Changing distribution patterns of selected conifers in the Quaternary of Europe caused by climatic variations

Dissertation
zur
Erlangung des Doktorgrades (Dr. rer. nat.)
der
Mathematisch-Naturwissenschaftlichen Fakultät
der
Rheinischen Friedrich-Wilhelms-Universität Bonn

vorgelegt von

Ruth Terhürne-Berson
aus
Essen

Bonn 2005

Angefertigt mit Genehmigung der Mathematisch-Naturwissenschaftlichen Fakultät der
Rheinischen Friedrich-Wilhelms-Universität Bonn

1. Referent: Prof. Dr. T. Litt
2. Referent: Prof. Dr. W. Barthlott

Tag der Promotion: 16.06.2005

Content

1. Introduction

1.1 Aims

Extreme climatic variations in the Quaternary of Europe did not only lead to an intense reduction of plant diversity, but also to significant changes in plant distribution. It is the aim of this work to exemplary investigate distributional changes of selected conifers that were exposed to different climatic impact during the last glacial-interglacial cycle using combined palaeobotanical datasets.

Within the scope of this PhD project, areal changes of two selected conifer species, *Abies alba* and *Picea abies*, are investigated in the course of different warm phases of the last glacial-interglacial cycle (Eemian, Brørup, Odderade and Holocene) and are compared with recent phylogeographical datasets to achieve a better understanding of chorology dynamics. The two species were chosen for this study, because they are widely distributed within Europe and moreover clearly respond to climatic changes. The aim is to locate glacial refugia of the two taxa in the respective periods as well as the reconstruction of potential migration routes and spread of fir and spruce during the warm stages of the investigated time span (126000 years to date).

The presented palaeobotanical reconstructions are based on both, macrofossil remains and pollen data. Synoptic studies of plant macrofossils provide independent tests of inferences from synoptic maps of pollen data, an approach the success of which is described and discussed for eastern North America (Jackson et al. 1997). Combined fossil datasets provide a more robust basis for locating glacial refugia and reconstructing the postglacial spread of the particular plant species.

Furthermore the present study also includes available phylogeographic datasets. Palaeobotanical data and results of molecular genetic investigations are compared in respect of the vegetational history of *Abies* and *Picea*.

1.2 State of research

Thanks to numerous publications dealing with the compilation of lastglacial and postglacial investigations on woody trees in Europe (e.g. Huntley and Birks 1983; Bennett et al. 1991; Lang 1994; Berglund et al. 1996) the state of research for this period has fundamentally improved over the past years. However, our palaeobotanical knowledge is so far mainly based on pollen data. There is a convenient basis of data for the Holocene. Large amounts of pollen finds are available from the "European Pollen Database" (EPD: http://medias.obs-mip.fr/paleo/epd/epd_main.html). Macrofossil evidences for selected trees were collected in the newly established "European Macrofossil Database" (EMD) at the Institute of Palaeontology in Bonn. Furthermore recent phylogeographic datasets were provided by colleagues of the EU-Project FOSSILVA (Dynamics of forest tree biodiversity: linking genetic, palaeogenetic and plant historical approaches). A detailed description of the present distribution range of *Picea* and *Abies* in Europe is given by Meusel et al. (1964) and Jalas and Suominen (1973). Compared to the history of postglacial immigration and spread of woody trees within the last 15000 years, the state of knowledge about changes in diversity patterns in previous interglacials is still inadequate. Even though numerous interglacial deposits in Europe contain a favourable set of palaeobotanical data (evidence of pollen and macroremains), a detailed overview on the distribution of woody trees is still missing. Important insights currently focus on single investigations of palaeobotanical evidences , such as 200 Eemian and Early Weichselian sites in northern central Europe (see e.g. Aalbersberg and Litt 1998).

Our palaeobotanical knowledge about the possible refugia and the spread of *A. alba* and *Picea abies* is mainly based on pollen data. *Abies* pollen maps for the Weichselian Lateglacial (Huntley and Birks 1983) suggest that fir was locally present in Italy and Greece. No direct evidence was available in Spain for that period. This assumption of two *Abies* refugia (Italy, Greece) is supported by long continuous pollen sequences through the last cold stage (summarised in Bennett et al. 1991). Lang (1994) identifies the southern Apennine Peninsula and the southern Balkan Peninsula as glacial refugia, whereas the Pyrenees or the Iberian Peninsula seem to be unlikely as potential refugia for *A. alba* according to the palynological investigations carried out by Reille (1988) and Reille and Lowe (1993). Lang (1994) reconstructs two major routes of spread; an easterly track from the southern Balkans through the Dinarids to the eastern Alps and Carpathians, and a westerly track from the southern Apennines to the Alps, Massif Central and the Pyrenees.

According to the current state of knowledge glacial refugia of *Picea* were found in three areas: the East Alps and Carpathians, the Balkan and Russia (Huntley and Birks 1983). Starting from these refugial areas the Lateglacial and Holocene spread took place along three major routes (Lang 1994). The North-European area of present-day spruce was colonised via a northern track coming from east and north-east. The colonisation of the hercynic-carpathian area started from the Carpathians in the south-east. The part of the distribution area covering today's alpine and southern European region was populated from the south-eastern Alps and possibly also from the adjacent Dinaric Mountains. The process of areal expansion of *Picea abies* during the last 15000 years shows clear differences between northern Europe and the mountainous areas in the south (Lang 1994). While the immigration into Fennoscandia did mostly not happen until 5000 B.P. (Giesecke and Bennett 2004), the spread into the hercynic Carpathians as well as to the alpine and south-east Europe was nearly completed by this time.

2. Stratigraphy and climate of the last glacial-interglacial cycle

2.1 Eemian

It is assumed that the Eemian interglacial, encompassing a time span from about 128000 to 117000 B.P., was similar to the present-days warm period. The duration of this interglacial can be calculated to about 11000 years by means of annualy laminated sediments from the German site Bispingen (Müller 1974).

Ice cores generally provide excellent climatic archives and give valuable insights into the palaeclimatology of the last glacial-interglacial cycle. At the beginning of the 1990s two deep ice cores, the Greenland Ice Core Project (GRIP) and the Greenland Ice Sheet Project 2 (GISP2) were drilled close to the crest of the Greenland Ice Sheet. According to investigations on these ice cores the colder parts of the Eemian were isotopically similar to the interstadials within the last glacial (Dowdeswell and White 1995), representing temperatures about 5°C cooler than the Holocene (Greenland Ice-core Project (GRIP) Members 1993). On the other hand the three warmest intervals of the Eemian are supposed to have been up to 4-5 °C warmer than today (Johnsen et al. 1995).

The stable oxygen isotope record from the GRIP core documents a dramatic climate instability within the Eemian (MIS-5e / marine isotope stage 5e) by rapid, high amplitude temperature oscillations. However, the Eemian part of the GRIP core contrasts with evidence from the GISP2 core (Fig. 1).

Also the comparison of the GRIP and GISP2 cores with two marine corings from the North Atlantic by McManus et al. (1994) does not confirm a significant Eemian climatic variability. The marine deposits rather show a more stable climate. Therefore the authors suggest localized phenomena to be responsible for the climatic instability of the GRIP ice core. Investigations on two other marine corings from the Norwegian Sea and the northern Atlantic studied by Cortijo et al. (1994) as well as Fronval and Jansen (1996) also differ from the GRIP's ice core record. They show continuous warm conditions for the entire interglacial. According to Fronval and Jansen (1996) Eemian temperature oscillations in the North Atlantic (and Europe) are possibly damped at lower latitudes, as is the case with the termination of the Holocene climate optimum.

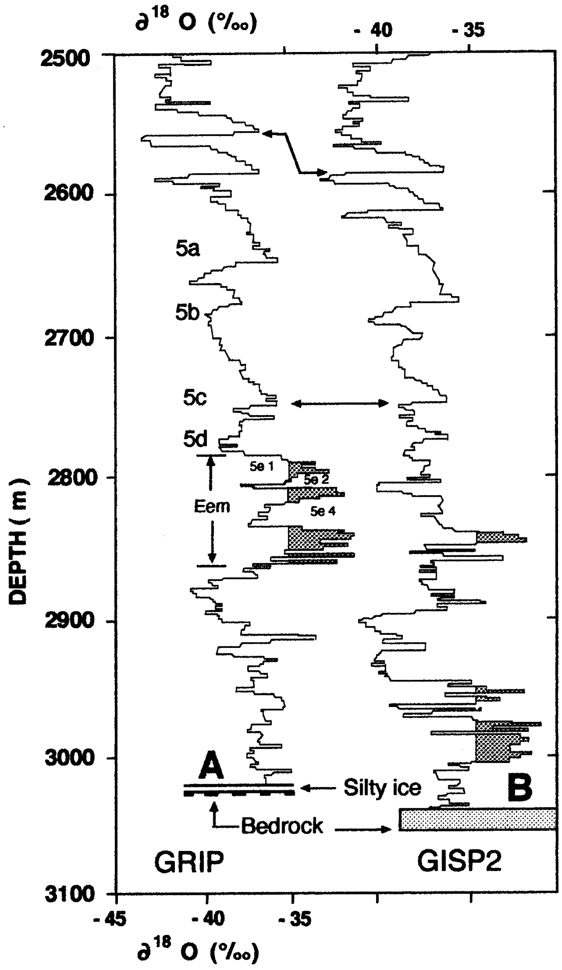


Fig. 1: The lower part of the stable oxygen isotope record from the GRIP and GISP 2 ice cores at Summit, Greenland (after Johnsen et al. 1995).

Field et al. (1994) investigated the correlation of the ice core results GRIP and GISP2 with pollen profiles from Bispingen/Germany (Müller 1974) and La Grande Pile/France (Woillard 1978). In doing so, they postulate noticeable climatic fluctuations and a mean temperature of up to -20°C for the coldest month in the middle of the Eemian. This disagrees with the presence of *Ilex aquifolium* and *Hedera helix* in both pollen diagrams, as well as numerous pollen diagrams close to these sites (Menke and Tynni 1984), as these species are generally supposed to be indicators for a relatively warm climate. Field et al. (1994) attribute this discrepancy to potential re-depositioning of older sediments. However, the results of Field et al. (1994) were particularly controverted by Aaby and Tauber (1995) and Litt et al. (1996), who formulated doubts in their methodical approach. Litt et al. (1996) suggest almost stable temperatures for the entire Eemian based on based on both palaeobotanical and stable isotope data the profile of Gröbern. Their assumptions are in accordance with most terrestrial pollen records within Europe, which support a continuous warm period for the last interglacial (e.g. Menke and Tynni 1984; Frenzel 1991; Litt 1994; Zagwijn 1996). The presence of the thermophilic indicator species *Ilex aquifolium* and *Hedera helix* in the pollen diagram of Bispingen (Müller 1974) and a great number of other Eemian pollen sites within north-west Europe imply a relatively mild climate.

The palaeoclimatic signal of a new ice core from central Greenland at the North Greenland Ice Core Project (NGRIP) site affirms a stable and warm period a least for the middle and late Eemian. Reaching back to 123000 years before present, this core contains the first continuous record for the late Eemian and the interception of the last glacial period to be recorded in a deep Greenland ice core (North Greenland Ice Core Project Members 2004). Furthermore, compared to the previously studied Greenland ice cores, the bottom ice of NGRIP is essentially undisturbed, whereas several authors (e.g. Grootes et al. 1993; Bender et al. 1994) supposed that the bottom 10% of at least one (and most probably both) of the cores GRIP and GISP2 was disturbed owing to ice folding close to the bedrock.

Most recent reconstructions of Eemian temperatures were carried out by Kühl and Litt (2003) using pollen data of three European sites. Two German sites, Bispingen and Gröbern, and the French site La Grande Pile were investigated by means of a newly established method based on probability density functions (*pdf*-method) and compared with previous reconstructions using other methods. The authors conclude that after a steep increase in January- as well as July-temperatures in the early phase of the interglacial, the most probable reconstructed climate appears slightly warmer than today. The models show relatively stable temperatures throughout the Eemian, however, there is evidence for a tendency towards cooler January temperatures.

2.1.1 Biostratigraphic correlation

In the past, different approaches were undertaken for north-western Europe to subdivide the Eemian interglacial into pollen zones according to specific biostratigraphic characteristics. There are just few differences between the different classifications. The most important classifications are compared in a regional context by Litt (2002), who also denominates the appropriate vegetational components according to their significance respectively commonness (Tab. 1).

The Netherlands		**Northern Germany**		**Northern Germany**		**Central Germany**		**Niederlausitz/ Brandenburg**		**South-western Poland**		**Central Poland**	
Zagwijn 1961		**Selle 1962** **Müller 1974**		**Menke & Tynni 1984**		**Litt 1994** **Litt et al. 1996**		**Erd 1973**		**Mamakowa 1989**		**Tobolski 1991**	
E6b	(Pinus)	VI	(Pinus)	VII	(Pinus)	7	(Pinus)	9	(Pinus, Betula)	E7	(Pinus)	7	(Pinus)
E6a	(Picea)	Vb	(Pinus, Picea, Abies)	VI	(Pinus, Picea, Abies)	6b	(Pinus, Picea, Abies)	8b	(Pinus, Alnus, Picea, Abies)	E6b	(Picea, Abies, Alnus, Pinus)	6	(Picea, Abies)
		Va	(Pinus, Picea, Carpinus)			6a	(Carpinus, Abies)	8a	(Carpinus, Alnus, Picea, Abies)	E6a	(Picea, Abies, Alnus, Pinus, Carpinus)		
E5b	(Carpinus, Picea)	IV	(Carpinus)	V	(Carpinus, Picea)	5	(Carpinus)	7	(Carpinus, Alnus, Corylus, Picea)	E5	(Carpinus, Corylus, Alnus)	5	(Carpinus)
E5a	(Carpinus)							6	(Carpinus, Alnus, Corylus, Taxus)				
E4b	(Taxus)	IIIc	(Tilia, Ulmus, Corylus)	IVb	(Corylus, Taxus, Tilia)	4b	(Corylus, Taxus, Tilia)	5	(Corylus,Taxus, Quercus, Alnus)	E4b	(Corylus, Quercus, Tilia, Carpinus)	4	(Corylus)
E4a	(Corylus)	IIIb	(Corylus)										
				IVa	(Quercetum mixtum, Corylus)	4a	(Quercetum mixtum, Corylus)	4	(Corylus, Quercus, Alnus)	E4a	(Corylus, Quercus, Tilia)		
E3b	(Quercus, Corylus)	IIIa	(Quercetum mixt., Corylus)										
E3a	(Quercus)	IIb	(Pinus, Quercetum mixtum)	III	(Pinus, Quercetum mixtum)	3	(Pinus, Quercetum mixtum)	3	(Pinus, Quercus, Betula)	E3	(Quercus, Fraxinus, Ulmus)	3	(Quercus)
E2b	(Pinus, Quercus)	IIa	(Pinus, Betula)	II	(Pinus, Betula)	2	(Pinus, Betula)	2	(Pinus, Betula, Ulmus)	E2	(Pinus, Betula, Ulmus)	2	(Pinus, Betula)
E2a	(Pinus, Ulmus)												
E1	(Betula, Pinus)	I	(Betula)	I	(Betula)	1	(Betula)	1	(Pinus, Betula)	E1	(Betula, Pinus)	1	(Betula)

Tab. 1: Stratigraphic subzones of the Eemian interglacial (after Litt 2002).

The work on hand is based on the classification of Menke and Tynni (1984). The authors distinguish seven pollen zones (I to VII) for the Eemian:

Zone I (birch) is characterized by a clear predominance of *Betula* pollen. A relative maximun of *Pinus* is significant for **zone II** (pine/birch), in which the amount of *Betula* pollen in general rapidly decreases. There is still a predominance of *Pinus* pollen in **zone III** (pine/mixed oak forest). However, the rates of *Betula* drop and values of mixed oak forest species (especially *Quercus*) rise. A rapid increase of the *Corylus* (and *Alnus*) values paired with further decreasing *Pinus* is characteristic for **zone IVa** (mixed oak/hazel). In this zone, pollen curves of *Taxus* and *Tilia* are set up. A culmination of *Taxus* and *Tilia* curves is representative for **zone IVb** (hazel/yew trees/lime trees). Initially, the values of hazel drop to the half, reaching an almost constant value within the following pollen zones. **Zone V** (hornbeam/spruce) is marked by the predominance of *Carpinus*. The values of *Corylus* decrease rapidly. In contrast to that, *Picea* as well as a little later also *Abies* gain more and more importance. The presence of thermophilic groves drops in **zone VI** (pine/spruce/fir). Besides, this zone is characterized by increasing *Pinus* values and concurrent decrease of the *Picea* rates. A one sided predominance of *Pinus* is symptomatic for **zone VII** (pine). As a general rule the presence of *Picea* diminishes at the boundary of zone VI to zone VII. In the upper part of zone VII *Betula* becomes more important again.

Menke and Tynni (1984) prove the regional availability of this zonal chronology by comparing several pollen diagrams of different Eemian occurences in central Europe. Further on, the authors mention several pollen diagrams from other central European areas, which in principle feature the same „basic operation sequence of forestal development". Fig. 2 shows two exemplary pollen diagrams of sites in northern and eastern Germany with a typical structure of pollen zones.

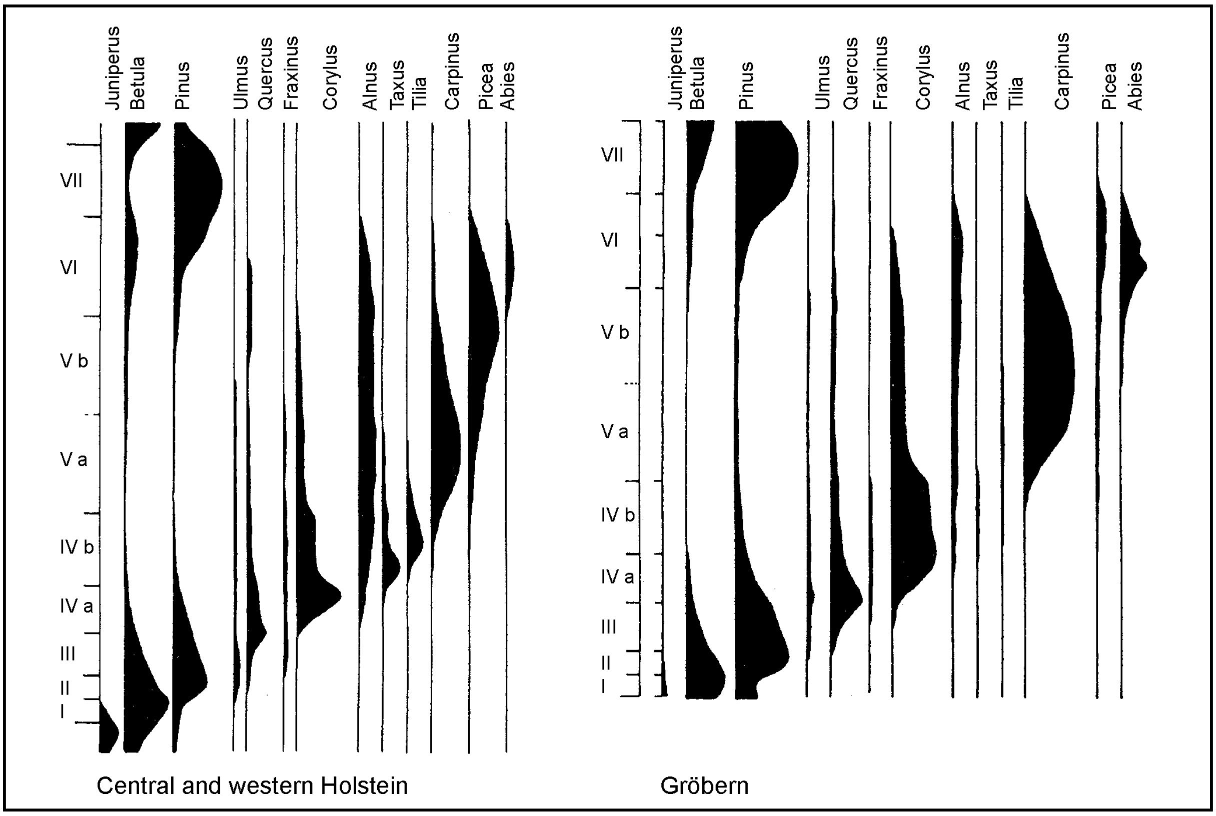


Fig. 2: Exemplary pollendiagrams of the Eemian interglacial in northern Germany (after Menke and Tynni 1984) and eastern Germany (after Litt 1994).

The diagrams are based on the duration of the respective periods determined by Müller (1974). Menke and Tynni (1984) agree with these specifications, however, they suggest a slightly longer term for zones I and II. The duration from the beginning of the pollen zone I to the end of the interglacial (zone VII) lasted about 11000 years (Müller 1974). Approximately 100 years of this period account for zone I, 200 years for zone II, 450 years for zone III, 1200 years for zone IVa, 1200 years for zone IVb, 4000 years for zone V, 2000 years for zone VI and 2000 years for zone VII (Litt 1994).

The „locus typicus“ for the Eemian is located along the Eem river close to the village Amersfoort/Netherlands (Zagwijn 1961).

2.2 Early Weichselian

The Weichselian Glacial encompasses a total of about 105000 years. Lang (1994) characterises the complete Weichselian Glacial as a long phase dominated by multiple temperature changes, by the end featuring cooler and probably even dryer climatic conditions.

This time span can be subdivided into three parts based on biostratigraphic evidences: the Early Weichselian, middle Weichselian (Pleniglacial) and late Weichselian (Lateglacial). The Early Weichselian comprises two rather long and warm interstadials (corresponding to Oxygen Isotope Stage (OIS) 5a and 5c), termed as Brørup and Odderade in northern Europe and St. Germain 1 and St. Germain 2 in the Alpine area respectively. Like nowadays both of these interstadials were characterized by the presence of forests within north-central Europe, though unlike the present predominance of temperate trees Early Weichselian forests were dominated by boreal trees (see Fig. 3). Incidentally open landscapes with cold steppe vegetation were prevalent for the most part of the Quaternary (Litt 2000).

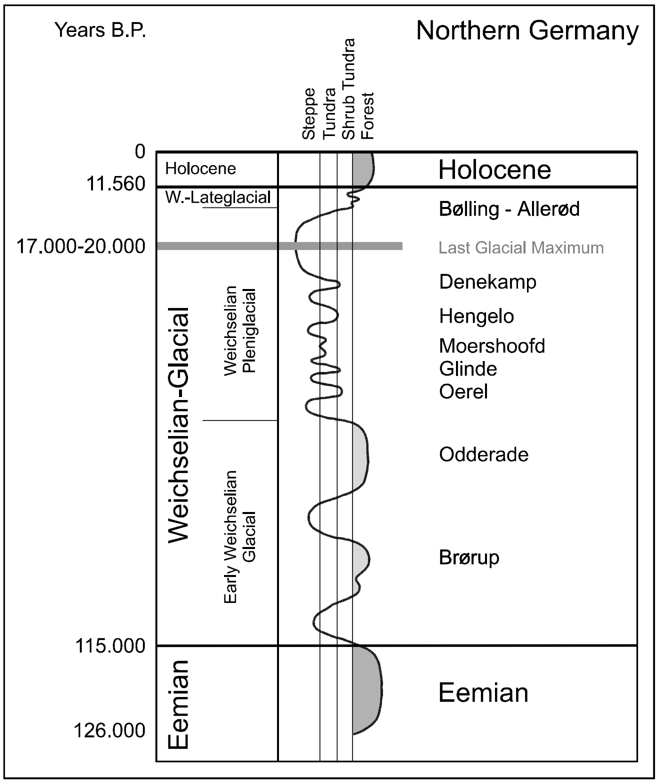


Fig. 3: Schematic representation of the last glacial-interglacial cycle in northern Germany (after Behre and Lade 1986). Dominating temperate forests are displayed in dark grey, dominating boreal forests in light grey.

In north-central Europe both interstadials, Brørup and Odderade, were quite similar in terms of their climatic conditions (Litt 1994). However, Ricken and Grüger (1988) point out that the flora of the Brørup probably contained more thermic demanding species than during the Odderade. Reconstructions of mean July and January palaeotemperatures for both interstadials as well as the adjacent stadials were undertaken by Caspers and Freund (1997) on the basis of pollen, macroremains and analyses of beetles (see Fig. 4). They show a quite „normal“ climatic change within the Odderade including increasing temperatures at the beginning and decreasing temperatures at the end of the interstadial, whereas to some extent severe changes occur particularly during the course of the early Brørup. Different pollen diagrams for this period of the Brørup show a clear subdivision into two parts by means of a noticeable climatic rebound. Therefore, some authors claim two independant interstadials, an older Amersfoort interstadial and a younger Brørup interstadial (Zagwijn 1961).

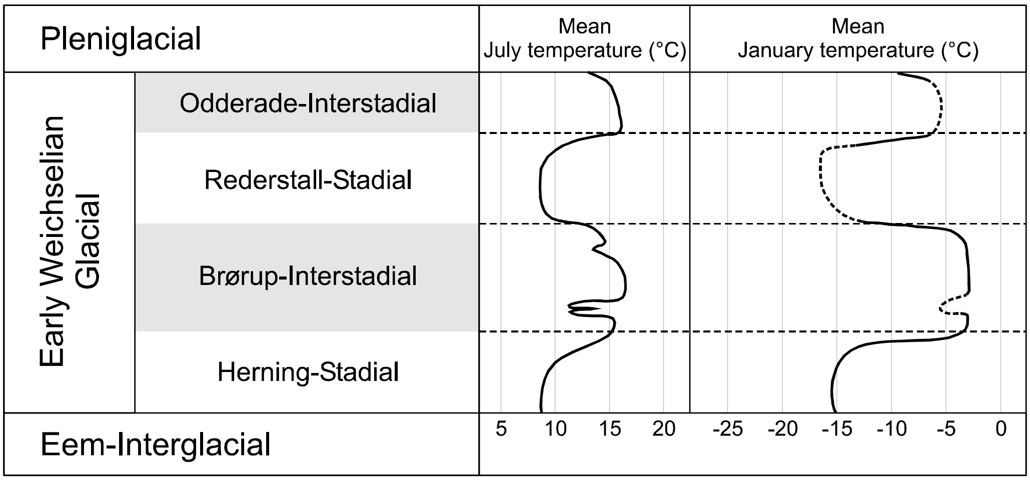


Fig. 4: Reconstruction of the palaeotemperatures in north-west Germany during the Early Weichselian (after Caspers and Freund 1997).

According to Aalbersberg and Litt (1998) the botanical evidence within Europe during the Brørup and the Odderade interstadial suggests that the minimum mean July temperatures rose to 15-16°C. During the coldest month these temperatures show a gradient between -13°C in the east and -5°C in the west. Summer times during these interstadials are supposed to have been relatively warm but short (Menke and Tynni 1984). A quite sharp climatic gradient became visible by means of palynological evidences (Litt 1994): boreal conifer-birch forests (including *Larix* and *Picea*) in north-central Europe confront with temperate oak-mixed forests (also including Carpinus) in south-west central Europe. Behre (1974) presumed, that the northern limit of distribution of thermophilic trees during the Brørup was located four to six degrees latitude further to the south of the site Osterwanna (northern Lower Saxony), which was reconfirmed by several subsequent studies in south-central Europe.

Zagwijn (1989) states that, in contrast to the Eemian, during the temperate intervals of the Early Weichselian the climate was cooler and more continental, related to persisting land-ice in the far northern part of the continent.

2.3 Lateglacial and Holocene

The Holocene and Lateglacial can be subdivided into different climatic sections with respect to specific climatic changes referred from the discontinous retreat of ice as well as migrational procedures and spread of plants. A detailed overview on the bio- and climatostratigraphic classifications (Tab. 2) of the Holocene and Lateglacial in northern, western and central Europe is given by Lang (1994).

	S.-Sweden (Nilsson 1935, Nilson 1964)	**Danmark** (Jessen 1935, Iversen 1954)	**British Isles** (Jessen 1949, Godwin 1956)	**Central Europe** (Firbas 1949, Firbas 1954)
Holocene	I/II Subatlantic (SA)	IX Subatlantic	VIII Subatlantic	IX/X Subatlantic
	2300	2500	2700	2800/2500
	III/IV Subboreal (SB)	VIII Subboreal	VIIb Subboreal	VIII Subboreal
	5300	5000	5000	4500
	V/VI Atlantic (AT)	VII Atlantic	VIIa Atlantic	VI/VII Atlantic
	8200	8000	7500	7500
	VII/VIII Boreal (BO)	V/VI Boreal	V/VI Boreal	V Boreal
	9900	9000	9500	8800/8500
	IX Preboreal (PB)	IV Preboreal	IV Preboreal	IV Preboreal
	10300	10300	10300	10100
Lateglacial	X Younger Dryas (DR 3)	III Younger Dryas	III Upper Dryas	III Younger subarctic period
	11100	11000	10800	11000
	XI Allerød (AL)	II Allerød	II Allerød	II Middle subarctic period
	12000	11700	12000	12000
	XII Older Dryas	Ic Older Dryas	I Lower Dryas	Ib Older subarctic period
		12000		
		Ib Bølling		
		12500		
		Ia Oldest Dryas		Ia Oldest deforested period

Tab. 2: Bio- and climatostratigraphic classifications of the Holocene and Lateglacial in northern, western and central Europe (after Lang 1994).

Since about 15000 B.P., following the Last Glacial Maximum, a re-warming is proved for central Europe. This warming did not take place as a linear continuous increase, but it was characterised by rapid high-frequency fluctuation (Litt 2000; also see Fig. 5). Correlations of the distinct Lateglacial climate show that these variations took a synchronous course at least for north-central Europe and Greenland (Litt et al. 2001).

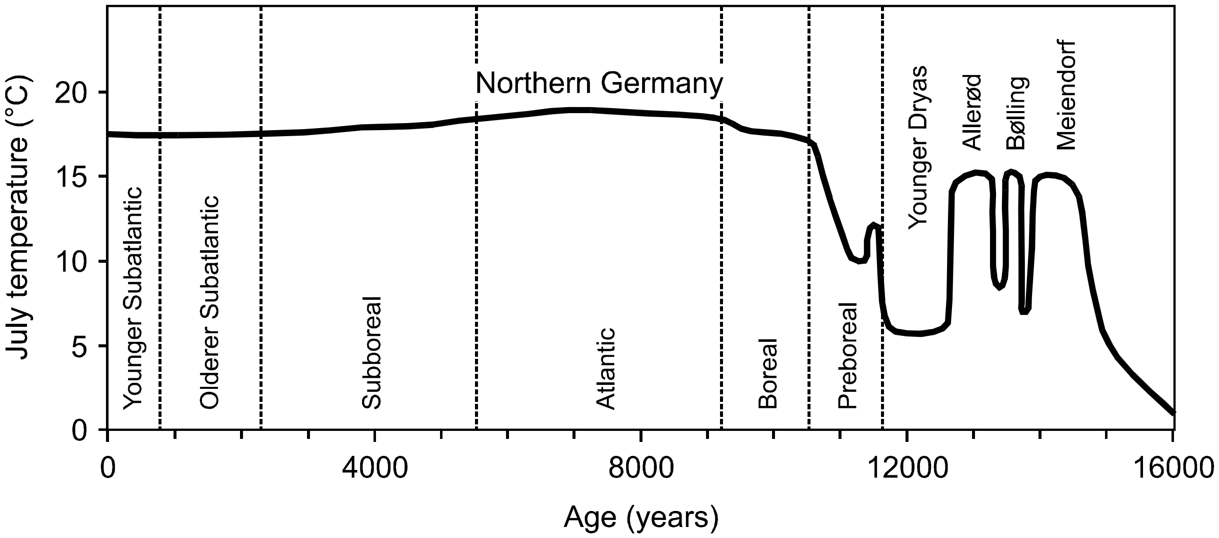


Fig. 5: Temperature changes in northern Germany during the last 16000 years (after Berner and Streif 2000).

According to Huntley and Birks (1983) the Lateglacial climate was probably considerably colder than today. Mediterranean-type vegetation locally present at 11000 and 10500 B.P. in southern Europe suggests less cooling in the south than in the north. A widespread aridity during the Lateglacial and the preceding Glacial Maximum is clearly documented by numerous investigations (most recent e.g., Briant et al. 2004; Frogley et al. 2001). The aridity on the continents was most likely caused by the strong surface air-flow from the continental regions to the oceans resulting from greater reduction in temperature on the continents compared with the oceans (Huntley and Birks 1983).

The abrupt increase of mean temperatures by at least 5-6°C 11560 years ago marks the beginning of the Holocene. This rapid increase took place within less than 15 years (Berner and Streif 2000). The onset of the Holocene in north-central Europe is supposed to be represented by the climatic amelioration that caused the final afforestation and immigration of thermophilic arboreal plants (Berglund et al. 1996). Afforestation of much of western and central Europe began early in the Lateglacial, when climatic conditiones were relatively humid, whereas farther east it did not occur until well into the Holocene because of the drier climate (Wright et al. 2003).

After Dowdeswell and White (1995) δ^{18}O-values in the ice corings GRIP and GISP2 show a relativly stable climate for the Holocene. According to their results particularly the Holocene part of the cores represent a period of exceptional climatic stability compared with the remainder of the cores. Thereby, the Holocene ice record is clearly distinguishable from the underlaying ice, which comprises evidences of cooler climate.

However, several striking climatic variations may be evidenced within the Holocene on a finer scale, such as the “Medieval warm period”, the “Migration period” (climatic pessimum), the “Roman climatic optimum” and the “Holocene climatic optimum” (see Fig. 6).

The Holocene climatic optimum occured between 9200 and 5700 B.P. (Berner and Streif 2000). Temperatures of this time frame are supposed to have been about 1-2°C higher than today in north-central Europe, though more humid. The period was particularly characterised by the onset of human activities (Litt 2003). Apparently, there is a damping of climatic oscillations by the termination of the Holocene climate optimum at lower latitudes (Fronval and Jansen 1996).

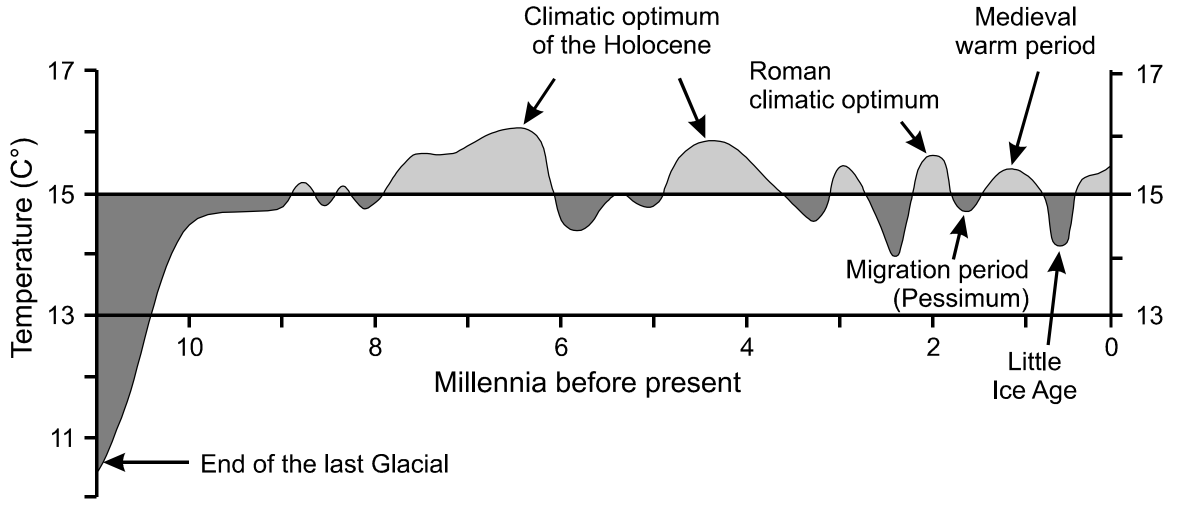


Fig. 6: Ground level mean temperatures of the northern hemisphere during the last 11000 years (after Schönwiese 1995).

It is often difficult to distinguish, whether observerd climatic changes are caused by natural or anthropogenic forcing. However, it can be hypothesised that humans responded to favourable and disfavourable climatic conditions in equal measure right from the start (Berner and Streif 2000). According to Ruddiman (2004) the interval between 8000 years ago and the industrial era was a time of significant and slowly increasing human impact on greenhouse-gas concentrations and global climate. Thus, Holocene climatic variability reflects a random balance between large-scale natural cooling and an almost equally large anthropogenic warming.

3. Material and methods

3.1 Pollen data

The pollen maps shown in this work are based on the following data sets:

- The Eemian maps contain 44 pollen sites for *Abies* (see appendix I) and 54 for *Picea* (see appendix V).
- For the Brørup 29 pollen sites were included for *Abies* (see appendix II) and 35 for *Picea* (see appendix VI).
- The maps for the Odderade are based on 23 pollen sites for *Abies* (see appendix III) and also 23 pollen sites for *Picea* (see appendix VII).
- Data from precedent warm phases of the last glacial-interglacial cycle predominantly result from examination of pollendiagrams and information about macroscopic plant remains from the appropriate original literature, which were organised in a special database. To the greatest possible extent this database includes just "high quality sites" that preferably fulfil the requirement of providing long and complete sequences of palaeobotanical record, at best the entire sequence of the corresponding interglacial. Moreover, the stratigraphic classification of these sites has to be doubtlessly confirmed.
- The pollen maps for the period since the last glacial are based on pollen sequences currently held in the EPD (European Pollen Database). A total of 208 sequences were used for *Abies* (see appendix IV) and 313 for *Picea* (see appendix VIII). For *Abies* four sites located in southern Bavaria, six sites from the "Bayrischer Wald" area and one site from northern Italy were additionally incorporated in this dataset (see "additional sites" in appendix IV). Pollen percentages from the EPD sequences are computed for every dated sample based upon a pollen sum of trees, shrubs and herbaceous plants, excluding aquatic plants and ferns.

3.2 Macrofossil data

The macrofossil inventory of former warm stages predominantly includes needles, seeds and wood as well as bud scales etc. For the Eemian five macroscopic evidences for *Abies* (see appendix I) and 14 for *Picea* (see appendix V) are included in this collection. Two macroscopic remains of *Abies* (see appendix II) and four records of *Picea* remains (see appendix VI) are mentioned for the Brørup. The dataset contains just one macrofossil evidence of *Abies* from the Odderade (see appendix III), while there are five macrofossil records of *Picea* (see appendix VII).

The macrofossil dataset for the Holocene is derived from the newly established European Macrofossil Database (EMD) (Institute of Palaeontology, University of Bonn) supported by the EU-Project FOSSILVA (Dynamics of forest tree biodiversity: linking genetic, palaeogenetic and plant historical approaches) designed to incorporate macrofossil plant remains throughout Europe.

This database includes 38 macrofossil sites for *Abies* so far; of these 21 sites are for *Abies alba* and 17 for *Abies* sp. respectively (see appendix IV). 33 sites are based on radiocarbon measurements and 5 dates were obtained by correlation with nearby sites. The dataset contains one site located in Switzerland, obtained from the Alpine Palynological Database, Bern, Switzerland (ALPADABA). The entire available macrofossil dataset for *Abies* mostly encompasses fragments of wood (charcoal) as well as stomata and needles.

In total, 197 macrofossil sites were used for *Picea*, 114 of these sites report findings of *Picea abies* and 84 *Picea* sp. (see appendix VIII). 181 sites are based on radiocarbon measurements, two dates derive from dendrochronological datings and 14 dates were inferred from correlations with nearby sites. The present dataset for *Picea* contains mostly wood (to some extent charcoal), needles, seeds and cones. Less common are finds of bud scales, cone-scales, strobiles, bark, stems, trunks, logs, hulls and branches.

Unlike pollen grains, which are abundant in sediments and may have experienced long distance transport over several kilometres, macrofossil remains are relatively rare but spatially more precise. Macrofossils hold several big advantages: firstly they are macroscopic plant remains, which provide concrete evidence of a taxon at the location where it is identified, secondly they can complete and confirm the pollen data, and finally they can frequently be identified to species level, while most pollen types are limited to genus or even family-level identification. Thus, the combination of the two types of bio-indicators leads to a more precise palaeoenvironmental reconstruction.

3.3 Chronologies

Dating of the pollen sequences encompassing the period from the last glacial to date was predominantly done by radiocarbon measurements on the sediments or on available plant remains. For the interpretation of observed palynological changes in pollen sequences there is a need to establish a reliable timescale to enable mapping at given time periods. Thus, for the pollen sites of the last glacial period a continuous chronology mainly was obtained by interpolating the radiocarbon measurements onto the sample depths throughout each record using suitable age/depth models. The network of all dated sites allowed us to extract samples for each time-slice and produce the appropriate maps. All these maps presented are based on uncalibrated ages B.P.

Absolute dating using radiocarbon measurements is not possible for the examinated previous warm stages, because due to the half life of the ^{14}C isotope this method is limited to a certain timeframe. According to Mason and Moore (1985) reliable ages can be obtained up to 50000 B.P. (including a maximum error of ±150 years). Lang (1994) states the restriction of radiocarbon analyses to the last 45000 years for metrological reasons, at most the measurable time span may include the last 70000 years.

