linear Pottery culture occurred in our country (Kaczanowski & Kozłowski 1998).

The vegetational changes during the climatic optimum were not only caused by the appearance and intensification of farming and stock-raising economy, which enhanced the disturbance of the primeval forest ecosystems (forest grazing, wood cutting for building, forest clearance for cultivation, etc.). They also resulted from the processes of natural transformation of phytocenoses caused by the diminishing role of once dominant protocratic components (among others *Pinus*, *Betula*, *Salix*).

In a set of the isopollen maps, the mediocratic element is represented unquestionably by ten taxa of trees and shrubs: *Acer*, *Alnus*, *Carpinus betulus*, *Corylus avellana*, *Fraxinus excelsior*, *Hedera helix*, *Quercus*, *Tilia*, *Ulmus*, and *Viscum* (Fig. 104). They can be divided into three groups according to the time of their most abundant appearance during the Holocene: 1. taxa showing dominant occurrence before 7500 yr BP, 2. taxa dominating between 7500 and 5000 yr BP, and 3. taxa present at that time but with the greatest expansion only after 5000 yr BP.

Corylus belongs to the group with maximal spread before 7500 yr BP. A distinct increase of *Corylus* contribution is recorded at ca. 9000 yr BP, and the maximal occurrence between 8500 and 8000 yr BP. About 7500 yr BP a decrease in *Corylus* expansion occurred. A wide time interval between 7000 and 4500 yr BP was marked by the stabilisation of this shrub in plant communities, as expressed by the domination of isoline 20%.

A few mediocratic plants had their greatest expansion between 7500 and 5000 yr BP. This group consists of *Ulmus*, *Fraxinus excelsior*, *Tilia*, *Hedera helix*, and *Viscum*.

The percentages of *Ulmus* pollen point to its maximal distribution between 7500 and 6000 yr BP, although at 8000 yr BP its values are almost the same. The maximal abundance of *Ulmus*, which lasted for almost two thousand years, started to decrease about 5500 yr BP, and after 4500 yr BP the evident regression of this tree occurred, especially in northern and western Poland. The main forest-forming role of *Ulmus* concurred with a diminishing contribution of *Pinus* and *Betula*, the two most important components of the postglacial protocratic element.

Fraxinus excelsior, which is undoubtedly underrepresented in paleopalynological material due to its weak pollen production, dominates at 6500–5000 yr BP. Approximately at the same time, from ca. 6500 to 5500 yr BP

Tilia, another tree underrepresented in pollen spectra, achieved its maximal spread.

The particular character of climate of the time interval 7500–5000 yr BP in the whole postglacial forest history is emphasised by the palynological temperature indicators *Viscum* and *Hedera helix*. *Viscum* shows maximal expansion between 7000 and 6000 yr BP and a decreasing tendency after 5500 yr BP. The dominance of *Hedera* comes slightly later, at 6000–5500 yr BP. Climatic preferences may explain a maximal occurrence of *Pteridium aquilinum* at 7000–5000 yr BP, yet it may have been connected also with the presence of the Mesolithic people.

Alnus, a taxon of waterlogged areas, opens the third group of mediocratic trees. In contrast to all the plants mentioned so far, two *Alnus* species (*A. incana* and *A. glutinosa*) build today their own communities, as they presumably did also at the time of the Holocene climatic optimum. Their participation in deciduous forests must have been effectively limited – just as today – by their limited competitiveness (Ellenberg 1996). The expansion of *Alnus* began at 8500 yr BP. However, the isopollen maps for the time intervals 7500, 7000, 6500, and 6000 yr BP are very similar and may provide evidence for the 2000-year period of their stabilized participation in the vegetation.

In non-waterlogged areas *Quercus* belongs to the most frequently represented components of mediocratic flora (though a sporadic occurrence of *Quercus* in waterlogged areas cannot be disregarded, for instance in some communities from the class *Alnetea glutinosae* (Sokołowski 1972). Although its greatest expansion fell in the Subboreal period (4500 yr BP), the role of *Quercus* in Poland has been considerable from at least 7000 yr BP. The beginning of expansion (which is not quite well understood because of the existence of island-shaped centres) is illustrated by the isopollen maps for 8000 and 7500 yr BP, and its progression is visible in the following two maps (7000 and 6500 yr BP). Between 6000–5500 yr BP the isopollen values became stable at the level of 10%. The next step in the expansion (above 15%) began around 5000 yr BP. The intensified expansion after a stable period 6000–5500 yr BP may have been related to the change of the structure of woodlands caused by a diminishing role of *Ulmus*, *Tilia*, and *Fraxinus*. This phenomenon has earlier been observed as a change of proportion of tree components of the classical curve of *Quercetum mixtum*, the upper part of which shows a clear dominance of *Quercus* pollen.

Acer species have been present in our forest flora from 7000 yr BP, yet only the 4000 yr BP map illustrates their maximal spread.

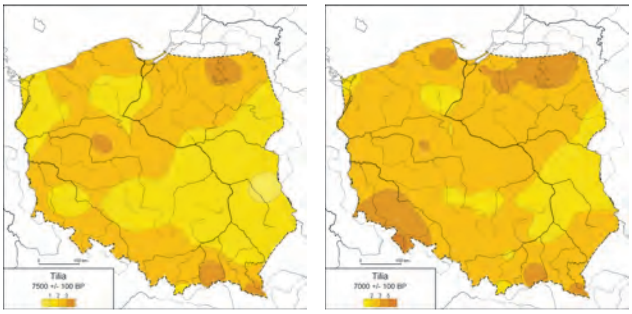
Mediocratic element also includes *Taxus boccata* (Tobolski 2002), which is poorly represented in the Holocene pollen diagrams but deserves close attention for several reasons. Attribution of *Taxus* to this element is determined by its optimal occurrence in the mesocratic phase of two earlier interglacials (Holsteinian and Eemian). The presence of *Taxus* in our forests should be discussed in connection with an out-of-date view about its late post-Atlantic migration to Poland, and a widespread but doubtful opinion about its great significance in the history of some woods. For instance, the great role of *Taxus* is wrongly attributed to the history of the Tuchola Forest. Today it is no longer argued that *Taxus* in Poland, as well as in the eastern Germany (Brande 1994), occurred in the mesocratic stage (Noryśkiewicz A.M. 2002). In order to be successful in invading stabilised forest communities, this poorly competitive and heavy-seeded taxon required, despite its favourable properties (e.g. dissemination by birds) – also favourable situations. One of them was suggested by Ralska-Jasiewiczowa and van Geel (1998) for the Gostynińskie Lake District, who related the expansion of *Taxus* to the existence of habitats created by Neolithic farmers. In the case of the Tuchola Forest area, at that time poorly inhabited favourite habitats for *Taxus* could have occurred on the shores of some lake islands (Tobolski 2002).

The history of forests in the Atlantic period would not be complete if basic information was limited to the presence of a mediocratic element. A few closing sentences should be devoted to the problem of declining terminocratic elements and an increasing significance of newcomers in the tree flora, especially of *Picea* (north-eastern Poland) and *Fagus*, which are generally identified neither with mediocratic nor terminocratic plants. A good example of the regression of terminocratic element at the time of the thermal optimum is represented by the isopollen maps of *Salix*. After its distinct presence in the early postglacial, the maps from 8000 yr BP onwards show quite a regular decline in pollen of this taxon, which is not naturally common. *Picea* was present in southern Poland already in the Late Glacial. In the period of 8000 to 5500 yr BP its range did not change substantially. At about 5000 yr BP it started to spread from a new direction of the north-east.

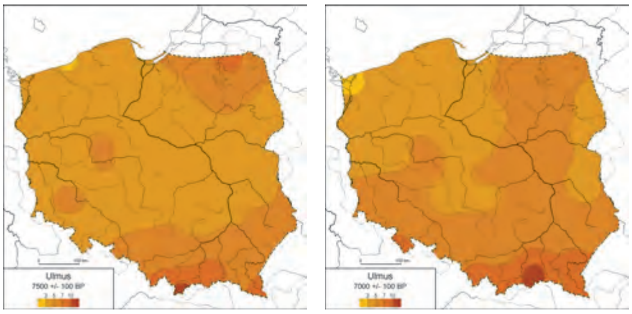
The fact that the onset of the Subboreal period was characterised by intensive changes in the forest composition, emphasised by the dynamics of the above-mentioned mediocratic taxa (*Acer*, *Quercus*, *Carpinus*), is also supported by the history of *Fagus sylvatica*. It seems that the expansion of this taxon in Poland best illustrates the beginning of intensive post-Atlantic transformations in the Subboreal and Subatlantic periods.

Fig. 104 (p. 402–403). Isopollen maps of selected tree taxa illustrating vegetation changes during the period 7500–5000 yr BP