Indeed dating of older sediments is possible via measurements of Uranium/Thorium as well as thermal luminescence, however both methods were scarcely applied for the European Eemian (e.g. see Krbetschek and Stolz 1994; Hall et al. 2002; Geyh et al. 1997; Onac et al. 2001). Due to this sparse amount of absolute datings the assignment to Eemian, Brørup or Odderade is generally carried out on the basis of representative biostratigraphical criteria.

3.4. Data extraction and mapping

For all sites reporting pollen for the Lateglacial and Holocene, pollen percentages were calculated from all samples with an age within a time-slice of +/- 250 years. The average was computed in cases were several samples occurred within this interval. The percentages for each time-slice were then used to produce the presented maps.

Eemian pollen records are included according to biostratigraphic considerations. Thus, the total time-span was divided into its specific pollen zones. The Eeminan distribution maps display maximum pollen values as well as macrofossil records of each of these zones.

It is not possible also to subdivide the two Early Weichselian interstadials according to their specific biostratigraphy. Therefore a single maximum pollen value is taken for each of the interstadials, Brørup and Odderade respectively. Additionally, the presence or absence of macroscopic remains is indicated for each site.

Pollen percentages in the maps are either plotted using circles with proportional sizes (for the last glacial period) or put in different colours according to their dimension (for previous integlacials). In most cases macrofossil finds are indicated on the original pollen diagrams, but some of the macrofossil records are presented as separate figures. Dating was either done on the macroremains themselves or correlated over the entire sequence with the help of existing measurements.

Maps of the last glacial period were produced on the basis of the pollen percentages as well as the macrofossil records at each time slice by using the software GMT (Wessel and Smith 1998, 1999), while maps of the previous interglacials were created with help of the software PanMap provided by PANGAEA (Database and Network of Geological and Environmental Data; http://www.pangaea.de). All maps are displayed in Mercator projection.

3.5 Pollen representation

Due to the fact that pollen are widely distribute via aerial transportation, very low percentages a a specific site do not prove the presence of a species for that site. Generally a taxon-specific "threshold" value of pollen percentages is chosen, which marks the limit of the probability of local presence. However, these values vary between different species, because of their distinctive pollen productivity and dispersal (Firbas 1949).

Huntley and Birks (1983) assume for their Holocene pollen distribution maps (13000-0 B.P.) that *Abies* pollen values ≥5% indicated a significant *Abies* component in the surrounding forest. They also presume that the relatively poor dispersal of *Abies* pollen suggests that values ≥2% are probably reliable indicators of local presence. For *Picea* pollen values ≥5% are expected to represent local presence, whereas values ≥25% are assumed to indicate areas where spruce-dominated forest is abundant (Huntley and Birks 1983). For *Picea abies* Giesecke and Bennett (2004) propose that a threshold of 1% terrestrial pollen is a conservative but robust indication of local or regional presence in forested areas. They agree that neither the 1% level nor the beginning of the continuous pollen curve should be applied to pollen diagrams obtained at or beyond the tree line to infer local presence. Particularly in connection with various macrofossil finds of Kullman (e.g 2001, 1986) it is suggested that early pollen percentages need to be disscussed according to site characteristics and the distance to possible source areas for long-distance dispersed pollen (Giesecke and Bennett 2004). However, all these assumptions on threshold values should be taken with caution especially in cold stages, when redeposition of pollen through erosion processes is common.

Hence, the presented maps do not show pollen data, which exclude low percentage records depending on a certain threshold value, but records are differentiated by using different sizes of dots or colours according to their appropriate pollen percentage value (encompassing a range of 0.1->10% for the last glacial period, 0.1-20% for *Abies* and 0.1->50% for *Picea* in the Weichselian interstadials as well as 0.1->50% for the Eemian). Instead of using specific threshold values to determine presence or absence in an area, the combined macroremains and the distribution of all pollen percentages provide more objective information. For that reason, even sequences reporting no pollen finds in an examined time frame where the corresponding taxon is generally present are displayed, because the lack of pollen finds may also point to a highly improbable presence of a taxon. In contrast to that a negative evidence of macrofossils is not significant.

4. Investigations on the spread of *Abies* during the last glacial-interglacial cycle (126000 years to date)

4.1 Present distribution of *Abies*

The present range of *Abies alba* is distributed throughout much of central and southern Europe, mostly in the montane region from the Pyrenees up to the Balkans (Fig. 7). Only north of the Carpathians, in southern Poland, does *A. alba* appear outside the mountain range in the lowlands (Meusel et al. 1964; Jalas and Suominen 1973).

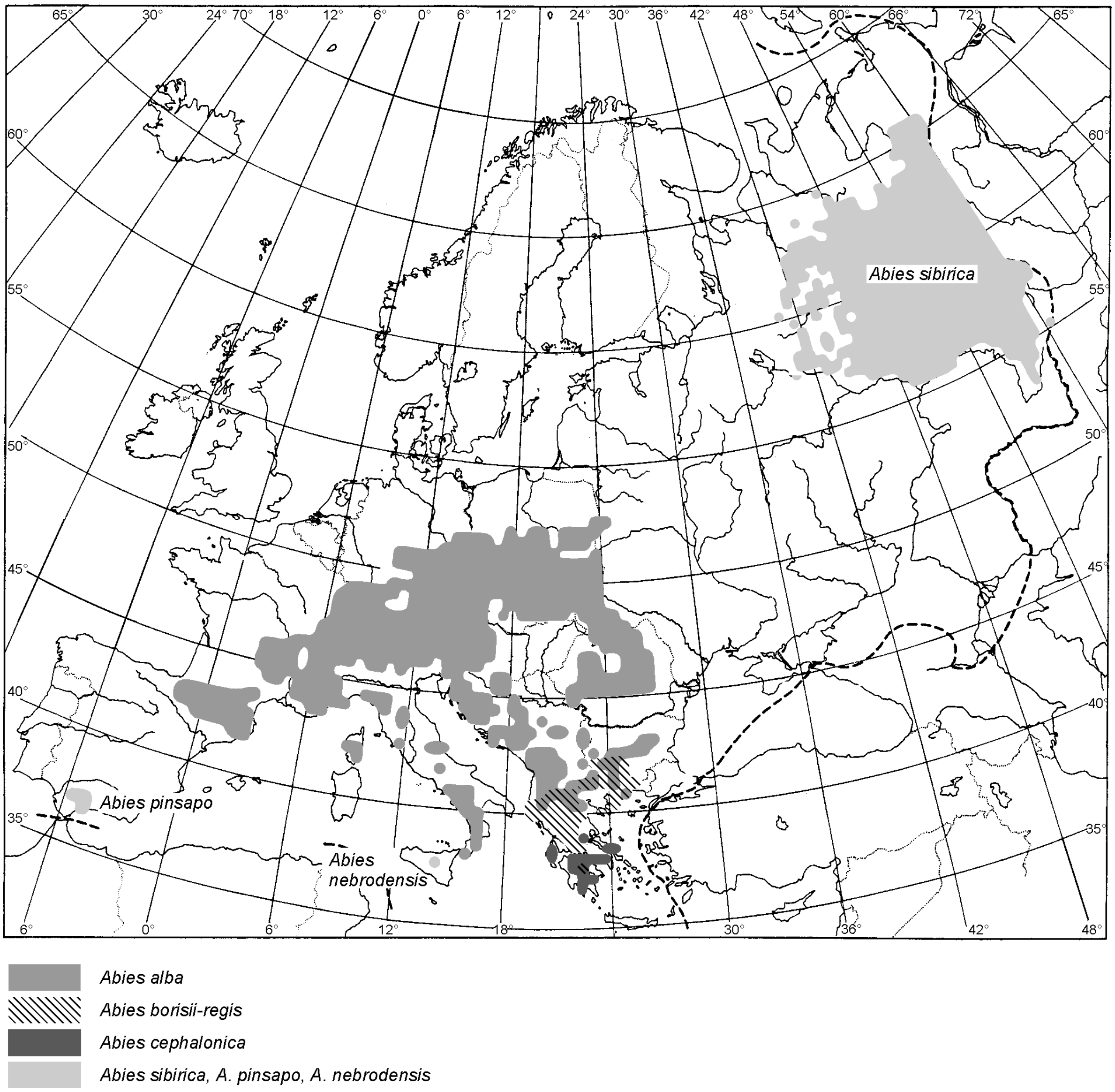


Fig. 7: Present range of *Abies* species in Europe (after Jalas and Souminen 1973).

Four species of *Abies* are restricted as endemics to different parts of the Mediterranean region (*A. pinsapo* in southern Spain, *A. nebrodensis* in Sicily, *A. cephalonica*, and *A. borisii-regis* in Greece). *A. sibirica* occurs only in the extreme north-east Europe, in the boreo-Russian zone.

4.2. Results from palaeobotanical data

4.2.1 Distribution pattern of *Abies* during the Eemian

PZ I (Fig. 8, top left)

Abies is reported just by from three European pollen sites within PZ I, even though numerous other profiles are available, which do not include any fir pollen finds. Two of the pollen sites, the location Mondsee in Austria (Klaus 1975; Drescher-Schneider 2000; Oeggl and Unterfrauner 2000) and Meikirch in Switzerland (Welten 1982b) steming from the western and eastern Alpine region respectively, show very low values (0.2%). They represent the potentially northernmost distribution of *Abies* in this time frame. Higher pollen percentages are mentioned from the site Valle di Castiglione (2.0%; Follieri et al. 1988; Follieri et al. 1998) situated in central Italy.

PZ II (Fig. 8, top right)

Also PZ II shows just a few sites representing *Abies*. A presence is still indicated by pollen from the Swiss site Meikirch (0.2; Welten 1982b) and Valle di Castiglione in central Italy (2.0%; Follieri et al. 1988; Follieri et al. 1998). Additionally there is a further site, Les Echets (Beaulieu and Reille 1984, 1989), which is situated in east-central France (0.2%). Furthermore macrofossil finds (including seeds, bud-scales and wood) are reported from the Austrian site Mondsee (Klaus 1975; Drescher-Schneider 2000; Oeggl and Unterfrauner 2000). Thus, the potential maximum northern distribution limit of *Abies* stays unaffected compared to the previous pollen zone.

PZ III (Fig. 8, bottom left)

Low value pollen sites in the east Alpine region consist within PZ III, even if they are represented by two sites, the German site Samerberg I (0.2%; Grüger 1979a,b) and the Austrian site Mondsee (0.25%; Klaus 1975; Drescher-Schneider 2000; Oeggl and Unterfrauner 2000). The site Mondsee also features macrofossil finds (seeds, bud-scales and wood). The pollen profile from east-central France, Les Echets (Beaulieu and Reille 1984, 1989) shows slightly increased fir values (1.5%). At Valle di Castiglione (Follieri et al. 1988; Follieri et al. 1998) in central Italy unchanged pollen percentages of 2.0% are observable. One pollen record including very low pollen (0.2%) of *Abies* is situated in central Poland (Glówczyn; Niklewski 1968). Possibly, this find suggests that climatic conditions in the east-central Europe slightly differed from the ones in north-central Europe. However, it must be pointed out that some westerly sites, which are located quite close to this pollen profile do not contain any pollen finds of *Abies* within this pollen zone at all. Thus, these finds could rather be the result of aerial pollen grain transportation.

PZ IVa (Fig. 8, bottom right)

Compared to PZ III the number of sites containing pollen precipitation of *Abies* nearly doubles within PZ IVa. There are still low pollen percentages of 0.2% at Samerberg I (Grüger 1979a,b) and 0.4% *Abies* pollen as well as macrofossil finds (seeds, bud-scales and wood) at Mondsee mentioned in the eastern Alps (Klaus 1975; Drescher-Schneider 2000; Oeggl and Unterfrauner 2000). Similar values are reported from individual sites in the north-west Alpine region, north-east Czechia, northern Germany as well as west-central Finland, though especially for north-central Europe still numerous profiles without any pollen record are present at the same time. A higher value of 1.5% is listed for the Polish site Góra Kalwaria (Sobolewska 1961). A total of three sites are identified in southern Europe, more precisely the Mediterranean region. In addition to the site Valle di Castiglione (2.0%; Follieri et al. 1988; Follieri et al. 1998) that was prevalent since the beginning of the Eem, two more pollen sites are registered from Greece. The north-west Greek site Ioannina (Tzedakis 2000; Tzedakis et al. 2002) indicates 5.0% and therefore represents the highest percentages of *Abies* in this particular pollen zone. In contrast the site Tenaghi Philippon TF1/TF2 (Tzedakis 2000; Wijmstra 1969) in north-central Greece just shows 0.5% of *Abies* pollen.

PZ IVb (Fig. 9, top left)

In comparison to the four previous pollen zones pollen percentages in PZ IVb rise to quite high values at several sites. Two of these sites, the German site Samerberg I (16.0%; Grüger 1979a,b) and the Austrian site Mondsee (8.0%; Klaus 1975; Drescher-Schneider 2000; Oeggl and Unterfrauner 2000) both also include macrofossil finds (seeds, bud-scales and wood at Mondsee; needles and seed wings at Samerberg I). Another two sites stem from the West Alps. They include the highest pollen percentages of *Abies* in this particular pollen zone with about 41.0% at the Swiss sites Gondiswil-Seilern (Wegmüller 1992) as well as minor percentages (1.2%) at Meikirch (Welten 1982b). A close by site, La Grande Pile (Woillard 1975, 1978; Beaulieu and Reille 1992a) in eastern France, shows 2.5% of *Abies* pollen. The two pollen sites from Greece, Ioannina (Tzedakis 2000; Tzedakis et al. 2002) and Tenaghi Philippon TF1/TF2 (Tzedakis 2000; Wijmstra 1969) report increased pollen values (5.0% and 7.0%), whereas Valle di Castiglione (Follieri et al. 1988; Follieri et al. 1998) persists indicating percentages of 2.0%.

All sites from north-central and northern Europe just show very low percentages of *Abies* pollen (0.1-1.0%). In addition, there are many sites containing no *Abies* pollen within this time frame. As in the previous pollen zone the northernmost of these sites is the location Mertuanoja (Eriksson et al. 1999) in Finland with pollen percentages of at most 0.2% *Abies*. It is generally assumed that all these minor values may have been caused by aerial transportation. So it can be supposed that the northernmost reach of *Abies* within PZ IVa was still limited to the Alpine area.

PZ V (Fig. 9, top right)

An extreme increase in the number of sites as well as the fir pollen percentages is visible within PZ V. Without any exception all investigated pollen sites show at least very low percentages of *Abies*. The highest pollen percentages in PZ V are still found in the Alpine region: The Swiss site Gondiswil-Seilern (Wegmüller 1992) features 53.0%, the French site Les Echets (Beaulieu and Reille 1984, 1989) 46.5%, the Austrian site Mondsee (Klaus 1975; Drescher-Schneider 2000; Oeggl and Unterfrauner 2000) 45.5% and the German site Samerberg I (Grüger 1979a,b) 38.0%. Macrofossil remains are reported from the sites Mondsee (seeds, bud-scales and wood) and Samerberg I (needles, seeds, seed wings and cone scales). Four further sites from the Alpine area (including one site from the Massif Central) show slightly lower pollen values between 29.0 and 17.0%. The three sites, which noted clear pollen finds of fir from the Mediterranean region in PZ IVb are still present within PZ V. Just one of them, the Greek site Tenaghi Philippon TF1/TF2 (Tzedakis 2000; Wijmstra 1969) shows somewhat increased percentages of *Abies* (6.0%).

Of great significance is a definite *Abies* presence in north-central Europe indicated by a great number of sites showing between 0.2 and 17.0% of pollen. One site also reports a macrofossil find (one needle), the Polish site Glówczyn (Niklewski 1968). Compared to the previous pollen zones the northern distribution limit of fir was remarkably shifted towards a northward direction.

Just two sites may indicate a presence of fir north of 55° latitude, the Estonian site Waewa-Ringen (0.2%; Thomson 1941) and the Swedish site Leveäniemi (0.5%; Robertsson 1991, 1997; Robertsson et al. 1997). Also one site is found in central Britain, the location Wing (Hall 1980), showing 0.2% of *Abies* pollen. However, the registered pollen percentages of the latter three sites are quite low and may rather be caused by aerial spread of loose pollen grains.

PZ VI (Fig. 9, bottom left)

PZ VI shows clear evidence of *Abies* within most of central and north-central Europe, indicated by the presence of predominantely high pollen percentage records. All sites of the Alpine region report more than 20.0% of *Abies* pollen. Like in PZ IVb and PZ V two of them also include macrofossil remains, the Austrian site Mondsee (seeds, bud-scales and wood; Klaus 1975; Drescher-Schneider 2000; Oeggl and Unterfrauner 2000) and the German site Samerberg I (needles, seeds, seed wings and cone scales; Grüger 1979a,b). A slightly lower pollen value of 18.5% is reported for the site Lac du Bouchet (H) (Reille et al. 1998) in the French Massif Central.

The presence of *Abies* is definitely proved for north-central Europe by a great number of locations showing pollen content between 0.1 and 37.0%. In comparison to PZ V *Abies* features remarkable pollen percentages also at sites from northernmost Germany. Macrofossil finds in north-central Europe are reported from the German site Schwindebeck (one seed scale, seeds and needles; Behre 1962) and the Polish site Imbramowice (wood; Mamakowa 1989).

Two sites are available in the Mediterranean region. The pollen percentage at the Greek site Ioannina (Tzedakis 2000; Tzedakis et al. 2002) is slightly increased at 13.0%, whereas the values at Valle di Castiglione (Follieri et al. 1988; Follieri et al. 1998) in central Italy remain constant at 2.0%. The pollen profile of the other easterly Greek site, Tenaghi Philippon TF1/TF2 (Tzedakis 2000; Wijmstra 1969) shows no more pollen of *Abies*, although the investigations at this location included this particular pollen zone.

No more pollen finds are noted north of 55° latitude, with the exception of the low percentage site of Wing (0.2%; Hall 1980) in Great Britain. Again, these finds can likely be attributed to aerial pollen dispersal.

PZ VII (Fig. 9, bottom right)

Abies pollen percentages clearly decrease at almost all sites in Europe within the outgoing Eemian (PZ VII). Except for the French site La Grande Pile (Woillard 1975, 1978; Beaulieu and Reille 1992a) containing about 28.0% of *Abies* pollen, no pollen site shows values of more than 10.0%. Also, at some of the investigated profiles there are no more fir pollen finds at all. However, the presence of *Abies* in Europe is still definitely documented for central and north-central Europe as well as some individual sites in southern Europe. In other respects highest pollen values are documented at the German site Samerberg I (10.0%; Grüger 1979a,b), the French site Ribains (9.0%; Beaulieu and Reille 1992b), Gröbern (9.0%; Litt 1994, 1990; Mai 1990a) in Germany and the Greek site Ioannina (7.5%; Tzedakis 2000; Tzedakis et al. 2002). Even though there are several sites left displaying just low percentages of *Abies* pollen (0.2-0.8%), especially in north-central Europe, the majority of sites still suggest northernmost Germany to be the northern distributional limit of fir at the end of the Eemian.

Macrofossil remains are reported from four sites, the Austrian site Mondsee (seeds, budscales and wood; Klaus 1975; Drescher-Schneider 2000; Oeggl and Unterfrauner 2000), the German site Samerberg I (needles; Grüger 1979a,b), the German site Schwindebeck (1/2 needle; Behre 1962) and the Polish site Imbramowice (wood; Mamakowa 1989).

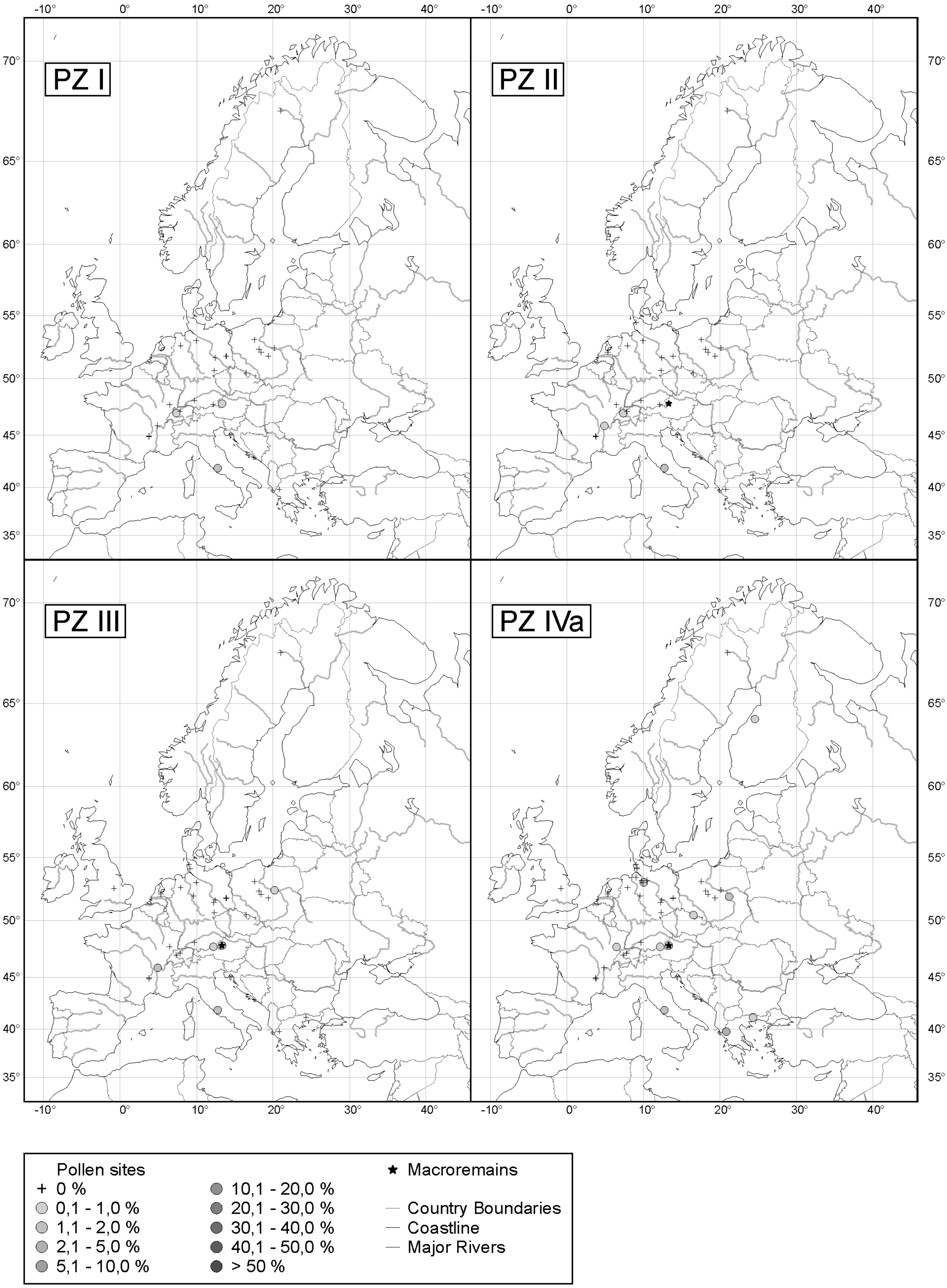


Fig. 8: Maximum pollen percentages and macrofossils of *Abies* within the Eem (PZ I-IVa).

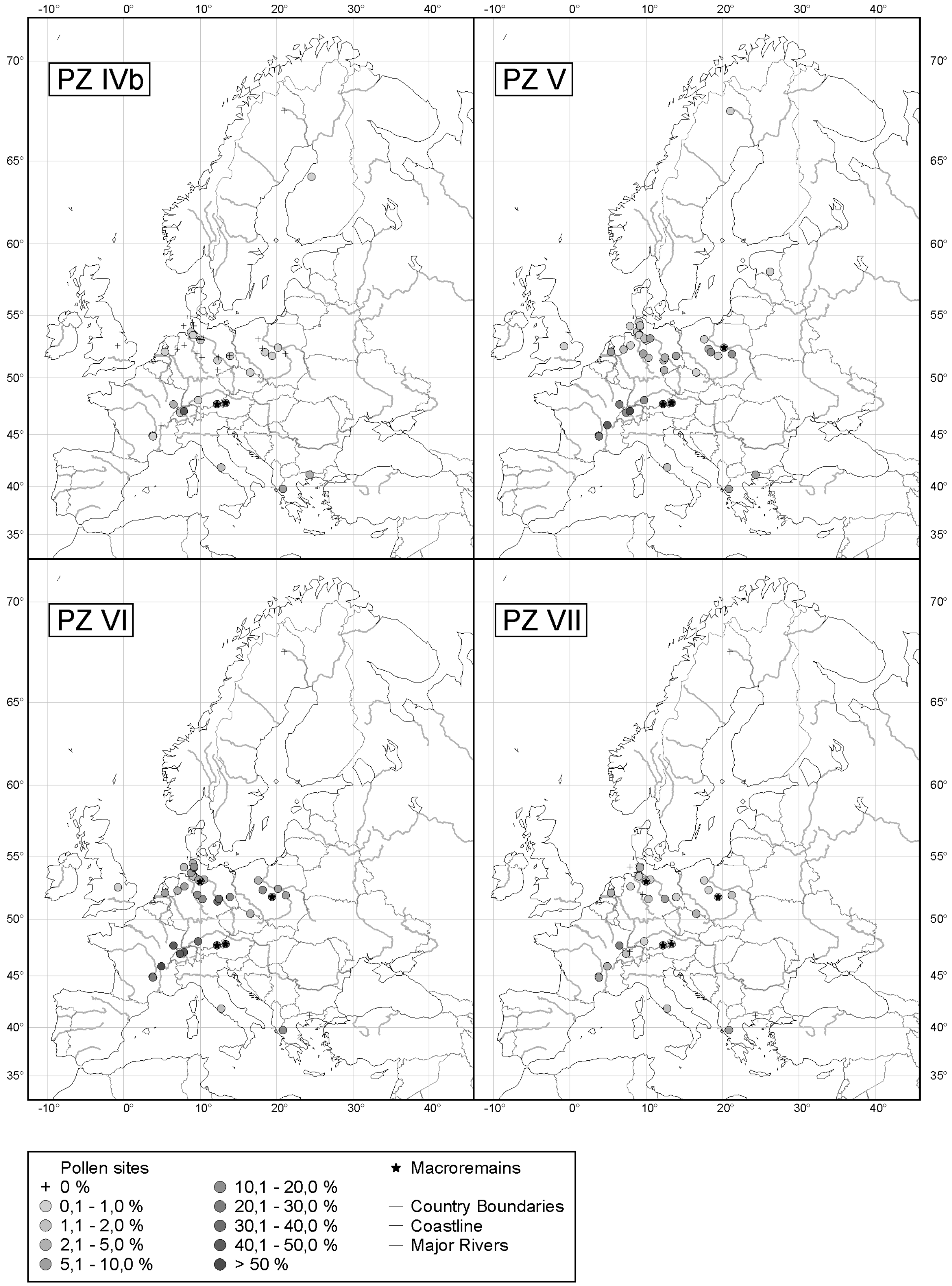


Fig. 9: Maximum pollen percentages and macrofossils of *Abies* within the Eem (PZ IVb-VII).

4.2.2 Distribution pattern of *Abies* during the Brørup

The maximum pollen percentages of *Abies* during the Brørup are found in the Mediterranean area, even though several sites with high pollen values as well as macrofossil finds occur in the Alpine region, likewise (Fig. 10). Maximum pollen percentages are known from three sites in central and southern Italy, Lagaccione (57.0%; Follieri et al. 1998; Magri 1999), Valle di Castiglione (25.0%; Follieri et al. 1988; Follieri et al. 1998) and Lago Grande di Monticchio (21.0%; Allen et al. 1999). Lower values are mentioned from the Greek site Ioannina (Tzedakis 2000; Tzedakis et al. 2002) with 17.0% of *Abies* pollen followed by the site Meikirch (Welten 1982b) in Switzerland (13.0%). Sites with *Abies* pollen percentages between 1.2 and 9.0% are predominantly located in the Alpine region, eastern France, the Massif Central and Greece. Among these are the French sites Les Echets (9.0%; Beaulieu and Reille 1984, 1989), La Grande Pile (7.0%; Woillard 1975, 1978), Tenagi Philippon (7.0%; Wijmstra 1969), Ribains (6.0%; Beaulieu and Reille 1992b) and Lac du Bouchet (D) (6.0%; Reille and Beaulieu 1990), the Austrian site Mondsee (4.5%; Klaus 1975; Drescher-Schneider 2000; Oeggl and Unterfrauner 2000) and the German sites Samerberg 1973 (3.0%; Grüger 1979a,b) and Jammertal (1.2%; Müller 2000, 2001).

The main distribution of *Abies* during the Brørup was quite similar to the one of the Holocene, however, there are some additional sites with less high pollen percentages in north-central Europe. Five pollen sites are available from this particular area showing values between 0.1 and 1.0%, but there are also four sites without any record of *Abies* in the investigated profile. The highest value (1.0%) in north-central Europe is reported from the site Neheim-Hüsten in Germany (Teunissen et al. 1972).

Just two macrofossil records are noted in the Brørup, one from Austria and one from southern Germany. Finds from the Austrian site Mondsee include seeds, needles, bud-scales as well as wood of *Abies* (Klaus 1975; Drescher-Schneider 2000; Oeggl and Unterfrauner 2000). Investigations at the German site Samerberg 1973 bore needles of *Abies* (Grüger 1979a,b).

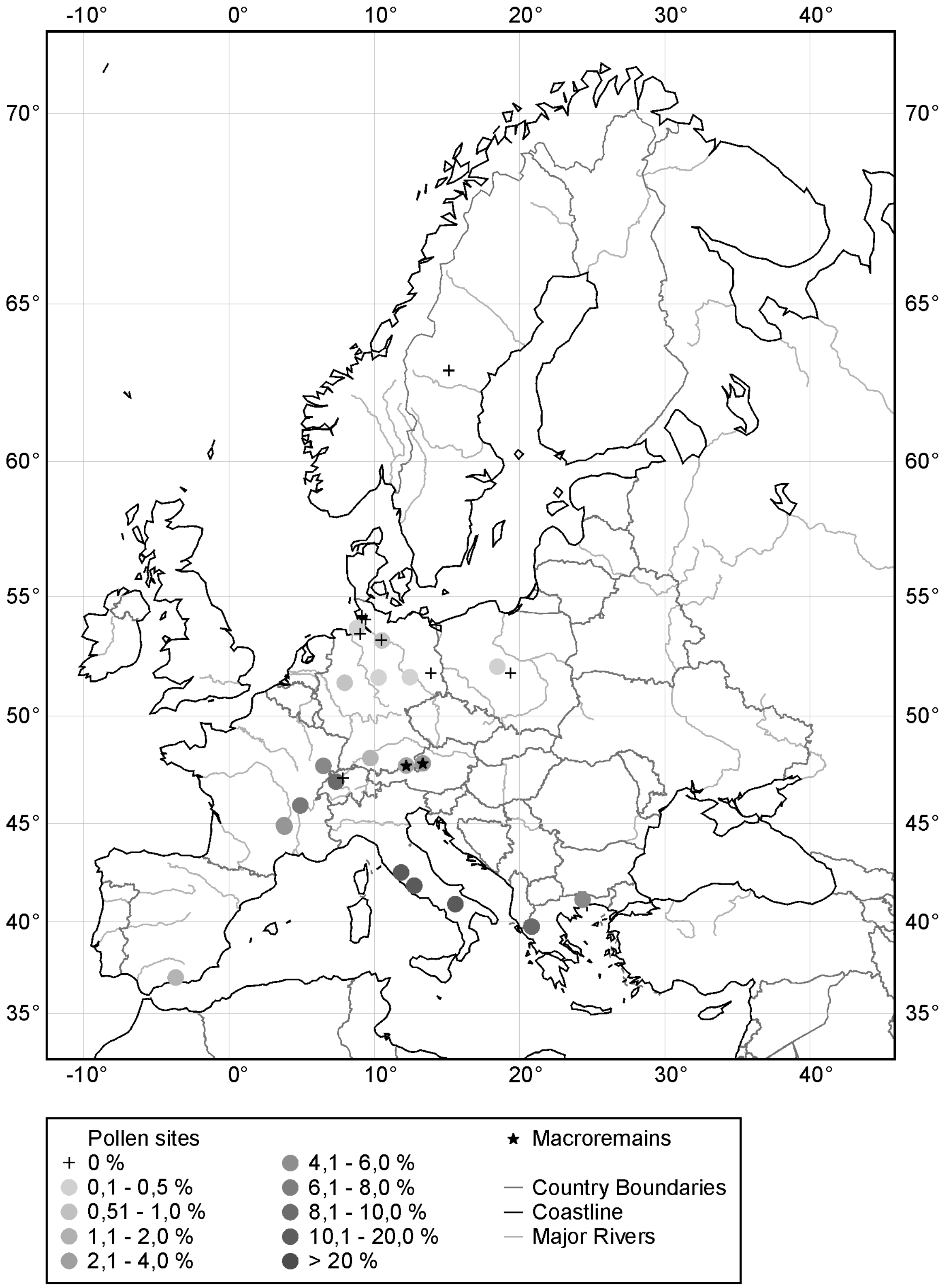


Fig. 10: Maximum pollen percentages and macrofossils of *Abies* within the Brørup.

4.2.3 Distribution pattern of *Abies* during the Odderade

Similar to the Brørup, clear evidences of *Abies* during the Odderade are know from the Mediterranean area, where the taxon certainly had its main distribution, though some finds are also reported from the Alpine region (Fig. 11). The maximum northern limit did not exceed far north of the Alps, thus, *Abies* was not distributed beyond its present range during the Odderade. Maximum pollen percentages are found in central and southern Italy: 22.0% at Lagaccione (Follieri et al. 1998; Magri 1999), 20.0% at Lago Grande di Monticchio (Allen et al. 1999) and 17% at Valle di Castiglione (Follieri et al. 1988; Follieri et al. 1998). Another quite high value is indicated by a site in Greece, Ioannina (Tzedakis 2000; Tzedakis et al. 2002), with about 8.0% of *Abies* pollen. Several sites situated in the northern part of the Alps, eastern France, the Massif Central as well as one in southern Spain reach lower percentages ranging between 0.2 and 3.0%. Macrofossils of *Abies* (seeds, bud-scales and wood) are just mentioned from one site in the Odderade, the site Mondsee in Austria (Klaus 1975; Drescher-Schneider 2000; Oeggl and Unterfrauner 2000).

Remarkably, none of the investigated sites in north-central Europe includes any pollen finds of *Abies*. Thus, during the Odderade this taxon definitely was not present further northward than the Alps.

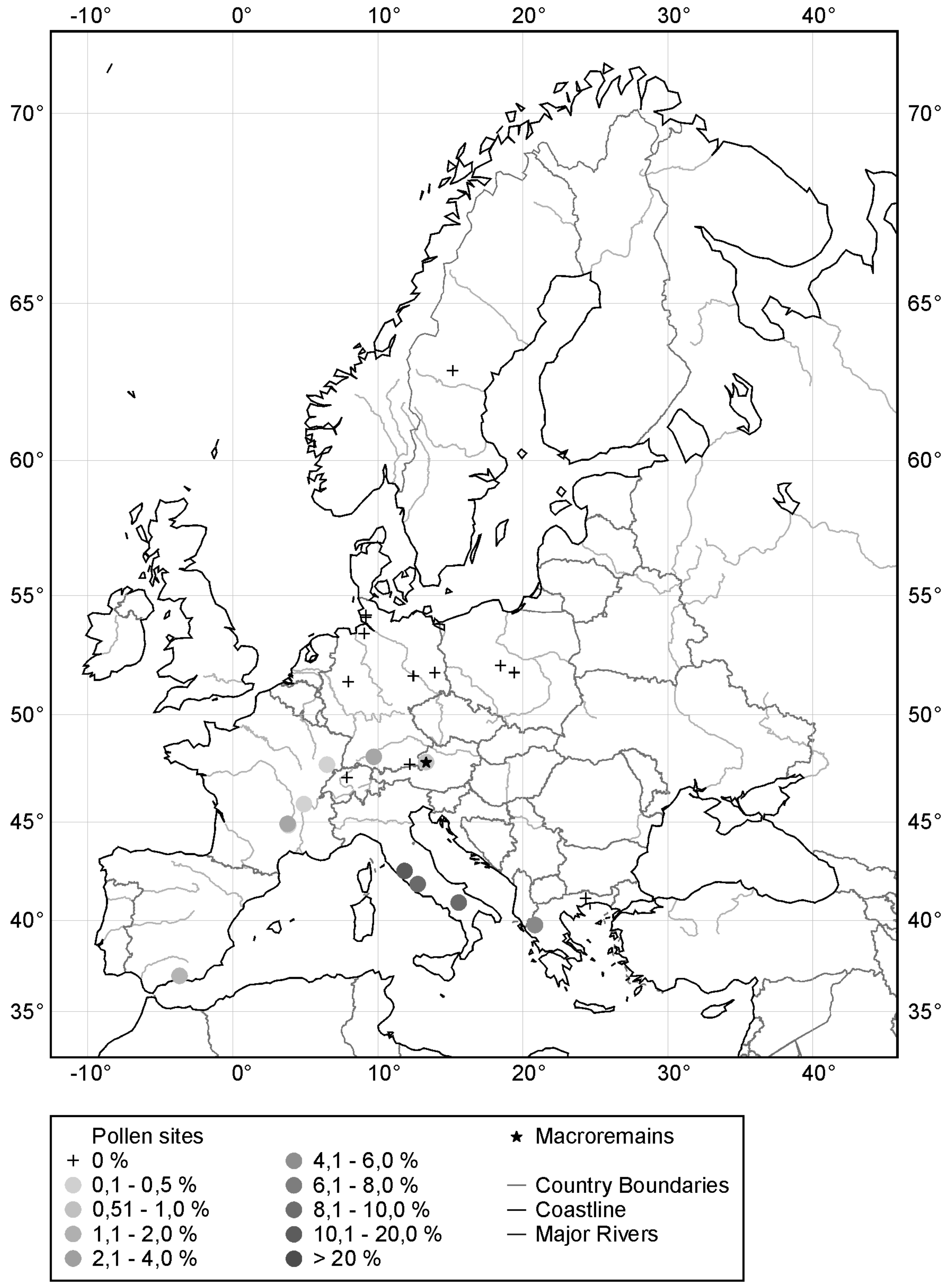


Fig. 11: Maximum pollen percentages and macrofossils of *Abies* within the Odderade.

4.2.4 Comparison of the distribution of *Abies* during the warm stages of the last glacial-interglacial cycle

Fig. 12 presents the northern distribution limits of *Abies* during Eemian, Brørup and Odderade resulting from pollen and macrofossil records, which were used for this study. Noticeably, the northern distribution limit of *Abies* during the Eemian lies much further northward than those of the Brørup and Odderade or the present-day limit. Thus, the distribution area of fir in the Eemian interglacial also included wide parts of north-central Europe.

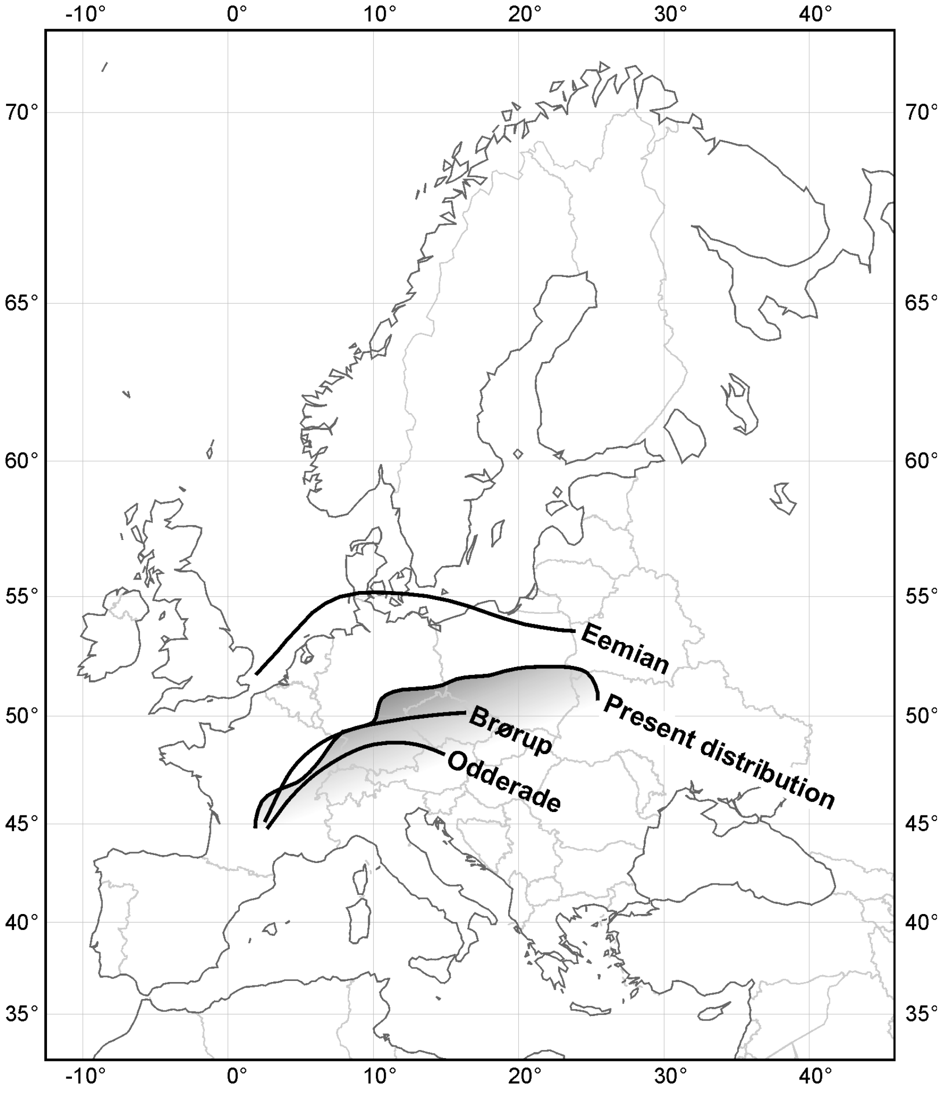


Fig. 12: Northern limits of *Abies* distribution during Eemian, Brørup and Odderade according to pollen and macrofossil finds of the present study.

In contrast to that, it is highly probable that *Abies* was restricted to the areas south of the Alps during both of the Early Weichselian stadials. The northern distribution limits are quite similar for the Brørup and Odderade. According to the palaeobotanical data *Abies* was restricted to the Alps and areas further south during the Odderade. Not a single sole palaeobotanical evidence is available from northerly areas. On the other hand, a slightly more northward distribution may be assumed for the Brørup according to several low percentage pollen sites in north-central Europe.

The course of the northern *Abies* limit during Brørup and Odderade could not be further determined for eastern Europe, because data coverage is too scarce. Thus, reliable presence of fir in the eastern Europe north of 45° latitude can only be inferred as far as the eastern Alps. Investigation of more sites in this area is needed to clarify the situation in east-central Europe.

The postulated distribution limits of *Abies* during the warm stages of the last glacial-interglacial cycle are in accordance with results of Zagwijn (1989, 1992), who investigated the distribution range of *Abies* during different warm phases of the Quaternary, however, unlike the present study, these examinations encompass the Eemian and Brørup, but do not include the Odderade.

Compared to the present range of *Abies* in Europe, its Eemian distribution reached considerably further towards the north than today. The difference of firs northern distribution limit accounts for at least 7° latitude. In contrast to today's rather SW-NE stretched course of the northern *Abies* distribution limit, it sooner followed a S-E trend within the Eemian. In this context it has to be pointed out that contrary to the Holocene the vegetation history in former warm stages, such as Eemian, Brørup and Odderade, could develop free of any anthropogenic influence. For instance during the Eemian the greater part of the Euro-Sibirian region was covered by forests and the same would be the case in the present, Holocene interglacial, had man not inferred (Zagwijn 1992). Thus, it can be assumed that the difference in firs northern distribution course between the Eemian and Holocene is caused by both, human impact and the effects of competition with other tree species during the Holocene.

The distributional limits of fir within the Brørup and Odderade are quite similar to the present-days range. Both show a SW-NE follow a course especially in the western part.

4.2.5 The spread of *Abies* throughout Europe since the last glacial period

Pleniglacial and Lateglacial (Fig. 13, 38000-11500 B.P.)

Fig. 13 presents macrofossil and pollen evidence from different time-slices within the Weichselian Pleniglacial (older than 12500 B.P.) and the older and middle part of the Lateglacial (12500-11500 B.P.). The EMD reports five sites with *Abies* from the Pleniglacial (between 38000-12500 B.P.). The oldest pollen data with reliable radiocarbon dates available in the EPD include sites between 20000 and 18000 B.P.

The oldest plant remains of *Abies* sp. from the Pleniglacial indicate an age of about 38000 B.P. The macrofossils were obtained from detrital sediments from the palaeolithic karst cave Divje babe I in the Idrija valley, Slovenia (Šercelj and Culiberg 1991). The geochronology of the sediment layers, which contained artefacts of the Moustérien type, is based on radiocarbon dating of charcoal fragments. Further macrofossil evidence of *Abies* prior to the Last Glacial Maximum (LGM) was obtained from the palaeolithic site Dolní Vĕstonice (Czechia), interpreted as a mammoth hunters' campsite with several fireplaces (Klíma 1963; Kneblová 1954). A radiocarbon date on charcoal material gives an age of 25600±170 B.P. The chronological frame is confirmed by two older ^{14}C dates from a clay pit with a similar archaeological inventory near Dolní Vĕstonice (28100±380 and 28900±300 B.P.) as well as two measurements on charcoal from the nearby palaeolithic site of Pavlov (26400±230 and 24800±150 B.P.). More recent investigation of Dolní Vĕstonice I, II and III by Damblon et al. (1996) included several dates from charcoal that also correspond to the data published by Klíma (1963).

The palaeolithic site of Šandalja II (Croatia) is also a karst cave encompassing strata between 27800±850 and 10830±70 B.P. (Culiberg and Šercelj 1995). A charcoal fragment of *Abies* was found at a depth of 4-5 m. The nearest ^{14}C dating was made on charcoal pieces of *Fagus sylvatica* at 5.20 m with an age of 21740±45 B.P., suggesting that the age of the *Abies* macrofossil is probably about 20000 B.P.

Charcoal analyses of material from the Altamira Grotto (Spain) show evidence for a Pleniglacial age for fossilised wood remains including those of *Abies*. Two ^{14}C measurements were processed using the “classical method” (15910±230 and 15500±700 B.P.; Uzquiano 1992a). However, *Abies* was probably present at this site earlier, as suggested by the finding of a wood fragment of cf. *Abies*, which was ^{14}C AMS dated to an age of about 17000 B.P. (Uzquiano 1992a; H. Valladas, personal communication).

A ^{14}C date based on charcoal is available from the site at Gazel, France (15070±270 B.P., Vernet 1980). Due to their poor preservation, the charcoal fragments could be anatomically identified only as "*Abies* or *Juniperus*". However, Vernet (1980) also describes the site at Belvis, Spain (approx. 60 km SW from Gazel), where a ^{14}C measurement was obtained from several charcoal pieces in the same layer, including one fragment of *Abies* dated at 12270±270 B.P.

Pollen records with absolute dating from the Pleniglacial are rare in Europe. The first evidence of *Abies* is documented in the EPD from the southern Balkans between 20000 and 18000 B.P. Quite high amounts of pollen are known, particularly from Ioannina in Greece (Bottema 1974; Tzedakis 2000; Tzedakis et al. 2002). Comparably high percentages of *Abies* were found at Banyoles in the Pyrenees between 16500 and 15500 B.P. (Perez-Obiol and Julia 1992) confirming the macrofossil record from Gazel in the same region (Vernet 1980). Pollen evidence of *Abies* from southern Italy is available from Lago Grande di Monticchio since 16500 B.P. (Watts 1985). The values of *Abies* pollen percentages drop between 15500 and 14500 B.P. in the southern Balkans, southern Italy and the Pyrenees. There is also a pollen record from a location in south-east France between 15500 and 14500 B.P. (Lac Long Inférieur; Beaulieu 1977). However, because of the very low pollen percentages, the presence of *Abies* trees in this area is questionable. Within these three areas, high amounts of *Abies* pollen are recorded during both the Pleniglacial and the Lateglacial. After the latter period, there are generally many more sites where palynological investigations have been undertaken. The pollen percentages from many sites increase steadily until the end of the Lateglacial. Several sites are available further north (i.e. Poland), but these just record small amounts of pollen probably caused by long-distant transport and/or redeposition of pollen grains. Numerous localities in north-central Europe show no evidence of *Abies* pollen in the Lateglacial sediment records.

End of the Lateglacial and early Holocene (Fig. 14, 11500-8500 B.P.)

To date there is a lack of *Abies* macroremains from between 11500 and 10500 B.P. In contrast, the density of investigated pollen sites for this time-slice shows a remarkable increase and the percentages of *Abies* pollen grains clearly rise. The northern sites still show low pollen percentages, whereas the records from Italy and Greece described in the previous section (Fig. 13) indicate more than 10% of *Abies* at this time. Moreover two more high percentage sites appear, one in north-west Italy and another one in south-east France. Only two macrofossil records from Switzerland are available from between 10500 and 9500 B.P. The earlier findings are documented from Les Embreux (Hubschmid and Lang 1985). The sediments in this mire were studied by means of 19 cores taken along two transects. According to Hubschmid and Lang (1985), needles of *Abies alba* were found in most of the cores at a frequency of 5%. From the site at Bedrina one ^{14}C dating was obtained from a horizon containing *Abies* stomata (about 10300 B.P., source ALPADABA). Furthermore, wood remains of *Abies alba* were dated to 9560±150 B.P. at this site (Zoller 1960). The distribution pattern of *Abies* pollen evidence during the early Holocene does not change much as compared to the end of the Lateglacial. In some parts of Europe the density of pollen sites increased, particularly in Czechia, Byelorussia, Scandinavia and Great Britain. The amount of macrofossil records clearly increases between 9500 and 8500 B.P. Nine *Abies* macrofossil finds occur in this time-slice. Most of them are located in Switzerland, south-east France, southern Italy and north-east Spain. *Abies* seems to be widely distributed throughout most of the southern part of Europe. Subsequently both, the number of sites as well as the recorded pollen percentages of *Abies* increases. Quite large amounts of pollen are recorded from the Pyrenees, southern France, Switzerland, Italy, Hungary and Greece. Unfortunately, there is a lack of data from the Balkan region. However, it can be supposed that *Abies* was prevalent in this area.

Middle Holocene (Fig. 15, 8500-5500 B.P.)

Between 8500 and 7500 B.P. the number of macrofossil records still remains the same even from the new sites. On the other hand, there is no more *Abies* macrofossil evidence recorded from southern Italy (Sicily). The pollen map generally shows an increasing quantity of pollen records and also rising percentages of *Abies* pollen. From 7500 B.P. onwards the number of macrofossil sites for *Abies* nearly doubles. Pollen values increase especially in the Alpine region, Greece, eastern Alps and the Hungarian basin. In the time-slice 6500 to 5500 B.P. there are increased numbers of macrofossil records in France and Switzerland. Additionally there are two new records from Greece and Bulgaria. At about 6000 B.P., *Abies alba* had largely reached its present-day limit (Fig. 15, bottom right). Later changes in distribution range and/or pollen percentages occur, which may indicate an increasing human impact. Therefore, we do not take into account more recent time-slices from the Holocene in our study since the *Abies* range could be strongly influenced by man.

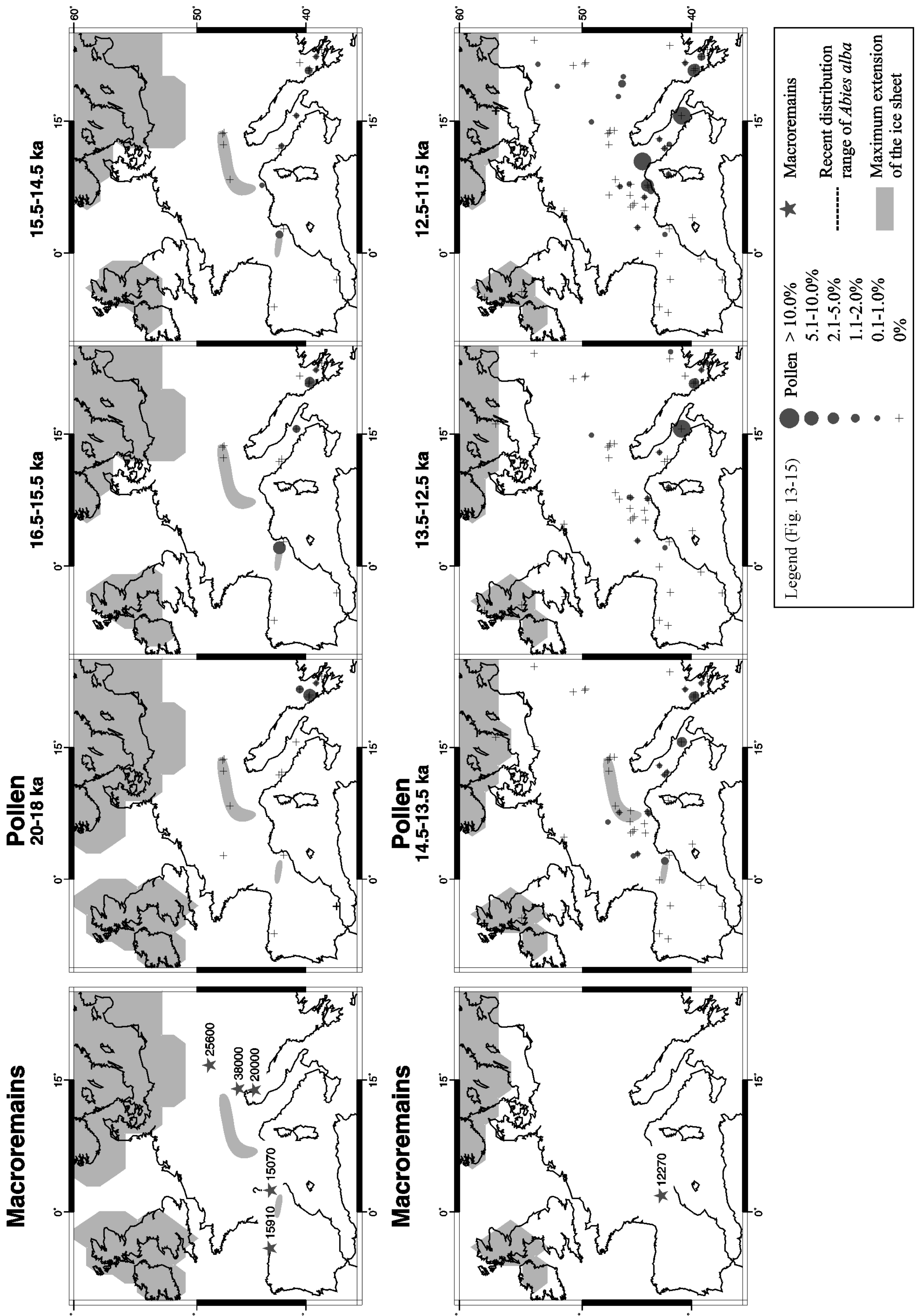


Fig. 13: Evidences of pollen and macrofossils of *Abies* for the Pleniglacial and Lateglacial (38000-11500 B.P.).

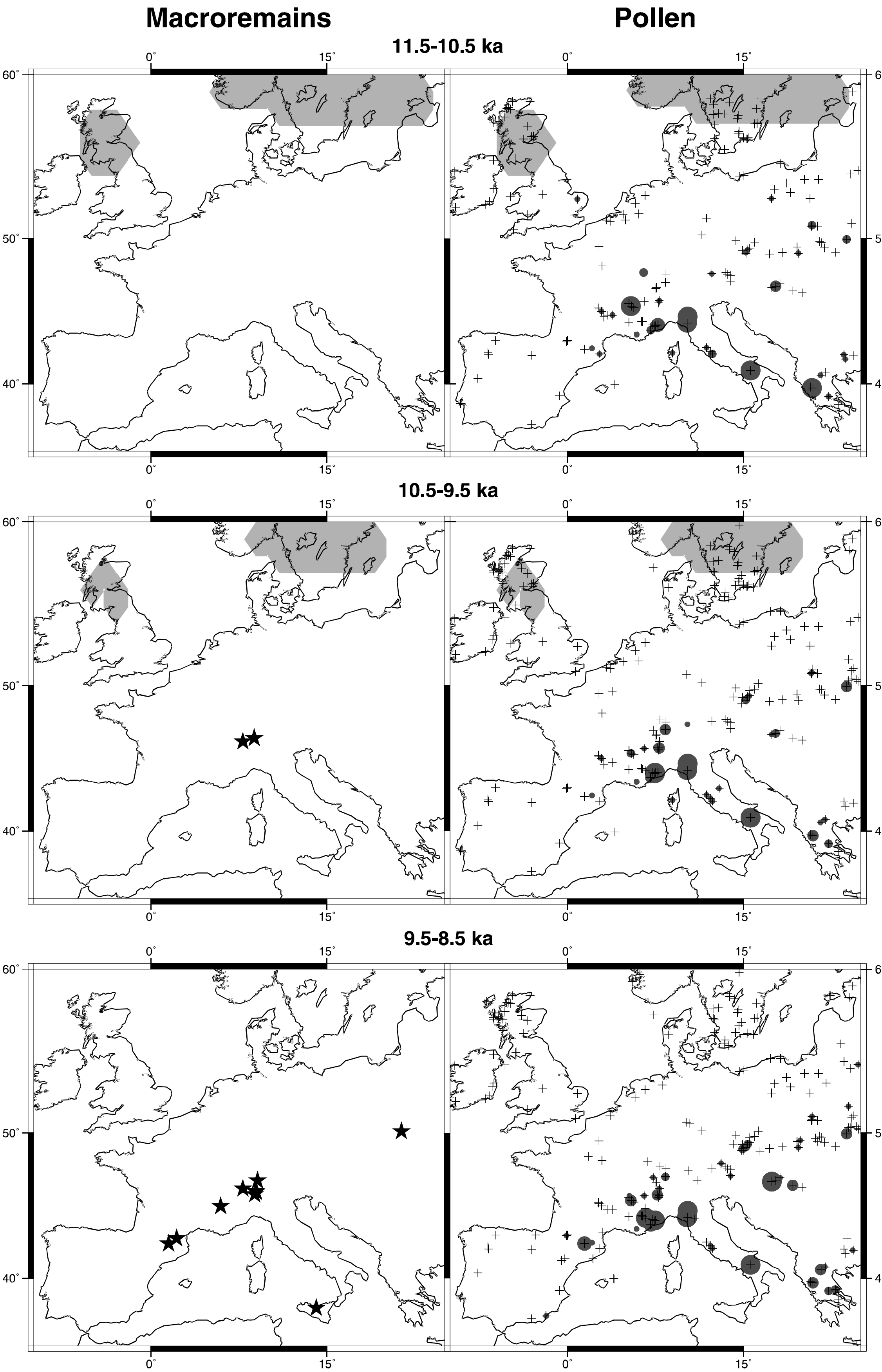
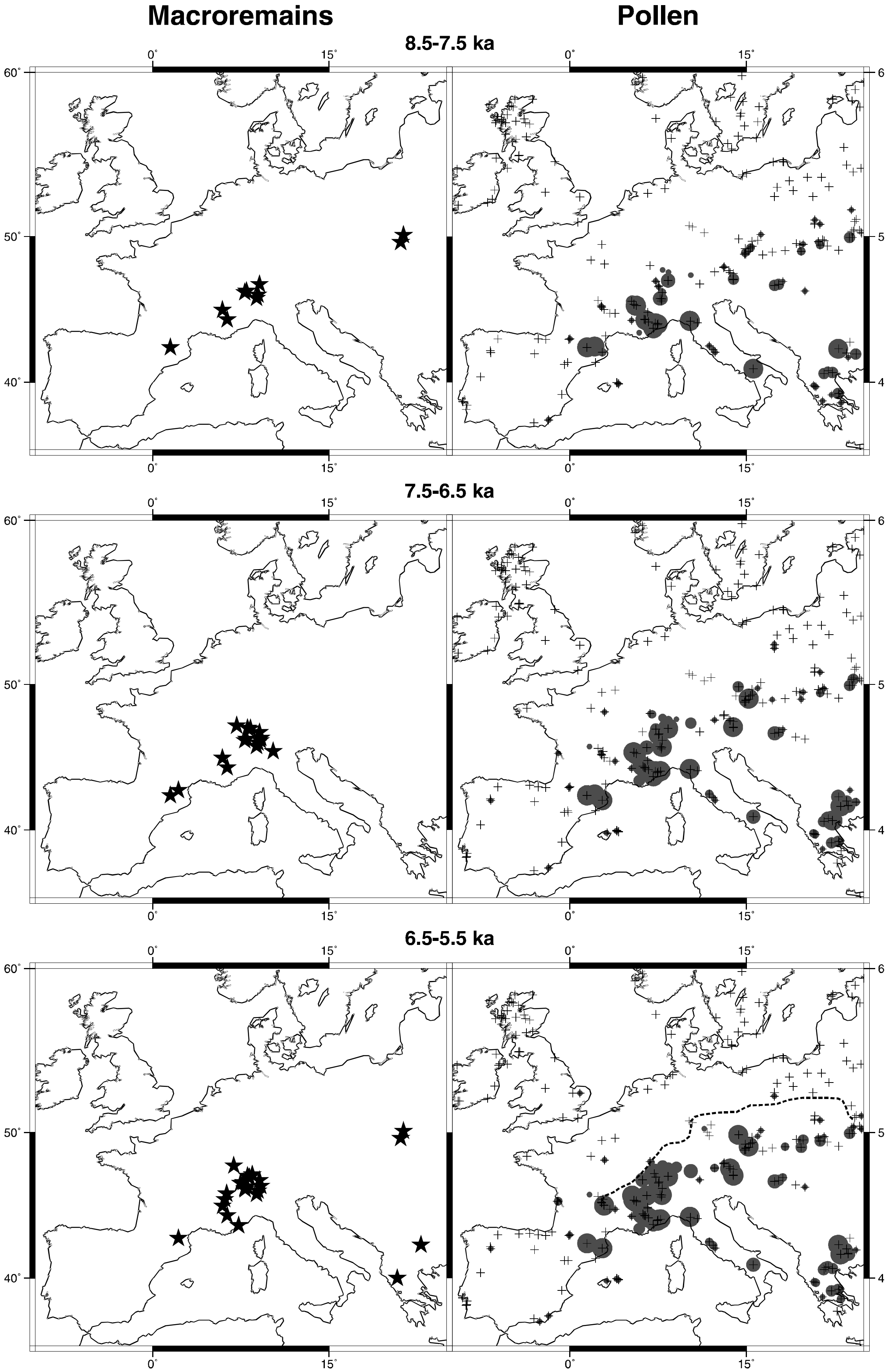


Fig. 14: Evidence of pollen and macrofossils of *Abies* at the end of the Lateglacial and early Holocene (11500-8500 B.P.).



Macroremains

Pollen

8.5-7.5 ka

7.5-6.5 ka

6.5-5.5 ka

Fig. 15: Evidence of pollen and macrofossils of *Abies* during the middle Holocene (8500-5500 B.P.).

4.3 Genetic data

Recent genetic datasets can provide crucial additional information about vegetational history processes, because every present genetic pattern of trees inevitably bears imprints of its past distribution. Thus, for numerous plants a long-term genetic legacy of refugial isolation was demonstrated for maternal refugial lineages. Recent genetic investigations of fir undertaken by Liepelt et al. (2002) deal with *Abies* gene flow during the postglacial. They show a strong subdivision of the *Abies* natural range according both the mitochondrial and the chloroplast DNA variation (Fig. 16 a, b). However, mitochondrial DNA of *Abies* is exclusively maternally inherited and thus dispersed by seeds, but chloroplast DNA is paternally inherited by pollen. Consequently the pattern of the paternally inherited marker displays a greater stirring of the genetic material. According to Liepelt et al. (2002), particularly the geographical distribution of the maternally inherited mitochondrial variation (Fig. 16 a) clearly supports the existence of at least two refugia with two recolonizing maternal lineages remaining largely separated throughout the range. Furthermore, the present results lead to the postulation that in wind-pollinated species an exchange of genetic information between refugia is possible by range-wide paternal introgression (Fig. 16 b).

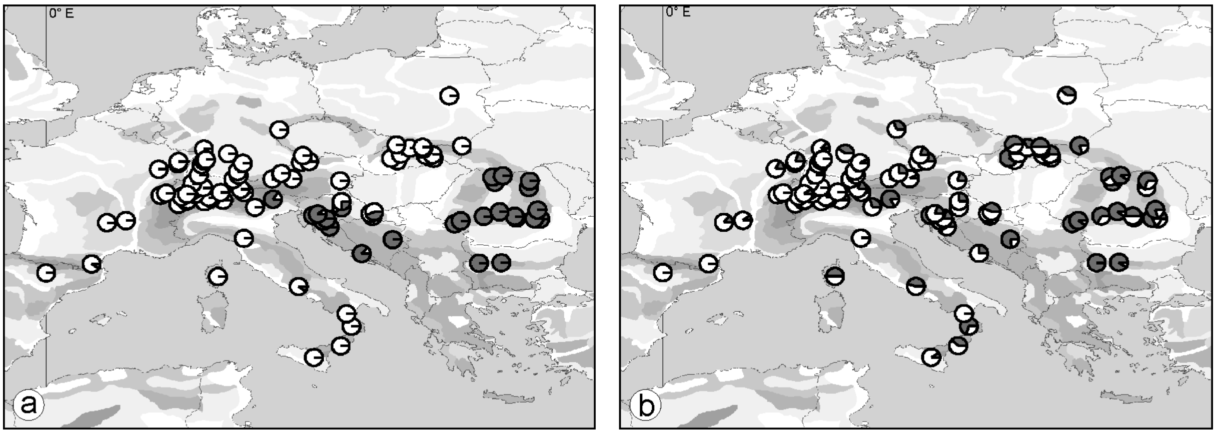


Fig. 16: Geographic maps of Europe showing DNA marker of 100 investigated *Abies alba* populations (Liepelt et al. 2002). (a) Maternally inherited *nad*5-4 marker. (b) Paternally inherited *psb*C marker. White and dark circles mark the presence of different alleles.

Potential refugia of the last glacial period and their contribution to the current range of silver fir by means of the large scale distribution of isozyme allele frequencies were identified by Konnert and Bergmann (1995) and Liepelt et al. (in prep.).

4.4 Discussion

There are several key questions to discuss with respect to palaeobotanical data:

(1) Do we have any strong pollen and/or macrofossil evidence for accurately locating the glacial refugia of *Abies* in Europe prior to the onset of the climate amelioration during the Weichselian Lateglacial?
(2) Did the distribution of *Abies* during the previous warm stages of the last glacial-interglacial cycle have any influence on its subsequent vegetational history?
(3) Which refugia played a major role for initiating the early migration and spread of *Abies alba* throughout Europe during the Weichselian Lateglacial and the Holocene?
(4) Can we reconstruct main migration routes of *Abies alba* during the Lateglacial and Holocene using both pollen and macrofossil remains?

4.4.1 Location of glacial refugia during the Weichselian

Only three sites in two different regions contained fir macroremains dated between 38000 and 20000 B.P. (Fig. 13). It must be stressed that these are localities with palaeolithic inventories from well-dated cave deposits and campsites (radiocarbon dates based on charcoal). Pollen data are not available during this time span in our data set. The two regions are:

a. Moravia, refugia type site Dolní Věstonice/Czechia (Klíma 1963), and
b. South-east Alps/north-west Balkans, refugia type site Šandalja II/Croatia (Culiberg and Šercelj 1995) and also Divje babe/Slovenia (Šercelj and Culiberg 1991; Turk et al. 1988-89).

According to Culiberg and Šercelj (1995), the charcoal remains at Šandalja II undoubtedly prove the presence of *Abies* in Slovenia during the Weichselian Glacial. The authors assume that the taxon occurred in dispersed groups or communities in ecological niches (microrefugia), and that there must have been numerous Pleistocene microrefugia for flora and fauna in these territories that enabled the early and abrupt thermophilic vegetation spread by the end of Pleistocene. However, based on the synoptic palaeobotanical data presented here, these sites, together with Dolní Věstonice, are suggested to be former temporary refugia, which may have existed before the glacial reached its maximum between 20000 and 17000 B.P. It is unlikely that they have played any role as "long-lasting" refugia in the lateglacial and postglacial migration history of *Abies alba* in Europe. Several pollen records from the eastern part of the Alps region are available from the LGM onwards. However, they do not show the presence of *Abies* earlier than 9000 B.P. (Figs. 13 and 14).

As to the locations of glacial refugia from which modern *Abies* populations may have originated, we should take into account only those palaeobotanical sites that indicate a more or less continuous presence between the Last Glacial Maximum and the Lateglacial with the onset of climate amelioration. Based on the combined pollen and macroremains (Fig. 13) we may identify three main regions as potential refugia for *Abies*:

(1) Pyrenees, refugia type site Altamira/Spain (macrofossils, Uzquiano 1992a) and Banyoles (pollen, Perez-Obiol and Julia 1992),
(2) Italy, refugia type site Lago Grande di Monticchio/Italy (pollen, Watts 1985), and
(3) Greece, refugia type site Ioannina (pollen, Bottema 1974; Tzedakis 2000; Tzedakis et al. 2002).

The scarcity of fossil macroremains available in the literature does not allow us to identify more refugial areas. However, the pollen data (Fig. 13: time-slices between 20000 and 14500 B.P.) suggest that there are additional potential refugial areas possibly located in south-east France and north-west Italy. During the end of the Pleniglacial there are few sites with very low percentages of *Abies* pollen (Fig. 13: 16500-15500 B.P.), whereas during the onset of the lateglacial climate amelioration these values increase remarkably (Fig. 13: 12500-11500 B.P.).

With respect to the refugial areas (2) and (3) mentioned above, there is a broad agreement in the literature. In earlier studies, Grüger (1977) and Schneider (1985) suggest that there were apparently refugia for *Abies* during the last glacial in the southern Apennine and the southern Balkan Peninsula (for the latter see also Bottema 1974). Based on *Abies* isopollen maps Huntley and Birks (1983) assume the local presence of fir in Greece and Italy at least for the Lateglacial (13000-10000 B.P.). Bennett et al. (1991) indicate potential refugial areas based on long continental pollen records especially in Italy and the Balkans.

Huntley and Birks (1983) formulate the hypothesis that *Abies* was possibly present prior to the Holocene in the Iberian Peninsula; however, there was no direct pollen evidence available for the occurrence of *Abies* during that time. Bennett et al. (1991) presume that the Iberian Peninsula was probably too arid and the mountain massifs too small to support viable populations of a range of forest trees, but they also mention that pollen records of this area are still sparse and require further examination. In any case, we have to take into consideration a very probable refugial area in the southern part of Spain for the endemic species *Abies pinsapo*, (see the Padul pollen record, Pons and Reille 1988). However, this is not relevant to potential refugia for *Abies alba*. As far as the Pyrenees are concerned, Lang (1994) explicitly excludes the possibility of refugia in this region based on work by Reille (1988) and Reille and Lowe (1993). The investigation of ten sites in the eastern part of the Pyrenees lead to the conclusion that *Abies* was not present in this region until about 10000 B.P. (Reille 1990). However, it should be mentioned that the site of La Borde shows low pollen values around 15000 B.P. Based on the current combined pollen and macroremains evidence presented here (Fig. 13) we suggest that the Pyrenees must be included as a real refugial area for silver fir. This raises a question concerning the role of the Pyrenees refugia as initial starting points for the spread of *Abies alba* northward (see discussion below).

The southern Balkans are a region with a high potential for refugial areas of *Abies*. Pollen finds date back to between 20000 and 18000 B.P. These high pollen percentages continue until the end of the Lateglacial. However, the pollen finds in Greece (Fig. 13) cannot be clearly assigned to the species *Abies alba* since there are other (minor) species present in that area and the accuracy of the pollen identification does not allow their distinction. The modern distribution pattern of the different *Abies* species (Jalas and Suominen 1973) shows either *A. alba*, *A. borisii-regis* or *A. cephalonica* may occur in this area (Fig. 7). According to Liu (1971) *A. borisii-regis* could be considered as a hybrid of *A. alba* and *A. cephalonica*. Unfortunately, macroscopic remains of *Abies* are completely unknown in this region. Additional sites in the central and northern part of the Balkans are needed to clarify the refugial situation in this area that so far is really *terra incognita*.

4.4.2 Potential migration routes during the Lateglacial and Holocene

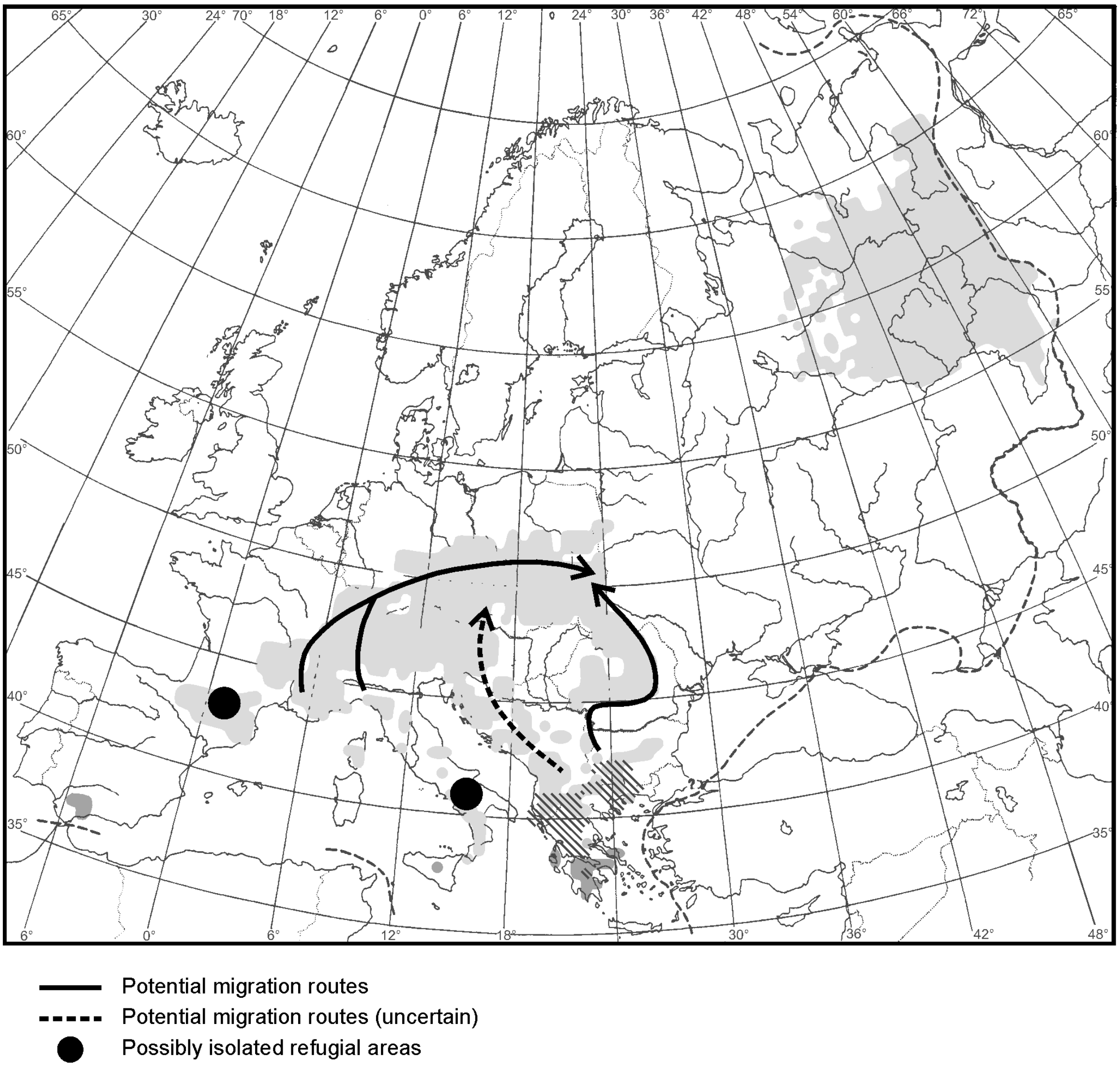


Fig. 17: Potential migration routes of *Abies* during the Lateglacial and Holocene.

According to the available evidence of refugia based on palaeobotanical data, it is theoretically conceivable that *Abies* migrated from the Pyrenees via central and eastern France to the north. Neither pollen nor macroremains clearly prove the existence of *Abies* in south-central France during the Pleni- and Lateglacial. Pollen percentages show low values during the Lateglacial and increase during the early Holocene (around 9500 B.P.). The fact that the records from the Pyrenees do not show a direct connection with the north could argue for an isolated refugial area that did not play any role in the spread of *Abies alba* (Fig. 17). This hypothesis corroborates the results of isozyme studies on gene markers by Konnert and Bergmann (1995) that indicate that the *Abies* populations in the Pyrenees are clearly separated from those of other European regions.

Conspicuously, present-days populations of spruce in the Pyrenees are in accordance with populations in central Europe in respect of their DNA markers (see Fig. 16), even though this refugial area probably had no influence on the postglacial spread of *Abies* in Europe. This apparent contradiction may be explained by the genetic legacy of former distribution pattern within previous warm phases. Genetic differentiation possibly occured within the Eemian interglacial, where *Abies* had a wide spread and continuous distribution throughout Europe.

The distribution maps show relatively high amounts of *Abies* pollen in southern Italy during the Pleni- and Lateglacial. According to the palaeobotanical findings, this area might have been a potential origin for *Abies* expansion to the north. Such a migration route cannot be described in detail because of the low pollen percentages in central Italy during the Pleni- and Lateglacial. Records from northern Italy do not start earlier than 12500 B.P. It is more likely that southern Italy (Calabria) represents an isolated area of silver fir (see Fig. 17), as initially proposed by Bergmann et al. (1990) and Konnert and Bergmann (1995) based on isozyme studies, and by Larsen (1986, 1989) based on plant ecophysiological investigations. According to Konnert and Bergmann (1995) both the Pyrenees and southern Italy sheltered distinct gene pools, which differed from those identified in central French or northern Italian populations. Both glacial refugia may have allowed the spread of autochthonous *Abies* populations. Willis (1996) suggested that these populations that remained isolated during the warm stages would carry the genetic differentiation on into the next glacial period.

Another potential area for the origin of the migration of fir into northern Europe could be expected in south-east France and north-west Italy (Fig. 17). Fir populations from these two areas could have combined in a potential migration route running along the western limit of the Alps. This assumption confirms the genetic survey carried out by Konnert and Bergmann (1995). These authors propose that silver fir spread to the north from a refugium located in central Italy via two routes: a “West Alpine route” (which is divided into the “Jura route” and the “Allgäu route”), as well as an “East Alpine route”. Isoenzyme investigations by Burga and Hussendörfer (2001) suggest an Italian gene pool as an origin for today’s western and eastern range of *Abies alba*. These results do not support the assumption of Konnert and Bergmann (1995), postulating a second migration path starting from a refugium located in central and/or eastern France (probably the “Massif Central”).

Konnert and Bergmann (1995) also suggest the existence of an introgression zone between the French and Italian refugia situated in central France as well as in an area along the north-west Alps. In contrast, Lang (1994) describes a possible track for fir populations going from the south of the Apennine Peninsula to the Alps and the low mountain ranges preceding them, also including the French Massif Central, and also to the Pyrenees. In addition, he suggests the speed of *Abies* migration to be about 75-120 m/a.

Several sites in the southern Balkans feature high amounts of pollen during the entire Pleni- and Lateglacial, indicating a potential refugial area. Although it is not possible to clearly assign these pollen findings from Greece to the species *Abies alba*, nevertheless this area may well have been one origin for the migration of fir into northern Europe. Because of the huge lack of palaeobotanical evidence from the central and northern Balkans this track unfortunately could not be proved from the available pollen and macrofossil records. Based on molecular-biological investigations, Konnert and Bergmann (1995) suggest a possible track running from a refugial area located in the southern and south-east Balkan Peninsula (Macedonia, Bulgaria, Romania), from where expansion occurred along the Dinaric Mountains to their northern border in Slovenia and along the Romanian Carpathians as far as the eastern parts of the Beskides (in Slovenia). Almost the same proposal was made by Lang (1994) who suggested an easterly migration branch of *Abies* starting from the southern Balkan Peninsula, leading via the Dinarids north-west to the eastern Alps and the low mountain ranges lying ahead of them as far as the Carpathians. Also Parducci et al. (1996) suggest through isoenzyme studies that *Abies alba* populations in the south-east Alps could have originated in a Balkan refuge.

Konnert and Bergmann (1995) further suppose that silver fir from the Balkan refugia could have met populations from the Italian refugia, developing an introgression zone that included the Beskides Mountains, High Tatra Mountains, Slovak Carpathians and Slovak Ore Mountains. This hypothesis agrees with the work of Liepelt et al. (2002), who proposed an introgression zone between an eastern Mediterranean and a western Mediterranean lineage in Croatia and Slovenia on the basis of maternally inherited genetic markers.

5. Investigations on the spread of *Picea* during the last glacial-interglacial cycle (126000 years to date)

5.1 Present distribution of *Picea*

Nowadays *Picea* is represented by two species in Europe (Fig. 18): *Picea abies* and *Picea omorika*. *P. abies* is distributed throughout the entire of northern Europe as well as the low mountain ranges and high mountains in the south and south-east (Jalas and Souminen 1973; Meusel et al. 1964). Actually two subspecies, *P. abies* subsp. *abies* and *P. abies* subsp. *obovata*, can be distinguished within the species by means of their cones. Some publications also use the synonymic term "*Picea excelsa*" for *Picea abies*.