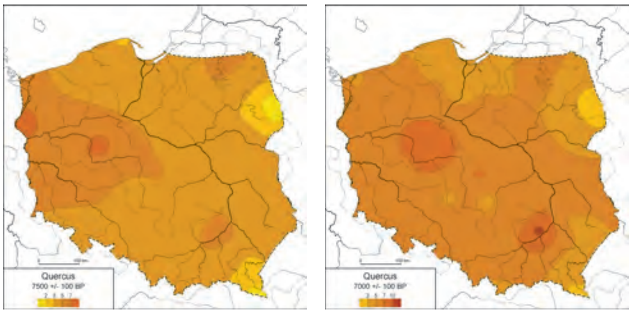
Tilia



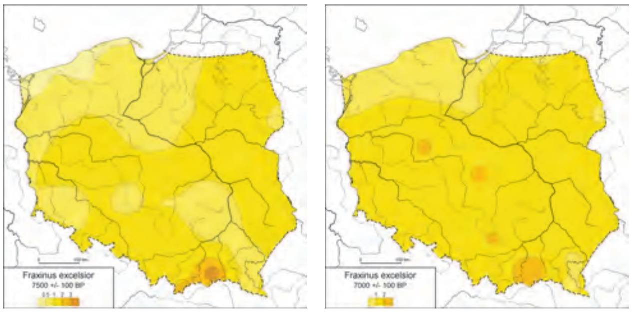
Ulmus



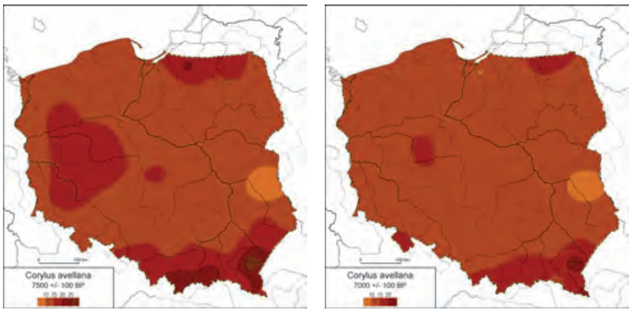
Quercus



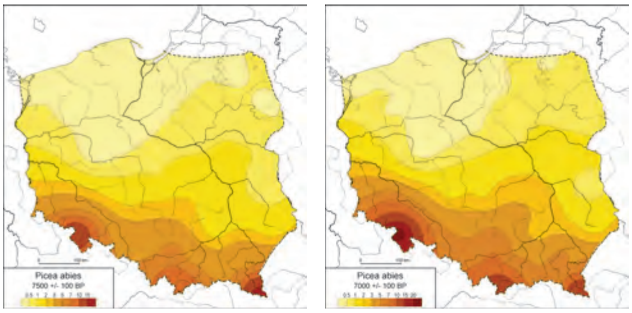
Fraxinus excelsior



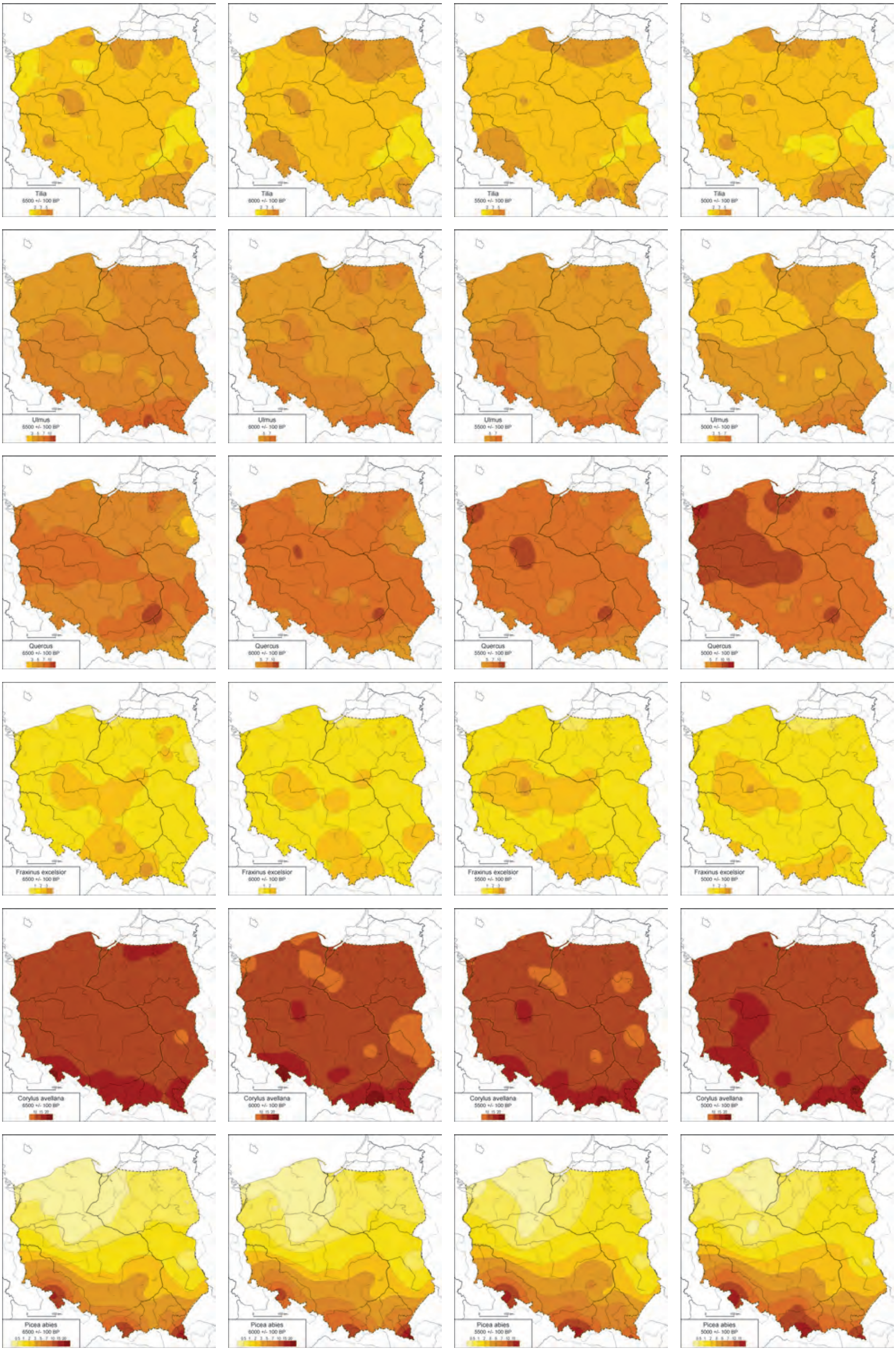
Corylus avellana



Picea abies



0.01 0.1 0.5 1 2 3 5 7 10 15 20 25 30 40 60


Tilia
6500 +/- 100 BP
Tilia
6000 +/- 100 BP
Tilia
5500 +/- 100 BP
Tilia
5000 +/- 100 BP
Ulmus
6500 +/- 100 BP
Ulmus
6000 +/- 100 BP
Ulmus
5500 +/- 100 BP
Ulmus
5000 +/- 100 BP
Quercus
6500 +/- 100 BP
Quercus
6000 +/- 100 BP
Quercus
5500 +/- 100 BP
Quercus
5000 +/- 100 BP
Fraxinus excelsior
6500 +/- 100 BP
Fraxinus excelsior
6000 +/- 100 BP
Fraxinus excelsior
5500 +/- 100 BP
Fraxinus excelsior
5000 +/- 100 BP
Corylus avellana
6500 +/- 100 BP
Corylus avellana
6000 +/- 100 BP
Corylus avellana
5500 +/- 100 BP
Corylus avellana
5000 +/- 100 BP
Picea abies
6500 +/- 100 BP
Picea abies
6000 +/- 100 BP
Picea abies
5500 +/- 100 BP
Picea abies
5000 +/- 100 BP

LATE HOLOCENE

5000–2500 ^{14}C yr BP (ca. 5700/5800–2550 cal yr BP)

MAGDALENA RALSKA-JASIEWICZOWA

The boundary at 5000 yr BP has generally been accepted as the end of optimum development of mixed deciduous forests (Atlantic chronozone). The subsequent period, defined as Subboreal chronozone (Mangerud et al. 1974), was characterized by profound environmental changes, including transformations of vegetation. The latter have resulted from various factors: climatic, pedogenic, anthropogenic, and also pathogenic processes. According to the prevailing opinion a cooling and rise of climate humidity occurred at the beginning of this period (Ralska-Jasiewiczowa & Starkel 1991), although data concerning this subject are not unequivocal. For example, the lowering of lake level observed in southern Sweden in its early phase (ca. 4900–4600 yr BP, Gaillard & Digerfeldt 1991) may indicate a decline of moisture, whereas in Poland a similar phase is marked at about 4000–3000 yr BP (Ralska-Jasiewiczowa & Starkel 1988). Some evidence such as enlargement of Alpine glaciers indicates that the fall of temperature could have taken place between 4000 and 3000 yr BP (Zolitschka 1992).

However, the results of natural processes commonly occurring then are indisputable, such as maturation and leaching/degradation of soils, as well as increasing human impact on vegetation, e.g. progressive land-occupation by Neolithic farmers. The effects of pathogenic factors are also evident, e.g. reduction of *Ulmus* participation in the forests, caused mainly by the Dutch elm disease. These reached a critical point around 5000 BP (Fig. 105). At the same time the other important reason of decline in *Ulmus* population seems to have been the activity of Neolithic farmers. By 4800 yr BP the proportions of *Ulmus* in the forests had already been much reduced throughout the entire lowland part of the country (pollen values up to 3%). At 4000 yr BP the higher elm representation is maintained only in the mountains and their forelands. This was probably the consequence of the occurrence there of mountain elm (*Ulmus scabra*), which is the species most resistant to this disease, and of the less intensive human activity in mountain areas. After 4000 yr BP the decline of *Ulmus* is marked in the mountains as well.

Tilia also declined in this period, starting evidently from the east (4500–4000 yr BP), where numerous marshy or poor-soil areas were unfavourable for this tree, which demands rather fertile slightly moist soils. By 3500 yr BP *Tilia* was still slightly more abundant in the regions around the Vistula river estuary and in south-western Poland in the mountains, with small centres persisting in the mountain depressions – the mid-Carpathian depression and the Moravian Gate. *Fraxinus*, although a poor pollen producer, appears from the isopollen maps as a more stabilized tree. Its occurrence declined slightly also from the east towards the north-west, but only since around 3500 yr BP.

Quercus, *Acer*, and *Corylus* had different histories at this time. *Quercus* and *Acer* reached their maximum Holocene distribution not earlier than by 4000 yr BP. *Corylus* remained quite abundant until around 4000 yr BP.

Between 5000 and 3800 yr BP, thus roughly at the time of these declines, the maximum development and then decline of Neolithic settlements took place in Poland (see the 4500 and 4000 yr BP maps for *Plantago lanceolata*, Cerealia, *Artemisia*, and *Rumex*, this volume). The areas of fertile soils devastated by extensive burning, forest clearance, grazing in the forests, and pasturage abandoned and then colonized temporarily by pioneer *Betula* and *Populus tremula*, were overgrown by regenerating scrub-forest communities. *Quercus*, favoured by farmers and partly saved during the clearings, could spread easily, and due to good light conditions flowered abundantly. *Corylus* also expanded. Probably in this way, between 5000 and 3700 yr BP, post-settlement, ecologically unstable communities dominated by *Quercus* and *Corylus* developed widely. Their expansion advanced from the north-west, additionally favoured by accessibility of the habitats available after reduction of *Ulmus* populations. These communities were very rare or even absent from the eastern part of the country, where marshy or sandy areas were dominated by *Pinus*, locally with *Betula*.

Between 4000 and 3500 yr BP slight decrease of *Corylus* started, first on those unfavourable areas in eastern Poland. A steeper decline of *Corylus* pollen curve is marked in many pollen diagrams by ca. 3700 yr BP. From around 3500 yr BP a distinct *Corylus* reduction followed throughout the country, except in the north. Those regions have still not been reached by a contiguous *Carpinus* expansion, which must have contributed to the *Corylus* retreat in most of Poland.

By ca. 4500 yr BP the late Holocene tree species *Carpinus*, *Fagus*, and *Abies*, which may have been already present in Poland somewhat earlier as scattered stands, started their distinct expansion from the south-east and south-west. All these trees appeared in Poland via the Carpathians. *Carpinus betulus* was present in the Southern Carpathians prior to 6000 yr BP (Farcas et al. 1999), *Fagus sylvatica* has been recorded in southern Bohemia and Moravia since 8000–7500 yr BP (Rybničkova & Rybniček 1996, Svobodova et al. 2001). Taberlet et al. (1998), on the basis of molecular studies, suggest the migration of *Fagus* from refugia in the Balkans and the Southern Carpathians. *Abies alba* came to the Carpathians from the Balkans and from northern Italy, and the introgression within *Abies* originating from different refugia and migrating along those two routes, took place in the Sudetes and the Western Carpathians (Konnert & Bergmann 1995).

A biological rate of *Carpinus* migration was the quickest due to its ecological features. Migrating from the direction of the Bieszczady Mountains and the mid-Carpathian low ranges, it expanded by 4000 yr BP in south-eastern Poland in the mountain foothill zone and reached the slightly moist fertile soils of the uplands. Already around 3500 yr BP, *Carpinus* spread quickly to the north-west and formed a broad forest area in the Wielkopolska region, occupying the lands left by the settlements of the Neolithic populations. Soils and also climate of those areas, hypothetically more continental than that of today (Tobolski 1991b), must have been very suitable for *Carpinus*, for this species, typical of the lower tree layer, could then have formed pure stands (up to 40% of *Carpinus* in the pollen spectra). At this time *Corylus* scrubs maintained still large concentrations in the Baltic Coastal Zone and in the northern lake districts, where *Carpinus* had not expanded. *Quercus* was particularly frequent in north-western Poland, where it started to build up forest communities with *Carpinus*, similar to present-day ones.

Fagus and *Abies* gradually occupied the lower montane forest zone of the Carpathians and the Sudetes. At 3500–3000 yr BP *Fagus* formed very strong centres in the Sudetes and particularly in the Eastern Carpathians, where it must have overgrown nearly entire mountain slopes. At 2500 yr BP it spread more abundantly into the Western Carpathians and on the south-Polish uplands. Between 3000 and 2500 yr BP the north-western centre of *Fagus* started to develop. *Abies* expanded frequently first in the Western Carpathians (ca. 3500 yr BP), then in the Sudetes (ca. 3000 yr BP), finally reaching the Eastern Carpathians between 3000 and 2500 yr BP.

Acer, a low pollen producer, seems to have occurred in Poland rather scarcely during the climatic optimum, somewhat more frequently in the mountains, but only locally. Between 5500 and 5000 yr BP it widened somewhat the acreage of its more numerous occurrences in the mountains and their forelands. Between 4500 and 4000 yr BP it expanded slightly but distinctly, at first in the whole central and the south-western part of Poland and then almost in the whole country. Its higher pollen values appearing between 4500 and 3500 yr BP in the mid-Carpathian lowering *sensu lato* might perhaps show some connection with the migration of *Fagus* (could it be then *Acer pseudoplatanus*, characteristic of the *Fagetalia* order and of the mountain communities of the *Acerion* alliance?). On the other hand, the mentioned spread of *Acer* in the entire lowlands of Poland, may have been connected with the activities of Neolithic tribes, as their herds of cattle were accompanied by the formation of natural hedges composed of the species of outskirt communities (Troels-Smith 1955, Groenman-van Waateringe 1978) of the *Rhamno*-*Prunetea* class, where *Acer campestre* is one of the characteristic species. In later times the more significant occurrence of *Acer* was limited to the mountains and uplands of southern Poland (*A. pseudoplatanus* mostly?).