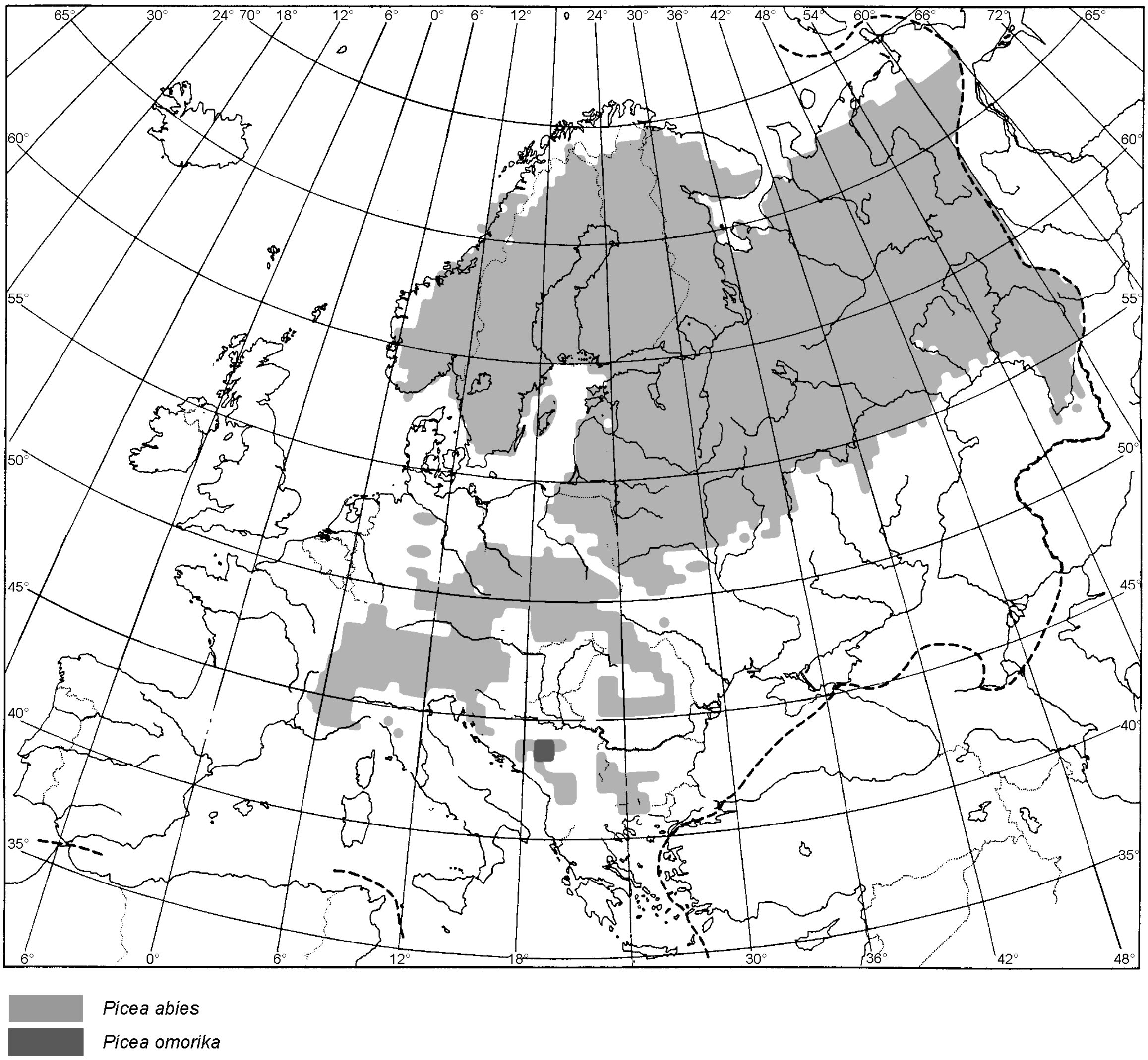


Fig. 18: Present range of *Picea* species in Europe (after Jalas and Souminen 1973).

Compared to *Picea abies*, *Picea omorika* is endemic to the Drina basin in Bosnia and Herzegovina. In all probability Lateglacial and Holocene pollen finds outside of the present range of *P. ormorika* can be assigned to *P. abies* (Lang 1994).

5.2 Results from palaeobotanical data

5.2.1 Distribution pattern of *Picea* during the Eemian

PZ I (Fig. 19, top left)

Most investigated sites show just very low pollen percentages (0.1-1.0%) or no pollen of *Picea* at the beginning of the Eemian (PZ I). These sites mainly spread over central and north-central Europe, also including single profiles from Italy (Valle di Castiglione; Follieri et al. 1988; Follieri et al. 1998), Great Britain (Bobbitshole; West 1957), southern Sweden (Leveäniemi; Robertsson 1991, 1997; Robertsson et al. 1997) and western Norway (Fjörsanger; Mangerud 1981). The southernmost finds of *Picea* pollen stem from the Italian site Valle di Castiglione (Follieri et al. 1988; Follieri et al. 1998). They do not exceed 0.2% at this location.

Two sites from the eastern and western Alpine region respectively clearly report the presence of spruce by 1.8% pollen at the Swiss site Meikirch (Welten 1982b) and even 6.2% at the Austrian site Mondsee (Klaus 1975; Drescher-Schneider 2000; Oeggl and Unterfrauner 2000). Findings at the site Mondsee also comprise macrofossil remains (seeds, needles, bud-scales of *Picea* sp. and wood determined as *Picea/Larix*). These pollen- and macrofossil finds obviously indicate that the distribution of *Picea* in central Europe was limited to the Alps by the initiation of the Eemian. However, a macrofossil find (wood identified as *Picea* sp.) was made at the Polish site Glówczyn (Niklewski 1968).

There is also one single notably high percentage pollen site, Seitevare (5.0%; Robertsson 1991), which is situated in northern Sweden.

PZ II (Fig. 19, top right)

Most investigated sites still do not show *Picea* pollen percentages exceeding values of 1.0% within PZ II. Like in the previous pollen zone the highest pollen percentages of *Picea* are mentioned for the sites Mondsee (10.0%) and Meikirch (1.8%) in the eastern and western Alps, respectively. The site Mondsee also exhibits macrofossil remains (seeds, needles, bud-scales of *Picea* sp. and wood determined as *Picea/Larix*; Klaus 1975; Drescher-Schneider 2000; Oeggl and Unterfrauner 2000). A further site indicates 4.0% of *Picea* pollen, the Swiss location Gondiswil-Seilern (Wegmüller 1992).

However, a couple of new sites that have non-irrelvant percentages of *Picea* pollen are seated in western Finland (Eriksson 1993), such as Viitala (2.5%), Norinkylä 3 (2.0%) and Vesiperä A (1.5%). Also the site Seitavare (Robertsson 1991) in northern Sweden, which was already present in PZ I persists within PZ II representing spruce pollen of 5.0%.

PZ III (Fig. 19, bottom left)

In PZ III, noticeably increasing values are indicated at several sites, especially in the Alpine region. The Swiss sites Meikirch (Welten 1982b) and Gondiswil-Seilern (Wegmüller 1992) in the western Alps report 7.0 and 3.0% of *Picea* pollen respectively. Higher values are shown by the Austrian site Mondsee (17.5%; Klaus 1975; Drescher-Schneider 2000; Oeggl and Unterfrauner 2000) and the German site Samerberg I (15.0%; Grüger 1979a,b) in the eastern Alps, both also containing macrofossil finds (seeds, needles, bud-scales of *Picea* sp. and *Picea/Larix* wood at Mondsee; needles and seed wings at Samerberg I).

Some sites in north-central Europe also have *Picea* pollen exceeding 1.0%, such as the German sites Wallensen (7.0%; Rabien 1953) and Neumark-Nord (1.5%; Litt 1994) as well as the southern Polish site Imbramowice (1.7%; Mamakowa 1989). Two sites including precipitation of spruce pollen are reported from Les Echets (Beaulieu and Reille 1984, 1989) in eastern France and the site Ribains (Beaulieu and Reille 1992b) in the Massif Central. However, they both do not pass a limit of 0.2%.

Decreasing percentages of spruce are evident at some of the Finish sites. Values do not rise above 0.2% in this particular pollen zone, whereas the content of *Picea* pollen at the Swedish site Seitavare (Robertsson 1991) still remains at 5.0%.

PZ IVa (Fig. 19, bottom right)

In PZ IVa there are just a few profiles left, which do not contain any *Picea* pollen at all. The highest values are still reported from the eastern Alpine sites. The percentages of spruce pollen go up to 38.0% at both sites Samerberg I (Grüger 1979a,b) and Mondsee (Klaus 1975; Drescher-Schneider 2000; Oeggl and Unterfrauner 2000). Both sites even document the sole finds of macrofossils (seeds, needles, bud-scales of *Picea* sp. and *Picea/Larix* wood at Mondsee; needles and seed wings at Samerberg I) within this time frame. Pollen values in the West Alps increased to 7.0% at the Swiss site Gondiswil-Seilern (Wegmüller 1992), but droped to 6.5% at Meikirch (Welten 1982b). Additionally the site La Grande Pile (Woillard 1975, 1978; Beaulieu and Reille 1992a) reports 2.5% of *Picea* pollen from eastern France.

At least half of the north-central European sites indicate increased values within PZ IVa, particularly the German sites Wallensen (8%; Rabien 1953), Quakenbrück (6%; Hahne et al. 1994a) and Neumark-Nord (3.5%; Litt 1994) as well as the Polish site Imbramowice (2.8%; Mamakowa 1989). Even one site, the locality Bobbitshole (West 1957), containing 2.0% of spruce pollen is known from the south-east of Great Britain.

Few changes of *Picea* pollen precipitation are recorded from Fennoscandia. Similarly to PZ IVa isolated sites situated in Norway, Sweden and Finland show values between 0.5 and 5.0%.

PZ IVb (Fig. 20, top left)

Most conspicuous for PZ IVb is the accumulation of quite high percentage sites (mostly exceeding 5.0%) in north-central Europe, especially in northern and north-central Germany. Percentages are as high as 54% at the German site Aschenhütte (Ricken and Grüger 1988). The site Hollerup (Andersen 1965) yet documents 9.0% of *Picea* pollen from northern Denmark. Remarkable is also a site from Estonia, the location Waewa-Ringen (Thomson 1941) which represents at most 2.0% of spruce pollen. In contrast, all pollen sites in central Poland, except for the site Góra Kalwaria (1.5%; Sobolewska 1961), do not exceed values of 0.8%. Macrofossil remains were found at four sites in north-central Europe, the German sites Schwindebeck (cones, needles and seeds determined as *Picea excelsa* as well as seeds, seed wings, wood and bud scales of *Picea* sp.; Behre 1962) and Aschenhütte (needles; Ricken and

Grüger 1988), the site Kamphuis (seeds of *Picea abies*; Geel et al. 1986) in the Netherlands and the Polish site Imbramowice (wood; Mamakowa 1989).

Further on the two east Alpine sites Mondsee in Austria (Klaus 1975; Drescher-Schneider 2000; Oeggl and Unterfrauner 2000) and Samerberg I (Grüger 1979a,b) in southern Germany still show particularly high pollen values (58.0 and 48.5% respectively) as well as coexisting macrofossil finds (seeds, needles, bud-scales of *Picea* sp. and *Picea/Larix* wood at Mondsee; needles, anthers and seed wings at Samerberg I).

Very sparse or no changes can be obseverd at the Fennoscandian sites, the locations in eastern France and Massif Central as well as in Italy.

PZ V (Fig. 20, top right)

The pollen percentages obviously rise at nearly all sites within PZ V. Notably high values of *Picea* pollen are reported from north-central Europe, all accounting for at least 7.0%. Highest values in this area are found in northern Germany. They reach 61.0% at the site Husum (Menke 1985), 44.0% at Rederstall II (Menke and Tynni 1984), 38.0% in Groß Todtshorn (Freund 1997; Caspers 1997) and still 38.0% at Odderade 7 (Averdieck 1967). Also a lot of macrofossils were found in north and north-central Germany, such as in Wallensen (needles, seeds, bud scales and cones of *Picea abies*; Rabien 1953), Odderade 7 (bark and a leaf; Averdieck 1967), Aschenhütte (wood; Ricken and Grüger 1988), Schwindebeck (cones, needles and seeds determined as *Picea excelsa* as well as seeds, seed wings, wood and bud scales of *Picea* sp.; Behre 1962) and Helgoland (seeds and seed wings; Behre 1970). One macrofossil find also stems from the site Kamphuis (seeds, seed wings and needles of *Picea abies*; Geel et al. 1986) in the eastern Netherlands.

In comparison to PZ IVb all Polish sites show extremely increased pollen percentages of spruce. The highest value of about 21.0% was obtained from the site Góra Kalwaria (Sobolewska 1961), however, also the site Zgierz-Rudunki (Jastzebska-Mamelka 1985) indicates only slightly lower percentages (20.0%).

Even higher values are evident at a site from Esthonia. The amount of *Picea* at this site, Waewa-Ringen (Thomson 1941), increased from 2.0% in PZ IVb to 59.0% in PZ V thus representing the highest value of spruce pollen for this time frame.

A couple of sites in the Alpine area remain at high pollen values, such as the Austrian site Mondsee (48.0%; Klaus 1975; Drescher-Schneider 2000; Oeggl and Unterfrauner 2000) and the German site Samerberg I (49.0%; Grüger 1979a,b), which also still contains macrofossil remains (seeds, needles, bud-scales of *Picea* sp. and *Picea/Larix* wood at Mondsee; needles, anthers and seed wings at Samerberg I).

Even most of the sites in Fennoscandia represent high pollen percentages of *Picea*. The highest values in this area are located at the Swedish site Leveäniemi (30.0%; Robertsson, 1991, 1997; Robertsson et al. 1997) and the Finnish site Evijärvi (33.0%; Eriksson 1993).

PZ VI (Fig. 20, bottom left)

For the majority of sites PZ VI displays the highest registred pollen percentages of *Picea* within the entire Eemian. Furthermore, the greatest amount of macrofossil remains is present in this pollen zone, especially in northern Germany and central Poland.

Peak values for this period can be found at sites in the Alpine area as well as in north-central Europe. The site Gondiswil-Seilern (Wegmüller 1992) in Switzerland features the highest percentages of spruce in this particular pollen zone. They are quoted to reach 73.0% at this location. High percentages of *Picea* are also reported from the Austrian site Mondsee (68.0%; Klaus 1975; Drescher-Schneider 2000; Oeggl and Unterfrauner 2000) and the German sites Husum (62.0%; Menke 1985), Samerberg I (57.0%; Grüger 1979a,b) and Rederstall II (56.0%; Menke and Tynni 1984). Like in the four previous pollen zones the sites Mondsee and Samerberg I also include macrofossil finds (seeds, needles, bud-scales of *Picea* sp. and *Picea/Larix* wood at Mondsee; needles, anthers and seed wings at Samerberg I).

A particularly high pollen value of spruce is also mentioned from the Esthonian site Waewa-Ringen (Thomson 1941) with about 65.0%. In the same way several high pollen percentages of *Picea* are displayed in Poland, such as Jozwin (45.0%; Tobolski 1991), Góra Kalwaria (44.0%; Sobolewska 1961) and Zgierz-Rudunki (35.0%; Jastzebska-Mamelka 1985).

Compared to the previous pollen zone, the pollen values of most Fennoscandian sites decrease, except for one site, the location Fjörsanger (Mangerud et al. 1981) in Norway, which indicates 44.0% of *Picea* pollen.

Even in PZ VI, the southernmost site, Valle di Castiglione (Follieri et al. 1988; Follieri et al. 1998) only exhibits 0.2 % of *Picea* pollen, a value, which did not change within all pollen zones of the Eemian. This value as well as the record of 0.2% in Wing (Hall 1980) argue against a presence of *Picea* in both areas. Probably, the documented pollen grains rather result of aerial pollen transportation.

PZ VII (Fig. 20, bottom right)

Picea pollen percentages drop at most sites at the end of the Eemian, however, they still clearly prove the presence of *Picea* for the Alpine area just as well as for north-central Europe. The highest values within PZ VII are reported from sites seated in the Alpine area, such as Gondiswil-Seilern (67.0%; Wegmüller 1992) and Meikirch (48.0%; Welten 1982b) in Switzerland as well as Samerberg I (63.0%; Grüger 1979a,b) in Germany. Like in PZ III-VI macrofossils are known from the locations Mondsee (seeds, needles, bud-scales of *Picea* sp. and wood of *Picea/Larix*) and Samerberg I (needles, anthers and seed wings).

Also quite high amounts of *Picea* pollen are displayed by the German site Aschenhütte (42.0%; Ricken and Grüger 1988) and the French site La Grande Pile (38.0%; Woillard 1975, 1978; Beaulieu and Reille 1992a). The presence of fir in the area of northern Germany is also confirmed by three locations of macrofossil finds, the sites Schwindebeck (cones, needles and seeds determined as *Picea excelsa* as well as seeds, seed wings, wood and bud scales of *Picea* sp.; Behre 1962), Aschenhütte (needles and wood; Ricken and Grüger 1988) and Wallensen (needles, seeds, bud scales and cones of *Picea abies*; Rabien 1953).

Compared to that, percentages of spruce pollen in eastern Germany and Poland drop considerably, they do no longer exceed a limit of 9.0%, as is documented at the Polish site Jozwin (Tobolski 1991).

Just two Fennoscandian sites were investigated for PZ VII. One of these, the site Seitavare (Robertsson 1991), still presents 5.0% of *Picea* pollen, whereas the other site, Leveäniemi (Robertsson 1991, 1997; Robertsson et al. 1997), does not reveal any find of spruce pollen at all, though it is quite close to Seitavare.

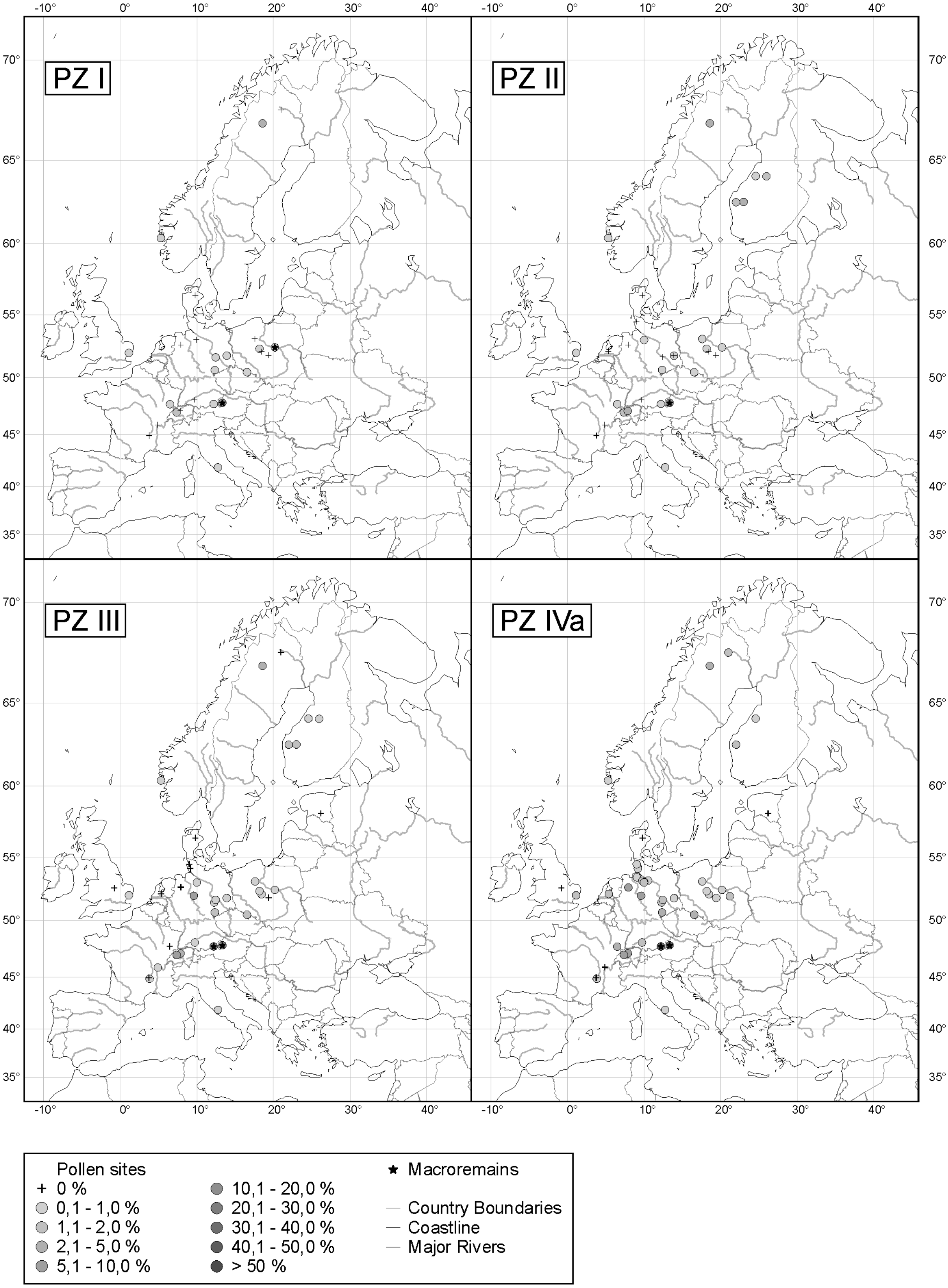


Fig. 19: Maximum pollen percentages and macrofossils of *Picea* within the Eem (PZ I-IVa).

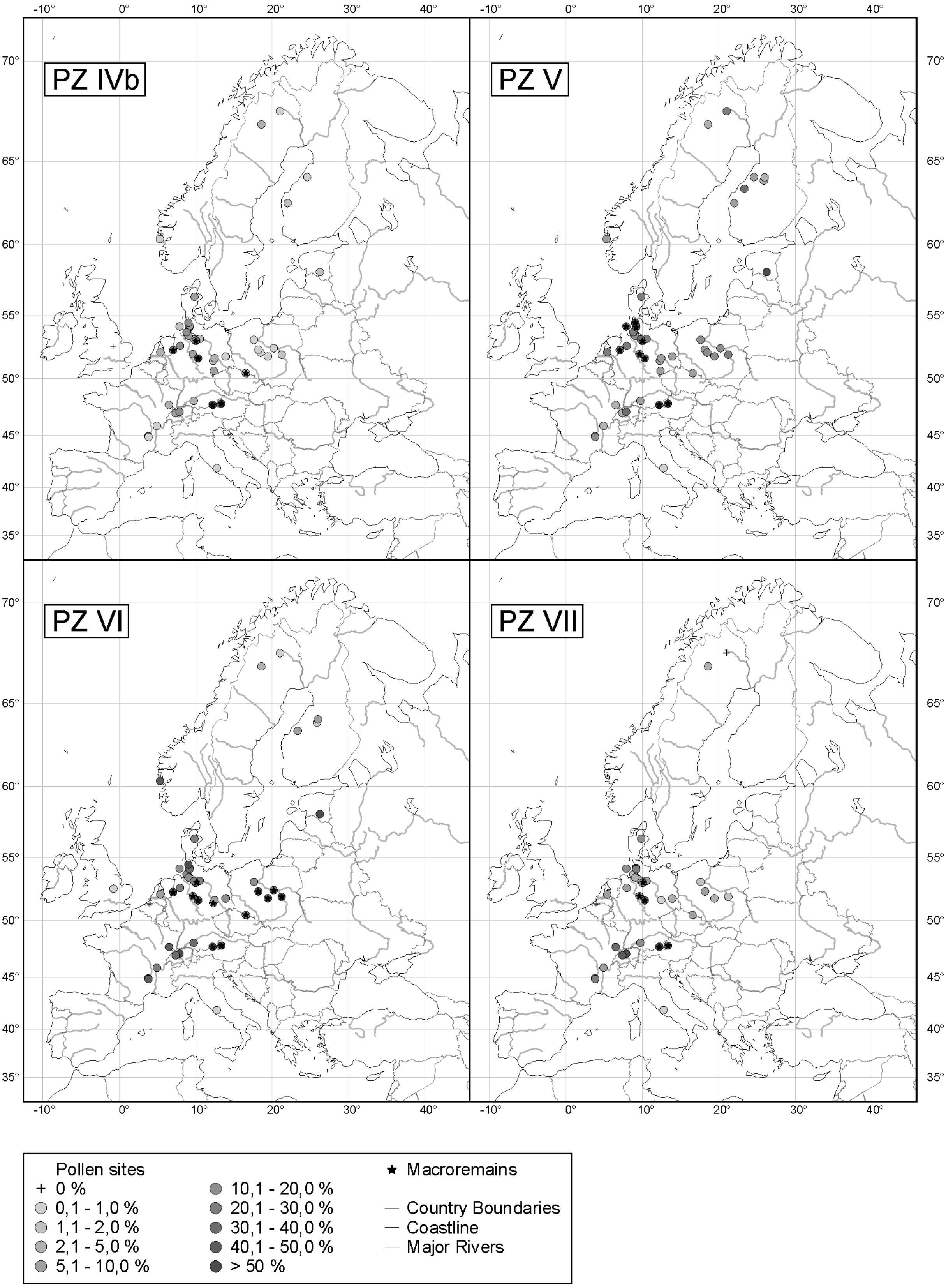


Fig. 20: Maximum pollen percentages and macrofossils of *Picea* within the Eem (PZ IVb-VII).

5.2.2 Distribution pattern of *Picea* during the Brørup

During the Brørup numerous sites accumulate in north-central Europe (Fig. 21). Another accumulation area is found in the Alps including two sites in eastern France and the Massif Central. This area has the highest pollen percentages of *Picea*, such as 87.0% at the site Gondiswil-Seilern in Switzerland (Wegmüller 1992), 83.0% at the site Samerberg 1973 in southern Germany (Grüger 1979a,b) and 82.0% at the Austrian site Mondsee (Klaus 1975; Drescher-Schneider 2000; Oeggl and Unterfrauner 2000). Several records in this area reveal lower, though still high amounts of pollen. Four of these sites are located in France, the sites Lac du Bouchet (D) (51.0%; Reille and Beaulieu 1990), Ribains (48.0%; Beaulieu and Reille 1992b), La Grande Pile (42.0%; Woillard 1975, 1978; Beaulieu and Reille 1992a) and Les Echets (37.0%; Beaulieu and Reille 1984, 1989). 47.0% of *Picea* pollen were determined for the site Amersfoort 3 in the Netherlands (Zagwijn 1961), 39.0% for the site Jammertal in Germany (Müller 2000, 2001) and 38.0% for the Swiss site Meikirch (Welten 1982b). The highest pollen values within north-central Europe are reported from the sites Brørup in Denmark (32.0%; Andersen 1961), Stenberget in Sweden (28.0%; Berglund and Lagerlund 1981) and Neheim-Hüsten in Germany (22.0%; Teunissen et al. 1972). The most northern site for the Brørup is the location Pilgrimstad in central Sweden (Robertson 1988) with a record of 2.0% of *Picea* pollen. Three sites in the Mediterranean area reach less high percentages of *Picea* pollen than in north-central Europe, the Italian sites Lagaccione (10%; Follieri et al. 1998; Magri 1999) and Valle di Castiglione (0.2%; Follieri et al. 1988; Follieri et al. 1998) and Tenagi Philippon II (2.5%; Wijmstra 1969) in Greece.

Four macrofossil sites are known for the Brørup, three from Germany and one from Austria. Needles, anthers and seed-wings of *Picea* as well as undefined remains of *Picea ormorika* are reported from the site Samerberg 1973 (Grüger 1979a,b) in southern Germany. Records from northern Germany include needles of *Picea abies* from the site Gröbern (Litt 1994) and *Picea* needles, buds and seeds from the site Aschenhütte (Ricken and Grüger 1988). Seeds, needles, bud-scales of *Picea* sp. and wood (determined as *Picea/Larix*) are found at the Austrian site Mondsee (Klaus 1975; Drescher-Schneider 2000; Oeggl and Unterfrauner 2000).

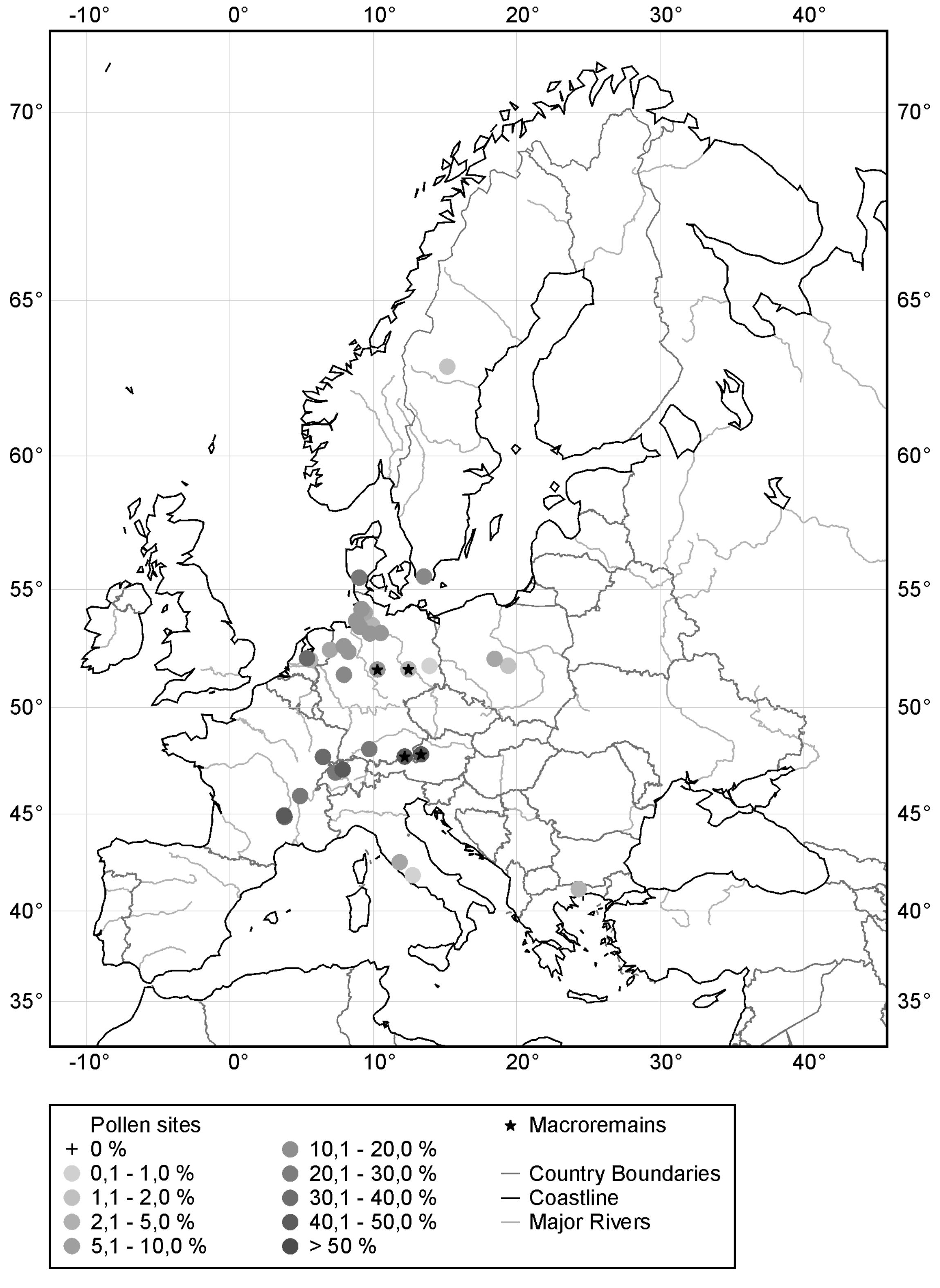


Fig. 21: Maximum pollen percentages and macrofossils of *Picea* within the Brørup.

5.2.3 Distribution pattern of *Picea* during the Odderade

The present dataset apparently includes less sites for the Odderade than for the Brørup. During this warm period *Picea* was widely present in central and north-central Europe. The highest pollen percentages are found in the Alpine region, eastern France, the Massif Central and central Italy (Fig. 22). They include the Austrian site Mondsee with 80.0% of *Picea* pollen (Klaus 1975; Drescher-Schneider 2000; Oeggl and Unterfrauner 2000), the site Samerberg 1973 in Germany (73.0%; Grüger 1979a,b) and the Swiss site Gondiswil-Seilern (71.0%; Oeggl and Unterfrauner 2000). Also three sites in eastern France, Lac du Bouchet (D) (Reille and Beaulieu 1990), La Grande Pile (Woillard 1975, 1978; Beaulieu and Reille 1992a) and Ribains (Beaulieu and Reille 1992b) as well as one in central Italy, Lagaccione (Follieri et al. 1998; Magri 1999) and one in southern Germany, Jammertal (Müller 2000, 2001), show quite high pollen percentages, ranging between 24.0 and 44.0%. Several sites are present in northern Germany, which mention *Picea* pollen values between 1.2 and 17.0%. Furthermore there are two sites from central Poland, one from central Italy and one from Greece indicating 0.5 and 1.8%. The most northerly pollen finds are reported from the site Pilgrimstad in central Sweden. *Picea* still has 5.0% of pollen at this high latitude (Robertson 1988).

Macrofossil finds (seeds, needles, bud-scales of *Picea* sp. and *Picea/Larix* wood) for the Odderade are specified from the site Mondsee in Austria (Klaus 1975; Drescher-Schneider 2000; Oeggl and Unterfrauner 2000). Needles, anthers and seed-wings of *Picea* were found at the southern German site Samerberg 1973 (Grüger 1979a,b). Three more macrofossil sites are located in northern Germany. Seeds and needles of *Picea abies* are reported from Gröbern (Litt 1994), seeds of *Picea abies* from Groß Todtshorn (Freund 1997) and numerous *Picea* needles as well as plenty of conifers periderm (presumably of *Picea*) from the site Neheim-Hüsten (Teunissen et al. 1972).

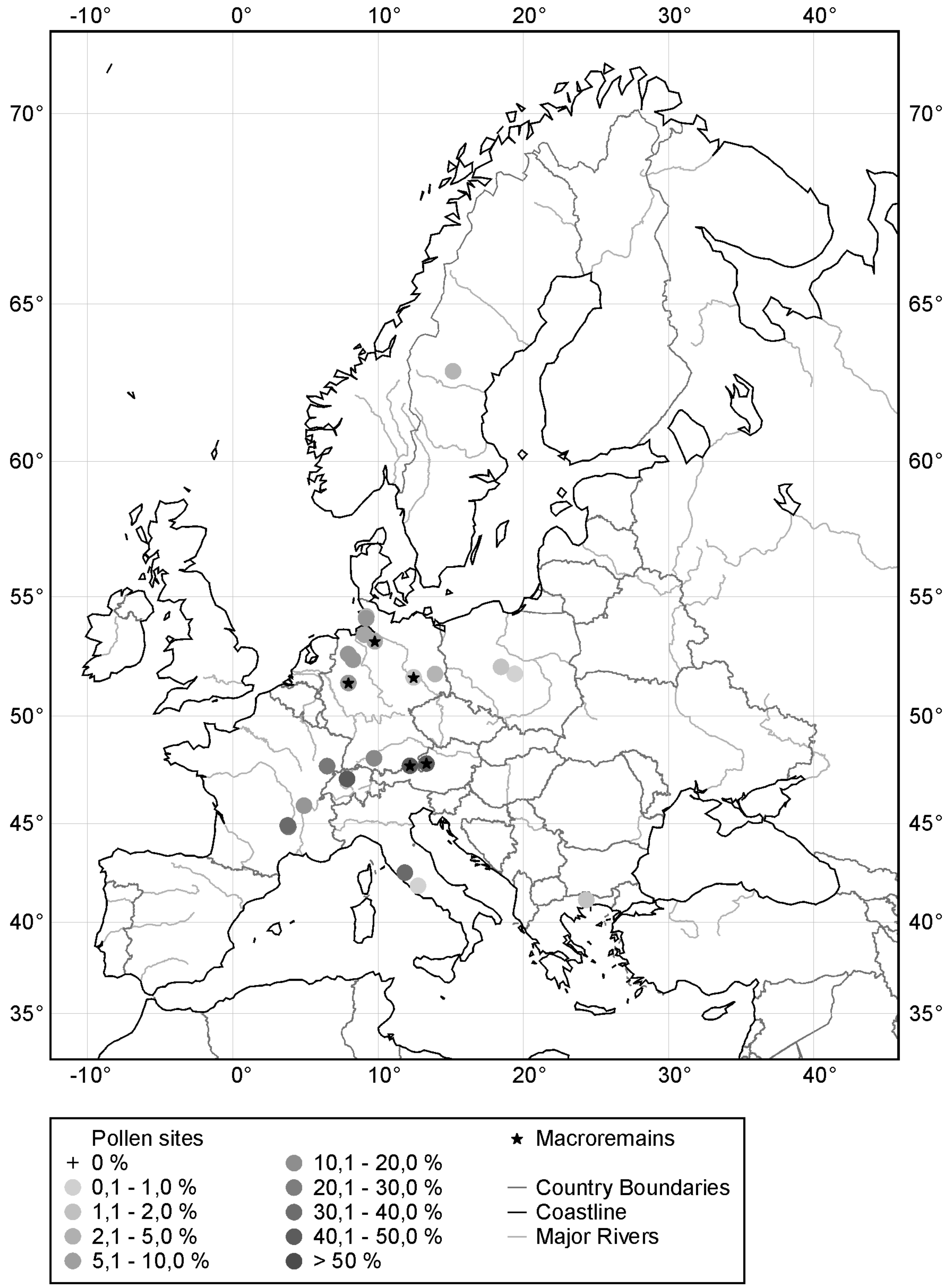


Fig. 22: Maximum pollen percentages and macrofossils of *Picea* within the Odderade.

5.2.4 Comparison of the distribution of *Picea* during the warm stages of the last glacial-interglacial cycle

The pattern of *Picea*'s maximum northern distribution limits during the Eemian, Brørup and Odderade is represented in Fig. 23. The distribution of spruce during all three warm stages followed a similar course at least at its western limit. However, clear changes emerge for its range in north-central Europe, particularly as the northermost limits are concerned.

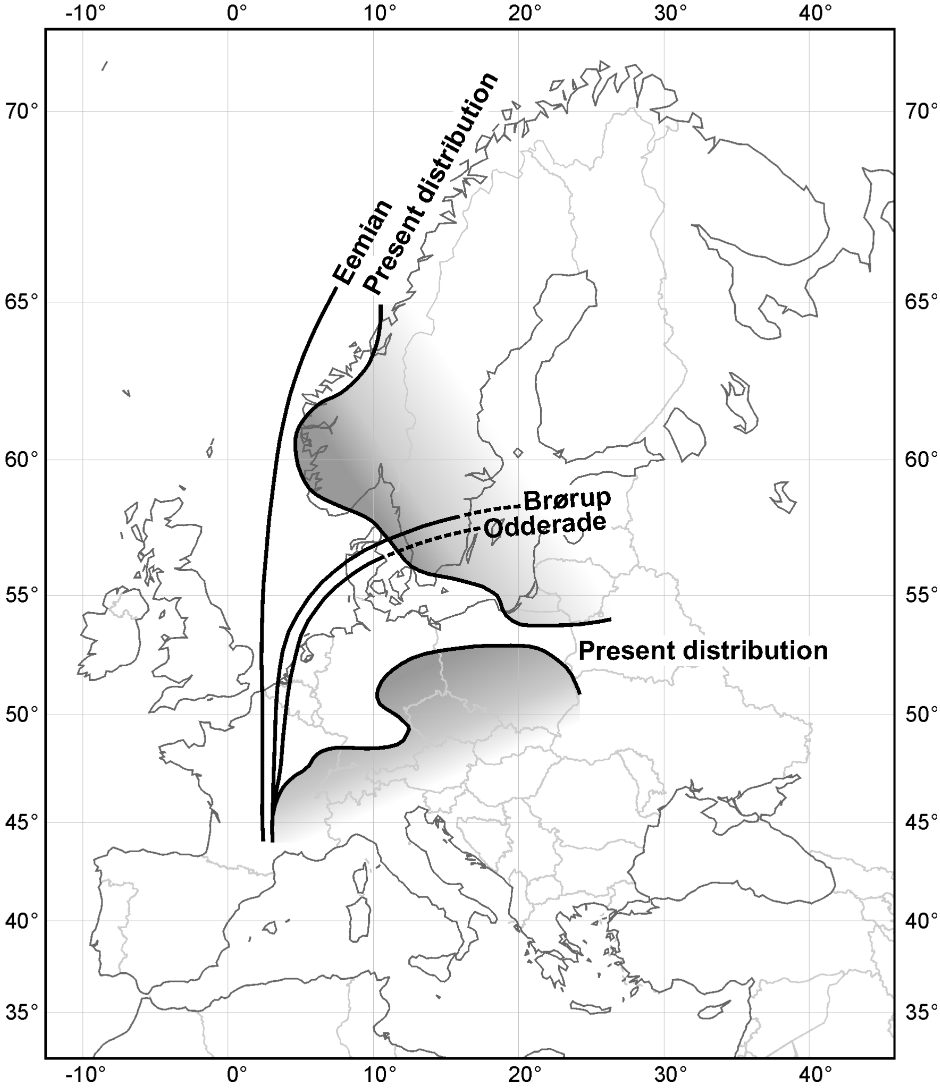


Fig. 23: Northern and western limits of *Picea* distribution during Eemian, Brørup and Odderade according to pollen and macrofossil finds of the present study.

The data suggest that the maximum range of *Picea* during the Eemian in northern Europe might have been located comparatively more to the west than during the Brørup and

Odderade. The northernmost Eemian site, Fjörsanger (Mangerud et al. 1981), still documents *Picea* pollen percentages of 44.0% above 60° latitude. By detailed investigations on the development of vegetation and climate of the Early and Pleni-Weichselian glacial period in the northern part of central Europe, Caspers and Freund (1997) concluded a definite presence of *Picea* during the Eemian in northernmost Germany by pollen values actually exceeding 60.0%, which also corresponds to the results of the present study.

During the Odderade and Brørup the maximum range of *Picea* seemingly was limited to northernmost Germany and southernmost Sweden, respectively. Little can be concluded for the distribution of *Picea* in the Scandinavian area during these warm stages. Due to a lack of data, the dataset contains just one site from Sweden. Thus the further northward course of *Picea*'s range is still uncertain.

Lang (1994) even argues for the doubtless existence of *Picea* on the British Isles during the Brørup and possibly also during the Eemian, but this hypothesis can not be affirmed by the present study. Just two sites of the British Isles are included in the dataset for the Eemian, which only show maximum values of 0.2 and 2.0% respectively, whereas no evidence is incorporated for the Brørup.

The presented data indicate the highest pollen percentages of *Picea* during the Brørup for the Alpine region, in accordance with results of Tobolski (1991), who already reported spruce maximum pollen percentages at a couple of sites in the Alps with more than 70.0%. Also, Menke and Tynni (1984) assumed that *Picea* became widely established within central Europe by the end of the Brørup.

Generally it can be concluded that due to the scarcity of palaeobotanical data in great parts of northern and eastern Europe the definite course of *Picea*'s range within the warm stages of the last glacial-interglacial cycle in these areas still remains questionable.

Even if there is a huge discrepancy in its over-all distribution, at least the western limits of the Eemian distribution of *Picea* concur with its present range. However, the recent natural distribution pattern of spruce shows a remarkable gap reaching from northern and western Germany along north-western and northern Poland to the east. According to the present data, it is highly probable that such “corridor” did not exist during the previous warm stages of the last glacial-interglacial cycle. Thus, Ravazzi (2002) suggests a longitudinally continuous distribution of spruce maintaining at least up to about 19500 B.P. Probably the gap still displays spruce genetic legacy, such that populations of different refugial areas met.

Starting from a distribution limit similar to today, both ranges during the Brørup and Odderade definitely include the greater parts of north-central Europe, even though the course of further northerly distributions is still uncertain. Compared to the Brørup it is more probable that, like nowadays, the natural range of *Picea* during the Odderade also encompassed parts of Scandinavia, whereas the northernmost part of Europe presumably was not populated by spruce.

5.2.5 The spread of *Picea* throughout Europe since the last glacial period

Pleniglacial (Figs. 24 and 25, 42000-12500 B.P.)

Figs. 2 and 3 present macrofossil and pollen evidences from different time slices of the Weichselian Pleniglacial (older than 12500 radiocarbon years B.P.). The EMD reports 26 sites of *Picea* from the Pleniglacial (between 42000-12500 B.P.), of which 13 sites actually show ages between 42000 and 20000 B.P. Compared to the macroremains, pollen evidences with absolute dating from the Pleniglacial are quite rare in Europe. The oldest pollen data with reliable radiocarbon datings available in the EPD include sites between 18000 and 15500 B.P., even though the pollen profiles at some sites go back as far as 21000 B.P.

Charcoal pieces of *Picea* from cultural layers at Willendorf II, Lower Austria (Haesarts, Damblon, Bachner and Trnka 1996), a major reference sequence for the Upper Palaeolithic, are the oldest plant remains from the Pleniglacial indicating an age of about 41700 +3700/-2500 B.P.

At the palaeolithic karst cave Divje babe I in the Idrija valley, Slovenia (Šercelj and Culiberg 1991), macrofossils of *Picea* were obtained from detrital sediments, also containing artefacts of the Moustérien type. Radiocarbon datings on charcoal fragments from these sediment layers, including several pieces of *Picea*, give an age of about 38000 B.P.

Two old Pleniglacial finds of *Picea* are recorded from Poland. Wood, identified as *Picea* or *Larix* sp., at the site Jedlicze (Pazdur et al. 1983) dates back to 36700±2100 B.P. A needle of *Picea* sp. as well as several remains of wood (*Larix* sp. vel *Picea* sp.) from Dobra in the western Carpathians (Środoń 1968) hold an age older than 32550±450 B.P. The radiocarbon measurement was made on *Pinus cembra* wood taken from a stratigraphically higher level. According to the author, the presence of *Picea excelsa* was also established by macroscopic plant remains in the lower layers at this site.

Macroscopic charcoal record, representing *Picea* sp. among others (*Pinus* sp. and *Juniperus* sp.) is obtained from the Hungarian site Solymár (Willis et al. 2000; Krolopp 1977). The radiocarbon measurement indicates an age of 32500±2170 B.P.

The conventional ^{14}C dating on *Picea* charcoal at the palaeolithic site Kostienki 14 (Damblon et al. 1996) in central Russia has given an age of 30080 +590/-500 B.P.

Fossil wood remains of *Picea abies* from an outcrop of a silty layer in Val Caltea, northern Italy (Fuchs 1970) were dated to 29350±460 B.P.

Two further sites of macrofossil finds from *Picea* are recorded from the Hungarian Plain (both see Willis et al. 2000; Krolopp 1977). Charcoal analysis of *Larix-Picea* at the archaeological site of Bodrogkeresztúr give an age of 28700±3000 B.P., at the site Mende charcoal pieces of *Picea* sp. indicate an age of 27200±1400 B.P. Several charcoal pieces from seven other sites in the Hungarian plain, the sites 6, 7, 8, 9, 10, 12 and 14 in the study of Willis et al. (2000), were also identified as *Picea* sp. The ages of these sites range between 28225±360 and 26618±532 B.P.

Jankovská et al. (2002) state measurements on *Picea* cones from fossil peat deposits at Šafárka (Slovakia, western Carpathians), which date back to 26509±480 B.P.

Charcoal analyses of material from the Hungarian site Veszprém (Willis et al. 2000; Krolopp 1977) show evidences for a Pleniglacial age. Fossil remains of wood, including pieces determined as "*Picea-Larix*" yield an age of 26350±3111 B.P.

A radiocarbon date of charcoal at the palaeolithic site of Dolní Věstonice (Czechia) (Klíma 1963), supposedly a former camp site of mammoth hunters with several fireplaces, gives an age of 25600±170 B.P. Two older ^{14}C datings from a clay pit with similar archaeological inventory near Dolní Věstonice (28100±380 and 28900±300 B.P.) as well as two charcoal measurements of the nearby palaeolithic site of Pavlov (26400±230 and 24800±150 B.P.) confirm this chronological framework. More recent investigations of Dolní Věstonice I, II and III of Damblon et al. (1996) also support the data of Klíma (1963).

Several datings on charcoal pieces from Hungary were undertaken by Willis et al. (2000): charcoal of *Picea* sp. give ages of 24030±317 B.P. at the site 17, 23571±486 B.P. at the site 19 and 23519±494 B.P. at the site Tokaj. In former studies, remains identified as "*Picea-Larix*" from the same site are believed to be 20350 years old (Geyh et al. 1969; Willis et al. 2000). Charcoal pieces mentioned as "*Larix-Picea*" at a further site in Hungary, Dunaszekesö (Willis et al. 2000; Krolopp 1977) were dated to 21740±320 B.P.

Several charcoal pieces of *Picea* sp. as well as some "coniferae indet." were found at the palaeolithic (Tardigravettian) site of Ovčja jama in Slovenia (Šercelj 1996). The radiocarbon age of all charcoal fragments (also comprising *Pinus* sp.) from the appropriate layer is 19544±500 B.P.

A collection of top quality material (mainly conifer charcoal) stems from the Moldavian site Cosautsi (Haesaerts et al. 1998). The content of *Picea* sp. in the anthracological composition of the cultural layer giving a maximum age of 19440±100 B.P. is quoted to be more than 50% of the total for the most part. Several other datings of the same layer (between 19410±100 B.P. in the lower part and 17030±180 B.P. in the upper part) support this age.

At the site Anhovo, Slovenia (Šercelj 1996) trees were deposited in fluvial glacial clays. A thin log of *Picea* (about 15 cm in diameter) has been radiocarbon dated to 18970±300 B.P.

One charcoal piece identified as "*Picea-Larix*" (together with a fragment determined as *Pinus sylvestris-Pinus cembra*) from a cultural layer of the loess site Ságvár, Hungary (Vogel and Waterbolk 1964; Willis et al. 2000) gives an age of 18900±100 B.P.

Macrofossil finds from the upper palaeolithic settlement of Madaras, north-eastern Telecska hills in Hungary (dated to 18080±405 B.P.), were assigned to "*Picea-Larix*" upon other taxa (Dobosi 1967; Willis et al. 2000).

The first Pleniglacial pollen finds are reported between 18000 and 15500 B.P. Two sites in north-west Russia (Lake Nero and Plesheevo Lake; source EPD) indicate more than 10% of *Picea* pollen. Some pollen evidence is reported from the Alpine region (2.1-5%) as well as from one site in the Massif Cenral (≤2%). Sparse *Picea* pollen are also found in the Pyrenees (0.1-1%).

Charcoal identified as "*Picea-Larix*" from a fire place in the Hungarian loess site Arka (Vogel and Waterbolk 1964; Willis et al. 2000) indicate an age of 17050±350 B.P. According to Vogel and Waterbolk (1964) the true age of this cultural layer might be higher, because practically all organic matter in the measured sample were dissolved in alkali.

Needles and seeds of *Picea abies* were collected from layers of fluviatile deposits at Smerek III in the Polish eastern Carpathians dating back to 16925±325 B.P. (Ralska-Jasiewiczowa 1980).

Pieces of charcoal, including three fragments of *Picea* (16830±150 B.P., after Šercelj 1996) were found during excavations at the cave of Županov spodmol, Slovenia (Osole 1976), which is interpreted as a hunting station of Tardigravettian/Mousterian times.

The age of "*Picea-Larix*" charcoal at Tápiósüly in the Carpathian basin of Hungary has been fixed as 16730±400 B.P. by radiocarbon analysis (Pécsi 1975; Willis et al. 2000).

No macrofossil finds are reported between 15500 and 14500 B.P. Percentages at most of the prior mentioned pollen sites drop in this appropriate period. There is just one site in north-west Russia (Lake Nero; source EPD) left, which shows 2.1-5% of *Picea* pollen. All other sites indicate no more than 2%.

There is no macrofossil evidence till the end of the Pleniglacial. Pleniglacial pollen percentages start increasing again not prior to 14500 B.P. The EPD reports two sites with high percentages of *Picea* pollen for the time-slice 14500 to 13500 B.P. They are situated in north-west Russia (one indicating more than 10% and one between 2.1-5%; Lake Nero and

Plesheevo Lake; source EPD). There is also a new record from central Italy exhibiting 1.1-2% *Picea* pollen.

In the next time-slice (13500-12500 B.P.) the pollen percentages of the Austrian site drop to 2.1-5%, though another site (5.1-10%) accrues close to it. Both Russian sites currently show high percentages (>10%). A further similarly high percentage site appears in northern Slovakia (source EPD). The percentages of *Picea* pollen from a site in the Massif Central arise again to 1.1-2%. Aside from these sites there are many new pollen sites mostly indicating no evidence of *Picea* or just very low percentages (0.1-1%).

Lateglacial and early Holocene (Fig. 26, 12500-9500 B.P.)

Two sites containing macrofossils of *Picea* are reported from north-west Romania by Björkman et al. (2002). A needle from the site Steregoiu has an age of 12365±115 B.P.. Younger datings of needles at the same site include ages of 9530±85 B.P., 9130±95 B.P. and 8300±85 B.P. Further finds of needles as well as one cone of *Picea* are mentioned from the site Preluca Tiganului with ages of 12230±105 B.P., 12065±115 B.P. and 11515±115 B.P.

Solely evidences of charcoal, identified as "*Larix-Picea*" were proved in a clay pit at Zalaegerszeg, Hungary (Geyh et al. 1969). Non-contaminated pieces could be dated to 12125±360 B.P. via a radiocarbon measurement.

Several seeds of *Picea* were obtained from a profile at Tarnowiec E in Poland (Harmata 1987). The profile is based on 12 radiocarbon datings of which the oldest reaches back to 11190±140 B.P. The macroremains of *Picea* appear earlier in the profile, they are presumably about 12000 years old.

Investigations in the Palughetto basin (Cansiglio Plateau, Italy) included ^{14}C datings on cones of *Picea abies* (Avigliano et al. 2000). A single cone from the composite section of 1995 and 1997 gives an age of 12000±340 B.P. This age is confirmed by a measurement on three cones in the 1994 section (11603±84 B.P.).

The density of investigated pollen sites remarkably increases between 12500 and 11500 B.P. Clear evidences (percentages >10%) are still indicated by two sites in north-west Russia and one in Austria. Additionally several records showing 5.1-10% as well as 2.1-5% of *Picea* pollen occur in Hungary, Slovakia, Czech Republic, Ukraina, Byelorussia, Lithuania, Latvia and south-east France.

Several remains of *Picea sp.* (bud scales and needels) with an age of about 11000 B.P. were found at the site Planclacke in Austria (Oeggl and Wahlmüller 1994). The age refers to a ^{14}C dating (11420±90 B.P.), which was received from sediments just below the finds.

Wood of *Picea abies* from Åreskutan 1 (central Sweden) gives an age of 11020±90 B.P. (Kullman 2001). Kullman also reports another wood find from the same site, which is slightly younger (10250±90 B.P.).

A needle of *Picea excelsa* occurred in the profile of Kępa, Poland (Gerlach et al. 1972). According to Środoń (1990) this find nearly dates back to about 11000 B.P.

The number of pollen sites slowly rises between 11500 and 10500 B.P. in which the observed percentages mostly do not exceed 10%. Just three sites in north-west Russia as well as on in northern Slovakia (source EPD) represent more than 10% *Picea* pollen.

Needles and other vegetative remains of *Picea abies* found at the Russian site Pichozero show ages between 10800 and 10000 B.P. (Wohlfarth et al. 2004).

Obidowicz (1990) describes some macrofossil finds of *Picea abies* from three other Polish sites (Puścizna Rękowiańska, Przymiarki and Bór na Czerwonem), which are supposed to be around 10000 years old. The closest ^{14}C dating is quoted as 8960±80 B.P. At another Polish site, Besko (Koperowa 1970), two seeds of *Picea excelsa* also show an age of approximately 10000 years (after Środoń 1990). Investigations at the site Roztoki A in Poland record seeds of *Picea* slightly older than 9920±95 B.P. (Harmata 1987). The corresponding radiocarbon age derives from a measurement of the peaty sediments nearby the finds.

Wood remains (10 vol. %) of *Picea abies* from the Czech mire Kameničky give an age of about 9500 B.P. The pieces were found closely above a layer, which yields an uncorrected ^{14}C date of 9985±220 B.P. (Rybníčková and Rybníček 1988). Several macroscopic evidences of *Picea* were also found in another Czech mire at Řásná (Rybníčková 1974). One seed of spruce could be identified in the coring close to a ^{14}C dating of 9610±150 B.P. Remains of wood and needles at the same site date back to about 7500 B.P.

Numerous finds of *Picea* cones at the site Sivárňa in Slovakia are dated to 9500±90 B.P. (Jankovská 1994).

Similarly is the age of *Picea* needles from the Austrian site Fuschlsee (Voigt 1996), that are at most 9500 years old. Several more needles prove the continuous presence of spruce at this site to date.

Between 10500 and 9500 B.P. the number of investigated pollen sites clearly increases just as the amount of pollen finds noticeable rises. Many sites show high percentages of *Picea* pollen (>10%). Most of them are located along a “stream” running from Austria and Hungary to the north-east up to the Onega lake region (Russia). Less high values (1.1-2% and 2.1-5%) are reported from south-east France, Switzerland and north-west Italy.

Middle and late Holocene (Figs. 27-29, 9500-500 B.P.)

Between 9500 and 8500 B.P. the number of macrofossil records remains all about the same compared to the previous time-slice. Two new sites are reported from Switzerland as well as one from northern Estonia.

Compared to that, pollen percentages of *Picea* significantly increase between 9500 and 8500 B.P., whereas the density of sites increases less strongly. There is a accumulation of high pollen percentage sites (more than 10%) in an area encompassing Austria, Hungary, the Czech Republic, Slovakia and southern Poland, which is in accordance with the location of macrofossil finds. A further site showing more than 10% *Picea* pollen is described from Lithuania.

The amount of macrofossil sites increases from 8500 B.P. onwards. Between 8500 and 7500 B.P. new sites accumulate particularly in north-central Sweden, Switzerland and the Czech Republic. There is also a new site from Romania.

The density of pollen sites slightly advances between 8500 and 7500 B.P. showing mostly high pollen percentages of *Picea* in the previously mentioned accumulation areas as well as the Baltic countries and north-west Russia. Pollen percentages up to 5% are also reported from one site at the southern Kola Peninsula (Russia).

There is also an increasing number of macrofossil records between 7500 and 6500 B.P. They still accumulate in the areas, which emerged in the previous time-slice.

Compared to the previous time-slice there is no big difference in the density of pollen sites and the given percentages of *Picea* pollen in this period, except there are two new high percentage sites (>10%) in southern Kareliya (Russia). Additionally some sites in eastern and western Bulgaria report sligthly increasing pollen values (1.1-5%).

Between 6500 and 5500 B.P. the amount of macrofossils nearly remains unaffected. The Swedish sites concentrate in the centre of the country. Several new sites occur in Switzerland as well as in the far north of Italy.

The evidence of high *Picea* pollen percentages persist between 6500 and 5500 B.P. Especially several baltic sites show increasing values. For the first time there are two high percentage sites (>10%) located in northern Kareliya (Russia) as well as one in central Poland. Pollen percentages of more than 10% are also shown by sites north and north-east of the Ladoga Lake (Russia) as well as in Hungary.

In comparison to the last time-slice a drop in the number of macrofossil sites in central Europe can be registered between 5500 and 4500 B.P. There are noticeable less sites in Switzerland, the Czech Republic and southern Poland, however, one new site from Austria was added. In contrast, the amount of northern European sites rises. Several new sites are reported from central Sweden as well as one from eastern Kola Peninsula (Russia).

At most sites pollen percentages of *Picea* increase in this particular period. Especially in Switzerland and south-east France values rise remarkably (at some sites to more than 10%). Definite increasing could also be found in some Kareliyan, eastern Russian, southern Finish, Romanian and Bulgarian sites.

Between 4500 and 3500 B.P. just two macrofossil sites from the Czech Republic and respectively southern Poland are left. Also the amount of Swedish records clearly decreases. However, one new site could be added for southern Finland.

Picea pollen percentages further on increase in this time-slice, especially in southern Kareliya (5.1->10%) and northern Finland (2.1-10%). At the same time there are clearly rising percentages in Estonia and western Russia. Individual sites in northern Poland and in north-west Italy also show more than 10% of *Picea* pollen.

There is no marked change in the amount of macrofossil sites between 3500 and 2500 B.P. Accumulations of sites are still found in central Sweden and Switzerland. Polish sites are no longer available in the dataset, but there are still two records from the Czech Republic and three new sites from Bulgaria.

Also the pollen percentages between 3500 and 2500 B.P. do not change notably. The values of the Bulgarian and Romanian sites slightly rise compared to the previous time-slice. In addition two new sites appear, one in eastern France and one in eastern Germany, each with more than 10% *Picea* pollen.

There are no more macrofossil records from central Sweden between 2500 and 1500 B.P. Just one northern Swedish site is reported for this period. There is still one site from the southern Kola Peninsula (Russia), three Bulgarian sites and an accumulation of finds in Switzerland. Additionally a new site occures at the coast of Croatia.

Between 2500 and 1500 B.P. the pollen record stays quite identical to the 3500-2500 B.P. time-slice. Just a few sites in Sweden currently report new noticeable high percentages of *Picea* pollen (two sites with more than 10% and two sites 5.1-10%).

There is a greater diversity in the location of macrofossil sites in central Europe between 1500 and 500 B.P. Macrofossil finds are reported from Switzerland, Austria, Germany and the Czech Republic. Two sites still occur in Bulgaria. The number of northern European sites re-increased by means of some records in central Sweden. Furthermore there is one new site from central Finland.

In the last time-slice, 1500 to 500 B.P., the pollen percentages of *Picea* are quite similar to the previous time-slice. New appreciable evidences are noted for southern Sweden (5.1-10%), Luxembourg (>10%) and central France (2.1-5%).

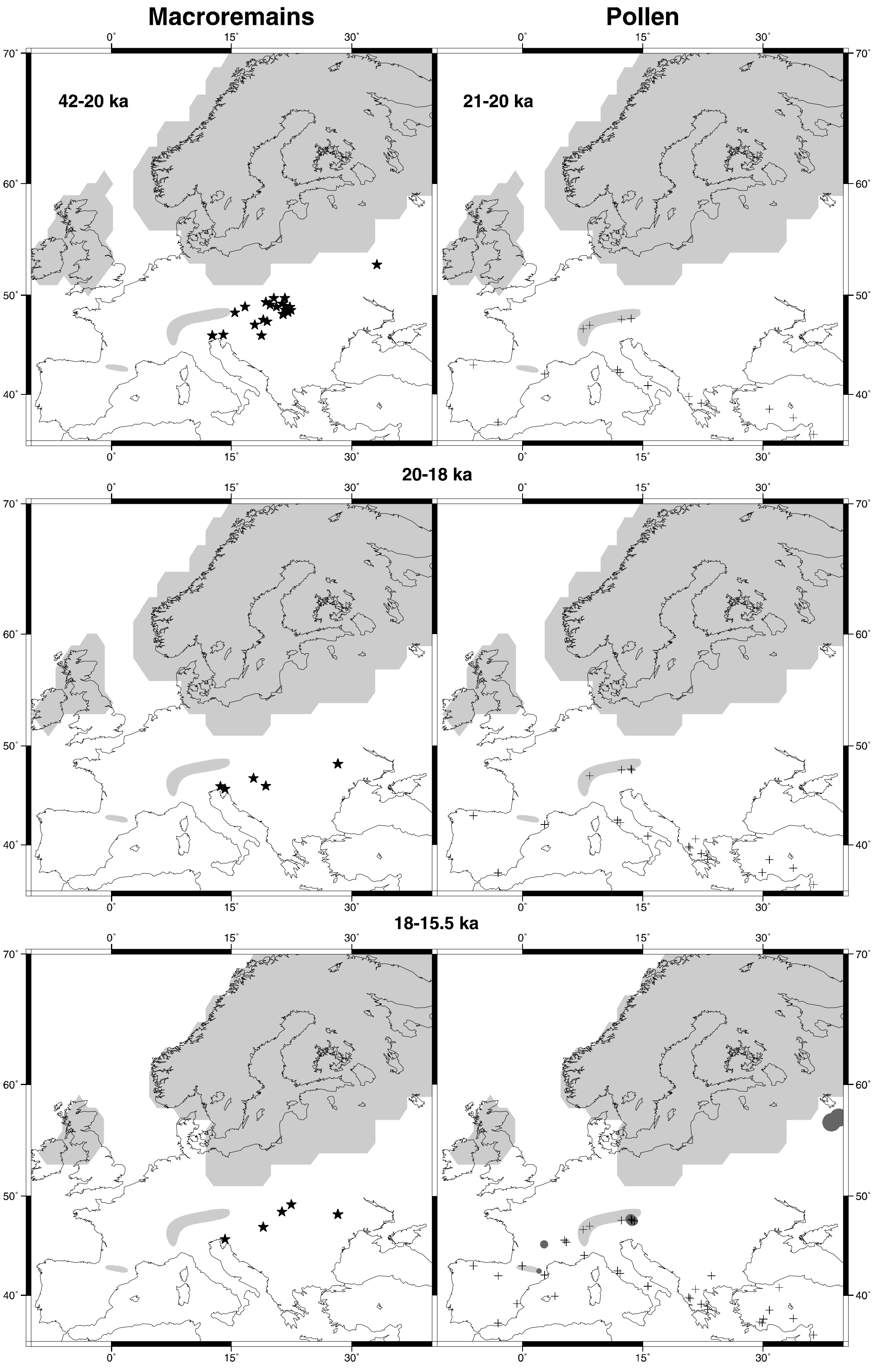


Fig. 24: Evidence of pollen and macrofossils of *Picea* during the Pleniglacial (42000/21000-15500 B.P.). (Legend: see Fig. 13).

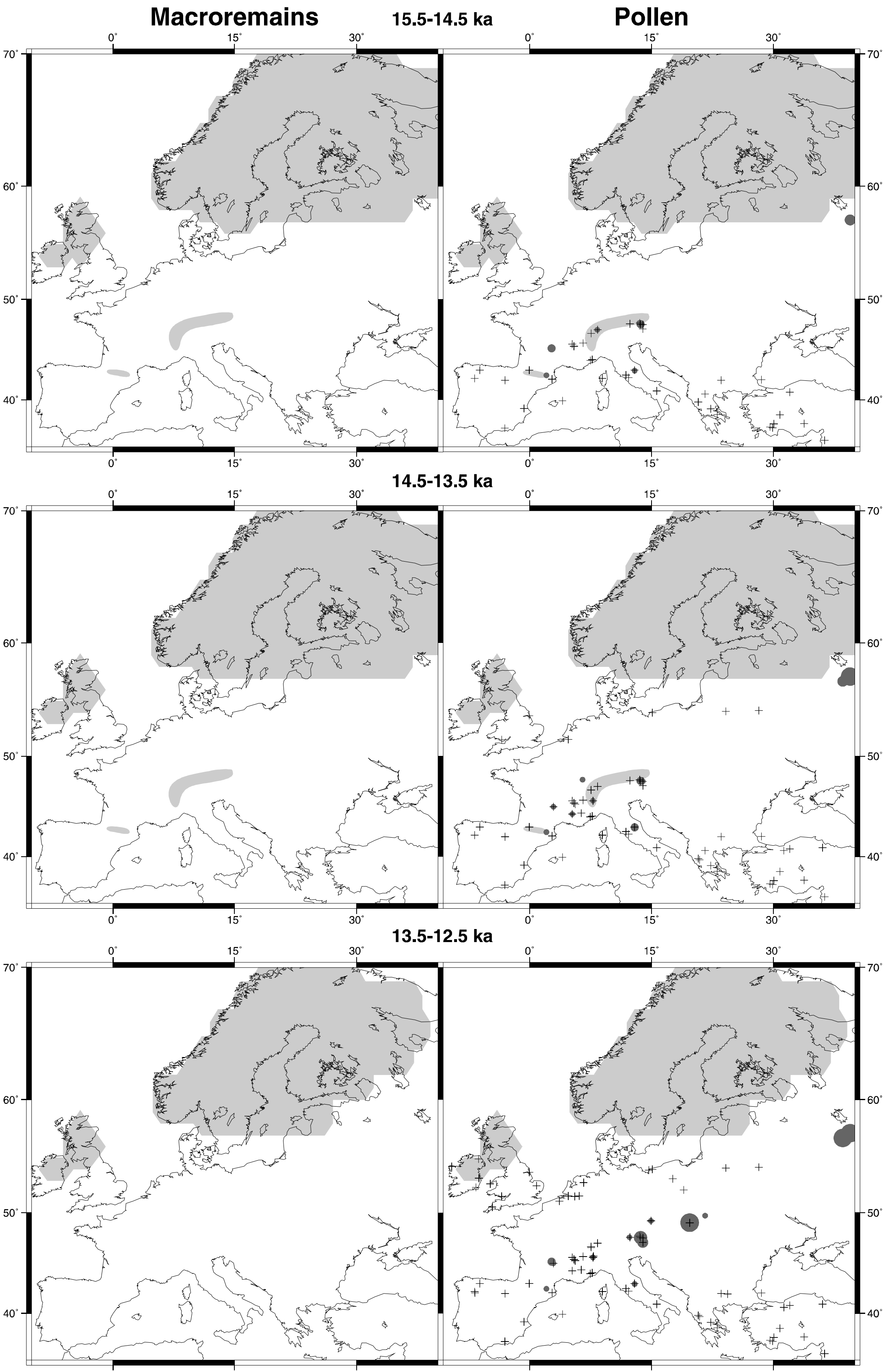


Fig. 25: Evidence of pollen and macrofossils of *Picea* at the end of the Pleniglacial (15500-12500 B.P.).

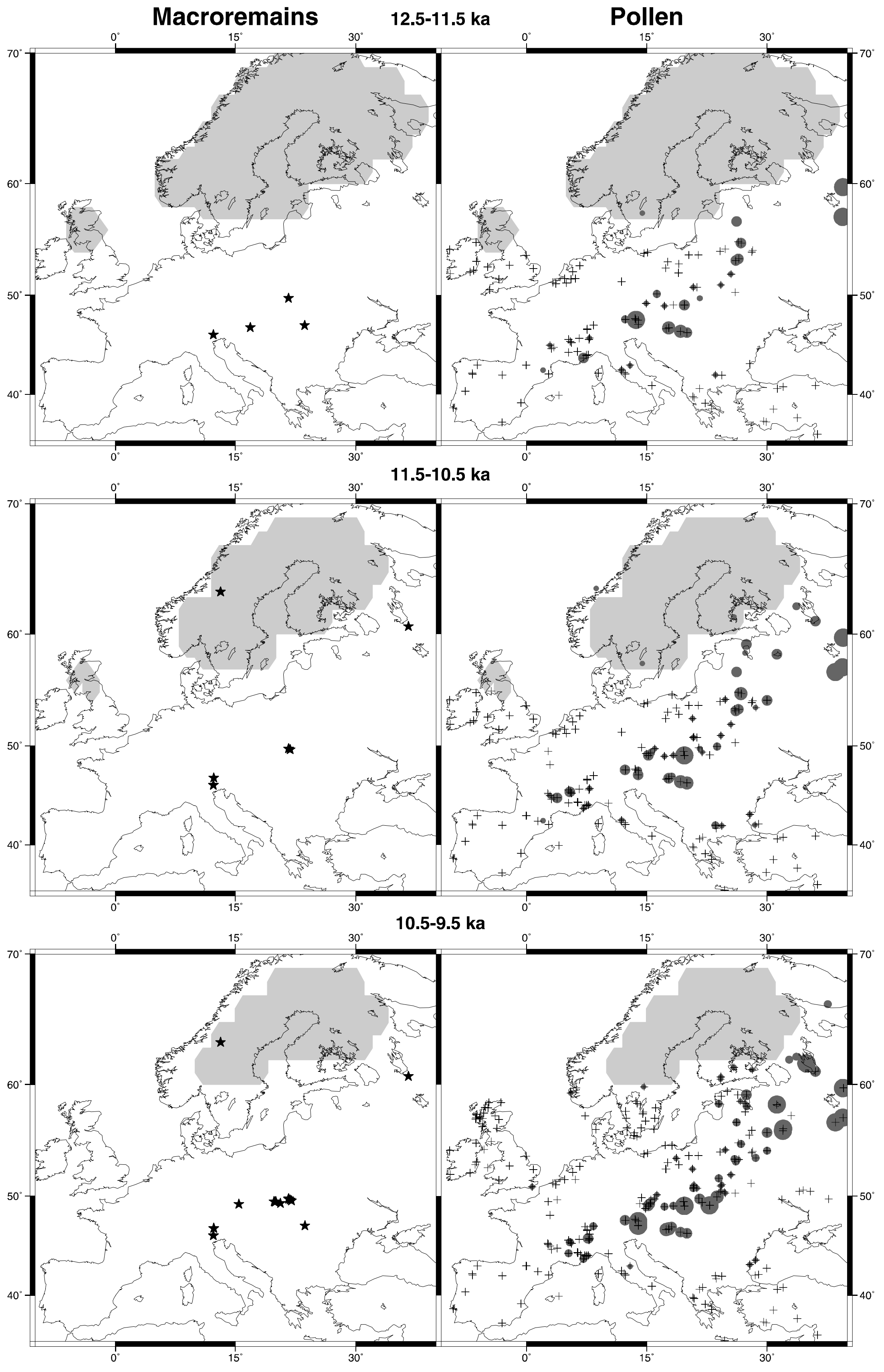
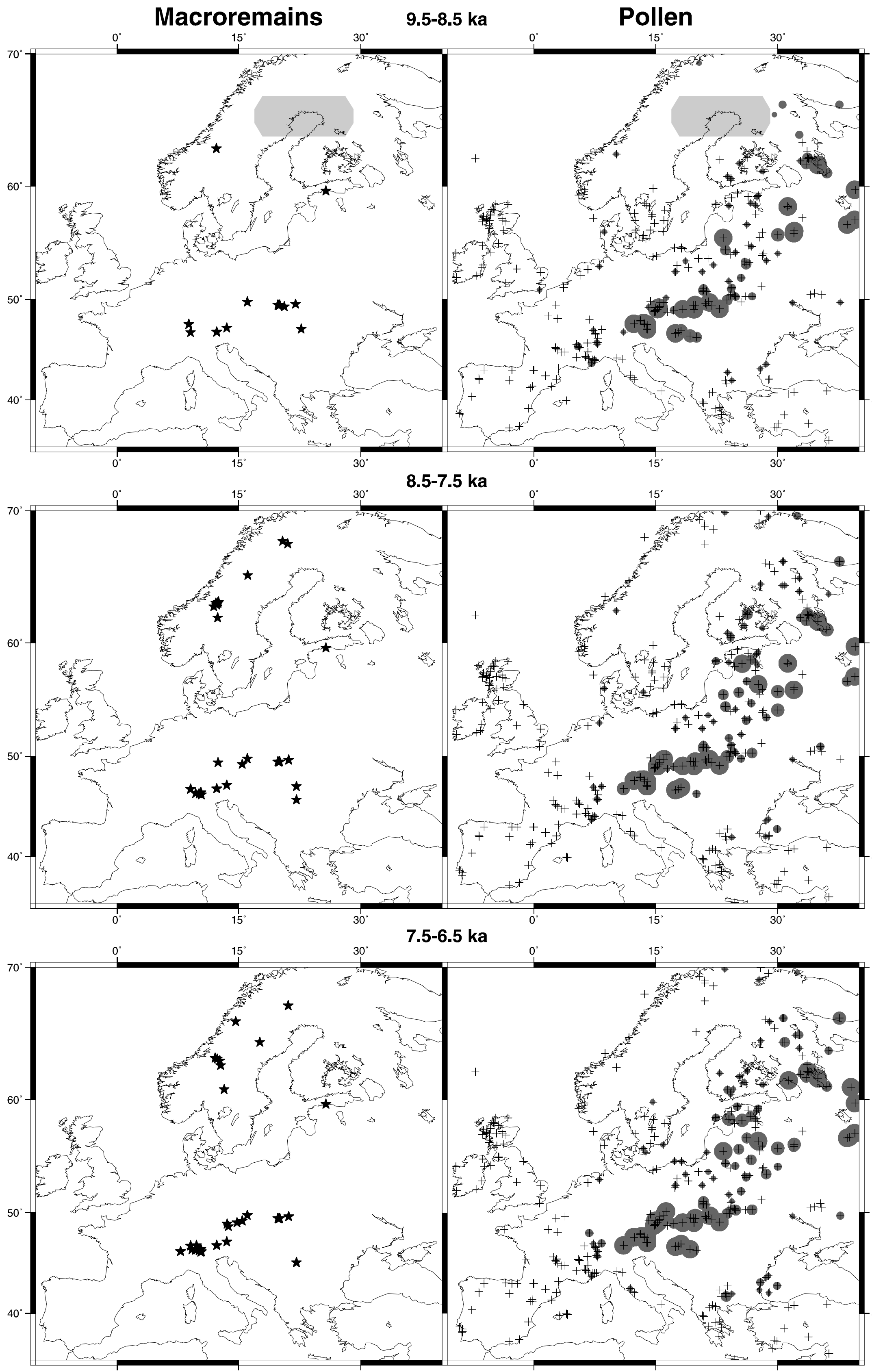


Fig. 26: Evidence of pollen and macrofossils of *Picea* during the Lateglacial and early Holocene (12500-9500 B.P.).



Macroremains

9.5-8.5 ka

Pollen

8.5-7.5 ka

7.5-6.5 ka

Fig. 27: Evidence of pollen and macrofossils of *Picea* during the early and middle Holocene (9500-6500 B.P.).

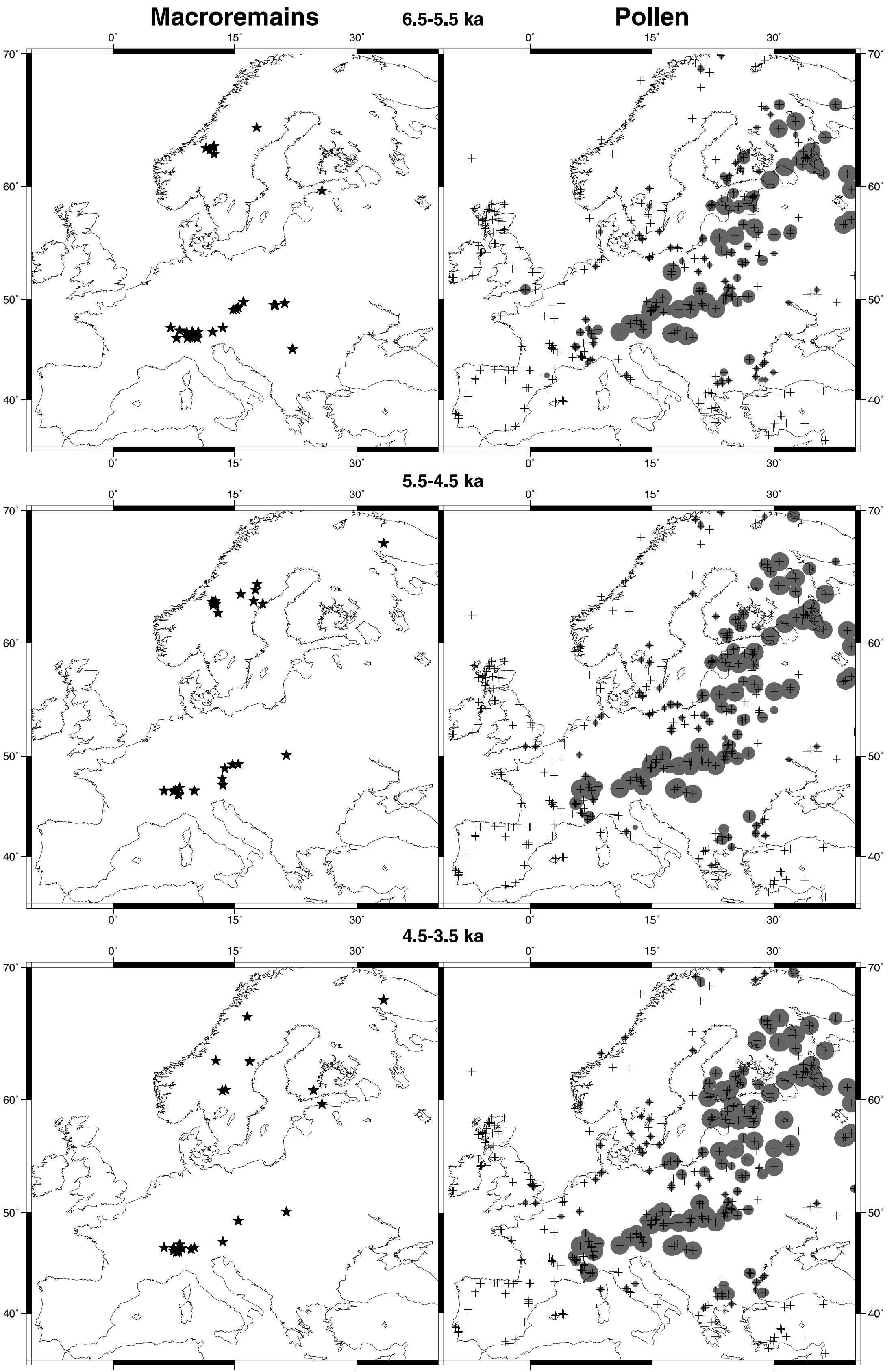


Fig. 28: Evidence of pollen and macrofossils of *Picea* during the middle Holocene (6500-3500 B.P.).