Between 5000 and 3500 yr BP distinct expansion of *Picea* occurred in Poland. Its range in the mountains extended northward into the upland areas, and the frequency of its occurrence increased. At 4500 yr BP a short-lasting link between the eastern and Western Carpathian ranges in the area of its 'mid-Carpathian gap' arose, persisting less distinctly until 3500 yr BP. About 4000 yr BP the north-eastern centre of *Picea* started to form.

During the period discussed the processes were active in the river valleys, such as filling up of ox-bows originating from shifting of river-beds, peat accumulation on the river terraces and subsequent covering of those peats with the flood deposits. At ca. 4000 yr BP the lowering of lake levels has been marked. All those phenomena resulted in appearance of numerous habitats suitable for riverine forests and carrs. The maximum Holocene extent of *Alnus* is observed during this time. Between 4000 and 3000 yr BP *Alnus* is represented almost throughout the country with pollen values of 15–20%, and locally even higher. Only in the mountains and in the continental forest-steppe area in Wołyń (east Poland) was *Alnus* less abundant.

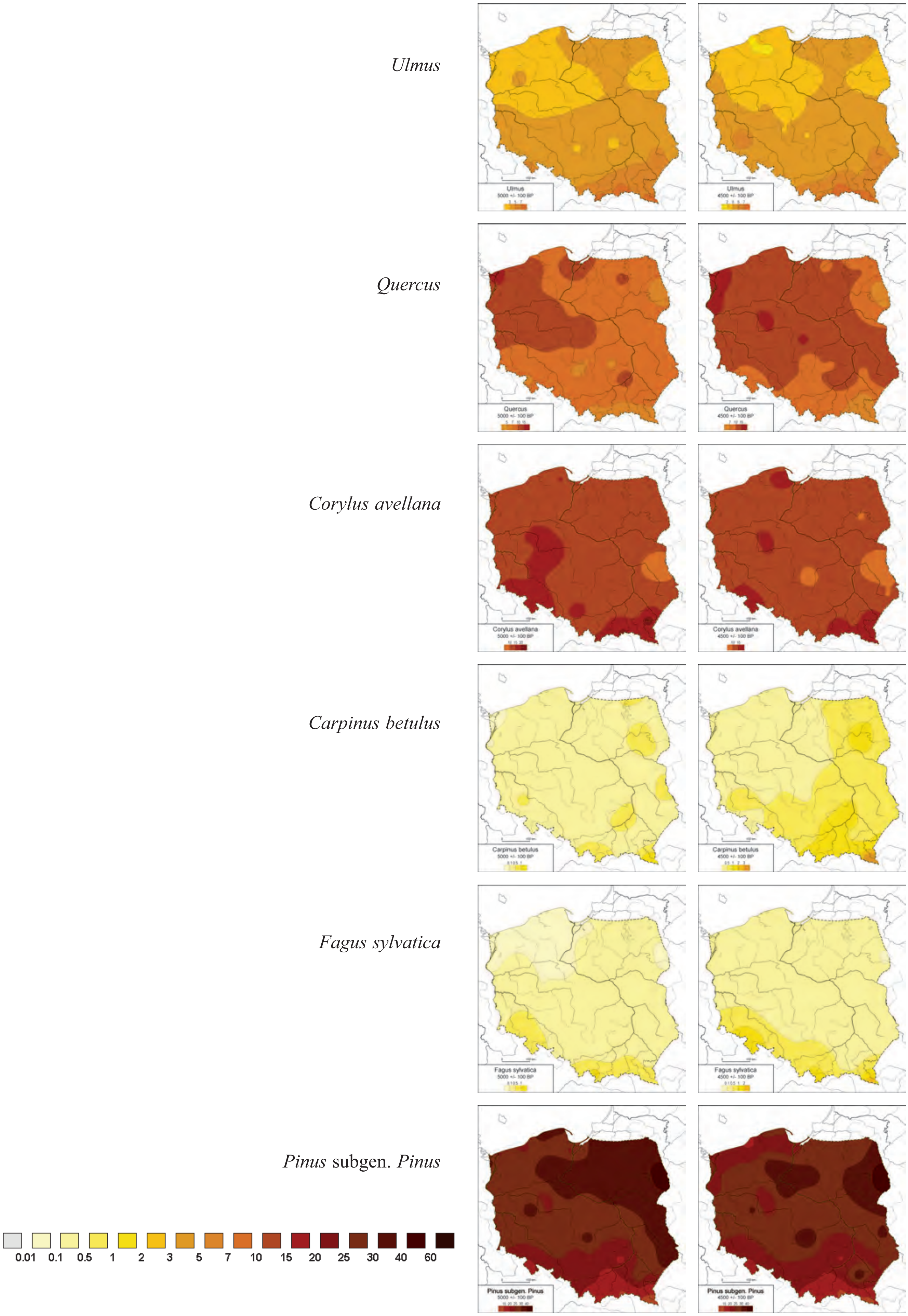
About 3300–3200 yr BP the first expansion and then development of the Lusatian culture progressed in Poland. The dominance of Lusatian tribes lasted until ca. 2500 yr BP, and the country was then densely populated, resulting in land-occupation also in inhospitable areas (poor soils, mountains, etc.), which previously were poorly populated or uninhabited. These processes caused further destruction of mesophilous forest species like *Quercus* and *Corylus* as well as *Tilia* and *Fraxinus*, which became already visible on 3000 yr BP maps, and much more drastically on those for 2500 yr BP, representing the decline of settlements of the Lusatian culture. Expansion of *Pinus*, reflected around 2500 yr BP, was also a result of considerable deforestation in central Poland and in the lake districts.

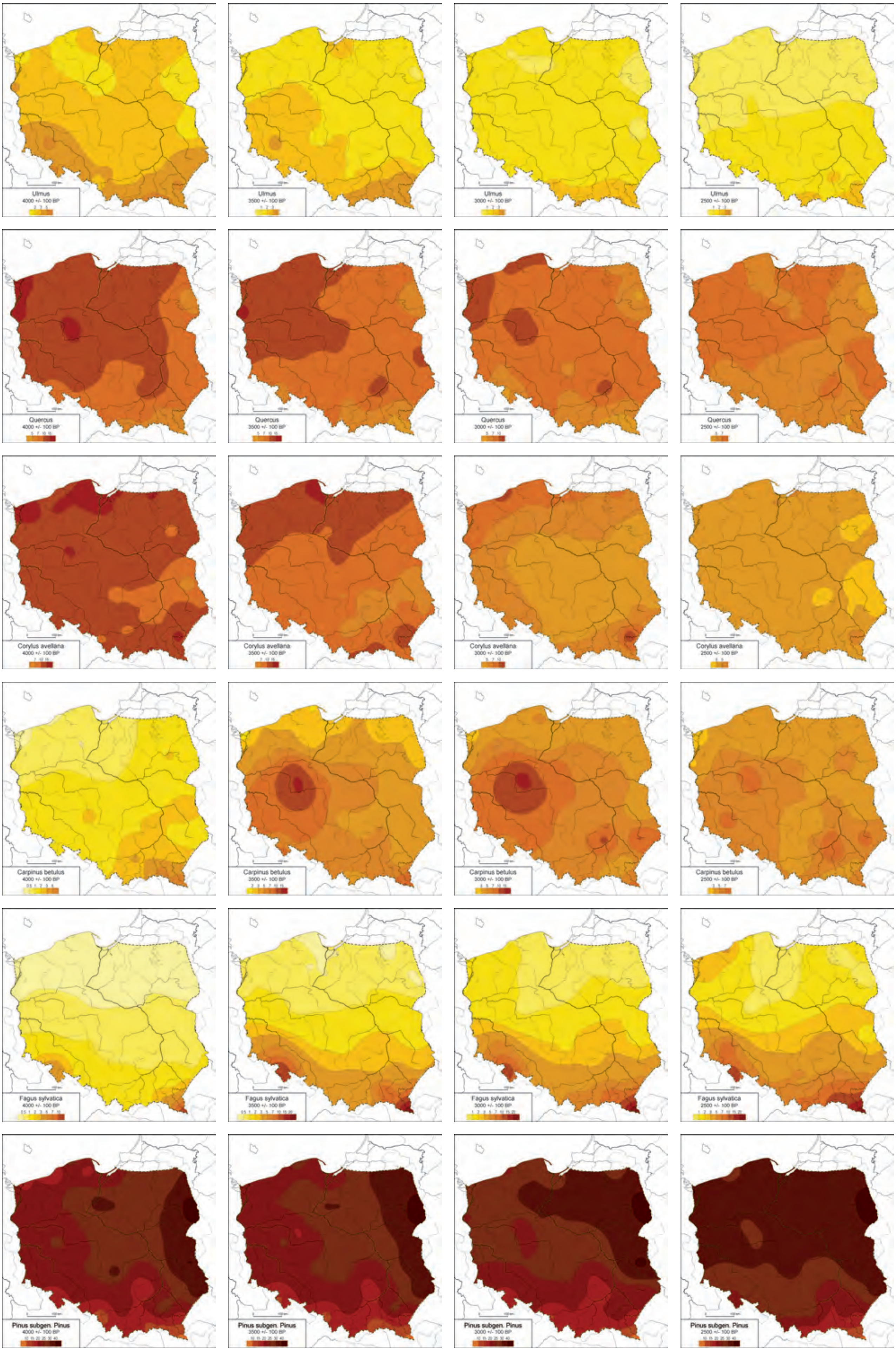
However, trees in the stage of expansion, such as *Carpinus* or *Fagus*, responded to these processes with some delay, if at all. The centre of *Carpinus* occurrence in the Wielkopolska region widened at 3000 yr BP into all of central Poland, and new smaller centres in the uplands of southern Poland were formed. Distinct destruction of *Carpinus* in the Wielkopolska region is marked only on the 2500 yr BP map. This picture does not fully reflect the record of the described processes, in particular in pollen diagrams from the Polish lowlands. Three expansion phases of *Carpinus* separated by two decreases are commonly reflected in these diagrams (Ralska-Jasiewiczowa et al. 2003b). The first maximum, occurring usually after 3500 yr BP is connected with the progress of *Carpinus* migration. The first decrease, caused most probably by the settlement activities of the Lusatian populations, generally began prior to 3000 yr BP. The renewed rather minor regeneration of *Carpinus* started after 2500 yr BP, with its culmination before 2000 yr BP. Those phenomena are poorly reflected on the isopollen maps drawn for a too coarse time resolution of the following time horizons. This and the next regeneration phase of the *Carpinus* forests marked at the 1500 yr BP is described in the next subchapter of the summary.

Fagus and *Abies*, spreading in the mountains and in adjacent areas during the time discussed, do not show on isopollen maps any distinct reaction to economic activities of the Lusatian populations. Both those trees, with some contribution of *Picea* or *Acer pseudoplatanus* were forming gradually the lower forest zone in the Polish mountains. The changes towards a cooler and more humid climate proceeding at that time favoured the development of *Fagus.* It is expressed in its expansion in western Poland and particularly in the north-western regions of the sea coastal zone, where at about 2500 yr BP a new centre of *Fagus* arose.

In this way the last important forest-forming tree species not only arrived in Poland, but also built up their present-day distribution ranges. The main processes of tree migrations in the Holocene have been completed. Thus, the conditions permitting the formation of all types of natural forest communities occurring in Poland recently have been fulfilled. Recapitulating described changes in vegetation pattern between 5000 and 2500 yr BP in the shortest way, it may be stated that during this period the majority of modern forest communities were formed in Poland.