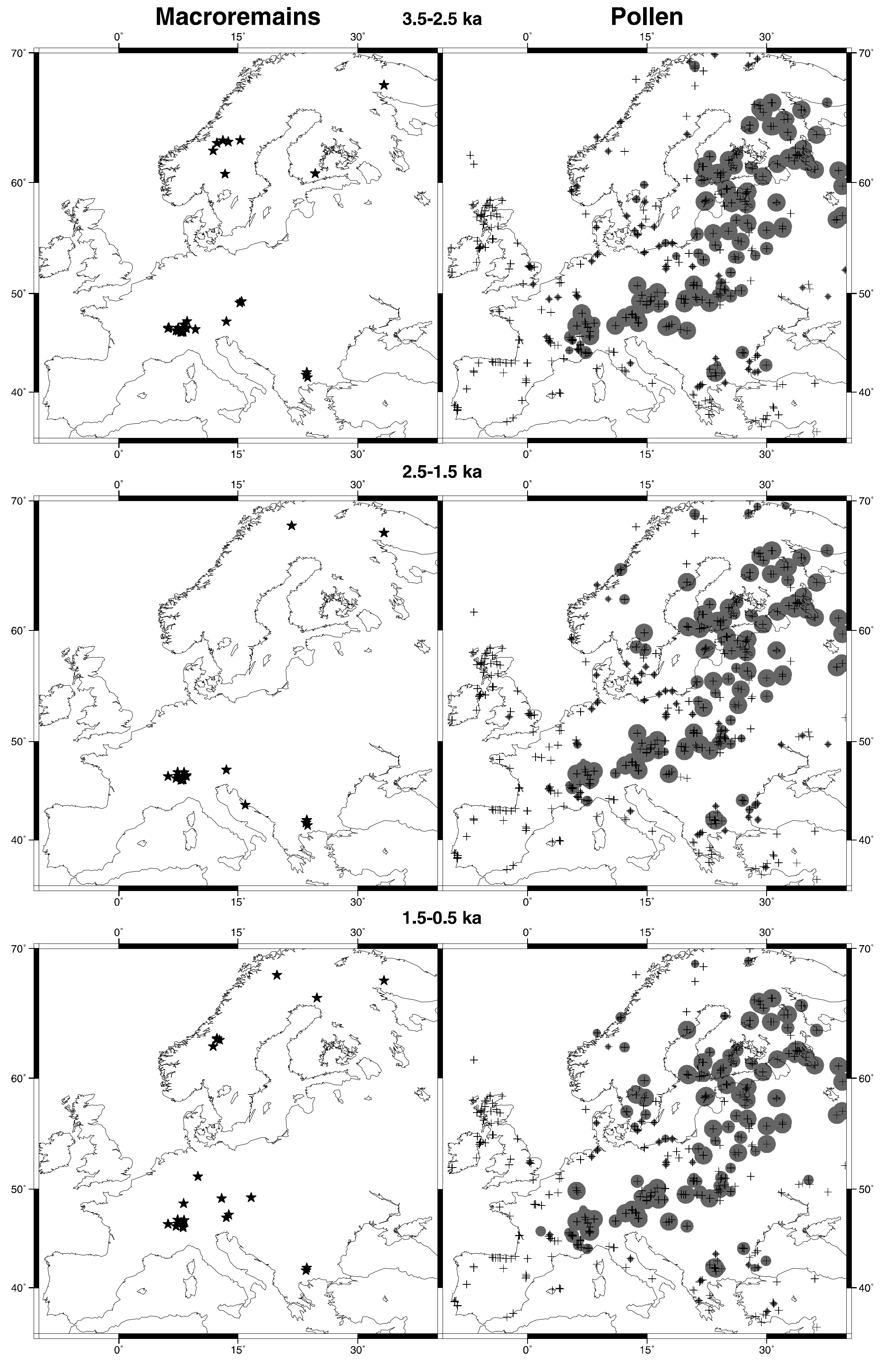


Fig. 29: Evidence of pollen and macrofossils of *Picea* during the late Holocene (3500-500 B.P.).

5.3 Genetic data

Results of recent investigations on mitochondrial gene material of *Picea abies* show pronounced population differentiation and a distinct geographical distribution pattern (Sperisen et al. 2001; Gugerli et al. 2001). A total of 18 mitochondrial DNA (mtDNA) variants was detected in a total of 940 trees, representing 90 populations of Norway spruce. A maximum parsimony analysis resulted in a tree with two main clades referred to as lineages A and B. According to Sperisen et al. (2001) these two lineages distinctively separate Norway spruce populations of north-eastern Europe (lineage A) from central and south-eastern Europe (lineage B) (see Fig. 30). The authors presume that these two spatially separated regions may be associated with putative glacial refugia in the Moscow area and the Carpathians or the Balkan Peninsula, respectively. Further it is hypothesised that specific size variants of the different lineages could be indicative of postglacial re-colonisation pathways. Two major gene pools (Alpine-Center European and Sarmathic-Baltic) of Norway spruce were also identified by previous genetic investigations based on chloroplast markers of Vendramin et al. (2000).

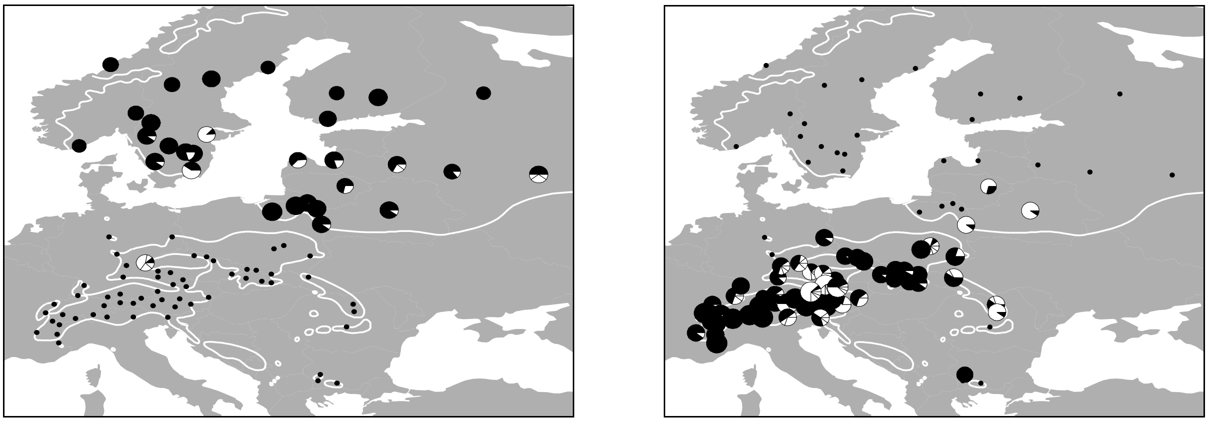


Fig. 30: Geographical distribution of selected most abundant mitochondrial size variants of lineages A (left) and B (rigth) of *Picea abies* within its natural range (after Sperisen et al. 2001).

Lagercrantz and Ryman (1990) revealed a clear geographical pattern of genetic variation throughout Europe, probably reflecting recent historical events related to the last glaciation, by intensive investigation on morphological and allozymic variations of *Picea abies*. They further claim for a considerable reduction of genetic variation in central European populations due to drastic restriction of population size (bottleneck effect) during this glacial period.

5.4 Discussion

The following questions should be discussed with main emphasis on palaeobotanical data:

(1) In which areas within Europe do we have strong evidence for glacial refugia of *Picea* on basis of the present palaeobotanical datasets?
(2) Did the distribution of *Picea* during the previous warm stages of the last glacial-interglacial cycle have any influence on its subsequent vegetational history?
(3) Where did the onset of migration start?
(4) Along which pathways did *Picea* spread through Europe in the Holocene?

5.4.1 Location of glacial refugia during the Weichselian

According to the palaeobotanical data seven regions may be identified as potential refugial areas for *Picea* (see Tab. 3). All records supporting these regions base on reliable ^{14}C datings. The Pleni- and Lateglacial macrofossil inventory includes some finds of wood, mostly charcoal pieces, which could not clearly be assigned to the species *Picea*, because wood anatomically often a clear-cut differentiation between *Picea* and *Larix* is not possible (see Schweingruber 1990). However, these records will although be mentioned in this context, because they may provide information on potentially additional remains of *Picea*. Compared to the macroremains pollen evidences with absolute dating from the Pleniglacial are quite rare in Europe. The oldest pollen data with reliable radiocarbon datings available in the EPD include sites between 18000 and 15500 B.P., even though the pollen profiles at some sites go back as far as 21000 B.P. Refugial areas of spruce proved by palaeobotany are:

1) East Alpine foreland,
2) South-east Alpine foreland,
3) North-west Carpathians,
4) Hungarian basin/Danubian plain,
5) Moldavian lowland,
6) Russian plain.

Two macrofossil sites as well as two pollen sites claim for the existence of a refugial area in the east Alpine foreland. First evidences are macroscopic remains of Pleniglacial age. They consist of charcoal, which was specified as *Picea*. The reliability of one of these sites, Dolní Věstonice, is also proved by several new radiocarbon datings showing ages between 32850±660 and 19640±540 B.P., which were obtained from more recent investigations on charcoal remains exclusively of conifers (including both *Picea* and *Pinus*) (Damblon et al. 1996). Furthermore two sites from the early Lateglacial in the east Alpine foreland report non-negligible amounts of *Picea* pollen (1.1-2.0% and 2.1-5.0%).

Several sites, mainly situated in Slovenia, argue for a refugial area in the south-east Alpine foreland. Clear first evidences are shown by Pleniglacial remains of *Picea* wood. Three sites reporting charcoal pieces (identified as *Picea* sp.) encompassing the time span from Pleni- to Lateglacial as well as a thin log of *Picea* from the Lateglacial support the potential of this region.

Another refugial area might have been seated within the north-west Carpathians. Explicit evidences for the presence of spruce are Pleniglacial finds of a needle (*Picea* sp.) from Poland (Środoń 1968) and cones from Slovakia (Jankovská et al. 2002). The same age is shown by finds of wood in this particular area even if they could just be identified as "*Picea* or *Larix* sp." and "*Larix* sp. vel. *Picea* sp." however. Seeds and needles of *Picea abies* from Poland are also mentioned for the Lateglacial. All listed sites in this region are situated in a collin-submontaneous altitude.

There is a strong evidence for a potential refugial area in the Hungarian basin/Danubian plain documented by means of numerous sites with macrofossil inventory in Hungary (see Willis et al. 2000). All these sites contain exclusively charcoal findings, mainly of Pleniglacial age. Most remains are identified as *Picea* sp., but there are also many finds, which could just be determined as "*Picea-Larix*" or "*Larix-Picea*". There are still clear evidences for the presence of spruce around the Lateglacial Maximum (LGM) as well as in the Lateglacial.

The Moldavian lowland may have been another refugial area for *Picea*. The evidence for this area is just given by one site with finds of charcoal from different species, however, pieces identified as *Picea* sp. form about 50% of the total charcoal amount of this location. This findings confirm the presence of spruce around the LGM in this region.

Noticeable evidence indicating the Russian plain as refugial area is given by three sites, particularly by two Lateglacial pollen sites showing percentages greater than 10% of *Picea*. First evidence for spruce in this region is given by one charcoal find (identified as *Picea*) slightly remote to the just mentioned pollen sites.

Pollen finds could argue for further refugial areas, which were located in the Massif Central (source EPD). *Picea* pollen are proved by one site showing just low pollen percentages (1.1-2.0%) by the end of the Weichselian Pleniglacial, whereas *Picea* pollen are not present in this region within most of the following time-slices.

	Refugia	**Site name**	**Country**	**Age (^{14}C)**	**Material**
1.	East Alpine foreland	Willendorf II	Austria	41700 +3700/-2500	charcoal pieces (*Picea*)
		Dolní Věstonice	Czech Republic	25600±170	charcoal pieces (including *Picea excelsa*)
		site EPD		18000-15500	pollen (2.1-5.0%)
		site EPD		18000-15500	pollen (1.1-2.0%)
2.	South-east Alpine foreland	Divje babe I	Slovenia	38000	charcoal pieces (*Picea*)
		Val Caltea	northern Italy	29350±460	wood remains (*Picea abies*)
		Ovčja jama	Slovenia	19544±500	charcoal pieces (*Picea* sp./coniferae indet.)
		Anhovo	Slovenia	18970±300	thin log (*Picea*)
		Županov spodmol	Slovenia	16830±150	charcoal (3 fragments of *Picea*)
3.	North-west Carpathians	Jedlicze	Poland	36700±2100	wood (*Picea* or *Larix* sp.)
		Dobra	Poland	32550±450	1 needle (*Picea* sp.) + several pieces of wood (*Larix* sp. vel *Picea* sp.)
		Šafárka	Slovakia	26509±480	cones (*Picea*)
		Smerek III	Poland	16925±325	needles + seeds (*Picea abies*)
4.	Hungarian basin/ Danubian plain	Solymár	Hungary	32500±2170	charcoal (*Picea* sp. among others)
		Bodrogkeresztúr	Hungary	28700±3000	charcoal (*Larix-Picea*)
		site 6	Hungary	28225±360	charcoal (*Picea* sp.)
		site 7	Hungary	27700±300	charcoal (*Picea* sp.)
		site 8	Hungary	27323±644	charcoal (*Picea* sp.)
		site 9	Hungary	27491±362	charcoal (*Picea* sp.)
		site 10	Hungary	27251±288	charcoal (*Picea* sp.)
		site 12	Hungary	26851±398	charcoal (*Picea* sp.)
		site 14	Hungary	26618±532	charcoal (*Picea* sp.)
		Bodrogkeresztúr	Hungary	26318±365	charcoal (*Picea* sp.)
		Mende	Hungary	27200±1400	charcoal (*Picea* sp.)
		Veszprém	Hungary	26350±3111	charcoal (*Picea-Larix*)
		site 17	Hungary	24030±317	charcoal (*Picea-Larix*)
		site 19	Hungary	23571±486	charcoal (*Picea* sp.)
		Tokaj	Hungary	23519±494	charcoal (*Picea* sp.)
		Dunaszekesö	Hungary	21740±320	charcoal (*Larix-Picea*)
		Tokaj	Hungary	20350±470	charcoal (*Picea-Larix*)
		Ságvár	Hungary	18900±100	one charcoal piece (*Picea-Larix*)
		Madaras	Hungary	18080±405	charcoal (*Picea-Larix*)
		Arka	Hungary	17050±350	charcoal (*Picea-Larix*)
		Tápiósüly	Hungary	16730±400	charcoal (*Picea-Larix*)
5.	Moldavian lowland	Cotautsi	Moldavia	19440±100	charcoal (50% content *Picea* sp.)
6.	Russian plain	Kostienki 14	Russia	30080+590/-500	charcoal (*Picea*)
		Lake Nero	Russia	18000-15500	pollen (>10%)
		Plesheevo Lake	Russia	18000-15500	pollen (>10%)
	Potential Refugia				
	Massif Central	site EPD	France	18000-15500	pollen (1.1-2.0%)

Tab. 3: Refugial areas of *Picea* according to palaeobotanical data.
(for detailed information see appendix)

5.4.2 The onset of spread during the late Pleniglacial and Lateglacial

Just two of the potential refugial areas as they were described for the last glacial, the east Alpine foreland and the Russian plain, maintain continuously existent from the LGM, during the Pleniglacial till the late Holocene, represented by pollen (>10%) and/or macrofossils. Definitely these areas are highly responsible for the onset of *Picea* spread within Europe. Three further regions of which two are not present during the three time-slices at the end of the Pleniglacial may also have been starting areas for migration. The South-east Alpine foreland, the north-west Carpathians as well as the Hungarian basin/Danubian plain show records of *Picea* around the LGM as well as continuous presence of records from 12500 B.P. onwards. Just in the north-west Carpathians *Picea* is already reported by pollen during the end of the Pleniglacial, since 13500 B.P. Due to the fact that there are no investigations on older sediments in this area, a presence of *Picea* for the beginning and middle of the Pleniglacial could not be proved by palaeobotanical data.

Further it can be assumed that there might have been a refugium in the Central Carpathians. Unfortunately there is a lack of palaeobotanical data in this area especially for the end of the Pleniglacial. Several sites documenting pollen- as well as macrofossil evidences are not known until 12500 B.P. The presence of *Picea* can not be proved previously at these sites, since the appropriate profiles do not include older sediments.

The role of the Massif Central is not easy to assess, because just single pollen finds of *Picea* are reported, however, they appear constantly up to 12500 B.P. According to long pollen profiles (e.g. Les Echets (Beaulieu and Reille 1984) and Ribains (Beaulieu and Reille 1992b) can be reckoned that spruce was present earlier in this area. It is not unlikely that populations persisted during the Pleni- and Lateglacial times, but disappeared during the following early Holocene possibly due to competitioning with other, particularly thermophilic, tree species. Probably the Massif Central did not have any influence on the migration history of *Picea*.

It is not possible to specify the role of the Moldavian lowland in respect of the spreading history of spruce, because data from this particular area is sparcely available.

Just isolated and low pollen finds occur in the western Alps. It is highly probable that these finds are caused by redepositioning processes and do not support this area to have influenced the postglacial spread of *Picea*.

5.4.3 Potential migration routes during the Lateglacial and Holocene

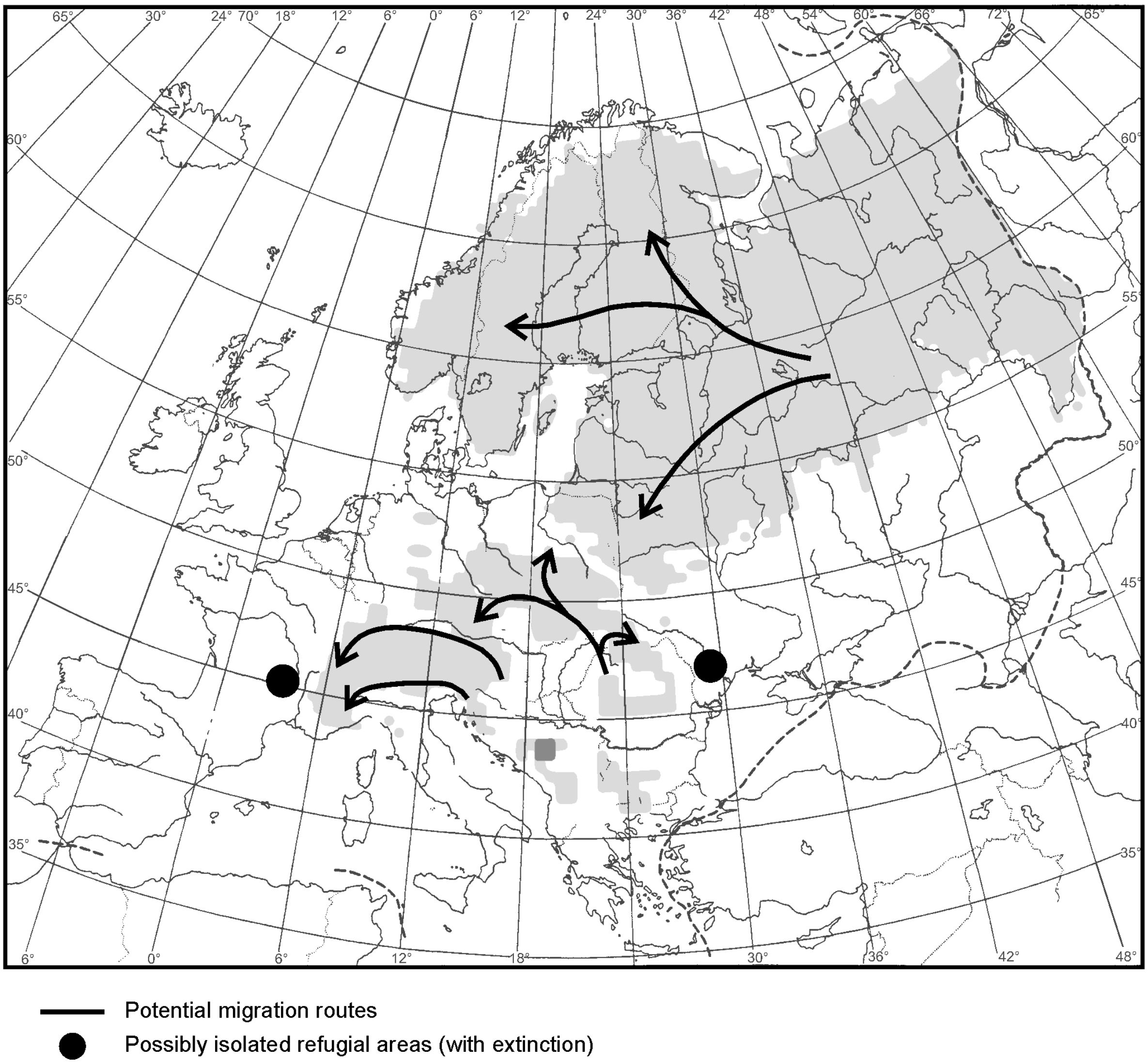


Fig. 31: Potential migration routes of *Picea* during the Lateglacial and Holocene.

After the initial onset of migration since 14500 B.P. *Picea* spread across Europe. Pollen- and macrofossil evidences show that the main emphasis of spread until 5500 B.P. concentrated on the eastern Alps, the northern Carpathians and the northern Balkan area. Since that time the distribution in these regions nearly remained unaffected until the present day. This is also in accordance with results of previous studies (Lang 1994). According to Ravazzi and Pini (2002) the late-glacial and early-middle Holocene expansion of *Picea* in the eastern and central Alps followed a general trend from east to west, along the main structural units of the Alpine chain, starting from the south-eastern Alps at the beginning of the Lateglacial

(Fig. 31). This major re-immigration of *Picea* from eastern Europe to France is commonly accepted from both pollen data analyses (e.g. Huntley and Birks 1983) and studies of morphological and allozymic variations (Lagercrantz and Ryman 1990). Several genetic investigations contributed to the re-invasional history of the Alpine area. Results from mtDNA analyses of Sperisen et al. (2001) support the hypothesis that some Alpine populations originated from the western parts of the Carpathian mountains. The same study revealed possible immigration pathways from central Europe into the south-eastern Alps, but also from the Balkan peninsula. In similar mtDNA studies, Gugerli et al. (2001) also favour a postglacial spread into the greater parts of the Alps mainly from central Europe, with an additional immigration route coming from southern European refugia. According to Collignon and Favre (2000) such a potential Balkan refugia of *Picea* could have been within the Dinaric mountains. Due to a great lack of palaeobotanical data within the central Balkans in this present study, it is not possible to evaluate the potential refugial character of this region. At least, an isolated refugium of *Picea omorika* can be assumed in the Drina Basin according to its present range.

Further genetic investigations (Vendramin et al. 2000) may on the one hand support the existence of refugia located in the central plains of the Italian peninsula as another potential area for the re-colonisation of the south-eastern Alps. This possibility was previously postulated by several authors, however, Scotti et al. (2000) dispute a potential refugium of spruce in Apennines of northern Italy due to their identification of a putative relict population in the Maritime Alps. The macrofossil data of the present study documents the presence of at least Pleniglacial *Picea* stands in south-east Alpine foreland. This would argue rather for the second speculation of Vendramin et al. (2000), that their genetic results could display a final step of a migration route starting from the Dinaric Alps and moving westward along the southern edge of the Alpine chain (see Fig. 31), an immigration course, which was already roposed by Kral (1977).

Between 12500 and 8500 just a few pollen sites report quite low percentages of *Picea* for the western Alps (eastern France). These sites clearly drop between 8500 and 5500 B.P. with an increasing amount of close-by sites containing no spruce pollen finds at all. Also macrofossil remains of *Picea* were not found further west than the central Alps earlier than 5500 B.P. As recently as 5500 B.P. the western Alps (including the Côte d'Azur) were re-colonised by easterly spruce stands. Investigations on RAPD (randomly-amplified-polymorphic DNA) markers undertaken by Collignon and Favre (2000) greatly contributed to the Postglacial history of *Picea abies* at the western margin of the Alps. In doing so they postulate the main re-immigration paths processed from the Jura mountains to the French Alps and Vosges on the basis of molecular relationships. Further a possible migratory path straight from central Switzerland and/or Black Forest to the Vosges is strongly suggested.

Traces of spruce pollen are displayed for the Massif Central in time-slice 12500 to 11500 B.P. One site also reports a quite high value in this region between 11500 and 10500 B.P. In contrast, not a single find of *Picea* is proved for this area between 10500 and 3500 B.P. As recently as 3500 B.P. very low percentages are mentioned, which persist up to the following time-slices. The pollen percentages of one site from the Massif Central actually increase between 1500 and 500 B.P, however, these finds are questionable, because this region does not belong to the present-day's natural distribution area of *Picea*.

It is generally assumed that a re-invasion of Europe, apart from refugia in the Dinaric Alps of the Balkan peninsula, occurred from glacial refuge zones located in the Moscow area and in the mountainous Carpathians in the east of Europe (Collignon and Favre 2000). In the present distribution maps a continuous presence of *Picea* pollen between 12500 and 500 B.P. is noted for the north-west Carpathians. Already for the Lateglacial, a clear presence of *Picea* is documented by quite high pollen percentages, which increase to more than 10% in the following time-slices. High values for this area persist up to 500 B.P., just slightly dropping between 2500 and 500 B.P.

The distribution of spruce in northern Europe mainly took place from 6500 B.P. onwards. Apparently, starting in the east, probably within central Russia and Moscow area respectively, colonisation of this area mainly followed a western and north-western direction (Fig. 31) with migration rates considerably higher than for the expansion in central Europe. Huntley and Birks (1983) estimate the velocity of expansion at rates of 80-240 m yr^{-1} in the southern areas of Europe, whereas migration into Fennoscandia occurred more rapidly, at rates up to 500 m yr^{-1}. Conspicuously there are numerous macrofossil finds from Norway and Sweden from 8500 B.P. onwards (Kullman 2001, 1998, 1996, 1995), though there are no additional reports of pollen findings until about 2500 B.P. Actually even two Swedish sites include macroscopic remains dating back to 11500 B.P. These data of Kullman will be discussed in detail within the following discussion part.

Lagercrantz and Ryman (1990) outline that spruce from two central European refugia, located in the Dinaric Alps (east of the Adriatic Sea) and in the Carpathians, appear to have spread north and west, whereas the Russian relicts expanded westward to Scandinavia and toward the south-west to meet spruce from other refugia in the area of the present eastern Poland. Thus, the postglacial history of Norway spruce in eastern Poland even is of special interest from the genetic point of view, because it is a region where two genetically different main areas came into contact. Due to investigations on allozyme variation of Lewandowski and Burczyk (2002) after the last glaciation spruce entered Poland first from southern refugia, and during the Boreal period from north-eastern refugia. The point and place in time where the two groups met is still uncertain, however, Środoń (1967) suggests a contact of the two groups during the Atlantic period (5000-3000 years before present). At present, a "spruceless zone" between the territories occupied by the two spruce ranges is proved (Lewandowski and Burczyk 2002), however, the provenances from eastern Poland are genetically intermediate between those from locations closer to the original refugia (Lagercrantz and Ryman 1990). Interestingly, virtually no significant genetic differentiation between southern and north-eastern populations in Poland was documented by the results of the studies of Lewandowski and Burczyk (2002), who assume gene flow as one possible explanation of this phenomenon. Further investigation with special interest on this particular area are surely needed to gain insight into the outstanding history of *Picea* in this part of Europe.

5.4.4 The controversal history of *Picea* in Fennoscandia

Several investigations of Kullman (2002, 2001, 2000, 1998, 1996, 1995) present a great amount of spruce megafossil data from Fennoscandia. Single sites occur from 11500 B.P. onwards, however, as recently as 8500 B.P. numerous finds are documented for this area. Most remains dated younger than 6000 B.P. stem from the eastern uplands and lowlands. According to the old finds Kullman (2002, 2000) hypothesises that *Picea* survived during the entire Weichselian glaciation close to the continental icesheet in western Scandinavia, with glacial refugia supposed to exist on the exposed shelf areas west and southwest of Norway, and started spreading from this areas in an eastward direction. Kullmans postulations mainly base on the trend that finds become younger to the east and the concept of a residual continental ice sheet east of Åreskutan, the site with the oldest megafossil finds, at the time to which the oldest remains were dated. However, the assumption of glacial refugia in the Scandes is in opposition to most palynological theories, which do not comprise glacial refugias in this area and generally regard *Picea abies* as a late-Holocene immigrant (e.g. Huntley and Birks 1983; Hafsten 1985, 1992).

Kullman (2002) discusses that the discoveries of macro- and megafossils somewhat concur with different lines of recent evidence (records and model simulations) suggesting that the

Scandinavian ice sheet (particularly over the mountain peaks) was thinner, less extensive and penetrated by nunataks earlier than the generally held opinion. The author further states that there are strong indications of substantial ice melting and warming in north-western Europe, thermally driven by rising summer insolation (Milankovitch cycles) favouring the early appearance of some tree species. Due to the postulated climatic conditions Kullman (2000) concludes that *Picea abies* appeared for the first time on an early deglaciated nunatak at the transition from Alleröd to Younger Dryas, whereas the species was strictly bound to higher elevations in the west during the early Holocene.

Kullman (2002) himself argues that his oldest radiocarbon dates conflict with the established glacial-morphological reconstructions and models of the initial deglaciation in this part of the Scandes (according to Lundquist 1986). However, a combined map including both the lines of ice recession and sites of *Picea* macrofossil finds shows that even the sites of the oldest and consequently most questionable finds were situated along the ice margin (see Fig. 32). Conspicuously most of Kullmans megafossil finds stem from an area in the west where an indentation of the ice sheet is documented between 9500 and 8500 B.P. clearly following the underlying topography. Lundquist (1986) proposes the recession of the ice margin towards the mountain areas of Norway was progressively influenced in its behaviour by local topography. Thus, the continental ice sheet in Fennoscandia, which had a thickness of at most 3 km (Miettinen 2004), was subdivided into domes and lobes situated in valleys enclosed by ice-free uplands after about 9000 B.P. possibly allowing certain tree species to establish small stands. Furthermore Lundquist (1986) states that the ice in the western part of Fennoscandia probably was more active due to a larger supply of precipitation and several readvances are known.

It is highly probable that the accumulated appearance of the macroscopic evidences is caused by the existence of several small stands of *Picea* within Fennoscandia descendant from fast expanding populations in north-west Russia and eastern Finland, rather than being evidence for glacial refugia on the continental shelf, a hypothesis, which is also represented by Giesecke and Bennett (2004). Probably these populations were quite small, so that they did not produce such great amounts of pollen precipitation, which could be visible in the present pollen distribution maps. However, Kullman (2000) mentions that an early immigration of spruce may be in accordance with at least stray finds or even long “tails” of *Picea* pollen deep into Holocene stratigraphy displayed in many published pollen diagrams, though in the past, those pollen generally have been considered as a result of long-distance transportation (Faegri 1950).

Also, Aas and Faarlund (1999) take into account that there must have been the possibility of an early expansion westwards of the spruce, long before the main expansion, also referring to previous studies. At any rate one has to take into account that there are not many sites reporting pollen from central Fennoskandia at all, particularly in the early Holocene. The investigation of more pollen sites in this part of Fennoscandia would help to clear the apparent contradiction of present macrofossil finds but no pollen records.

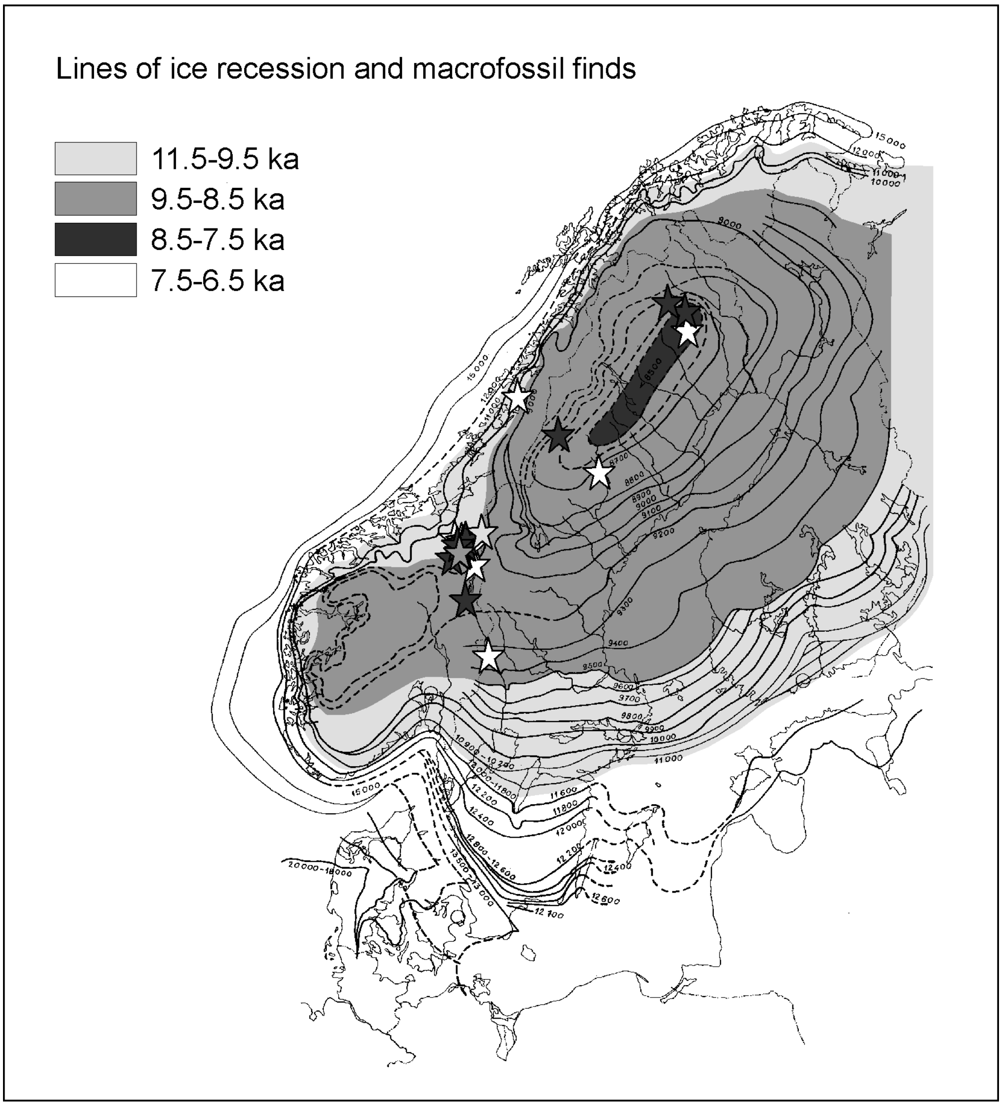


Fig. 32: Lines of ice recession in Scandinavia (after Lundquist 1986) and macrofossil finds according to the dataset of the present study.

An early Holocene migration of spruce westwards into Sweden and Norway from easterly locations could be rendered possible via a direct connection during the extensive dry-fall of the Ancylus-Lake. Following to the Ancylus-Regression the Baltic Sea partly became mainland between about 9000 and 8000 B.P., however, the draining of the Ancylus lake into the Northern Sea is still in disput (e.g. see Björck 1995; Lemke et al. 1998; Brenner and Meemken 2002). Maybe also an earlier migration of *Picea* was possible, because, according to Tikkanen and Oksanen (2002) in the Gulf of Bothnia a certain amount of new land emerged even during the transgressive Ancylus period due to the fact that the rate of land uplift consistently exceeded the water level rise. Kuusela (1990) states ample evidence from Finland that *Picea* seeds may blow 200-300 km over snow surfaces. Thus, tree-line environments in the Scandes Mountains may have been points at which seeds travelling on the ice-crusted snow became trapped and suitable habitats for small stands of trees could establish (Giesecke and Bennett 2004).

For the immigration history of spruce in northern Europe the present study confirms the main conclusions of Giesecke and Bennett (2004). The authors presume the spread of *Picea abies* in Fennoscandia and adjacent areas to be separated into two phases, (1) a rapid early Holocene spread out of Byelorussia and northern Russia at low population density giving rise to small outpost populations, possibly as far as the Scandes Mountains, and (2) a mid- to late Holocene front-like spread at high population densities moving from east to west into the Baltic Republics and Finland, into northern Scandinavia and then moving south and west towards its present-day distributional limits.

6. Conclusions

The present work shows that localisation of potential glacial refugia of fir and spruce simply is possible by using datasets from palaeobotany. Furthermore, the comparison of palaeobotanical data and recent molecular genetic allows to reconstruct the immigration history. Just by the combination of genetic and palaeobotanical data, it is possible to identify, which refugia had an influence on the spread of these trees in Europe.

However, it should be stressed that the network of palaeobotanical data is still uneven, particularly for previous warm stages, and that further data would help to improve the present interpretations.

Vegetation history of Abies during the last glacial-interglacial cycle

1. The most recent pollen data confirm long-lasting refugia of *Abies,* such as southern Italy and Greece as already suggested in previous studies.
2. Based on pollen and macrofossil evidence we can identify a another important refugial area in the Pyrenees.
3. Pollen data suggest additional potential refugia in south-east France and north-west Italy.
4. On the basis of comparison between palaeobotanical data and isozyme studies on gene markers, it is unlikely that the refugia of *Abies* in southern Italy or in the Pyrenees played any role in the postglacial migration and spread of *Abies* throughout Europe. These populations are separate and isolated.
5. It is highly likely that *Abies alba* migrated into northern Europe from an origin in south-east France and north-west Italy.
6. A further origin for the migration of fir into northern Europe may have been Greece.
7. However, a lack of pollen and macrofossil data from the central and northern Balkans means that the proposed easterly migration routes cannot so far be reconstructed on the basis of palaeobotany alone. Nevertheless the molecular biological data support this hypothetical track.

Vegetational history of Picea during the last glacial-interglacial cycle

1. Both, pollen and macrofossil data of the present study prove the existence of long-lasting refugia of *Picea* in the east Alpine foreland and the Russian plain.
2. Further refugial areas, based on the occurrence of pollen and macrofossils, are suggested to be located in the south-east Alpine foreland, the north-west Carpathians, the Hungarian plain and the Moldavian lowland.
3. Pollen data likely imply an additional possible refugial area in the Massif Central.
4. The role of the Massif Central according to the migration history of spruce could not be accurately assessed. However, it is unlikely that this area had any influence on the post-glacial spread of *Picea* throughout Europe. The populations are supposed to be isolated and extinct to date.
5. Due to the scarcity of available sites it was not possible to specify the role of the Moldavian lowland in respect of the spreading history of spruce. These populations are also considered as isolated and extinct to date.
6. It is highly probable that *Picea* migrated into central Europe from refugial areas in the east Alpine foreland and south-east Alpine foreland following a general trend from east to west.
7. Further origins of migration of spruce into central Europe may have been the Hungarian plain and north-western Carpathians, however, there is still a lack of data.
8. Populations from central Russia and the Moscow area were responsible for the spread of *Picea* into Scandinavia and the eastern Baltic states.
9. Certainly, populations of spruce originating from different refugial areas came into contact in eastern Poland, causing a present-day "spruceless zone" as well as introgression species.
10. The apparent contradiction of the presence of macrofossils but absence of pollen records in Fennoscandia may be caused by the existence of very small stands of *Picea*, which did not produce sufficient amounts of pollen precipitation.
11. However, the results of the present study argue for an immigration of spruce into Fennoscandia following an east to west route.

Acknowledgements

I wish to thank Prof. T. Litt for providing me with an interesting research topic and for support and advice throuhout the course of this investigation. Many thanks also to Prof. W. Barthlott for being second referee.

This project would not have been possible without the constant encouragement of Arne and my family, particularly Winni, Ursula, Judith, Dirk and Anna. Furthermore, I am thankful to my working group, Georg, Norbert, Frank und Beate, for their assistance and helpful comments on my work within the past years. Special thanks also to Dany for her outstanding friendship and every day support with tea. I also wish to thank all members of the institute for the pleasant daily atmosphere, Georg and Martin, in particular.

I am much obliged to my FOSSILVA colleagues Rachid, Birgit, Sascha, Christoph and Mari Mette for constant discussion and providing of essentiel information.

The contribution of pollen data to the EPD produced by individual pollen analysts is greatfully acknowledged, as is the facility afforded by the EPD. The synthetic interpretation of these data, however, is that of the present authors.

I also thank all the contributors of macrofossil data, which have been used in this study, particularly M. Latałowa for helpful discussion of the Polish sites as well as to W. O. van der Knaap and B. Ammann for useful information on the occurrence of macrofossils in the Alpine region.

The study was supported by the EU-project FOSSILVA (Dynamics of forest tree biodiversity: linking genetic, palaeogenetic and plant historical approaches, EVK2-1999-00244) and by a grant from the German Research Council (DFG) within the scope of the Research Training Group “Evolution and Biodiversity in Space and Time”.

References

AABY, B. & TAUBER, H. (1995): Eemian climate and pollen.- Nature, **376**: 27-28.

AALBERSBERG, G. & LITT, T. (1998): Multiproxy climate reconstructions for the Eemian and Early Weichselian.- J. Quaternary Sci., **13 (5)**: 367-390; (Wiley & Sons).

AAS, B. & FAARLUND, T. (1999): Macrofossils versus pollen as evidence of the Holocene forest development in Fennoscandia.- AmS-Rapport, **12B**: 307-346; Stavanger.

ALLEN, J. R. M., BRANDT, U., BRAUER, A., HUBBERTEN, H.-W., HUNTLEY, B., KELLER, J., KRAML, M, MACKENSEN, A., MINGRAM, J., NEGENDANK, J. F. W., NOWACZYK, N. R., OBERHÄNSLI, H., WATTS, W. A., WULF, S. & ZOLITSCHKA, B. (1999): Rapid environmental changes in southern Europe during the last glacial period.- Nature, **400**: 740-743.

AMMANN, B. (1988): Periods of rapid environmental change around 12500 and 10000 years B.P., as recorded in Swiss lake deposits.- Journal of Paleolimnology, **1**: 267-277; Belgien (Kluwer Academic Publishers).

ANDERSEN, S. TH. (1961): Vegetation and its Environment in Denmark in the Early Weichselian Glacial (Last Glacial).- Danm. Geol. Unders., II. R., **75**: 1-175; København.

ANDERSEN, S. T. (1965): Interglacialer og interstadialer i Danmarks kvartær.- Medd. fra Dansk Geol. Forening, **15 (4)**: 486-506; København.