Fig. 105 (p. 408–409). Isopollen maps of selected tree taxa illustrating vegetation changes during the period 5000–2500 yr BP


Ulmus
Ulmus 5000 +/- 100 BP
Ulmus 4500 +/- 100 BP
Quercus
Quercus 5000 +/- 100 BP
Quercus 4500 +/- 100 BP
Corylus avellana
Corylus avellana 5000 +/- 100 BP
Corylus avellana 4500 +/- 100 BP
Carpinus betulus
Carpinus betulus 5000 +/- 100 BP
Carpinus betulus 4500 +/- 100 BP
Fagus sylvatica
Fagus sylvatica 5000 +/- 100 BP
Fagus sylvatica 4500 +/- 100 BP
Pinus subgen. *Pinus*
Pinus subgen. Pinus 5000 +/- 100 BP
Pinus subgen. Pinus 4500 +/- 100 BP
0.01
0.1
0.5
1
2
3
5
7
10
15
20
25
30
40
60


Ulmus
4000 +/- 100 BP
2 3 5
Ulmus
3500 +/- 100 BP
1 2 3
Ulmus
3000 +/- 100 BP
1 2 3
Ulmus
2500 +/- 100 BP
1 2 3
Quercus
4000 +/- 100 BP
5 7 10 15
Quercus
3500 +/- 100 BP
5 7 10 15
Quercus
3000 +/- 100 BP
5 7 10
Quercus
2500 +/- 100 BP
5 7
Corylus avellana
4000 +/- 100 BP
7 10 15
Corylus avellana
3500 +/- 100 BP
7 10 15
Corylus avellana
3000 +/- 100 BP
5 7 10
Corylus avellana
2500 +/- 100 BP
Carpinus betulus
4000 +/- 100 BP
0.5 1 2 3 5
Carpinus betulus
3500 +/- 100 BP
2 3 5 7 10 15
Carpinus betulus
3000 +/- 100 BP
3 5 7 10 15
Carpinus betulus
2500 +/- 100 BP
3 5 7
Fagus sylvatica
4000 +/- 100 BP
0.5 1 2 3 5 7 10
Fagus sylvatica
3500 +/- 100 BP
0.5 1 2 3 5 7 10 15 20
Fagus sylvatica
3000 +/- 100 BP
1 2 3 5 7 10 15 20
Fagus sylvatica
2500 +/- 100 BP
1 2 3 5 7 10 15 20
Pinus subgen. Pinus
4000 +/- 100 BP
10 15 20 25 30 40
Pinus subgen. Pinus
3500 +/- 100 BP
10 15 20 25 30 40
Pinus subgen. Pinus
3000 +/- 100 BP
10 15 20 25 30 40
Pinus subgen. Pinus
2500 +/- 100 BP
10 15 20 25 30 40

LATE HOLOCENE PERIOD OF INCREASING HUMAN IMPACT

2500–100 ^{14}C yr BP (ca. 2550 – -50 cal yr BP)

MIROSŁAW MAKOHONIENKO

The youngest part of the Holocene chronostratigraphy, including the last 2500 yr BP (from about 600 BC in calendar years), is distinguished as the Subatlantic chronozone (Mangerud et al. 1974). At this time the transformation of the vegetation in Poland, apart from the natural aspects connected mainly with climatic fluctuations, was influenced principally by anthropogenic factors. During this period no new forest-forming components appeared due to natural migration. The main outlines of the Holocene distribution of *Fagus*, *Picea*, and *Abies* were already established. However, forest areas underwent considerable changes through both successive restriction of their spread and modification of their composition and structure due to human influence.

The beginning of the Subatlantic period (ca. 2500 BP) occurred in the early stage of history of material culture, marked by iron-production knowledge. The earliest phase of the Iron Age, the Hallstatt Period, is dated according to archaeological sources to 700–400 BC (Godłowski & Kozłowski 1983). Palaeoclimatic reconstructions for Poland indicate essential climatic fluctuations at a threshold of the period discussed. Considering a broader period of time from about 2700 to 2000 yr BP, tendency to increased precipitation connected with cooling is recorded (Ralska-Jasiewiczowa & Starkel 1991). Isopollen maps for 2500 yr BP show significant changes in spatial representation of forest-forming components (Fig. 106). In lowland areas and partly in mountain foothills regression of previously developed *Carpinus* stands, which formed a characteristic component of the late Holocene deciduous forests took place. Reduction in *Carpinus* representation was manifested in western Poland, including the Wielkopolska, Kujawy area and part of Silesia (Late Holocene and *Carpinus* chapters, this volume). The palynological profiles from the Wielkopolska-Kujawy Lowland confirm univocally the anthropogenic basis of destruction of the forests of that time (Tobolski 1990, Noryśkiewicz B. 1995). *Quercus*, *Ulmus*, and *Fraxinus* were extirpated, too. Intensification of anthropogenic influences during Hallstatt time was a continuation of previous settlement processes occurring in the Bronze Age (see the 3000 yr BP horizon). However, clearings of *Carpinus* forests are marked on a greater scale only on the 2500 yr BP map. They are the most significant in the western part of the country. It seems to be connected with intensified development of settlement in the younger Iron Age in western Poland, which were closer to the sphere of influence of eastern centres of the Hallstatt culture. As a result of anthropogenic pressure on deciduous forests, *Pinus sylvestris* and *Betula pendula* encroached in secondary succession into the clearings within disturbed forest communities, and in the case of *Betula* occupying ecotones between forest and open spaces. Increase in *Betula* and *Pinus* was especially marked in the lowland.

At the 2500 yr BP horizon the second stage of *Fagus* expansion into Poland took place, this time from the north-west, being a direction of favourable geographic elements with oceanic provenance. At this time *Fagus sylvatica* expanded in some parts of western and central Pomerania in the seacoast belt (Late Holocene, this volume). Its migration proceeded during the following 500 years. As in the earlier encroachment of *Picea* from the boreal region in the north-east, the migration of *Fagus* is regarded as a natural process caused by climatic reasons (Ralska-Jasiewiczowa & Starkel 1991), but supported by anthropogenic factors. According to the isopollen maps *Fagus* migration from the north-west and *Picea* migration from the north-east into Poland were not synchronous. *Picea* expansion from the boreal area happened about 1500 years earlier.

Around 2000 yr BP the pattern of isopolls on the maps indicates the next changes in the development of the cultural landscape of Poland. The accepted time horizon in calendar years about 50 BC might have corresponded with the close of the younger pre-Roman Period, described also as the Late La Tène Period. The method of map construction as well as the range of calibration error of radiocarbon dates may actually ascribe discussed horizon also to the beginnings of

1 century AD, belonging to the period of Roman influence. In the horizon dated to 2000 yr BP *Secale cereale* pollen gained in importance indicating the spread of rye cultivation (Wasylikowa 1983, *Secale cereale*, this volume). Its records for the first time reached values up to 0.5% of a total sum of trees and herbs. At this initial phase of rye cultivation a pattern of the isopollen lines may indicate its development mainly in the major part of the country west of the Vistula and to the south of San rivers, with the exception of the Western Pomerania. An increase in *Rumex* representation throughout the country also occurred then. This indicated further development of meadow communities on acid soils, impoverished in consequence of their excessive pasturage. The pattern of *Rumex* and *Secale* isopolls are generally concurrent. Their less intense concurrence is visible at the eastern outskirts of the country. The highest representations of both taxa were noticed in southern Poland in the upper Vistula river basin. Forest grazing may be indirectly inferred from the widening range and increase in records of *Juniperus*, which is a species gaining its importance as a result of clearings and pasturage. This increase concerns mainly southern Poland in the upper and middle Vistula river basin. The highest values of *Juniperus* together with rather high records of *Rumex*, *Artemisia*, and *Plantago lanceolata* appear in the Kraków region, where in the younger pre-Roman Period the development of the Tyniec group settlement, represented by the population of Celtic origin, was recorded.

The isopollen pattern reflects the general increase of settlements and intensification of agriculture in the younger pre-Roman Period, resulting from influence of the Celtic culture, and continuing throughout the Roman Period. The settlement and economic rise was connected with introduction of permanent arable cultivation in the land-rotation system, replacing the earlier slash-and-burn system. From the younger pre-Roman Period through the Roman Period people of the Przeworsk culture settled the greater part of Poland.

Around 2000 yr BP, during a time of intensive development of settlement processes at the end of the Late La Tène Period and the beginning of Roman Period, the amount of *Quercus* pollen increased distinctly in most of the country. The tendency towards rise of *Quercus* representation, connected clearly with the phase of intensive settlements of the Przeworsk culture, was noticed earlier on a smaller scale in the diagrams from the central Wielkopolska area (Makohonienko 2000). Thus an increase in *Quercus* contribution is then in opposition to the lower records of this tree, both in the preceding phase of the intensive settlement of the Lusatian culture (2500 yr BP), as well as during following settlement phase from the Early Medieval Period (the 1000 yr BP time horizon). This phenomenon may have been stimulated by warming of the climate at the turn of the epochs, expressed by higher summer temperatures (Bortenschlager 1982, Patzelt 1980, after Ralska-Jasiewiczowa & Starkel 1991) and/or by anthropogenic factors, such as leaving *Quercus* during clearings of other species or wider forest grazing on dry grounds, as seen in analogies known from the historic times. According to Faliński and Pawlaczyk (1993) in the northwestern Poland ‘grazing of cattle in the forest performed for a long time resulted in extermination of hornbeam from the composition of thermophilous types of dry oak-lime-hornbeam forests and in forming the pure oak stands with high amount of meadow and xerothermic species in the herb layer – so called ‘well-lighted oak forest’. According to these authors the origin of at least some part of the recent stands of well-lighted *Quercus* forests is connected with mass cattle grazing in the forest. This phenomenon was very common in some regions up to the middle of the 20th century. It is very probable that pollen spectra of the 2000 yr BP horizon reflect to some extent this type of economy.

During the succeeding time-horizon of ca. 1500 yr BP (ca. 500 AD) the recurrence of forest communities characterized the vegetation development in Poland. Regeneration of the forest cover is best reflected by the increasing amount of *Carpinus* and high representation of *Quercus*. This phase corresponds with settlement regression occurring during the Migration Period, its onset dated in Poland at about 450 AD. *Carpinus* expansion is accompanied by decreasing amounts of some synanthropic plants such as *Rumex*, *Artemisia*, and *Plantago lanceolata*, confirming progressing reduction of cultural landscape. At the 1500 yr BP horizon decrease of anthropogenic indicators is partial. However, it should be kept in mind that isopollen values represent a mean value from the period of 1500±100 yr BP, influencing considerably a discussed time interval. A picture compiled from the set of isopollen maps indicates the highest degree of natural forest regeneration in the Pomerania areas, north of the Noteć river valley. Relatively higher amounts of herbs (NAP), including *Artemisia* and *Rumex*, have been recorded in the south-eastern Poland, comprising the Vistula and San river basins. The oldest sites connected with the early-Slavonic settlements and represented by the finds of the Prague culture (Parczewski 1997) are known from this area. They are dated to the close of the 5th and the first half of the 6th century AD.

Regeneration of the forest communities with *Carpinus*, shown at the 1500 yr BP map, was not durable. The picture for 1000 yr BP presents transformation of natural environment of Poland, in a scale unnoticed before, caused by anthropopressure. The limits of forest extent are recorded by reduction in *Carpinus*, *Quercus*, *Tilia*, and *Fraxinus* and to some extent also *Ulmus.* The regions displaying the highest level of deforestation (NAP within the range of 20–30%) are Małopolska in the river basin of the upper Vistula, Wielkopolska in the Warta river basin, and

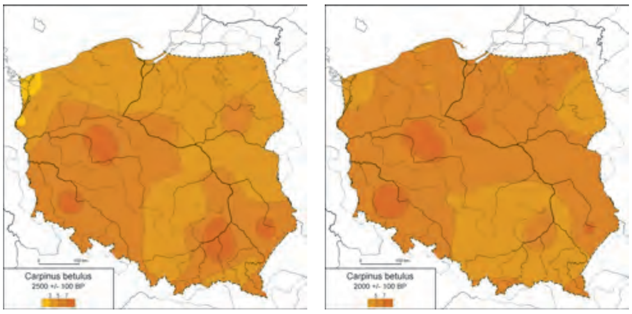
Western Pomerania in the lower Odra river catchment. In those areas and particularly in the regions of central Wielkopolska and Małopolska the highest values of plants of synantropic habitats appear, namely – *Rumex*, *Plantago lanceolata*, Chenopodiaceae, and partly also *Artemisia*. This picture corresponds very well with the leading role of the Kraków Land and central Wielkopolska in Poland of 11th century. At that time all of the analysed anthropogenic indicators attain high values in middle Wielkopolska between Poznań and Gniezno, distinguishing thus the central area of the Polish State formation by the first Piast Dynasty. Settlement and economic activity are expressed by much wider appearance of open lands used by Slavonic population for cereal cultivation, as is well illustrated by the rise in *Secale* occurrence. Significant decrease in *Alnus* amounts throughout the country suggests wider exploitation of waterlogged areas. Transformation of marshy grounds leads to development of the secondary communities of brushwood with *Salix*. At this time the only forest-forming species that gains significantly due to anthropopressure is *Pinus*. Development of pine forests as a result of secondary succession as well as economic use of forests is once more expressed in development of *Juniperus*. Its role in the understory of transformed forest communities shows an increasing tendency during subsequent centuries. *Betula*, despite its pioneer predisposition, has displayed stable tendency towards a decline in the landscape since the Middle Ages. The process of Medieval deforestation intensified during the following centuries, as expressed by a further decrease in the amount of all the forest-forming components apart from *Pinus*. In consequence of this, as shown by the isopollen maps of the 100±100 yr BP horizon, it comes to a domination of open communities with anthropogenic vegetation.

A scale of clearings and transformation of forest environments of Poland due to human activity during the last 2500 years can be illustrated well by *Carpinus* example. *Carpinus betulus* determines the specific character of many recent species of deciduous forests of the *Carpinion betuli* alliance, occurring in the meso- and eutrophic habitats of both the lowlands and the montane foothill zone. Oak-hornbeam forests with lime are in central Europe climax communities i.e. stable natural communities conditioned by macroclimate (Matuszkiewicz W. 2001). Reduction of the climax communities with *Carpinus* in Poland with passing time is well expressed by the sets of isopollen maps. In the last phase of significant regeneration of the forest acreages, during the Migration Period (1500 BP), the mean percentage values of *Carpinus betulus* recorded in the fossil pollen spectra were between 7 and 15% of the pollen sum in about 2/3 of the country. This indicates the significant or dominating role of *Quercus-Carpinus-Tilia* forest communities in the landscape. At this time the maximum pollen values of *Carpinus* for Poland occurring in Wielkopolska exceeded 49% (Filbrandt 1991). The isopollen map of *Carpinus* in the phase prior to the Medieval settlement (1000 yr BP) does not record any areas where its mean representation would have been lower than 2%. The map for the times close to the present day (100 yr BP) shows *Carpinus* values below 2% in about 3/4 of the country, indicating the marginal role of this species in the landscape. On this map *Carpinus* nowhere reaches values above 5%. Estimated calculations of W. Matuszkiewicz (1990) regarding the potential natural plant communities of Poland suggest 41.6% of the area for the oak-hornbeam forests with lime, which is well confirmed in the pre-Medieval phase of vegetation development. The actual area of *Quercus-Carpinus-Tilia* forest communities in Poland, according to the rough estimates (Matuszkiewicz J.M. 2002) is at present about 740 km^2, which is barely about 0.2% of the country area.

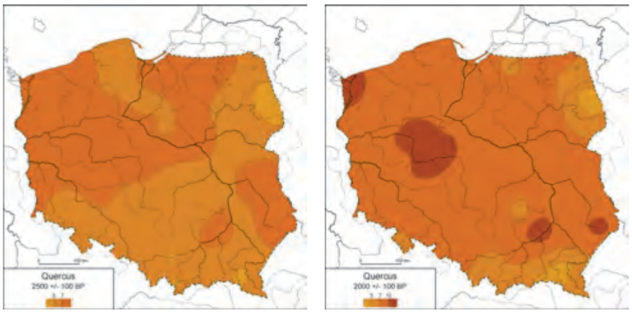
Degree of synanthropization of the recent vegetation in Poland, presented by Faliński (1975), distinguishes the areas of high anthropogenic changes in the Wielkopolska-Kujawy Lowland, in a part of the Mazovian area, and in the Kraków Land. According to the Holocene reconstruction of the vegetation pattern this results from the long-lasting process of anthropogenic transformation of vegetation going back to the prehistoric periods.

Fig. 106 (p. 414–415). Isopollen maps of selected tree and herb taxa illustrating vegetation changes during the period 2500–100 yr BP

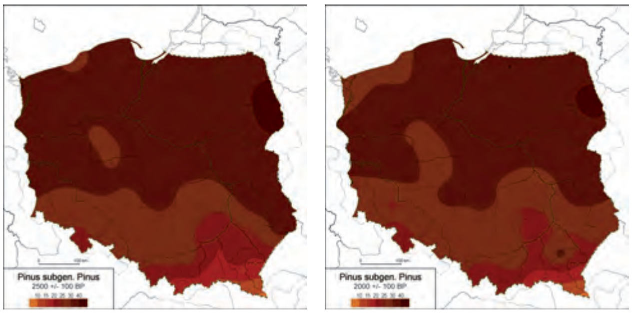
Carpinus betulus



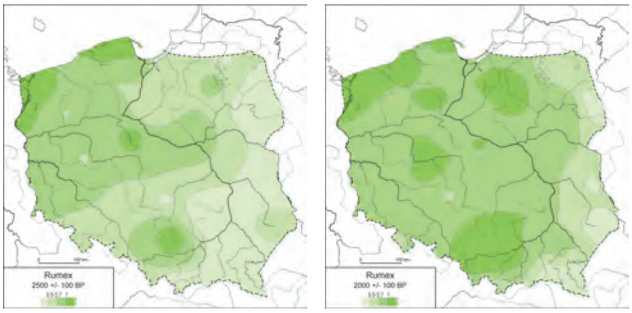
Quercus



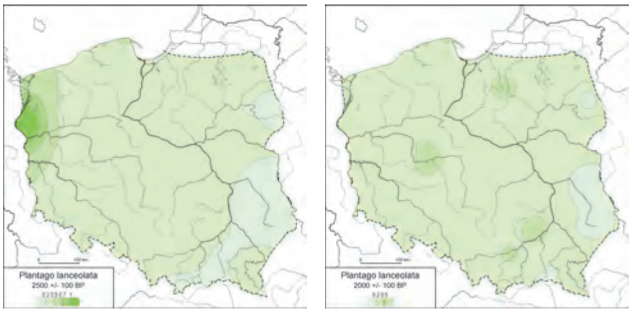
Pinus subgen. *Pinus*



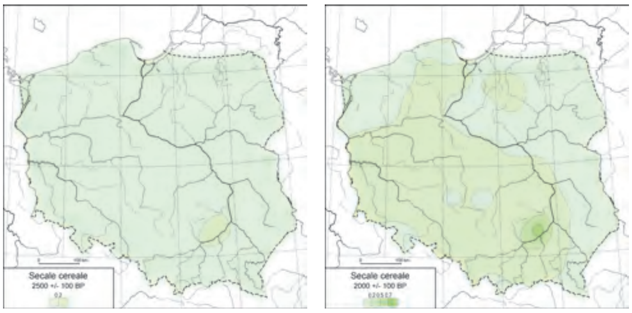
Rumex

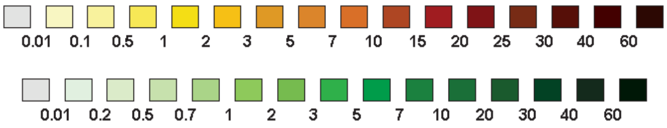


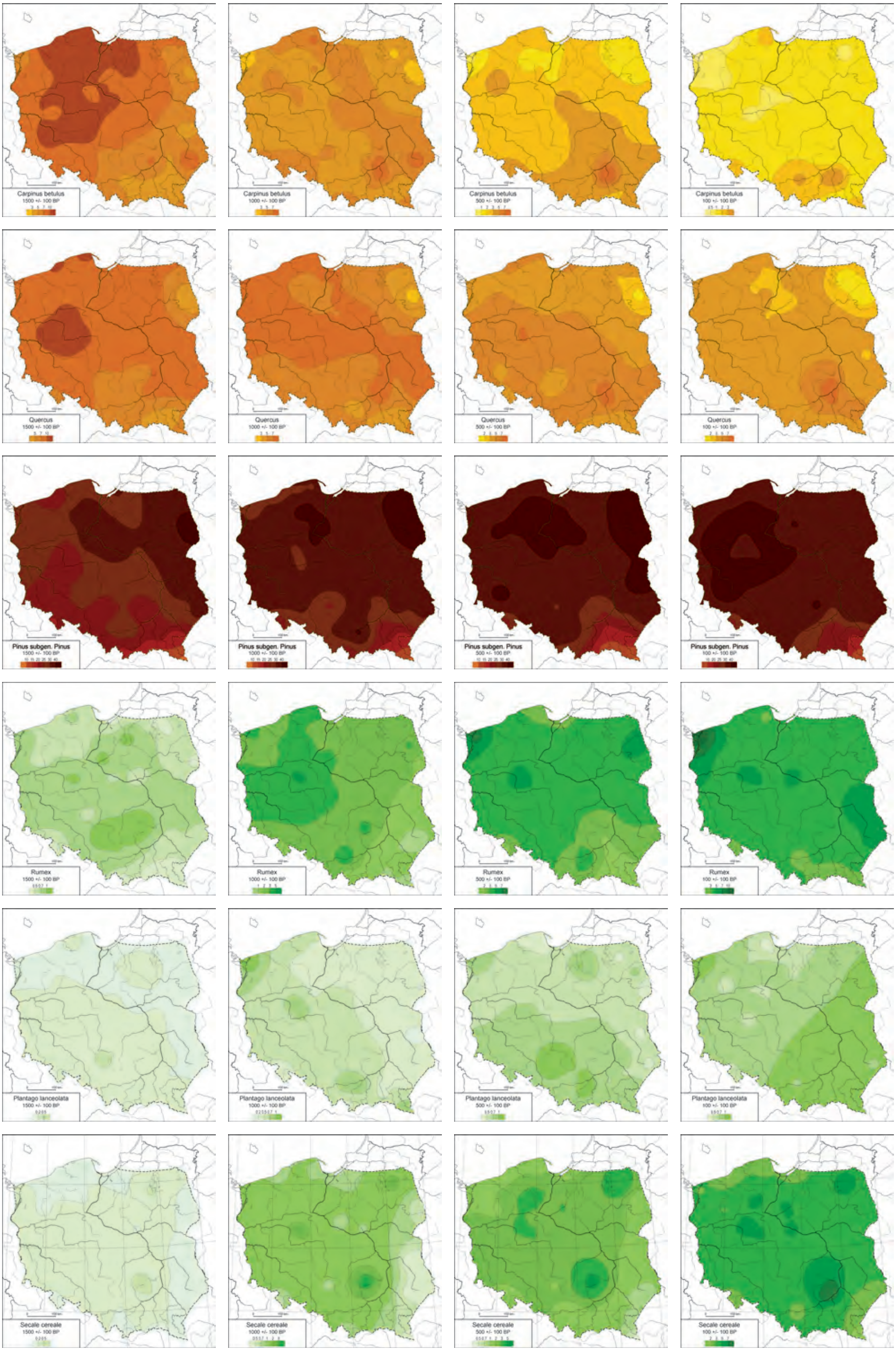
Plantago lanceolata



Secale cereale






Carpinus betulus
1500 +/- 100 BP
Carpinus betulus
1000 +/- 100 BP
Carpinus betulus
500 +/- 100 BP
Carpinus betulus
100 +/- 100 BP
Quercus
1500 +/- 100 BP
Quercus
1000 +/- 100 BP
Quercus
500 +/- 100 BP
Quercus
100 +/- 100 BP
Pinus subgen. Pinus
1500 +/- 100 BP
10 15 20 25 30 40
Pinus subgen. Pinus
1000 +/- 100 BP
10 15 20 25 30 40
Pinus subgen. Pinus
500 +/- 100 BP
10 15 20 25 30 40
Pinus subgen. Pinus
100 +/- 100 BP
10 20 25 30 40
Rumex
1500 +/- 100 BP
Rumex
1000 +/- 100 BP
Rumex
500 +/- 100 BP
Rumex
100 +/- 100 BP
Plantago lanceolata
1500 +/- 100 BP
Plantago lanceolata
1000 +/- 100 BP
Plantago lanceolata
500 +/- 100 BP
Plantago lanceolata
100 +/- 100 BP
Secale cereale
1500 +/- 100 BP
Secale cereale
1000 +/- 100 BP
Secale cereale
500 +/- 100 BP
Secale cereale
100 +/- 100 BP

APPENDIX

SITES USED FOR DRAWING THE ISOPOLLEN MAPS OF POLAND

DOROTA NALEPKA

Distribution of sites used for drawing the isopollen maps is presented in Fig. 107. The list of these sites is contained in Table 2. The order of sites in Table 2 corresponds to the order of entrance of the data into the isopollen data base. Table 3 contains the list of sites in alphabetic order.