APPLEBY, P.G. (unpubl. 1998a): Report on the radiometric dating of two peat cores from central and southern Switzerland.- Environmental Radioactivity Research Centre, Liverpool.

APPLEBY, P.G. (unpubl. 1998b): Report on the radiometric dating of two peat cores from Älbi Flue and Aletschwald, Switzerland. Environmental Radioactivity Research Centre, Liverpool.

AVERDIECK, F.-R. (1967): Die Vegetationsentwicklung des Eem-Interglazials und der Frühwürm-Interstadiale von Odderade/Schleswig-Holstein.- Fundamenta, **B/2**: 101-125.

AVIGLIANO, R., DI ANASTASIO, G., IMPROTA, S., PERESANI, M. & RAVAZZI, C. (2000): A new late glacial to early Holocene palaeobotanical and archaeological record in the Eastern Pre-Alps: the Palughetto basin (Consiglio Plateau, Italy).- Journal of Quaternary Science, **15** (8): 789-803.

BEAULIEU, J.-L. DE (1977): Contribution pollenanalytique à l'histoire tardiglaciaire at Holocène de la végétation des Alpes méridionales françaises.- Thesis; Univ. Aix-Marseille.

BEAULIEU, J.-L. DE & REILLE, M. (1984): A long Upper Pleistocene pollen record from Les Echets, near Lyon, France.- Boreas, **13**: 111-132; (Oslo).

BEAULIEU, J.-L. DE & REILLE, M. (1989): The transition from temperate phases to stadials in the long Upper Pleistocene sequence from Les Echets (France).- Palaeogeography, Palaeoclimatology, Palaeoecology, **72**: 147-159; Amsterdam (Elsevier).

BEAULIEU, J.-L. DE & REILLE, M. (1992a): The last climatic cycle at La Grande Pile (Vosges, France). A new pollen profile.- Quaternary Science Reviews, **11**: 431-438; (Pergamon).

BEAULIEU, J.-L. DE & REILLE, M. (1992b): Long Pleistocene pollen sequences from the Velay Plateau (Massif Central, France). I. Ribains maar.- Veget. Hist. Archaeobot., **1**: 233-242; Heidelberg (Springer).

BEHRE, K.-E. (1962): Pollen- und diatomeenanalytische Untersuchungen an letztinterglazialen Kieselgurlagern der Lüneburger Heide.- Flora, **152**: 325-370, 8 Abb., 3 Taf.; Jena (Fischer).

BEHRE, K.-E. (1970): Die Flora des Helgoländer Süßwasser-"Töcks", eines Eem-Interglazials unter der Nordsee.- Flora, **159**: 133-146.

BEHRE, K.-E. (1974): Die Vegetation im Spätpleistozän von Ostwanna/Niedersachsen.- Geol. Jb., **A 18**: 3-48, 8 Abb, 5 Taf.; Hannover (Schweizerbart).

BEHRE, K.-E. & LADE, U. (1986): Eine Folge von Eem und 4 Weichsel-Interstadialen in Oerel/Niedersachsen und ihr Vegetationsablauf.- Eiszeitalter u. Gegenwart, **36**: 11-36, 12 Abb., 2 Tab., 2 Taf.; Hannover (Schweizerbart).

BENDER, M., SOWERS, T., DICKSON, M.-L., ORCHARDO, J., GROOTES, P., MAYEWSKI, P. A. & MEESE, D. A. (1994): Climate correlations between Greenland and Antarctica during the past 100,000 years.- Nature, **372**: 663-666.

BENNETT, K. D., TZEDAKIS, P. C. & WILLIS, K. J. (1991): Quaternary refugia of north European trees.- Journal of Biogeography, **18**: 103-115.

BERGLUND, B. E. & LAGERLUND, E. (1981): Eemian and Weichselian stratigraphy in South Sweden.- Boreas. **10**: 323-362; Oslo.

BERGLUND, B. E., BIRKS, H. J. B., RALSKA-JASIEWICZOWA, M. & WRIGHT, H. E. (1996): Palaeoecological events during the last 15000 years.- 764 S.; Chichester (Wiley & Sons).

BERGMANN, F., GREGORIUS, H. R. & LARSEN, J. B. (1990): Levels of genetic variation in European silver fir (*Abies alba*). Are they related to the species' decline?- Genetica, **82**: 1-10.

BERNER, U. & STREIF, H. (Hrsg.) (2000): Klimafakten. Der Rückblick - Ein Schlüssel für die Zukunft.- 2. Aufl., 238 S.; Stuttgart (Schweizerbart).

BERTOLANI MARCHETTI, D., ACCORSI, C. A., AROBBA, D., BANDINI MAZZANTI, M., BERTOLANI, M., BIONDI, E., BRAGGIO, G., CIUFFI, C., DE CUNZO, T., DELLA RAGIONE, S., FORLANI, L., GUIDO, A. M., LOLLI, F., MONTANARI, C., PAOLI, P., RAIMONDO, F. M., ROSSITTO, M. & TREVISAN GRANDI, G. (1984): Recherches géobotaniques sur les Monts Madonie (Sicile du Nord).- Webbia, **38**: 329-348.

BJÖRCK, S. (1995): A review of the history of the Baltic Sea, 13.0-8.0 ka BP.- Quaternary International, **27**: 19-40; (Pergamon).

BJÖRKMAN, L., FEURDEAN, A., CINTHIO, K., WOHLFARTH, B. & POSSNERT, G. (2002): Lateglacial and early Holocene vegetation development in the Gutaiului Mountains, northwestern Romania.- Quaternary Science Reviews, **21**: 1039-1059.

BOTTEMA, S. (1974): Late Quaternary vegetation history of northwestern Greece.- Thesis Univ. Groningen, pp. 190.

BOZILOVA, E. (1995): The upper forest limit in the Rila Mts. in postglacial time- Palaeoecological evidence from pollen analysis, macrofossil plant remains and ^{14}C dating.- Advances in Holocene Palaeoecology in Bulgaria, 1-8; Sofia - Moscow (Pensoft Publ.).

BOZILOVA, E., TONKOV, S. B. & PAVLOVA, D. K. (1986): Pollen and plant macrofossil analyses of the lake Suho Ezero in the south Rila mountains.- Annuaire de l'université de Sofia, **80**: 48-57.

BRENNER, W. & MEEMKEN, H.-J. (2002): Öko- und chronostratigraphische Korrrelierung der Zentralen Ostsee mit der Kieler Bucht anhand organisch-wandiger Mikrofossilien.- Meyniana, **54**: 17-40, 10 Abb., 1 Tab.; Kiel.

BRIANT, R. M., COOPE, G. R., PREECE, R. C., KEEN, D. H., BOREHAM, S., GRIFFITHS, H. I., SEDDON, M. B. & GIBBARD, P. L. (2004): Fluvial system response to late Devensian (Weichselian) aridity, Baston, Lincolnshire, England.- Journal of Quaternary Science, **19(5)**: 479-495; (Wiley & Sons).

BURGA, C. A. (1987): Gletscher- und Vegetationsgeschichte der Südrätischen Alpen seit der Späteiszeit.- Denkschriften der Schweizerischen Naturforschenden Gesellschaft, **101**: 162 S.; Basel (Birkhäuser).

BURGA, C. A. & HUSSENDÖRFER, E. (2001): Vegetation history of *Abies alba* Mill. (silver fir) in Switzerland - pollen analytical and genetic surveys related to aspects of vegetation history of *Picea abies* (L.) H. Karsten (Norway spruce).- Veget. Hist. Archaeobot., **10**: 151-159; Heidelberg (Springer).

CASPERS, G. (1997): Die eem- und weichselzeitliche Hohlform von Groß Todtshorn (Kr. Harburg; Niedersachsen) – Geologische und palynologische Untersuchungen zu Vegetation und Klimaverlauf der letzten Kaltzeit.- In: FREUND, H. & CASPERS, G. (1997 a): Vegetation und Paläoklima der Weichsel-Kaltzeit im nördlichen Mitteleuropa - Ergebnisse paläobotanischer, -faunistischer und geologischer Untersuchungen.- Schriftenreihe der Deutschen Geologischen Gesellschaft, **4**: 7-59; Hannover.

CASPERS, G. & FREUND, H. (1997): Die Vegetations- und Klimaentwicklung des Weichsel-Früh- und –Hochglazials im nördlichen Mitteleuropa.- In: FREUND, H. & CASPERS, G. (1997 a): Vegetation und Paläoklima der Weichsel-Kaltzeit im nördlichen Mitteleuropa - Ergebnisse paläobotanischer, -faunistischer und geologischer Untersuchungen.- Schriftenreihe der Deutschen Geologischen Gesellschaft, **4**: 201-249; Hannover.

CASTELLETTI, L. & LEONI, L. (1987): I resti vegetali macroscopi. In: ACCORSI, C.A., BANDINI, M., BIAGI, P., CASTELLETTI, L., CREMASCHI, M., LEONI, L. & PARVARANI, M. (1987): Il sito mesolitico Sopra Fienile Rossino. Natura Bresciana **23**: 268-276.

CHERDYNTSEV, V. V., ALEKSEYEV, V. A., KIND, N. V., FOROVA, V. S. & SULERZHITSKIY, C. D. (1968): Geological Institute Radiocarbon Dates I.- Radiocarbon Vol. **10**, Nr. 2: 419-425.

CLEVERINGA, P., MEIJER, T., LEEUWEN, R. J. W. VAN, WOLF, H. DE, POUWER, R., LISSENBERG, T. & BURGER, A. W. (2000): The Eemian stratotype locality at Amersfoort in the central Netherlands: a re-evaluation of old and new data.- Geologie en Miijnbouw / Netherlands Journal of Geoscience, **79 (2/3)**: 197-216; Utrecht.

COLLIGNON, A. M. & FAVRE, J. M. (2000): Contribution to the Postglacial History at the Western Margin of *Picea abies*' Natural Area Using RAPD Markers.- Annals of Botany, **85**: 713-722.

COTIJO, E., DUPLESSY, J. C., LABEYRIE, L., LECLAIRE, H., DUPRAT, J. & WEERING, T. C. E. VAN (1994): Eemian cooling in the Norwegian Sea and North Atlantic ocean preceding continental ice-sheet growth.- Nature, **372**: 446-449.

COUTEAUX, M. (1982): Recherches pollenanalytiques en Oisans: Le plateau de Brande (Alpe d´Huez, Isère, France).- Bulletin Société Royale de Botanique de Belgique, **115**: 91-106.

CULIBERG, M. & ŠERCELJ, A. (1995): Anthracotomical and palynological research in the palaeolithic site Šandalja II (Istria, Croatia). Razprave IV, Razreda SAZU, XXXVI, **3**, Ljubljana:49-57.

DAMBLON, F., DUBAR, M., NICOL-PICHARD, S. & VERNET, J.-L. (1988): Paléoécologie du pays niçois à la fin de la période atlantique.- Inst. fr. Pondichéry, trav. sec. sci. tech., t. **XXV**: 11-25.

DAMBLON, F., HAESAERTS, P. & VAN DER PLICHT, J. (1996): New datings and considerations on the chronology of upper palaeolithic sites in the great eurasiatic plain. Préhistoire Européenne, **9**: 177-231.

DIGERFELDT, G., BEAULIEU, J.-L. DE, GUIOT, J. & MOUTHON, J. (1997): Reconstruction and palaeoclimatic interpretation of the Holocene lake-level changes in Lac de Saint-Léger, Haute-Provence, southeast France.- Palaeogeography, Palaeoclimatology, Palaeoecology, **136**: 231-258.

DOBOSI, V. (1967): A recent upper palaeolithic settlement in the Great Hungarian Plain.- Archeológiai Értesito **94**: 184-193.

DOWDESWELL, J. A. & WHITE, J. W. C. (1995): Greenland ice core records and rapid climate change.- Pil. Trans. R. Soc. Lond. A, **352**: 359-371; (The Royal Society).

DRESCHER-SCHNEIDER, R. (1997): Ergebnisse der pollen- und großrestanalytischen Untersuchungen im Gebiet der Plankenalm, Dachstein (Österreich).- Mitteilungen der Anisa, 18. Jg., Heft **1/2**: 46-61; Haus i. E..

DRESCHER-SCHNEIDER, R. (1999): Pollen and Macrofossil Analysis in a subalpine dung pile on the eastern Dachstein Plateau (Austria) – Possibilities and limits of interpretation.- Universitätsforschungen zur prähistorischen Archäologie, **55**: 225-230.

DRESCHER-SCHNEIDER, R. (2000): Die Vegetations- und Klimaentwicklung im Riss/Würm-Interglazial und im Früh- und Mittelwürm in der Umgebung von Mondsee. Ergebnisse der pollenanalytischen Untersuchungen.- Mitt. Komm. Quartärforsch., **12**: 39-92, 12 Abb., 9 Tab..

DUBAR, M. (1986): L'Environment côtier des Alpes-Maritimes á la fin de la transgression versilienne d'apres l'etude biostratigraphique du site de L'Etoile á Nice (France).- Revue de Paléobiologie, **5 (2)**: 289-310; Genève.

ERD, K. (1973): Pollenanalytische Gliederung des Pleistozäns der Deutschen Demokratischen Republik.- Z. geol. Wiss., **1 (9)**: 1087-1103, 8 Abb., 1 Tab.; Berlin.

ERD, K. (1991): Vegetationsentwicklung und Pollenanalysen im Eem-Interglazial und Weichsel-Interglazial von Schönfeld, Kreis Calau.- Natur und Landschaft in der Niederlausitz, **1**: 71-81; Cottbus.

ERIKSSON, B. (1993): The Eemian pollen stratigraphy and vegetational history of Ostrobothnia, Finland.- Geological Survey of Finland, Bulletin **372**: 1-36, 15 Fig.; Espoo.

ERIKSSON, B., GRÖNLUND, T. & UUTELA, A. (1999): Biostratigraphy of Eemian sediments at Mertuanoja, Pohjanmaa (Ostrobothnia), western Finland.- Boreas, **28**: 274-291; Oslo.

FAEGRI, K. (1950): Studies on the Pleistocene of Western Norwa. IV. On the immigration of *Picea abies* (L.) Karst.- Naturvitenskapelig rekke, **1**: 1-52; (Universitetet i Bergen Årbok).

FAVRE, P. & JACOMET, S. (1998): Branch wood from the lake shore settlements of Horgen Scheller, Switzerland: Evidence for economic specialisation in the late Neolithic period.- Veget. Hist. Archaeobot., **7**: 167-178.

FELBER, H. (1974): Vienna Radium Institute Radiocarbon Dates V.- Radiocarbon Vol. **16**, Nr.2: 277-283.

FELBER, H. (1980): Vienna Radium Institute Radiocarbon Dates X.- Radiocarbon Vol. **22**, Nr.1: 108-114.

FIELD, M. H., HUNTLEY, B. & MÜLLER, H. (1994): Eemian climate fluctuations observed in a European pollen record.- Nature, **371**: 779-783.

FIRBAS, F. (1949): Spät- und nacheiszeitliche Waldgeschichte Mitteleuropas nördlich der Alpen, Allgemeine Waldgeschichte.- 480 S.; Jena (Gustav Fischer).

FIRBAS, F. (1954): Die Vegetationsentwicklung im Spätglazial von Wallensen im Hils.- Nachr. Akad. Wiss. Göttingen, Math.-Physik. Kl. IIb, Biol.-Physiol.-Chem. Abt. 1954, 37-50.

FOLLIERI, M., MAGRI, D. & SADORI, L. (1988): 250,000-year pollen record from Valle di Castiglione (Roma).- Pollen et Spores, **XXX, 3-4**: 329-356.

FOLLIERI, M., GIARDINI, M., MAGRI, D. & SADORI, L. (1998): Palynostratigraphy of the last glacial period in the volcanic region of central Italy.- Quaternary International, **47**: 3-20; (Pergamon).

FRENZEL, B. (1991): Das Klima des letzten Interglazials in Europa.- In: FRENZEL, B. (1991): Klimageschichtliche Probleme der letzten 130000 Jahre.- 451 S., 159 Abb., 22 Tab.: S. 51-78; Stuttgart/New York (Fischer).

FREUND, H. (1997): Die Vegetation im Weichsel-Früh- und –Hochglazial von Groß Todtshorn (Kr. Harburg; Niedersachsen) anhand botanischer Makroreste.- In: FREUND, H. & CASPERS, G. (1997): Vegetation und Paläoklima der Weichsel-Kaltzeit im nördlichen Mitteleuropa - Ergebnisse paläobotanischer, -faunistischer und geologischer Untersuchungen.- Schriftenreihe der Deutschen Geologischen Gesellschaft, **4**: 61-86; Hannover.

FREUND, H., MEYER, K.-J., CASPERS, G. & Höfle, H.-C. (1997): Pollenstratigraphische Untersuchungen zum Eem-Interglazial und Börup-Interglazial von Barendorf (Kr. Lüneburg; Niedersachsen).- In: FREUND, H. & CASPERS, G. (1997 a): Vegetation und Paläoklima der Weichsel-Kaltzeit im nördlichen Mitteleuropa - Ergebnisse paläobotanischer, -faunistischer und geologischer Untersuchungen.- Schriftenreihe der Deutschen Geologischen Gesellschaft, **4**: 157-174; Hannover.

FROGLEY, M. R., GRIFFITHS, H. I. & HEATON, T. H. E. (2001): Historical biogeography and Late Quaternary environmental change of Lake Pamvotis, Ioannina (north-western Greece): evidence from ostracods.- Journal of Biogeography, **28**: 745-756; (Blackwell).

FRONVAL, T. & JANSEN, E. (1996): Rapid changes in ocean circulation and heat flux in the Nordic seas during the last interglacial period.- Nature, **383**: 806-810.

FUCHS, F. (1970): Studien zur Karst- und Glazialmorphologie in der Monte-Cavallo-Gruppe/Venezianische Voralpen. Frankfurter Geographische Hefte **47**: 26-109.

GÁBORI-CSÁNK, V. (1960): A Ságvári Telep Abszolút Kormeghatározása.- Archeológiai Értesíto, **87**: 125-129.

GAILLARD, M.-J. (1984): Evolution de la Végétation du Moyen-Pays Romand. Dissertationes Botanicae **77**, 322 pp.

GEEL, B. VAN, KLINK, A. G., PALS, J. P. & WIEGERS, J. (1986): An Upper Eemian lake deposit from Twente, Eastern Netherlands.- Review of Palaeobotany and Palynology, **47**: 31-61; Amsterdam (Elsevier).

GEHRIG, R. (1989): Pollenanalytische und geomorphologische Untersuchungen im Eigental (LU).- Unveröff. Diplomarbeit Geogr. Inst. Univ. Zürich, 89 S..

GEHRIG, R. (1991): Pollenanalytische Untersuchungen zur Vegetationsgeschichte des Pilatusgebietes.- Mitt. Naturf. Ges. Luzern, **32**: 127-143; Luzern.

GEHRIG, R. (1997): Pollenanalytische Untersuchungen zur Vegetations- und Klimageschichte des Val Camonica (Norditalien).- Dissertationes Botanicae, **276**: 152 S.; Berlin – Stuttgart (Cramer).

GERLACH, T., KOSZARSKI, L., KOPEROWA, W. & KOSTER, E. (1972): Sédiments lacustres postglaciaires dans la dépression de Jasło-Sanok.- Studia Geomorphologica Carpatho-Balcanica, **Vol. VI**: 37-61; Krakow.

GEYH, M. A., SCHWEITZER, F., VÉRTES, L. & VOGEL, J. C. (1969): Neue chronologische Angaben zur Würm-Vereisung in Ungarn.- Földrajzi Értesíto, **18**: 5-18.

GEYH, M. A., HENNIG, G. & OEZEN, D. (1997): U/Th-Datierung interglazialer und interstadialer Niedermoortorfe und lignite - Stand und Zukunft.- In FREUND, H. & CASPERS, G. (Hrsg.) (1997): Vegetation und Paläoklima der Weichsel-Kaltzeit im nördlichen Mitteleuropa - Ergebnisse paläobotanischer, -faunistischer und geologischer Untersuchungen.- Schriftenreihe der Deutschen Geologischen Gesellschaft, **4**: 187-199, 10 Abb., 5 Tab.; Hannover.

GIESECKE, T. & BENNETT, K. D. (2004): The Holocene spread of *Picea abies* (L.) Karst. in Fennoscandia and adjacent areas.- Journal of Biogeography, **31**: 1523-1548.

GIL, E., GILOT, E., KOTARBA, A., STARKEL, L. & SZCZEPANEK, K. (1974): An early holocene landslide in the Niski Beskid and its significance for paleogeographical reconstructions.- Studia Geomorphologica carpatho - Balcanica, **Vol. VIII**: 69-83; Krakow.

GODWIN, H. (1956): The History of the British Flora. A Factual Basis for Phytogeography.- 384 pp; Cambridge (University press).

GREENLAND ICE-CORE PROJECT (GRIP) MEMBERS (1993): Climate instability during the last interglacial period recorded in the GRIP ice core.- Nature, **364**: 203-207.

GROOTES, P. M., STUIVER, M., WHITE, J. W. C., JOHNSEN, S. & JOUZEL, J. (1993): Comparison of oxygen isotope records from the GISP2 and GRIP Greenland ice cores.- Nature, **366**: 552-554.

GRÜGER, E. (1977): Pollenanalytische Untersuchung zur würm-zeitlichen Vegetationsgeschichte von Kalabrien (Süditalien).- Flora, **166**: 475-489.

GRÜGER, E. (1979a): Die Seeablagerungen vom Samerberg/Obb. und ihre Stellung im Jungpleistozän.- Eiszeitalter u. Gegenwart, **29**: 23-34, 4 Abb., 1 Tab.; Hannover.

GRÜGER, E. (1979b): Spätriß, Riß/Würm und Frühwürm am Samerberg in Oberbayern - ein vegetationsgeschichtlicher Beitrag zur Gliederung des Jungpleistozäns.- Geologica Bavarica, **80**: 5-64, 3 Abb., 6 Tab., 3 Beil..; München.

GUGERLI, F., SPERISEN, C., BÜCHLER, U., MAGNI, F., GEBUREK, T., JEANDROZ, S. & SENN, J. (2001): Haplotype variation in a mitochondrial tandem repeat of Norway spruce (*Picea abies*) populations suggest a serious founder effect during postglacial re-colonisation of the western Alps.- Molecular Ecology, **10**: 1255-1263; (Blackwell).

HAESAERTS, P., DAMBLON, F., BACHNER, M. & TRNKA, G. (1996): Revised stratigraphy and chronology of the Willendorf II sequence, Lower Austria. Archaeol. Austriaca **80**: 25-42.

HAESAERTS, P., BORZIAK, I., VAN DER PLICHT, J. & DAMBLON, F. (1998): Climatic events and Upper Paleolithic chronology in the Dniester basin: new ^{14}C results from Cosautsi. Radiocarbon **40** (2): 649-657.

HAFSTEN, U. (1985): The immigration and spread of spruce forest in Norway, traced by biostratigraphical studies and radiocarbon datings. A preliminary report.- Norsk geogr. Tidsskr., **39**: 99-108; Oslo.

HAFSTEN, U. (1992): The immigration and spread of Norway spruce (*Picea abies* (L.) Karst.) in Norway.- Norsk Geografisk Tidsskrift, **46**: 121-158.

HAHNE, J (1991): Untersuchungen zur spät- und postglazialen Vegetationsgeschichte im nördlichen Bayern (Rhön, Grabfeld, Lange Berge).- Flora, **185**: 17-32; Jena (Fischer).

HAHNE, J. (1992): Untersuchungen zur spät- und postglazialen Vegetationsgeschichte im nordöstlichen Bayern (Bayrisches Vogtland, Fichtelgebirge, Steinwald).- Flora, **187**: 169-200; Jena (Fischer).

HAHNE, J., KEMLE, S., MERKT, J. & MEYER, K.-D. (1994a): Eem-, weichsel- und saalezeitliche Ablagerungen der Bohrung "Quakenbrück GE 2".- Geol. Jb., **A 134**: 9-69, 29 Abb., 1 Tab.; Hannover (Schweizerbart).

HAHNE, J., MENGELING, H., MERKT, J. & GRAMANN, F. (1994b): Die Hunteburg-Warmzeit („Cromer-Komplex“) und Ablagerungen der Elster-, Saale- und Weichsel-Kaltzeit in der Forschungsbohrung Hunteburg GE 58 bei Osnabrück.- Geol. Jb., **A 134**: 117-166, 21 Abb., 4 Tab.; Hannover.

HALLIK, R. & KUBITZKI, K. (1961): Über die Vegetationsentwicklung des Weichsel-Interstadials aus Hamburg-Bahrenfeld.- Eiszeitalter uund Gegenwart, **12**: 92-98; Öhringen/Württ..

HALL, A. M., GORDON, J. E., WHITTINGTON, G., DULLER, G. A. T. & HEIJNIS, H. (2002): Sedimentology, palaeoecology and geochronology of Marine Isotope Stage 5 deposits on the Shetland Islands, Scotland.- J. Quaternary Sci., **17 (1)**: 51-67; (Wiley & Sons).

HALL, A. R. (1980): Late Pleistocene deposits at Wing, Rutland.- Phil. Trans. R. Soc. Lond., **B 289**: 135-164.

HARMATA, K. (1987): Late-Glacial and Holocene history of vegetation at Roztoki and Tarnowiec near Jasło (Jasło-Sanok Depression).- Acta Palaeobotanica, **27 (1)**: 43-65.

HEITZ, CH. (1975): Vegetationsentwicklung und Waldgrenzschwankungen des Spät- und Postglazials im Oberhalbstein (Graubünden/Schweiz) mit besonderer Berücksichtigung der Fichteneinwanderung.- Beiträge zur geobotanischen Landesaufnahme der Schweiz, **55**: 5-63.

HÖLZER, A. & HÖLZER, A. (1987): Paläoökologische Moor-Untersuchungen an der Hornisgrinde im Nord-Schwarzwald.- Carolinea, **45**: S. 43-50; Karlsruhe.

HUBSCHMID, F. & LANG, G. (1985): Les Embreux - Holocene environments of a mire in the Swiss Jura Mountains.- Diss. Bot., **87**: 115-125; Vaduz.
HUNTLEY, B. & BIRKS, H. J. B. (1983): An atlas of past and present pollen maps for Europe: 0-13000 years ago.- 667 S.; Cambridge (University Press).

IVERSEN, J. (1954): The late-glacial flora of Denmark and its relation to climate and soil. In: IVERSEN, J. (ed.) (1954): Studies in Vegetational History in honour of Knut Jessen.- Danm. Geol. Unders., **II/80**: 87-119.

JACKSON, S. T., OVERPECK, J. T., WEBB-III, T., KEATTCH, S. E. & ANDERSON, K. H. (1997): Mapped plant-macrofossil and pollen records of Late Quaternary vegetation change in eastern North America.- Quat. Sci. Rev., **16**: 1-70; (Pergamon).

JALAS, J. & SUOMINEN, J. (1973): Atlas Florae Europaeae. Distribution of vascular plants in Europe. 2. Gymnospermae (Pinaceae to Ephederaceae).- 38 pp.; Helsinki.

JANKOVSKÁ, V. (1980): Paläogeobotanische Rekonstruktion der Vegetationsentwicklung im Becken Třeboňská pánev während des Spätglazials und Holozäns.- Vegetace ČSSR, **A 11**: 141 S.; Praha.

JANKOVSKÁ, V. (1987): The development of the Mokré Louky meadows: A palaeoecological study of a deposit situated near Třeboň, Czechoslovakia, and dating back to the Post-Glacial Period.- Folia Geobot. Phytotax., **22**: 199-216; Praha.

JANKOVSKÁ, V. (1994): Die Entwicklung der Vegetationsdecke der Becken am Fuße der hohen Tatra vom Ende der Eiszeit bis zur Gegenwart.- Zborník Prác o Tatranskom Národnom Parku, **31**: 73-84.

JANKOVSKÁ, V., CHROMY, P. & NIŽNIANSKÁ, M. (2002): Šafárka – first palaeobotanical data of the character of the Last Glacial vegetation and landscape in the West Carpathians (Slovakia). Acta Palaeobotanica, **42** (1): 39-50.

JANSSEN, L. R. (1974): Vogesen Symposium 1974. Geomorphologische, bodenkundliche und paläobotanische Untersuchung von den Zentralvogesen.- Manuskript; Wageningen.

JASTRZĘBSKA-MAMEŁKA, M. (1985): The Eemian Interglacial and Early Vistulian at Zgierz-Rudunki in the Łódź Plateau (Poln. mit engl. abstract).- Acta Geographica Lodziensia, **53**: 1-75.

JESSEN, K. (1935): Archaeological dating in the history of North Jutlands vegetation.- Acta Archaeologica, **5**: 185-214.

JESSEN, K. (1949): Studies in the late quaternary deposits and flora history of Ireland.- Proc. Roy. Irish Acad., **52**, **B 6**: 85 ff; Dublin.

JOHNSEN, S. J., CLAUSEN, H. B., DANSGAARD, W., GUNDESTRUP, N. S., HAMMER, C. U. & TAUBER, H. (1995): The Eem stable isotope record along the GRIP Ice Core and its interpretation.- Quaternary Research, **43**: 117-124.

JUVIGNE, E. (1977): La zone de dispersion des poussières émises par une des dernières eruption du volcan du Laachersee (Eifel).- Z. Geomorph., **NF 21 (3)**: 323-342; Berlin.

KHOTINSKIY, N. A. (1984): Holocene vegetation history. In: Velichko, A. A. (1984): Late quaternary environments of the Soviet Union.- pp. 179-200; Minneapolis (University of Minnesota Press).

KLAUS, W. (1975): Das Mondsee-Interglazial, ein neuer Florenfundpunkt der Ostalpen.- Jahrb. OÖ. Musealverein, I. Abh., **120**: 315-344, 5 Abb., 5 Phototaf.; Linz.

KLEIBER, H. (1974): Pollenanalytische Untersuchungen zum Eisrückzug und zur Vegetationsgeschichte im Oberengadin I.- Bot. Jahrb. Syst., **94**, 1: 1-53; Stuttgart.

KLÍMA, B. (1963): Dolní Vestonice. Výzkum tábořiště lovců mamutů v letech 1947-1952.- Nakladatelství Československé Akademie Věd, 427 pp.; Praha.

KNAAP, W. O. VAN DER & AMMANN, B. (1997): Depth-age relationships of 25 well-dated Swiss Holocene pollen sequences archived in the Alpine Palynological Data-Base.- Revue Paléobiol., **16 (2)**: 433-480; Geneve.

KNAAP, W. O. VAN DER, LEEUWEN, J. F. N. VAN, FANKHAUSER, A. & AMMANN, B. (2000): Palynostratigraphy of the last few centuries in Switzerland based on 23 lake and mire deposits: chronostratigraphic pollen markers, regional patterns, and local histories.- Review of Palaeobotany and Palynology, **108**: 85-142.

KNEBLOVÁ, V. (1954): Fytopaleontologický rozbor uhlíků z paleolitického sídlište v Dolních Vestonicích. Anthropozoikum 3: 297-299.

KOFF, T. & KANGUR, M. (2003): Vegetation history in northern Estonia during the Holocene based on pollen diagrams from small kettlehole and lake sediments.- In: Tonkow, S. (ed.): Aspects of Palynology and Palaeoecology. Festschrift in honour of Elissaveta Bozilova. 113-126; Sofia-Moscow (Pensoft).

KONNERT, M. & BERGMANN, F. (1995): The geographical distribution of genetic variation of silver fir (*Abies alba, Pinaceae*) in relation to its migration history.- Pl. Syst. Evol., **196**: 19-30; Heidelberg (Springer).

KOPEROWA, W. (1970): Late-Glacial and Holocene history of the vegetation of the eastern part of the "Jasło-Sanok Doły" (Flysch Carpathians).- Acta Palaeobotanica, **Vol. XI (2)**: 1-43; Krakow.

KOPONEN, M. & NUORTEVA, M. (1973): Über subfossile Waldinsekten aus dem Moor Piilonsuo in Südfinnland.- Acta Entomologica Fennica, **29**: 4-84.

KRAL, F. (1977): Verbreitungsgeschichte der Fichte im Alpenraum. In: SCHMIDT-VOGT, H. (1977): Die Fichte. Band 1, pp. 180-186; Hamburg, Berlin (Paul Parey).

KRBETSCHEK, M. R. & STOLZ, W. (1994): Lumineszenz-Datierungen an pleistozänen Sedimenten aus Tagebauen des Mitteldeutschen und Lausitzer Braunkohlereviers.- In: EISSMANN, L. & LITT, T. (Hrsg.) (1994): Das Quartär Mitteldeutschlands.- Altenbg. nat. wiss. Forsch., **7**: 289-295, 2 Abb., 2 Tab.; Altenburg.

KREMENETSKI, C., VASCHALOVA, T. & SULERZHITSKY, L. (1999): The Holocene vegetation history of the Khibiny Mountains: implications for the postglacial expansion of spruce and alder on the Kola Peninsula, northwestern Russia.- Journal of Quaternary Science **14** (1): 29-43.

KROLOPP, E. (1977): Absolute chronological data of the quaternary sediments in Hungary.- Földrajzi Közlemények, **25**: 230-232.

KÜHL, N. & LITT, T. (2003): Quantitative time series reconstruction of Eemian temperature at three sites using pollen data.- Veget. Hist. Archaeobot., **12**: 205-214.

KÜSTER, H. (1986): Werden und Wandel der Kulturlandschaft im Alpenvorland.- Germania, **64(2)**: 533-559.

KÜSTER, H. (1988): Vom Werden einer Kulturlandschaft.- VCH, Weinheim.

KÜSTER, H. (1989): The history of the landscape around Auerberg, Southern Bavaria: A pollen analytical study. In: Birks, H.H., Birks, H.J.B., Kaland, P.E., Moe, D. (eds) The cultural landscape - past, present and future.- pp 301-310, Cambridge (University Press).

KÜTTEL, M. (1979): Pollenanalytische Untersuchungen zur Vegetationsgeschichte und zum Gletscherrückzug in den westlichen Schweizeralpen.- Ber. Schweiz. Bot. Ges., **89**: 9-62.

KÜTTEL, M. (1990): Zur Vegetationsgeschichte des Gotthardgebietes.- Mitteilungen der Naturforschenden Gesellschaft Luzern, **31**: 99-111 + 2 Plates.

KULLMAN, L. (1986): Recent tree-limit history of *Picea abies* in the southern Swedish Scandes.- Can. J. For. Res., **16**: 761-771.

KULLMAN, L. (1995): New and firm evidence for Mid-Holocene appearance of Picea abies in the Scandes Mountains, Sweden.- Journal of Ecology, **83**: 439-447.

KULLMAN, L. (1996): Norway spruce present in the Scandes Mountains, Sweden at 8000 BP: new light on Holocene tree spread.- Global Ecology and Biogeography Letters, **5**: 94-101.

KULLMAN, L. (1998): Palaeoecological, biegeographical and palaeoclimatological implications of early Holocene immigration of Larix sibirica Ledeb. into the Scandes Mountains, Sweden.- Global Ecology and Biogeography Letters, **7**: 181-188.

KULLMAN, L. (2000): The geoecological history of *Picea abies* in northern Sweden and adjacent parts of Norway. A contrarian hypothesis of Postglacial tree immigration patterns.- Geo-Öko, **21**: 141-172; Bensheim.

KULLMAN, L. (2001): Immigration of Picea abies into North-Central Sweden. New evidence of regional expansion and tree-limit evolution.- Nord. J. Bot., **21(1)**: 39-54; Copenhagen.

KULLMAN, L. (2002): Boreal tree taxa in the central Scandes during the Late-Glacial: implications for Late-Quaternary forest history.- Journal of Biogeography, **29**: 1117-1124.

KUUSELA, K. (1990): The Dynamics of Boreal Coniferous Forest.- 172 pp; Finnish National Fund for Research and Development, Helsinki.

LAGERCRANTZ, U. & RYMAN, N. (1990): Genetic structure of Norway Spruce (*Picea abies*): concordance of morphological and allozymic variation.- Evolution, **44**: 38-53.

LANG, G. (1994): Quartäre Vegetationsgeschichte Europas.- 462 S., 177 Abb., 54 Tab.; Jena / Stuttgart / New York (Fischer).

LANG, G. & TOBOLSKI, K. (1985): Hobschensee - Lateglacial and holocene environment of a lake near the timberline. In LANG, G. (ed.) (1985): Swiss Lake and Mire Environments during the last 15000 years.- Diss. Bot., **87**: 209-228; Vaduz.

LARSEN, J. B. (1986): Das Tannenstreben. Eine neue Hypothese zur Klärung dieser rätselhaften Komplexkrankheit der Weißtanne (*Abies alba* Mill.).- Forstwissenschaftliches Centralblatt, **105**: 381-396.

LARSEN, J. B. (1989): Waldbauliche Probleme und Genökologie der Weißtanne (*Abies alba* Mill.).- Allgemeine Forst- und Jagdzeitung, **160**, 39-43.

LEMKE, W., ENDLER, R., TAUBER, F., JENSEN, J. B. & BENNIKE, O. (1998): Late- and postglacial sedimentation in the Tromper Wiek, northeast of Rügen (western Baltic).- Meyniana, **50**: 155-173.

LEROYER, CH. & HEINZ, CH. (1992): Complémentarité des études palynologiques et anthracologiques: les exemples pyrénéens de La Balma Margineda (Andorre) et de Belesta (Pyrénées-Orientales, France).- Bull. Soc. bot. Fr., **139**, Actual. Bot. (2/3/4): 281-295.

LEVANIČ, T. & ČUFAR K. (1997): Construction of a slovene dinaric silver fir (*Abies alba* Mill.) regional chronology. Dendrochronologia **15**: 183-190.

LEWANDOWSKI, A. & BURCZYK, J. (2002): Allozyme Variation of *Picea abies* in Poland.- Scand. J. For. Res., **17**: 487-494.

LIEPELT, S., BIALOZYT, R. & ZIEGENHAGEN, B. (2002): Wind-dispersed pollen mediates postglacial gene flow among refugia.- Proc. Natl. Acad. Sci. USA, **99**: 14590-14594.

LIEPELT, S., CHEDDADI, R., BEAULIEU, J.-L. DE, FADY, B., GOMORY, D., HUSSENDÖRFER, E., KONNERT, M., LITT, T., LONGAUER, R., TERHÜRNE-BERSON, R. & ZIEGENZAGEN, B. (in prep.): Biogeography and evolutionary history of *Abies alba* Mill. - a synthesis based on palaeobotany and genetics.

LITT, T. (1990): Pollenanalytische Untersuchungen zur Vegetations- und Klimaentwicklung während des Jungpleistozäns in den Becken von Gröbern und Grabschütz.- Altenbg. nat. wiss. Forsch., **5**: 92-105, 5 Abb., 3 Tab.; Altenburg.

LITT, T. (1994): Paläoökologie, Paläobotanik und Stratigraphie des Jungquartärs im nordmitteleuropäischen Tiefland (Unter besonderer Berücksichtigung des Elbe-Saale-Gebietes).- Diss. Bot., **227**: 1-185, 50 Abb., 10 Tab., 4 Beilg.; Berlin/Stuttgart (Cramer).

LITT, T. (2000): Waldland Mitteleuropa - die Megaherbivorentheorie aus paläobotanischer Sicht.- Berichte aus der bayrischen Landesanstalt für Wald- und Forstwirtschaft, **27**: 49-64; Freising (LWF).

LITT, T. (2002): Die Bedeutung der Eemwarmzeit für die terrestrische Stratigraphie, Paläoökologie und Paläoklimatologie.- Terra Nostra, **2002/6**: 197-203.

LITT, T. (2003): Environmental response to climate and human impact in central Europe during the last 15,000 years - a German contribution to PAGES-PEPIII. Editorial.- Quaternary Science Reviews, **22/1**: 1-4.

LITT, T., JUNGE, F. & BÖTTGER, T. (1996): Climate during the Eemian in north-central Europe - a critical review of the palaeobotanical and stable isotope data from central Germany.- Veget. Hist. Archaeobot., **5**: 247-256; Heidelberg (Springer).

LITT, T., BRAUER, A., GOSLAR, T., MERKT, J., BAŁAGA, K., MÜLLER, H., RALSKA-JASIEWICZOWA, M., STEBICH, M. & NEGENDANK, J. F. W. (2001): Correlation and synchronisation of Lateglacial continental sequences in northern central Europe based on annually laminated lacustrine sediments.- Quat. Sci. Rev., **20**: 1233-1249; (Elsevier).

LIU, T. S. (1971): A monographh of the genus *Abies*.- Dept. Forestry, Coll. Agriculture, National Taiwan Univ.; Taipei.

LOTTER, A. F. (1988): Paläoökologische und paläolimnologische Studie des Rotsees bei Luzern. Pollen-, großrest-, diatomeen- und sedimentanalytische Untersuchungen.- Diss. Bot., **124**: 1-187; Berlin/Stuttgart (Cramer).

LOTTER, A. F. (1991): Absolute dating of the late-glacial period in Switzerland using annually laminated sediments.- Quaternary Research, **35**: 321-330.

LOTTER, A. F. (1997): Exkursionführer zur 21. Moorexkursion: Waldgrenzprobleme und hochauflösende Stratigraphien.- 87 S.; Bern.