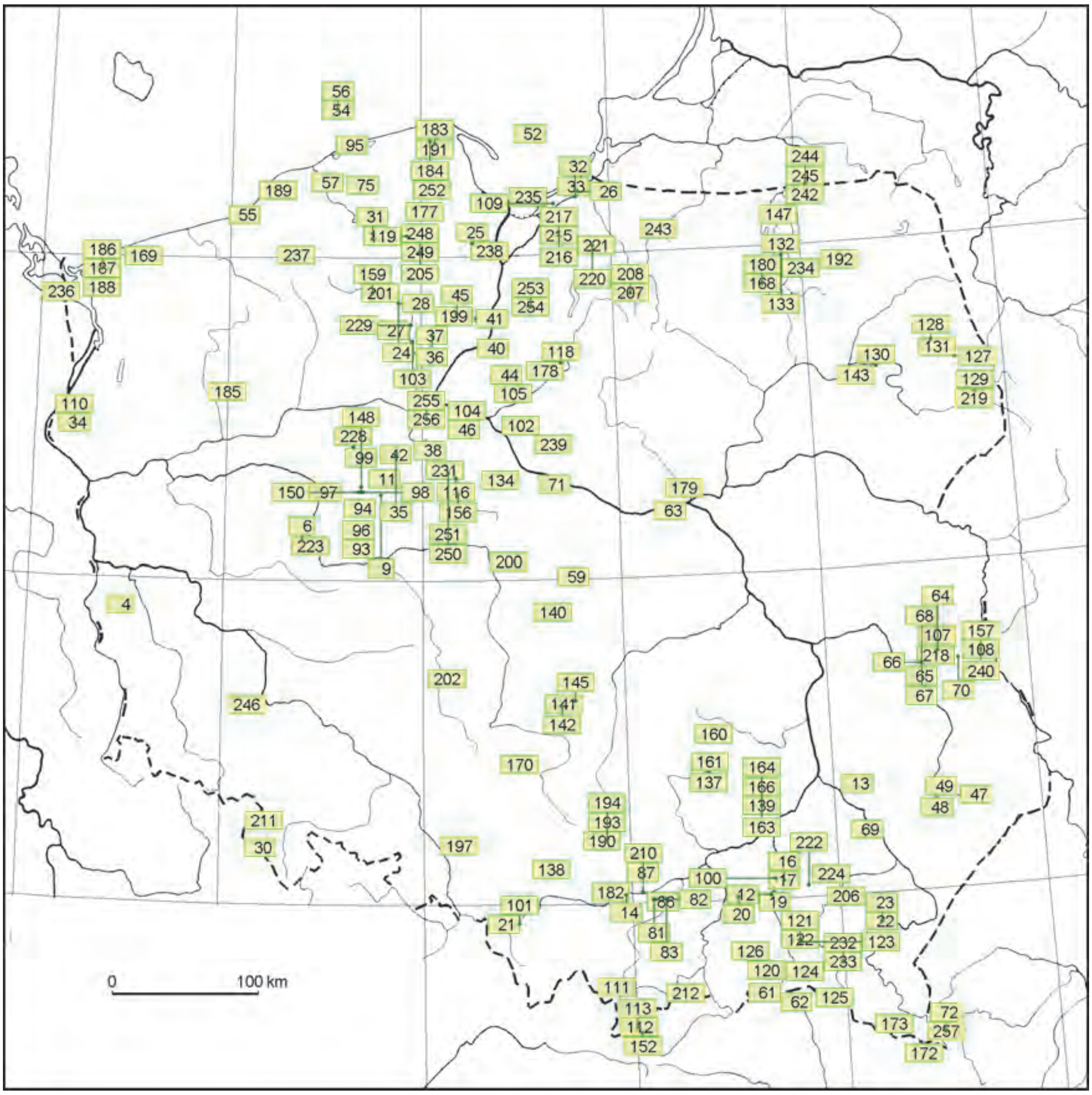


Fig. 107. Distribution of sites used for drawing the isopollen maps; 1–257 – identification numbers of profiles in the isopollen data base

Table 2. List of sites used for drawing the isopollen maps; * – identification number of profile in the isopollen data base and on the maps; ** – calendar dates of varve sediments converted to ^{14}C BP age

No.	No. izo*	Name of site with profile symbol	Geographic coordinates	References	Number of dates	
					^{14}C dates	Estimated dates
1	2	3	4	5	6	7
1	4	Jasień (Jas-12)	51°50´N, 14°58´E	Nowaczyk & Okuniewska-Nowaczyk 1996, Okuniewska-Nowaczyk 1996		5
2	6	Lake Skrzynka (Sk)	52°15´N, 16°47´E	Okuniewska-Nowaczyk 1987, 1992, Ołtuszewski 1957, Szafrański 1968, 1973	10	4
3	9	Lake Świętokrzyskie (Sw 3/91)	52°32´N, 17°35´E	Makohonienko 1997, 2000		12
4	11	Lake Głęboczek (Gl 1/91)	52°38´N, 17°37´E	Makohonienko 1997, 2000		7
5	12	Podgrodzie (PA)	50°01´N, 21°20´E	Alexandrowicz et al. 1981	4	4
6	13	Imielty Ług (ImŁ)	50°40´N, 22°14´E	Mamakowa 1962		6
7	14	Kraków-Rondo (KrR)	50°03´N, 19°56´E	Mamakowa 1970		4
8	16	Brzeźnica C (BC)	50°06´N, 21°28´E	Kowalkowski et al. 1981		3
9	17	Brzeźnica D (BD)	50°06´N, 21°28´E	Kowalkowski et al. 1981	1	2
10	19	Grabiny-Latoszyn (Grl B)	50°02´N, 21°22´E	Mamakowa et al. 1981	1	
11	20	Tarnów-Gumniska (TG)	50°01´N, 21°01´E	Brud & Mamakowa 2001		3
12	21	Bąków near Drogomyśl (Bk)	49°53´N, 18°45´E	Mamakowa 1997 (unpubl.)	1	2
13	22	Podbukowina I (PbI)	49°49´N, 22°23´E	Mamakowa 1962		7
14	23	Podbukowina II (bottom) (PbII)	49°49´N, 22°23´E	Mamakowa 1962		6
15	24	Suszek (Su) (lake)	53°43´N, 17°46´E	Miotk-Szpiganowicz 1989, 1992		7
16	25	Lake Godziszewskie (Go)	54°05´N, 18°33´E	Miotk 1986, Bogaczewicz-Adamczak & Miotk-Szpiganowicz 1987		7
17	26	Zalew Wiślany (Vistula Lagoon) (IIIa-ZW)	54°23´N, 19°41´E	Bogaczewicz-Adamczak & Miotk 1985		3
18	27	Kęsowo (upper part) (Ks) (lake)	53°33´N, 17°43´E	Miotk-Szpiganowicz 1989, 1992		6
19	28	Mały Suszek (MS) (lake)	53°43´N, 17°46´E	Miotk-Szpiganowicz 1989, 1992	5	9
20	30	Zieleniec (ZL)	50°21´N, 16°24´E	Madeyska 1989, Kuźniewski 1958, Stark 1936	6	4
21	31	Sierżno (Sr)	50°21´N, 16°24´E	Miotk-Szpiganowicz unpubl.	4	3
22	32	Zalew Wiślany (Vistula Lagoon) (2a)	54°21´N, 19°39´E	Zachowicz 1985		7
23	33	Zalew Wiślany Piaski (Vistula Lagoon) (Ib)	54°25´N, 19°38´E	Zachowicz 1985		9
24	34	Chojna 1/85	52°57´N, 14°26´E	Krupiński 1985 (unpubl.), 1988, 1991		5
25	35	Biskupin Mire (TB)	52°47´N, 17°44´E	Niewiarowski & Noryśkiewicz A.M. 1995		6
26	36	Lake Mukrz (M1)	53°31´N, 18°07´E	Noryśkiewicz A.M. 2002		13
27	37	Lake Mukrz II (MII)	53°31´N, 18°07´E	Noryśkiewicz A.M. 2002	1	11
28	38	Pakość (Pa/70	52°46´N, 18°05´E	Noryśkiewicz B. unpubl.		10
29	40	Rudnickie Małe (RMł/74) (lake)	53°26´N, 18°45´E	Drozdowski 1974, Drozdowski & Berglund 1976	1	6
30	41	Lake Zawada (Z/99)	53°37´N, 18°35´E	Noryśkiewicz B. & Tobolski 2003	2	7
31	42	Lake Biskupin (B/4)	52°47´N, 17°44´E	Noryśkiewicz B. 1993, 1994, 1995, Niewiarowski et al. 1995, Niewiarowski & Noryśkiewicz B. 1999		12
32	44	Czystochleb 1992 (Cz/92)	53°16´N, 18°53´E	Filbrandt-Czaja & Noryśkiewicz B. 2003, Filbrandt-Czaja et al. 2003	2	9
33	45	Osie (O/83)	53°39´N, 18°23´E	Bednarek 1991	1	4
34	46	Dzikowo (Dz)	52°56´N, 18°26´E	Tomczak 1987		8
35	47	Tarnawatka	50°33´N, 23°23´E	Bałaga 1998	6	3
36	48	Krasnobród	50°33´N, 23°00´E	Bałaga 1998	6	3
37	49	Kosobudy	50°37´N, 23°03´E	Bałaga 1998	2	1
38	52	Basen Gdański 2 (El/96)	54°45´N, 19°11´E	Mojski (ed.) 1995		4
39	54	Ławica Słupska (14097)	54°55´N, 17°08´E	Uścinowicz & Zachowicz 1991	2	
40	55	Lake Jamno 2	54°16´N, 16°09´E	Dąbrowski et al. 1985, Zachowicz 1972, 1985		8
41	56	Ławica Słupska (14097B)	54°55´N, 17°08´E	Uścinowicz & Zachowicz 1991	5	
42	57	Słupsk (S)	54°28´N, 17°07´E	Zachowicz 1990		3
43	59	Witów I	52°01´N, 19°31´E	Wasylikowa 1964, 2001	4	3
44	61	Regetovka (Re)	49°25´N, 21°16´E	Wacnik 1995, 1999, 2000, Wacnik et al. 2001b	4	1
45	62	Kružlová (Kr)	49°21´N, 21°34´E	Wacnik 2000, 2001, Wacnik et al. 2001b	4	1

Table 2. Continued

1	2	3	4	5	6	7
46	63	Wilków (Wil 900)	52°24´N, 20°31´E	Konecka-Betley et al. 1996	5	
47	64	Moszne	51°27´N, 23°07´E	Bałaga et al. 1992, 1995	7	2
48	65	Lake Łukcze (ŁI)	51°23´N, 22°57´E	Bałaga 1990		4
49	66	Łukcze (ŁII)	51°23´N, 22°57´E	Bałaga 1990	1	2
50	67	Łukcze (ŁIII)	51°23´N, 22°57´E	Bałaga 1990	2	3
51	68	Łukcze (ŁIV)	51°23´N, 22°57´E	Bałaga 1990	4	2
52	69	Kopki	50°23´N, 22°18´E	Bałaga & Taras 2001	6	1
53	70	Krowie Bagno	51°24´N, 23°19´E	Bałaga et al. 1980/81, Bałaga 2003; unpubl.	3	3
54	71	Lake Gościąż (G1/87)	52°35´N, 19°21´E	Ralska-Jasiewiczowa et al. 1998	258[**]	
55	72	Tarnawa Wyżna (Ta I)	49°07´N, 22°55´E	Ralska-Jasiewiczowa 1972, 1980, 1989		14
56	75	Poganice (Po4F)	54°27´N, 17°24´E	Nalepka 1993		3
57	81	Podłężówka (Pł 17)	50°01´N, 20°12´E	Nalepka 1991, 1994a, b		5
58	82	Podłężówka (Pł 40)	50°01´N, 20°13´E	Nalepka 1991, 1994a, b		3
59	83	Stanisławice (S2)	50°01´N, 20°19´E	Nalepka 1991, 1994a, b, 2003		6
60	86	Błoto (Pel 4)	50°00´N, 20°17´E	Nalepka 1991, 1994a, b		2
61	87	Pleszów (Pl-861)	50°04´N, 20°06´E	Nalepka 1991, 1994a, b	2	5
62	93	Giecz (G-2/90)	52°12´N, 17°21´E	Milecka 1998	3	8
63	94	Lake Baba (Ba/91)	52°25´N, 17°22´E	Milecka 1998		11
64	95	Kluki 74	54°42´N, 17°17´E	Tobolski 1987, 1997	20	
65	96	Giecz (G-1/89)	52°19´N, 17°21´E	Milecka 1998	3	6
66	97	Lake Skrzetuszewskie (S/84)	52°33´N, 17°21´E	Tobolski 1991b	9	2
67	98	Lake Skrzetuszewskie (S/87)	52°33´N, 17°21´E	Tobolski 1990	14	1
68	99	Lake Lednickie (V/86)	52°33´N, 17°23´E	Litt & Tobolski 1991		10
69	100	Wola Żyrakowska (WŻ 3)	50°07´N, 21°23´E	Starkel & Granoszewski 1995		4
70	101	Bronów (W-1)	49°53´N, 18°54´E	Granoszewski 1998b (unpubl.)	2	5
71	102	Lake Steklin (J. Ste 6/82)	52°57´N, 19°01´E	Marciniak 1987, Noryśkiewicz B. 1982a, Noryśkiewicz B. & Ralska-Jasiewiczowa 1989	1	8
72	103	Zamrzenica (Z/82)	53°29´N, 17°55´E	Noryśkiewicz B. 1982b		8
73	104	Czarne Błota (CzBł/78)	53°03´N, 18°28´E	Niewiarowski & Noryśkiewicz B. 1983		5
74	105	Napole (Nap/97)	53°09´N, 18°57´E	Filbrandt-Czaja & Noryśkiewicz B. 2003, Filbrandt-Czaja et al. 2003	1	2
75	107	Lake Moszne C	51°27´N, 23°07´E	Bałaga 2003, unpubl.		2
76	108	Lake Perespilno 200	51°26´N, 23°33´E	Bałaga et al. 1998, Goslar et al. 1999	52	
77	109	Zalew Wiślany (Vistula Lagoon) (ZW6)	54°19´N, 19°25´E	Zachowicz unpubl.		2
78	110	Chojna (2/85)	52°57´N, 14°26´E	Krupiński 1985 (unpubl.), 1988, 1991		8
79	111	Puścizna Rękowiańska (PR)	49°29´N, 19°49´E	Obidowicz 1990	8	1
80	112	Czarny Staw Gąsienicowy (CzS) (lake)	49°14´N, 20°01´E	Obidowicz 1996	5	
81	113	Zielony Staw Gąsienicowy(ZS) (lake)	49°14´N, 20°00´E	Obidowicz 1996	5	
82	116	Lake Gopło III	52°38´N, 18°21´E	Jankowska 1980		14
83	118	Lake Strażym (J. Str 6/87)	53°20´N, 19°27´E	Kuc et al. 1993, Noryśkiewicz B. 1987a, b, Ralska-Jasiewiczowa et al. 1985		10
84	119	Korne (Ko/64)	54°08´N, 17°52´E	Kępczyński & Noryśkiewicz B. 1982, Szupryczyński 1967	2	6
85	120	Jasło	49°33´N, 21°20´E	Harmata 1995b, Wójcik 1987		5
86	121	Roztoki b (Roz. b)	49°44´N, 21°35´E	Harmata 1995b, Wójcik 1987		4
87	122	Roztoki a (Roz. a)	49°44´N, 21°35´E	Harmata 1987, 1995b, Wójcik 1987	2	1
88	123	Tarnowiec (Tar)	49°43´N, 21°36´E	Harmata 1987, 1995a,b, Wójcik 1987	7	1
89	124	Cergowa Góra 1994	49°32´N, 21°42´E	Szczepanek 2001, Więckowski & Szczepanek 1963, Wacnik et al. 2001b	10	1
90	125	Jasiel 1981	49°22´N, 21°53´E	Szczepanek 1987, 1989a, Wacnik et al. 2001b	5	
91	126	Szymbark	49°38´N, 21°06´E	Gil et al. 1972, 1974, Szczepanek 1989a, Wacnik et al. 2001b	5	
92	127	Stare Biele (SB I)	53°14´N, 23°32´E	Kupryjanowicz 2000, Żurek 2000		10
93	128	Machnacz (M-III)	53°21´N, 23°18´E	Kupryjanowicz 1991, 1994, Żurek 1990, 1992		14
94	129	Rabinówka (R)	53°01´N, 23°43´E	Kupryjanowicz 1999 (unpubl.)		5
95	130	Żurawisko (Ż)	53°13´N, 22°43´E	Kupryjanowicz 1995 (unpubl.)		4

Table 2. Continued

1	2	3	4	5	6	7
96	131	Kładkowe Bagno (KB V)	53°18´N, 23°22´E	Kupryjanowicz (2004), Brzostowska 2001 (unpubl.)		8
97	132	Nietlice (N10)	53°56´N, 21°48´E	Kupryjanowicz 2002		4
98	133	Nietlice (N11)	53°56´N, 21°48´E	Kupryjanowicz 2002		2
99	134	Osłonki (Os 949)	52°37´N, 18°48´E	Gąsiorowski & Nalepka 2004		5
100	137	Słopiec 79/80	50°47´N, 20°47´E	Szczepanek 1961, 1982, 1989b, 2000	17	
101	138	Jęzor-Jaworzno 1998	50°13´N, 19°13´E	Szczepanek & Stachowicz-Rybka 2004	6	4
102	139	Czajków 1	50°34´N, 21°17´E	Karczmarz & Szczepanek 1982, Szczepanek 1971a		6
103	140	Aleksandrów (Aleks 0)	51°48´N, 19°18´E	Balwierz unpubl.		10
104	141	Bełchatów z.I	51°14´N, 19°23´E	Balwierz & Goździk 1997	1	5
105	142	Bełchatów z.III	51°13´N, 19°22´E	Balwierz & Goździk 1997	1	4
106	143	Lake Maliszewskie (Mal. I)	53°10´N, 22°30´E	Balwierz & Żurek 1987, 1989	4	1
107	145	Napoleonów (NAP I)	51°15´N, 19°30´E	Balwierz 1980		4
108	147	Lake Dgał Wielki/Pieczarki (P6/95)	54°11´N, 21°48´E	Filbrandt-Czaja 2000		8
109	148	Lake Kamionek (Ka/87)	52°35´N, 17°23´E	Filbrandt 1991, Filbrandt-Czaja 1998	2	7
110	150	Lake Linie (Lin2/87)	52°33´N, 17°24´E	Filbrandt-Czaja 1998	1	8
111	152	Przedni Staw (lake)	49°12´N, 20°03´E	Krupiński 1983/84, Wicik 1979		6
112	156	Potrzymiech (Pot/98)	52°32´N, 18°22´E	Molewski & Noryśkiewicz B. 2000	1	4
113	157	Lake Perespilno 202	51°26´N, 23°33´E	Bałaga et al. 2002	8	1
114	159	Lake Wielkie Gacno (main profile)	53°47´N, 17°30´E	Hjelmroos-Ericsson 1981	17	3
115	160	Suchedniów	51°01´N, 20°51´E	Szczepanek 1961, 2000		3
116	161	Górno	50°51´N, 20°48´E	Szczepanek 1961, 2000		5
117	163	Czajków 3-III	50°34´N, 21°17´E	Karczmarz & Szczepanek 1982, Szczepanek 1971a	1	2
118	164	Czajków 4	50°34´N, 21°17´E	Karczmarz & Szczepanek 1982, Szczepanek 1971a	1	4
119	166	Czajków 2-II	50°34´N, 21°17´E	Karczmarz & Szczepanek 1982, Szczepanek 1971a	2	6
120	168	Lake Mikołajki (Mik)	53°46´N, 21°35´E	Ralska-Jasiewiczowa 1964, 1966, Ralska-Jasiewiczowa & Latałowa 1996		14
121	169	Niechorze (N-1 bis)	54°00´N, 15°03´E	Brykczyńska 1978, Kopczyńska-Lamparska et al. 1984, Ralska-Jasiewiczowa & Rzętkowska 1987	1	6
122	170	Walenczów (Wal.)	50°52´N, 18°56´E	Ralska-Jasiewiczowa 1977	2	3
123	172	Wołosate (Woł.)	49°03´N, 22°42´E	Ralska-Jasiewiczowa 1980		6
124	173	Smerek (SM 1)	49°11´N, 22°26´E	Ralska-Jasiewiczowa 1972, 1980		9
125	177	Lake Raduńskie Dolne	54°17´N, 18°03´E	Gołębiewski 1976		6
126	178	Lake Oleczno (OL 3/96)	53°17´N, 19°17´E	Filbrandt-Czaja 1999		4
127	179	Lake Błędowo III	52°32´N, 20°40´E	Bińka et al. 1988,1991, Bińka & Szeroczyńska 1989		8
128	180	Lake Mikołajki (Mik.84)	53°46´N, 21°35´E	Ralska-Jasiewiczowa unpubl., Ralska-Jasiewiczowa & Latałowa 1996	5	
129	182	Cholerzyn (CH)	50°04´N, 19°47´E	Lipka 1989, Madeyska & Obidowicz 2001	5	1
130	183	Darżlubie Forest (P. Darż./78)	54°42´N, 18°10´E	Latałowa 1982, 1989b	10	3
131	184	Żarnowiec (Żar/76, Żar/75)	54°43´N, 18°07´E	Latałowa 1982, 1989c	7	3
132	185	Sicienko (S/1998)	53°10´N, 16°00´E	Latałowa unpubl.	3	10
133	186	Kołczewo (K-0)	53°55´N, 14°40´E	Latałowa 1989d, 1992	14	4
134	187	Lake Racze (R-1)	53°55´N, 14°40´E	Latałowa 1992	8	6
135	188	Wolin (W-II)	53°50´N, 14°40´E	Latałowa 1989d, 1992, 1999b	8	1
136	189	Żurawiec (Słowińskie Bagno) (SB-1)	54°25´N, 16°30´E	Latałowa 1989b, Latałowa unpubl.	7	1
137	190	Wolbrom (WOL-1)	50°23´N, 19°46´E	Latałowa 1976, 1989a, Latałowa & Nalepka 1987	2	11
138	191	Orle 76	54°40´N, 18°10´E	Latałowa 1988b	1	6
139	192	Miłuki (Mil 1/97)	53°53´N, 22°22´E	Milecka unpubl.		8
140	193	Wolbrom (WOL-2)	50°23´N, 19°46´E	Latałowa 1976, 1989a, Latałowa & Nalepka 1987	11	5
141	194	Wolbrom (WOL-3)	50°23´N, 19°46´E	Latałowa 1976, 1989a, Latałowa & Nalepka 1987	3	8

Table 2. Continued

1	2	3	4	5	6	7
142	197	Sławięcice (S)	50°22´N, 18°20´E	Nita unpubl.		2
143	199	Dury 1/98	53°38´N, 18°21´E	Milecka 2001, Kowalewski & Milecka 2003		10
144	200	Rośle	52°07´N, 18°52´E	Krajewski & Balwierz 1984	2	
145	201	Lake Ostrowite (OST/99)	53°47´N, 17°35´E	Milecka & Szeroczyńska 2002, 2004	10	4
146	202	Węglewice (W-I)	51°24´N, 18°14´E	Tobolski 1965	1	8
147	205	Juszki B2 (JuB)	54°02´N, 18°00´E	Miotk-Szpiganowicz unpubl.	1	2
148	206	Mleczka I/6	49°59´N, 22°03´E	Zernitskaya et al. 2003		5
149	207	Woryty (Wor 80) (upper part)	53°45´N, 20°12´E	Dąbrowski (ed.) 1981, Pawlikowski et al. 1982, Ralska-Jasiewiczowa & Latałowa 1996		5
150	208	Woryty (Wor 82) (lower part)	53°45´N, 20°12´E	Dąbrowski (ed.) 1981, Pawlikowski et al. 1982, Ralska-Jasiewiczowa & Latałowa 1996	7	2
151	210	Pleszów (compilation)	50°04´N, 20°06´E	Wasylikowa et al. 1985	5	
152	211	Batorowskie peat-bog (WTB/6)	50°31´N, 16°26´E	Marek 1998, Stark 1936		4
153	212	Bryjarka (Bry.)	49°26´N, 20°28´E	Pawlikowa 1965		2
154	215	Lake Druzno 1a (lower part)	54°07´N, 19°28´E	Zachowicz & Kępińska 1987, Zachowicz et al. 1982		4
155	216	Lake Druzno 1A (upper part)	54°07´N, 19°28´E	Zachowicz & Kępińska 1987, Zachowicz et al. 1982		5
156	217	Lake Druzno 1A (lower part)	54°07´N, 19°28´E	Zachowicz & Kępińska 1987, Zachowicz et al. 1982		2
157	218	Lake Karaśne	51°25´N, 23°06´E	Bałaga 2003	3	2
158	219	Julianka (Ja)	52°58´N, 23°42´E	Kupryjanowicz unpubl.		8
159	220	Stary Cieszyn (St.C/9)	54°03´N, 19°49´E	Noryśkiewicz B. et al. 2000, 2002		2
160	221	Stary Cieszyn (St.C/2)	54°03´N, 19°49´E	Noryśkiewicz B. et al. 2000, 2002	2	
161	222	Wolica Ługowa (WŁ-1)	50°04´N, 21°42´E	Madeja 2002a, b, Starkel et al. 2002		3
162	223	Bogulin (Bg)	52°13´N, 16°52´E	Okuniewska-Nowaczyk unpubl.	3	6
163	224	Świlcza (SW-1)	50°05´N, 21°55´E	Madeja unpubl.	1	
164	228	Lake Łekneńskie (Ł2/96)	52°50´N, 17°18´E	Milecka 1997, 2000a, c		9
165	229	Tuchola (T4)	53°35´N, 17°54´E	Obremska & Lamentowicz M. unpubl.		8
166	231	Bożejewice (B1/97) (lower part)	52°41´N, 18°14´E	Makohonienko unpubl.		6
167	232	Besko (Bes 1) (upper part)	49°35´N, 21°59´E	Koperowa 1970		4
168	233	Besko (Bes 1) (lower part)	49°35´N, 21°59´E	Koperowa 1970	2	3
169	234	Lake Miłkowskie (M4/98)	53°51´N, 21°50´E	Wacnik 2003 (unpubl.), Wacnik et al. 2001a		14
170	235	Stegna Oczyszczalnia	54°19´N, 19°09´E	Zachowicz unpubl.	2	1
171	236	Zalew Szczeciński (Szczecin Lagoon) I	53°46´N, 14°25´E	Wypych 1980		7
172	237	Lake Kwiecko (K-1)	54°01´N, 16°42´E	Madeja 2003 (unpubl.)	1	7
173	238	Gniszewo	54°02´N, 18°44´E	Zachowicz unpubl.		5
174	239	Lake Mielno (Miel.5)	52°52´N, 19°21´E	Kępczyński 1960	1	7
175	240	Lake Perespilno 505	51°26´N, 23°33´E	Bałaga 2003	1	1
176	242	Sapallen-Sapałówka S	54°15´N, 22°05´E	Gross 1939		5
177	243	Lingenau-Łęgnowo Ł	54°08´N, 20°31´E	Gross 1939		5
178	244	Zedmar ZrA (upper part)	54°22´N, 22°06´E	Gross 1938		5
179	245	Zedmar ZrA (lower part)	54°22´N, 22°06´E	Gross 1938		2
180	246	Kunice (Kun 6)	51°14´N, 16°15´E	Marek & Siedlak 1972, Marek & Casparie 1988	1	7
181	248	Juszki (B1) (upper part)	54°02´N, 18°00´E	Miotk-Szpiganowicz unpubl.	1	6
182	249	Juszki (B1) (lower part)	54°02´N, 18°00´E	Miotk-Szpiganowicz unpubl.		2
183	250	Sławsko (1/97) (upper part)	52°40´N, 18°16´E	Milecka 2000b	1	1
184	251	Sławsko (1/97) (lower part)	52°40´N, 18°16´E	Milecka 2000b	2	4
185	252	Stążki (St) (slightly modified)	54°25´N, 18°08´E	Szafrański 1961		9
186	253	Lake Klasztorne (K1) (upper part)	53°41´N, 19°09´E	Noryśkiewicz B. 1997	1	1
187	254	Lake Klasztorne (K1) (lower part)	53°41´N, 19°09´E	Noryśkiewicz B. 1997	1	2
188	255	Lake Jezuickie (Je/88) (upper part)	53°00´N, 18°03´E	Noryśkiewicz B. unpubl.		4
189	256	Lake Jezuickie (Je/88) (lower part)	53°00´N, 18°03´E	Noryśkiewicz B. unpubl.		4
190	257	Tarnawa Wyżna (TaII) (lower part)	49°07´N, 22°55´E	Ralska-Jasiewiczowa 1980	5	

Table 3. Alphabetic list of the sites used for drawing the isopollen maps; * – identification number of profile in the isopollen data base and on the maps

Name of site with profile symbol	No. izo*
Aleksandrów (Aleks 0)	140
Basen Gdański 2 (El/96)	52
Batorowskie peat-bog (WTB/6)	211
Bąków near Drogomyśl (Bk)	21
Bełchatów z.I	141
Bełchatów z.III	142
Besko (Bes 1) (lower part)	233
Besko (Bes 1) (upper part)	232
Biskupin Mire (TB)	35
Błoto (Pel 4)	86
Bogulin (Bg)	223
Bożejewice (B1/97) (lower part)	231
Bronów (W-1)	101
Bryjarka (Bry.)	212
Brzeźnica C (BC)	16
Brzeźnica D (BD)	17
Cergowa Góra 1994	124
Chojna (2/85)	110
Chojna 1/85	34
Cholerzyn (CH)	182
Czajków 1	139
Czajków 2-II	166
Czajków 3-III	163
Czajków 4	164
Czarne Błota (CzBł/78)	104
Czarny Staw Gąsienicowy (CzS) (lake)	112
Czystochleb 1992 (Cz/92)	44
Darżlubie Forest (P. Darż./78)	183
Dury 1/98	199
Dzikowo (Dz)	46
Giecz (G-1/89)	96
Giecz (G-2/90)	93
Gniszewo	238
Górno	161
Grabiny-Latoszyn (Grl B)	19
Imielty Ług (ImŁ)	13
Jasiel 1981	125
Jasień (Jas-12)	4
Jasło	120
Jęzor-Jaworzno 1998	138
Julianka (Ja)	219
Juszki (B1) (lower part)	249
Juszki (B1) (upper part)	248
Juszki B2 (JuB)	205
Kęsowo (upper part) (Ks) (lake)	27
Kluki 74	95
Kładkowe Bagno (KB V)	131
Kołczewo (K-0)	186
Kopki	69
Korne (Ko/64)	119
Kosobudy	49
Kraków-Rondo (KrR)	14
Krasnobród	48
Krowie Bagno	70

Name of site with profile symbol	No. izo*
Kružlová (Kr)	62
Kunice (Kun 6)	246
Lake Baba (Ba/91)	94
Lake Biskupin (B/4)	42
Lake Błędowo III	179
Lake Dgał Wielki/Pieczarki (P6/95)	147
Lake Druzno 1a (lower part)	215
Lake Druzno 1A (lower part)	217
Lake Druzno 1A (upper part)	216
Lake Głęboczek (Gl 1/91)	11
Lake Godziszewskie (Go)	25
Lake Gopło III	116
Lake Gościąż (G1/87)	71
Lake Jamno 2	55
Lake Jezuickie (Je/88) (lower part)	256
Lake Jezuickie (Je/88) (upper part)	255
Lake Kamionek (Ka/87)	148
Lake Karaśne	218
Lake Klasztorne (K1) (lower part)	254
Lake Klasztorne (K1) (upper part)	253
Lake Kwiecko (K-1)	237
Lake Lednickie (V/86)	99
Lake Linie (Lin2/87)	150
Lake Łekneńskie (Ł2/96)	228
Lake Łukcze (ŁI)	65
Lake Maliszewskie (Mal. I)	143
Lake Mielno (Miel.5)	239
Lake Mikołajki (Mik)	168
Lake Mikołajki (Mik.84)	180
Lake Miłkowskie (M4/98)	234
Lake Moszne C	107
Lake Mukrz (M1)	36
Lake Mukrz II (MII)	37
Lake Oleczno (OL 3/96)	178
Lake Ostrowite (OST/99)	201
Lake Perespilno 200	108
Lake Perespilno 202	157
Lake Perespilno 505	240
Lake Racze (R-1)	187
Lake Raduńskie Dolne	177
Lake Skrzetuszewskie (S/84)	97
Lake Skrzetuszewskie (S/87)	98
Lake Skrzynka (Sk)	6
Lake Steklin (J. Ste 6/82)	102
Lake Strażym (J. Str 6/87)	118
Lake Świętokrzyskie (Sw 3/91)	9
Lake Wielkie Gacno (main profile)	159
Lake Zawada (Z/99)	41
Lingenau-Łęgnowo Ł	243
Ławica Słupska (14097)	54
Ławica Słupska (14097B)	56
Łukcze (ŁII)	66
Łukcze (ŁIII)	67
Łukcze (ŁIV)	68

Table 3. Continued

Name of site with profile symbol	No. izo*
Machnacz (M-III)	128
Mały Suszek (MS) (lake)	28
Miłuki (Mil 1/97)	192
Mleczka I/6	206
Moszne	64
Napole (Nap/97)	105
Napoleonów (NAP I)	145
Niechorze (N-1 bis)	169
Nietlice (N10)	132
Nietlice (N11)	133
Orle 76	191
Osie (O/83)	45
Osłonki (Os 949)	134
Pakość (Pa/70	38
Pleszów (compilation)	210
Pleszów (Pl-861)	87
Podbukowina I (PbI)	22
Podbukowina II (bottom) (PbII)	23
Podgrodzie (PA)	12
Podłężówka (Pł 17)	81
Podłężówka (Pł 40)	82
Poganice (Po4F)	75
Potrzymiech (Pot/98)	156
Przedni Staw (lake)	152
Puścizna Rękowiańska (PR)	111
Rabinówka (R)	129
Regetovka (Re)	61
Rośle	200
Roztoki a (Roz. a)	122
Roztoki b (Roz. b)	121
Rudnickie Małe (RMł/74) (lake)	40
Sapallen-Sapałówka S	242
Sicienko (S/1998)	185
Sierżno (Sr)	31
Sławięcice (S)	197
Sławsko (1/97) (lower part)	251
Sławsko (1/97) (upper part)	250
Słopiec 79/80	137
Słupsk (S)	57
Smerek (SM 1)	173
Stanisławice (S2)	83

Name of site with profile symbol	No. izo*
Stare Biele (SB I)	127
Stary Cieszyn (St.C/2)	221
Stary Cieszyn (St.C/9)	220
Stążki (St) (slightly modified)	252
Stegna Oczyszczalnia	235
Suchedniów	160
Suszek (Su) (lake)	24
Szymbark	126
Świlcza (SW-1)	224
Tarnawa Wyżna (TaI)	72
Tarnawa Wyżna (TaII) (lower part)	257
Tarnawatka	47
Tarnowiec (Tar)	123
Tarnów-Gumniska (TG)	20
Tuchola (T4)	229
Walenczów (Wal.)	170
Węglewice (W-I)	202
Wilków (Wil 900)	63
Witów I	59
Wola Żyrakowska (WŻ 3)	100
Wolbrom (WOL-1)	190
Wolbrom (WOL-2)	193
Wolbrom (WOL-3)	194
Wolica Ługowa (WŁ-1)	222
Wolin (W-II)	188
Wołosate (Woł.)	172
Woryty (Wor 80) (upper part)	207
Woryty (Wor 82) (lower part)	208
Zalew Szczeciński (Szczecin Lagoon) I	236
Zalew Wiślany (Vistula Lagoon) (2a)	32
Zalew Wiślany (Vistula Lagoon) (IIIa-ZW)	26
Zalew Wiślany (Vistula Lagoon) (ZW6)	109
Zalew Wiślany Piaski (Vistula Lagoon) (Ib)	33
Zamrzenica (Z/82)	103
Zedmar ZrA (lower part)	245
Zedmar ZrA (upper part)	244
Zieleniec (ZL)	30
Zielony Staw Gąsienicowy(ZS) (lake)	113
Żarnowiec (Żar/76, Żar/75)	184
Żurawiec (Słowińskie Bagno) (SB-1)	189
Żurawisko (Ż)	130

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