LOTTER, A.F., AMMANN, B. & STURM, M. (1992): Rates of change and chronological problems during the late-glacial period. Climate Dynamics **6**: 233-239.

LOTTER, A. F., AMMANN, B., HAJDAS, I., STURM, M. & VAN LEEUWEN, J. (1996): Faulenseemoos revisited: new results from an old site.- PACT **50**-II.5: 133-144.

LUNDQUIST, J. (1986): Late Weichselian glaciation and deglaciation in Scandinavia.- In: SIBRAVA, V., BOWEN, D. Q. & RICHMOND, G. M. (eds) (1986): Quaternary Glaciations in the Northern Hemisphere.-Quaternary Science Reviews, **5**: 269-292.

MAI, D.-H. (1990a): Die Flora des Interglazials von Gröbern (Kreis Gräfenhainchen).- Altenbg. nat. wiss. Forsch., **5**: 106-115, 1 Taf., 1 Tab.; Altenburg.

MAI, D.-H. (1990b): Die Flora des Interglazials von Grabschütz (Kreis Delitzsch).- Altenbg. nat. wiss. Forsch., **5**: 116-137, 1 Taf., 1 Tab.; Altenburg.

MAGRI, D. (1999): Late Quaternary vegetation history at Lagaccione near Lago Bolsena (central Italy).- Review of Palaeobotany and Palynology, **106**, 171-208; (Elsevier).

MAMAKOWA, K. (1989): Late Middle Polish Glaciation, Eemian and Early Vistulian vegetation at Imbramowice near Wrocław and the pollen stratigraph of this part of the Pleistocene in Poland.- Acta Palaeobotanica, **29 (1)**: 11-176.

MANGERUD, J., SØNSTEGAARD, E., SEJRUP, H.-P. & HALDORSEN, S. (1981): A continuous Eemian-Early Weichselian sequence containing pollen and marine fossils at Fjøsanger, western Norway.- Boreas, **10**: 138-208; Oslo.

MARINOVA, E. & TONKOV, S. (2003): Macrofossil records of tree species in the sediments of Lake Panichishte (Northwestern Rila Mts.).- International Scientific Conference "75 years of the Forest Research Institute of Bulgarian Academy of Sciences", Proceedings, vol. 1: 266-270; Sofia.

MARKGRAF, V. (1969): Moorkundliche und vegetationsgeschichtliche Untersuchungen an einem Moorsee an der Waldgrenze im Wallis.- Botanische Jahrbücher, **89**: 1-63.

MASON, B. & MOORE, C. B. (1985): Grundzüge der Geochemie.- 340 S., 97 Abb., 66 Tab.; Stuttgart (Enke).

MATTHEY, F. (1971): Contribution à l'étude de l'évolution tardi- et postglaciaire de la végétation dans le Jura central.- Beitr. geobot. Landesaufn. Schweiz, **53**: 1-86.

MATTHEY, F. (1985): Das Moorprofil „Chüealp". in VÖGELE, A. E.: Untersuchungen zur Geomorphologie und jungquartären Talgeschichte des Dischma (Davos Kt. Graubünden), S. 115-120.

MCMANUS, J. F., BOND, G. C., BROECKER, W. S., JOHNSEN, S., LABEYRIE, L. & HIGGINS, S. (1994): High-resolution climate records from the North Atlantic during the last interglacial.- Nature, **371**: 326-329.

MENKE, B. (1970): Ergebnisse der Pollenanalyse zur Pleistozän-Stratigraphie und zur Pliozän-Pleistozän-Grenze in Schleswig-Holstein.- Eiszeitalter u. Gegenwart, **21**: 5-21; Öhringen/Württ..

MENKE, B. (1985): Palynologische Untersuchungen zur Transgression des Eem-Meeres im Raum Offenbüttel/Nord-Ostsee-Kanal.- Geol. Jb., **A 86**: 19-26, 1 Abb., 1 Taf.; Hannover (Schweizerbart).

MENKE, B. & TYNNI, R. (1984): Das Eeminterglazial und das Weichselfrühglazial von Rederstall/Dithmarschen und ihre Bedeutung für die mitteleuropäische Jungpleistozän-Gliederung.- Geol. Jb., **A 26**: 3-120, 18 Abb., 7 Tab., 9 Taf.; Hannover (Schweizerbart).

MEUSEL, H., JÄGER, E. & WEINERT, E. (1964): Vergleichende Chorologie der zentraleuropäischen Flora.- Bd. I, Karten, 258 S..

MIETTINEN, A. (2004): Holocene sea-level changes and glacio-isostasy in the Gulf of Finland, Baltic Sea.- Quaternary International, **120**: 91-104; (Elsevier).

MÜLLER, H. (1974): Pollenanalytische Untersuchungen und Jahresschichtenzählungen an der eem-zeitlichen Kieselgur von Bispingen/Luhe.- Geol. Jb., **A 21**: 149-169, 5 Abb., 3 Tab.; Hannover (Schweizerbart).

MÜLLER, U. C. (2000): A Late-Pleistocene pollen sequence from the Jammertal, southwestern Germany with particular reference to location and altitude as factors determing Eemian forest composition.- Veget. Hist. Archaeobot., **9**: 125-131; (Springer).

MÜLLER, U. (2001): Die Vegetations- und Klimaentwicklung im jüngeren Quartär anhand ausgewählter Profile aus dem südwestdeutschen Alpenvorland.- TGA, Reihe D, **7**: 1-118, 30 Abb., 3 Tab.; Tübingen.

MULLER, D., DAVID, F. & WICHA, S. (2000): Impact de l'exposition des versants et de l'anthropisation sur la dynamique forestière dans les Alpes du Sud (France).- Géographie physique et Quaternaire, **54**: 231-243.

NIKLEWSKI, J. (1968): The Eemian Interglacial at Główczyn near Wyszogród (Central Poland) (Poln. mit engl. abstract).- Monographiae Botanicae, **XXVII**: 125-193.

NILSSON, T. (1935): Die pollenanalytische Zonengleiderung der spät- und postglazialen Bildungen Schonens.- Geol. Fören., Stockholm, Förhandl., **57**: 385-562.

NILSSON, T. (1964): Standardpollendiagramme und 14C-Datierungen aus dem Ageröds Mosse im mittleren Schonen.- Lunds Univ. Årsskr. N. F., **59/7**: 1-52.

NORTH GREENLAND ICE CORE PROJECT MEMBERS (2004): High-resolution record of Northern Hemisphere climate extending into the last interglacial period.- Nature, **431**: 147-151.

NORYŚKIEWICZ, B. (1978): The Eemian Interglacial at Nakło on the River Noteć (N Poland).- Acta Palaeobotanica, **XIX (1)**: 67-112.

NYDAL, R., GULLIKSEN, S., LÖVSETH, K. & SKOGSETH, F. (1985): Trondheim natural Radiocarbon measurements IX.- Radiocarbon, Vol. **27**, Nr. 3: 525-609.

OEGGL, K. & UNTERFRAUNER, H. (2000): Die Pflanzenreste des Riss/Würm-Interglazials und des Würmglazials von Mondsee.- Mitt. Komm. Quartärforsch., **12**: 93-121; Wien (Österr. Akademie der Wissenschaften).

OEGGL, K. & WAHLMÜLLER, N. (1994): Holozäne Vegetationsentwicklung an der Waldgrenze der Ostalpen: Die Plancklacke (2140)/Sankt Jakob im Defreggen, Osttirol.- In LOTTER, A. F. & AMMANN, B. (eds.) (1994): Festschrift Gerhard Lang.- Diss. Bot. **234**: 389-411; Berlin/Stuttgart (Cramer).

OEGGL, K. & WAHLMÜLLER, N. (1997): Die Waldgrenze in den Zentralalpen während des Mesolithikums. In: Alpine Vorzeit in Tirol.- Begleitheft zur Austellung, 65 S.; Innsbruck.

ONAC, B. P., BJÖRKMAN, L., BJÖRCK, S., CLICHICI, O., TAMAS, T., PEATE, D. & WOHLFARTH, B. (2001): The First Dated Eemian Lacustrine Deposit in Romania.- Quaternary Research, **56**: 62-65.

OSOLE, F. (1963): Mlajši Paleolitik iz Ovče jame.- Arheološki vestnik, **13-14**: 129-143; Ljubljana.

OSOLE, F. (1976): Paleolitik iz Županovega spodmola pri Sajevčah. Das Palaeolithikum aus Županov spodmol bei Sajevče.- Poročilo o raziskovanju paleolita, neolita in eneolita v Sloveniji, **V**: 7-28; Ljubljana.

OBIDOWICZ, A. (1990): Eine pollenanalytische und moorkundliche Studie zur Vegetationsgeschichte des Podhale-Gebietes (West-Karpaten).- Acta Palaeobotanica, **30(1,2)**: 147-219.

PARADUCCI, L., VILLANI, F., WANG, X.-R. & CHERUBINI, M. (1996): Genetic variation of *Abies alba* in Italy.- Hereditas, **125**: 11-18.

PAZDUR, M. F., AWSIUK, R., BLUSZCZ, A., PAZDUR, A., WALANUS, A. & ZASTAWNY, A. (1983): Gliwice Radiocarbon dates IX. Radiocarbon, Vol. **25,** No. 3: 843-866.

PÉCSI, M. (1975): Lithostratigraphical subdivision of the loess sequences in Hungary.- Földrajzi Közlemények, **23**: 217-229.

PEREZ-OBIOL, R. & JULIA, R. (1992): Climatic Change on the Iberian Peninsula Recorded in a 30.000-yr Pollen Record from Lake Banyoles.- Quaternary Research, **41**: 91-98.

PONEL, P. & LOWE, J. J. (1992): Coelopteran, pollen and radiocarbon evidence from the Prato Spilla "D" succession, N. Italy.- Comtes-Rendus de l'Académie des Sciènces, Paris, **315**, **II:** 1425-1431.

PONEL, PH., BEAULIEU, J.-L. DE & TOBOLSKI, K. (1992): Holocene palaeoenvironments at the timberline in the Taillefer Massif, French alps: a study of pollen, plant macrofossils and fossil insects.- The Holocene, **2,2**: 117-130; Norwich.

PONS, A. & REILLE, M. (1988): The Holocene- and upper Pleistocene pollen record from Padul (Granada, Spain): A new study.- Palaeogeography, Palaeoclimatology, Palaeoecology, **66**: 243-263; Amsterdam (Elsevier).

RABIEN, I. (1953): Die Vegetationsentwicklung des Interglazials von Wallensen in der Hilsmulde.- Eiszeitalter u. Gegenwart, **3**: 96-127; Öhringen/Württ. (Hohenlohe).

RALSKA-JASIEWICZOWA, M. (1980): Late-Glacial and Holocene vegetation of the Bieszczady Mts. (Polish Eastern Carpathians).- PańStowe Wydawnictwo Naukowe (PNW), 202 pp; Warszawa-Kraków.

RAVAZZI, C. (2002): Late Quaternary history of spruce in southern Europe.- Review of Palaeobotany and Palynology, **120 (1/2)**: 131-177; (Elsevier).

RAVAZZI, C. & PINI, R. (2002): The Late-Glacial and Early-Middle Holocene spruce expansion in the Eastern and Central Alps: A discussion and new data.- Razprave IV. Razreda Sazu, **XLIII-2**: 241-263, Fig. 5; Ljubljana.

REILLE, M. (1988): Nouvelles analyses polliniques de la tourbière de la Moulinasse: versant nord-oriental des Pyrénées (France).- Lab. Bot. Hist. Pal., 21 pp.

REILLE, M. (1990): Recherches pollenanalytiques dans l'extrémité orientale des Pyrénées: données nouvelles, de la fin du Glaciaire à l'Actuel.- Ecologia Mediterranea, **XVI**: 317-357.

REILLE, M. & BEAULIEU, J.-L. DE (1990): Pollen analysis of a long upper Pleistocene continental sequence in a Velay maar (Massif Central, France).- Palaeogeography, Palaeoclimatology, Palaeoecology, **80**: 35-48; Amsterdam (Elsevier).

REILLE, M. & LOWE, J. J. (1993): A re-evaluation of the vegetation history of the eastern Pyrenees (France) from the end of the last glacial to the present.- Quat. Sci. Rev., **12**: 47-77.

REILLE, M., ANDRIEU, V., BEAULIEU, J.-L. DE, GUENET, P. & GOEURY, C. (1998): A long pollen record from Lac du Bouchet, Massif Central, France: For the period ca. 325 to 100 ka BP (OIS 9c to OIS 5e).- Quaternary Science Reviews, **17**: 1107-1123; (Elsevier).

REYNAUD, CH. & TOBOLSKI, K. (1974): Etude paléobotanique d'une basse terrasse du fleuve Kemi (Tervola, Finlande) basée sur la palynologie et l'identification des restes macroscopiques.- Aquilo Ser. Bot., **13**: 35-52.

RICKEN, W. & GRÜGER, E. (1988): Vegetationsentwicklung, Paläoböden, Seespiegelschwankungen: Untersuchungen an eem- und weichselzeitlichen Sedimenten vom Südrand des Harzes.- Eiszeitalter u. Gegenwart, **38**: 37-51, 8 Abb., 1 Tab.; Hannover (Schweizerbart).

ROBERTSON, A.-M. (1988): Biostratigraphical studies of interglacial and interstadial deposits in Sweden.- USDQR Rep. **10**; Stockholm.

ROBERTSSON, A.-M. (1991): The Last Interglacial in northernmost Sweden.- Quaternary International, **10-12**: 173-181; (Pergamon).

ROBERTSSON, A.-M. (1997): Reinvestigation of the interglacial pollen flora at Leveäniemi, Swedish Lapland.- Boreas, **26**: 81-89; Oslo.

ROBERTSSON, A.-M., SVEDLUND, J.-O., ANDRÉN, T. & SUNDH, M. (1997): Pleistocene stratigraphy in the Dellen region, central Schweden.- Boreas, **26**: 237-260; Oslo.

RODMANN, C. (1987): Ein Pollendiagramm vom Origliosee. Palynologische Untersuchungen zur Spät- und Nacheiszeit im Südtessin.- Unveröff. Diplomarbeit Bot. Inst. Univ. Basel, 77 S.

RÖSCH, M. (1986): Zwei Moore im westlichen Bodenseegebiet als Zeugen prähistorischer Landschaftsveränderungen.- Telma, **16**: 83-111.

RÖSCH, M. (1989): Pollenprofil Breitnau-Neudorf: Zum zeitlichen Verlauf der holozänen Vegetationsentwicklung im südlichen Schwarzwald.- Carolinea, **47**: 15-24.

RÖSCH, M. (1990): Vegetationsgeschichtliche Untersuchungen im Durchenbergried.- In: Siedlungsarchäologie im Alpenvorland 2. Forschungen und Berichte zur Vor- und Frühgeschichte in Baden-Württemberg, **37**: 9-64.

RÖSCH, M. (1992): Human impact as registered in the pollen record - some results from western Lake Constance.- Vegetation History and Archaeobotany, **1**: 101-109.

RÖSCH, M. (1993): Prehistoric land use as recorded in a lake shore core at Lake Constance.- Vegetation History and Archaeobotany, **2**: 213-232.

RÖSCH, M. & FISCHER, E. (2000): A radiocarbon dated Holocene pollen profile from the Banat mountains (Southwestern Carpathians, Romania).- Flora, **195**: 277-286, Jena.

RUDDIMAN, W. F. (2004): Early Anthropogenic Overprints on Holocene Climate.- PAGES News, **12, 1**: 18-19.

RYBNIČEK, K. & RYBNIČKOVÁ, E. (1968): The history of Flora and Vegetation on the Bláto mire in Southeastern Bohemia, Czechoslovakia (Palaeoecological Study).- Folia Geobotanica et Phytotaxonomica, **3**: 117-142; Praha.

RYBNIČEK, K. & RYBNÍČKOVÁ, E. (1977): Mooruntersuchungen im oberen Gurgltal, Ötztaler Alpen.- Folia Geobot. Phytotax., **12**: 245-291; Praha.

RYBNÍČEK, K., DICKSON, J. & RYBNÍČKOVÁ, E. (1998): Flora and vegetation at about A.D. 1100 in the vicinity of Brno, Czech Republic.- Vegt. Hist. Archaeobot., **7**: 155-165; Berlin (Springer).

RYBNÍČKOVÁ, E. (1974): Die Entwicklung der Vegetation und Flora im südlichen Teil der Böhmisch-Mährischen Höhe während des Spätglazials und Holozäns.- Vegetace ČSSR, **A 7**: 149 S.; Praha.

RYBNÍČKOVÁ, E. & RYBNÍČEK, K. (1988): Holocene Palaeovegetation and Palaeoenvironment of the Kameničská kotlina Basin (Czechoslovakia).- Folia Geobotanica et Phytotaxonomica, **23**: 285-302; Praha.

SCHLOSS, S. (1979): Pollenanalytische und stratigraphische Untersuchungen im Sewensee. Ein Beitrag zur spät- und postglazialen Vegetationsgeschichte der Südvogesen.- Diss. Bot., **52**: 1-138; Vaduz.

SCHNEIDER, R. (1985): Analyse palynologique dans l'Aspromonte en Calabre (Italie méridionale).- Cahiers ligures de préhistoire et de protohistoire N.S., **2**: 279-288.

SCHNEIDER, R. & TOBOLSKI, K. (1985): Lago di Ganna - Late-glacial and Holocene environments of a lake in the Southern Alps. In LANG, G. (ed.) (1985): Swiss lake and environments during the last 15000 years.- Diss. Bot., **87**: 229-271; Vaduz.

SCHÖNWIESE, C.-D. (1995): Klimaänderungen.- 224 S.; Berlin, Heidelberg (Springer).

SCHWEINGRUBER, F. H. (1990): Anatomie europäischer Hölzer. Anatomy of European woods.- 800 S.; Bern (Paul Haupt).

SCOTTI, I., VENDRAMIN, G. G., MATTEOTTI, L. S., SCARPONI, C., SARI-GORLA, M. & BINELLI, G. (2000): Postglacial recolonisation routes for *Picea abies* K. in Italy as suggested by the analysis of sequence-characterized amplified region (SCAR) markers.- Molecular Ecology, **9**: 699-708.

SELLE, W. (1962): Geologische und vegetationskundliche Untersuchungen an einigen wichtigen Vorkommen des letzten Interglazials in Nordwestdeutschland.- Geol. Jb., **79**: 295-352, 1 Taf., 17 Abb., 11 Tab.; Hannover.

ŠERCELJ, A. (1996): The origins and development of forests in Slovenia.- Slovenska Akademija Znanosti in Umetnosti, Razred za naravoslovne vede, Dela (Academia Scientiarum et Artium Slovenica, Classis IV: Historia Naturalis, Opera), **35**: 5-135; Ljubljana.

ŠERCELJ, A. & CULIBERG, M. (1991): Palynological and anthracotomical investigations of sediments from the Divje Babe I Palaeolithic site. Razprave IV. Razreda SAZU XXXII, **4**, Ljubljana: 129-152.

SOBOLEWSKA, M. (1961): Flora of the Eemian Interglacial from Góra Kalwaria (Central Poland) (Poln. mit engl. abstract).- Inst. Geol., Biul., **169**: 73-90, 3 fig.; Warsaw.

SPERISEN, C., BÜCHLER, U., GUGERLI, F., MÁTYÁS, G., GEBUREK, T. & VENDRAMIN, G. G. (2001): Tandem repeats in plant mitochondrial genomes: application to the analysis of population differentiation in the conifer Norway spruce.- Molecular Ecology, **10**: 257-263; (Blackwell).

SRDOČ, D., SLIEPČEVIC, A., OBELIC, B. & HORVATINČIC, N. (1979): Rudjer Bošković Institute Radiocarbon measurements V.- Radiocarbon, Vol. **21**, Nr.1: 131-137.

ŚRODOŃ, A. (1967): The common spruce in the Quaternary of Poland.- Acta Palaeobot., **8** (**2**): 3-61.

ŚRODOŃ, A. (1968): On the vegetation of the Paudorf Interstadial in the Western Carpathians. Acta Palaeobotanica, **9** (**1**): 3-27.

ŚRODOŃ, A. (1983): The history of fir in Poland (Jodła pospolita w historii naszych Lasów).- Nasze drezewa Leśne, Monografie Popularnonaukowe, **4**: 9-39; Polska Akademia Nauk, Instytut Dendrologii.

ŚRODOŃ, A. (1990): Postglacial history of the common spruce (*Picea excelsa* (LAM.) Lk.) in the low Beskids separating the east from the west Carpathians.- Acta Palaeobotanica, **30(1,2)**: 221-226.

STALLING, H. (1983): Untersuchungen zur nacheiszeitlichen Vegetationsgeschichte des Meißners (Nordhessen).- Flora, **174**: 357-376; Jena.

STALLING, H. (1987): Untersuchungen zur spät- und postglazialen Vegetationsgeschichte im Bayerischen Wald.- Dissertation zur Erlangung des Doktorgrades der Mathematisch-Naturwissenschaftlichen Fachbereiche der Georg-August-Universität zu Göttingen, 154 S.; Göttingen.

STEFANOVA, I. (1997): New data on the Late Holocene vegetative succession in the Northern Pirin Mountains: pollen and macrofossil analysis of depositions from the peat bogs of Goce Delchev and Visokata Ela.- Phytologia Balcanica, **3**/2-3: 53-63.

SZCZEPANEK, K. (1971): The Staszów karst in the light of palaeobotanical studies (South Poland).- Acta Palaeobotanica, Vol. **XII**, Nr. 2: 64-140; Kraków.

TESSIER, L., BEAULIEU, J.-L. DE, COUTEAUX, M., EDOUARD, J.-L., PONEL, PH., ROLANDO, CH., THINON, M., THOMAS, A. & TOBOLSKI, K. (1993): Holocene palaeoenvironments at the timberline in the French Alps – a multidisciplinary approach.- Boreas, **22 (3)**: 244-254; Oslo.

TEUNISSEN, D., BRAUM, F. J. & TEUNISSEN-VAN OORSCHOT, H. (1972): Eine weichselfrühglaziale Torf-/Tonschicht in periglazialen Hangsedimenten von Neheim-Hüsten im Ruhrtal.- Fortschr. Geol. Rheinld. u. Westf., **21**: 303-316, 3 Abb., 1 Tab.; Krefeld.

THIEBAULT, S. (1994): Evolution de la vegetation holocene à la Balme de Thuy (Haute-Savoie, France), l'apport de l'anthracologie.- Revue de Paléobiologie, **13/2**: 341-350; Genève.

THOMSON, P. W. (1941): Die Klima- und Waldentwicklung des von K. Orviku entdeckten Interglazials von Ringen bei Dorpat/Estland.- Z. dt. geol. Ges., **93**: 274-282; Hannover

TIKKANEN, M. & OKSANEN, J. (2002): Late Weichselian and Holocene shore displacement history of the Baltic Sea in Finland.- Fennia, **180**, **1**-2: 9-20.

TINNER, W. & CONDERA, M (1995): Indagini paleobotanice sulla storia della vegetazione e degli incendi forestali durante l'olocene al Lago di Origlio (Ticino meridionale).- Bollettino della Società ticinese di scienze naturali, **83 (1-2)**: 91-106.

TOBOLSKI, K. (1986): Palaeobotanical studies of the Eemian interglacial and Early Vistulian, Władysławów in the vicinity of Turek. (Preliminary report).- Quaternary Studies in Poland, **7**: 91-101; Poznan.

TOBOLSKI, K. (1991): Biostratigraphy and Palaeoecology of the Eemian Interglacial and the Vistulian glaciation of the Konin region (Poln. mit engl. abstract).- In STANKOWSKI, W. (ed.): Przemiany środowiska geograficznego obszaru Konin-Turek, S. 45-87; Poznań (Universitätsverlag).

TONKOV, S. B & BOZILOVA, E. (1992): Palaeoecological investigation of Tschokljovo Marsh (Konjavska Mountain).- Annuaire de l'université de Sofia, **83**: 5-16.

TURK, I., DIRJEC, J. & CULIBERG, M. (1988-89): Divje Babe I – Novo paleolitsko najdišče in Skupinsko Grobišče jamskega medveda.- Arheološki vestnik, **39-40**: 13-60.

TZEDAKIS, P. C. (2000): Vegetation variability in the Greece during the last interglacial.- Geologie en Miijnbouw / Netherlands Journal of Geoscience, **79 (2/3)**: 355-367; Utrecht.

TZEDAKIS, P. C., LAWSON, I. T., FROGLEY, M. R., HEWITT, G. M. & PREECE, R. C. (2002): Buffered Tree Population Changes in a Quaternary Refugium: Evolutionary Implications.- Science, **297**: 2044-2047.

UZQUIANO, P. (1992a): L'Homme et le bois au Paléolithique en région Cantabrique, Espagne. Exemples d'Altamira et d'Buxu.- Bull. Soc. bot. Fr., **139 (2/3/4)**: 361-372.

UZQUIANO, P. (1992b): The late glacial/postglacial transition in the Cantabrian Cordillera (Asturias and Cantabria, Spain) based on charcoal analysis.- Palaios, 7 (5): 540-547.

VENDRAMIN, G. G., DEGEN, B., PETIT, R. J., ANZIDEI, M., MADAGHIELE, A. & ZIEGENHAGEN, B. (1999): High level of variation at *Abies alba* chloroplast microsatellite loci in Europe.- Molecular Ecology, **8**: 1117-1126.

VENDRAMIN, G. G., ANZIDEI, M., MADAGHIELE, A., SPERISEN, C. & BUCCI, G. (2000): Chloroplast microsatellite analysis reveals the presence of population subdivision in Norway spruce (*Picea abies* K.).- Genome, **43**: 68-78.

VERNET, J.-L. (1980): La vegetation du bassin de l'Aude, entre pyrenees et Massif Central, au tardiglaciaire et au postglaciaire d'apres l'analyse anthracologique.- Review of Palaeobotany and Palynology, **30**: 33-55; Amsterdam (Elsevier).

VÉRTES, L. (1964): Das Jungpaläolithikum von Arka in Nord-Ungarn.- Quartär, **15/16**: 79-132.

VOGEL, J. C. & WATERBOLK, H. T. (1964): Groningen Radiocarbon Dates V.- Radiocarbon, Vol. **6**: 349-369.

VOIGT, R. (1996): Paläolimnologische und vegetationsgeschichtliche Untersuchungen an Sedimenten aus Fuschlsee und Chiemsee (Salzburg und Bayern).- Dissertationes Botanicae, **270**: 1-303.

WATTS, W. A. (1985): A long pollen record from Laghi di Monticchio, southern Italy: a preliminary account.- J. geol. Soc. London, **142**: 491-499, 2 figs..

WEGMÜLLER, S. (1966): Über die spät- und postglaziale Vegetationsgeschichte des südwestlichen Jura.- Beitr. geobot. Landesaufn. Schweiz, **48**: 1-144; Bern (Hans Huber).

WEGMÜLLER, S. (1976): Pollenanalytische Untersuchungen über die Siedlungsverhältnisse der frühneolithischen Station Egolzwil 5.- Sonderdruck der naturwissenschaftlichen Beiträge aus: Archäologische Forschungen, 141-162; Zürich.

WEGMÜLLER, S. (1992): Vegetationsgeschichtliche und stratigraphische Untersuchungen an Schieferkohlen des nördlichen Alpenvorlandes.- Denkschriften der Schweizerischen Akademie der Wissenschaften, **102**: 1-82; Basel Boston Berlin (Birkhäuser).

WEGMÜLLER, S. & LOTTER, A. F. (1990): Palynostratigraphische Untersuchungen zur spät- und postglazialen Vegetationsgeschichte der nordwestlichen Kalkalpen.- Botanica Helvetica, **100/1**: 37-73; Basel (Birkhäuser).

WELTEN, M. (1982a): Vegetationsgeschichtliche Untersuchungen in den westlichen Schweizer Alpen: Bern-Wallis.- Denkschriften der Schweizerischen Naturforschenden Gesellschaft, **Bd. 95**: 1-104, 37 Diagramme (Extraheft); Basel (Birkhäuser).

WELTEN, M. (1982b): Pollenanalytische Untersuchungen im Jüngeren Quartär des nördlichen Alpenvorlandes des Schweiz.- Beiträge zur Geologischen Karte der Schweiz, 156: 174 S., 17 Fig., 8 Tab.; Bern.

WESSEL, P. & SMITH, W. H. F. (1998): New, improved version of the Generic Mapping Tools released.- EOS Transactions AGU, **79 (49)**: p. 579.

WESSEL, P. & SMITH, W. H. F. (1999): The Generic Mapping Tools Technical Reference and Cookbook.- Version 3.3, pp.132.

WEST, R. G (1957): Interglacial deposits at Bobbitshole, Ipswich.- Phil. Trans. R. Soc. Lond., **B 241**: 1-31.

WICK, L. & TINNER, W. (1997): Vegetation changes and timberline fluctuations in the Central Alps as indicators of Holocene climatic oscillations.- Arctic and Alpine Research, Vol. **29**, **No. 4**: 445-458.

WIJMSTRA, T. A. (1969): Palynology of the first 30 metres of a 120 m deep section in Northern Greece.- Acta Bot. Neerl., **18(4)**: 511-527.

WILLIS, K. J. (1992): The late Quaternary vegetational history of northwest Greece. II. Rezina marsh.- New Phytol., **121**: 119-138.WILLIS, K. J. (1996): Where did all the flowers go? The fate of temperate European flora during glacial periods.- Endeavour, **20**: 110-114.

WILLIS, K. J., RUDNER, E. & SÜMEGI, P. (2000): The Full-Glacial Forests of Central and Southeastern Europe. Quaternary Research **53**: 203-213.

WOHLFARTH, B., SCHWARK, L., BENNIKE, O., FILIMONOVA, L., TARASOV, P., BJÖRKMAN, L., BRUNNBERG, L., DEMIDOV, I. & POSSNERT, G. (2004): Unstable early-Holocene climatic and environmental conditions in northwestern Russia derived from a multidisciplinary study of a lake-sediment sequence from Pichozero, southeastern Russian Karelia.- The Holocene, **14,5**: 732-746.

WOILLARD, G. M. (1975): Recherches palynologiques sur le Pléistocène dans l'est de la Belgique et dans les Vosges lorraines.- Acta Geographica Lovaniensia, **14**: 1-118; Louvain la Neuve.

WOILLARD, G. M. (1978): Grand Pile peat bog: A continuous pollen record for the last 140,000 years.- Quaternary Research, **9**: 1-21, 5 Fig., 1 Tab..

WRIGHT, H. E., Jr., AMMANN, B., STEFANOVA, I., ATANASSOVA, J., MARGALITADZE, N., WICK, L. & BLYAKHARCHUK , T. (2003): Late-glacial and Early-Holocene Dry Climates from the Balkan Peninsula to Southern Sibiria.- Aspects of Palynology and Palaeoecology, *Festschrift in honour of Elissaveta Bozilova*: 127-136; Sofia–Moscow (Pensoft).

ZAGWIJN, W. H. (1961):Vegetation, climate and radiocarbon datings in the Late Pleistocene of the Netherlands. Part I: Eemian and Early Weichselian.- Meded. geol. St., N.S. **14**: 15-45.

ZAGWIJN, W. H. (1989): Vegetation and climate during warmer intervals in the Late Pleistocene of Western and Central Europe.- Quaternary International, **3/4**: 57-67.

ZAGWIJN, W. H. (1992): Migration of vegetation during the Quaternary in Europe.- Courier Forsch.-Inst. Senckenberg, **153**: 9-20, 11 Fig.; Frankfurt a. M.

ZAGWIJN, W. H. (1996): An analysis of Eemian climate in Western and Central Europe.- Quaternary Science Reviews, **15**: 451-469; (Elsevier).

ZOLLER, H. (1960): Pollenanalytische Untersuchungen zur Vegetationsgeschichte der insubrischen Schweiz.- Denkschriften der Schweizerischen Naturforschenden Gesellschaft, Band **LXXXIII**, Abh. 2: 45-157; Zürich.

ZOLLER, H., SCHINDLER, C. & RÖTHLISBERGER, H. (1966): Postglaziale Gletscherstände und Klimaschwankungen im Gotthardmassiv und Vorderrheingebiet.- Verhandlungen der Naturforschenden Gesellschaft in Basel, Band 77, Heft **2**: 97-164.

ZOLLER, H. & KLEIBER, H. (1971): Vegetationsgeschichtliche Untersuchungen in der montanen und subalpinen Stufe der Tessintäler.- Verhandlungen der Naturforschenden Gesellschaft in Basel, Band **81**, Nr. 1: 1-156.

ZWAHLEN, R. (1985): Lörmoos - Late-glacial and Holocene environments of an ancient lake on the Central Swiss Plateau. In LANG, G. (ed.) (1985): Swiss lake and environments during the last 15000 years.- Diss. Bot., **87**: 171-184; Vaduz.

Appendix

Appendix I

List of pollen and macrofossil sites used for the *Abies* maps (Eemian)

Site name	Latitude/ Longitude	Author(s)	Macroremains
Amersfoort 1	(52.0927/05.2322)	Zagwijn (1961) and Cleveringa et al. (2000)	X
Aschenhütte	(51.4036/10.1807)	Ricken and Grüger (1988)	N
Barendorf 3	(53.1348/10.3121)	Freund et al. (1997)	X
Bispingen	(53.0420/09.5928)	Müller (1974)	X
Glówczyn	(52.2915/20.1136)	Niklewski (1968)	Y
Gondiswil-Seilern	(47.0845/07.5220)	Wegmüller (1992)	X
Góra Kalwaria	(51.5831/21.1331)	Sobolewska (1961)	N
Grabschütz	(51.2826/12.1638)	Litt (1990, 1994) and Mai (1990b)	N
Grevenhof	(53.0607/10.0220)	Behre (1962)	X
Gröbern	(51.4128/12.2719)	Litt (1990, 1994) and Mai (1990a)	N
Groß Todtshorn	(53.1248/09.4642)	Caspers (1997) and Freund (1997)	N
Helgoland	(54.1117/07.5339)	Behre (1970)	N
Husum	(54.2825/09.0253)	Menke (1985)	X
Imbramowice	(50.2825/16.3342)	Mamakowa (1989)	Y
Ioannina	(39.4500/20.5100)	Tzedakis (2000) and Tzedakis et al. (2002)	X
Jammertal	(48.0600/09.4344)	Müller (2000, 2001)	X
Jozwin	(52.2340/18.1124)	Tobolski (1991)	N
Kamphuis	(52.2042/07.0226)	Geel et al. (1986)	N
Kittlitz	(51.5008/13.5603)	Erd (1973)	X
Lac du Bouchet (H)	(44.5500/03.4700)	Reille et al. (1998)	X
La Grande Pile	(47.4400/06.3014)	Woillard (1975, 1978) and de Beaulieu and Reille (1992a)	X
Les Echets	(45.5213/04.5455)	de Beaulieu and Reille (1984, 1989)	X
Leveäniemi	(67.3800/21.0100)	Robertson (1991, 1997) and Robertson et al. (1997)	X
Meikirch	(47.0034/07.2205)	Welten (1982b)	X
Mertuanoja	(64.0700/24.3500)	Eriksson et al. (1999)	X
Mondsee	(47.5107/13.2046)	Klaus (1975), Drescher-Schneider (2000) and Oeggl and Unterfrauner (2000)	Y
Naklo	(53.0925/17.3527)	Noryskiewicz (1978)	N
Neumark-Nord	(50.3929/12.2120)	Litt (1994)	N

Odderade 7	(54.0828/09.1129)	Averdieck (1967)	N
Oerel	(53.2859/09.0325)	Behre and Lade (1986)	X
Osterwanna II	(53.4437/08.4840)	Behre (1974)	X
Quakenbrück	(52.4030/07.5721)	Hahne at al. (1994 a)	N
Rederstall I	(54.1346/09.1219)	Menke and Tynni (1984)	X
Ribains	(44.5035/03.4950)	de Beaulieu and Reille (1992b)	X
Samerberg I	(47.4500/12.1200)	Grüger (1979a,b)	Y
Schönfeld	(51.4930/13.5430)	Erd (1991)	X
Schwindebeck	(52.0730/10.0658)	Behre (1962)	Y
Tenagi Philippon TF1/TF2	(41.1000/24.2000)	Wijmstra (1969) and Tzedakis (2000)	X
Valle di Castiglione	(41.5330/12.4535)	Follieri et al. (1988) and Follieri et al. (1998)	X
Waewa-Ringen	(58.0843/26.1453)	Thomson (1941)	X
Wallensen	(52.0107/09.3716)	Rabien (1953)	N
Wing	(52.3650/-00.4505)	Hall (1980)	N
Wladyslawow	(52.0800/18.2800)	Tobolski (1986, 1991)	N
Zgierz-Rudunki	(51.5039/192520)	Jastzebska-Mamelka (1985)	N

Appendix II

List of pollen and macrofossil sites used for the *Abies* maps (Brørup)

Site name	Latitude/ Longitude	Author(s)	Macroremains
Aschenhütte	(51.4036/10.1807)	Ricken and Grüger (1988)	N
Barendorf 2	(53.1348/10.3121)	Freund et al. (1997)	X
Barendorf 3	(53.1348/10.3121)	Freund et al. (1997)	X
Gondiswil-Seilern	(47.0845/07.5220)	Wegmüller (1992)	X
Gröbern	(51.4128/12.2719)	Litt (1990, 1994) and Mai (1990a)	N
Ioannina	(39.4500/20.5100)	Tzedakis (2000) and Tzedakis et al. (2002)	X
Jammertal	(48.0600/09.4344)	Müller (2000, 2001)	X
Keller	(54.0437/09.2534)	Menke (1970)	X
Kittlitz	(51.5008/13.5603)	Erd (1973)	X
Lac du Bouchet (D)	(44.5500/03.4700)	Reille and de Beaulieu (1990)	X
Lagaccione	(42.3400/11.5100)	Follieri et al. (1998) and Magri (1999)	X
Lago Grande di Monticchio	(40.5600/15.3500)	Allen et al. (1999)	X
La Grande Pile	(47.4400/06.3014)	Woillard (1975, 1978) and de Beaulieu and Reille (1992a)	X
Les Echets	(45.5213/04.5455)	de Beaulieu and Reille (1984, 1989)	X
Meikirch	(47.0034/07.2205)	Welten (1982b)	X
Mondsee	(47.5107/13.2046)	Klaus (1975), Drescher-Schneider (2000) and Oeggl and Unterfrauner (2000)	Y
Neheim-Hüsten	(51.2703/07.5800)	Teunissen et al. (1972)	N
Odderade 5	(54.0828/09.1129)	Averdieck (1967)	N
Oerel	(53.2859/09.0325)	Behre and Lade (1986)	X
Osterwanna II	(53.4437/08.4840)	Behre (1974)	N
Padul	(37.0000/-03.4000)	Pons and Reille (1988)	X
Pilgrimstad	(62.5800/150100)	Robertson (1988)	X
Rederstall I	(54.1346/09.1219)	Menke and Tynni (1984)	X
Ribains	(44.5035/03.4950)	de Beaulieu and Reille (1992b)	X
Samerberg 1973	(47.4500/12.1200)	Grüger (1979a,b)	Y
Tenagi Philippon II	(41.1000/24.2000)	Wijmstra (1969)	X
Valle di Castiglione	(41.5330/12.4535)	Follieri et al. (1988) and Follieri et al. (1998)	X
Wladyslawow	(52.0800/18.2800)	Tobolski (1986, 1991)	N
Zgierz-Rudunki	(51.5039/192520)	Jastzebska-Mamelka (1985)	N

Appendix III

List of pollen and macrofossil sites used for the *Abies* maps (Odderade)

Site name	Latitude/ Longitude	Author(s)	Macroremains
Gondiswil-Seilern	(47.0845/07.5220)	Wegmüller (1992)	X
Gröbern	(51.4128/12.2719)	Litt (1990, 1994) and Mai (1990a)	N
Ioannina	(39.4500/20.5100)	Tzedakis (2000) and Tzedakis et al. (2002)	X
Jammertal	(48.0600/09.4344)	Müller (2000, 2001)	X
Kittlitz	(51.5008/13.5603)	Erd (1973)	X
Lac du Bouchet (D)	(44.5500/03.4700)	Reille and de Beaulieu (1990)	X
Lagaccione	(42.3400/11.5100)	Follieri et al. (1998) and Magri (1999)	X
Lago Grande di Monticchio	(40.5600/15.3500)	Allen et al. (1999)	X
La Grande Pile	(47.4400/06.3014)	Woillard (1975, 1978) and de Beaulieu and Reille (1992a)	X
Les Echets	(45.5213/04.5455)	de Beaulieu and Reille (1984, 1989)	X
Mondsee	(47.5107/13.2046)	Klaus (1975), Drescher-Schneider (2000) and Oeggl and Unterfrauner (2000)	Y
Neheim-Hüsten	(51.2703/07.5800)	Teunissen et al. (1972)	N
Odderade 5	(54.0828/09.1129)	Averdieck (1967)	N
Oerel	(53.2859/09.0325)	Behre and Lade (1986)	X
Padul	(37.0000/-03.4000)	Pons and Reille (1988)	X
Pilgrimstad	(62.5800/150100)	Robertson (1988)	X
Rederstall I	(54.1346/09.1219)	Menke and Tynni (1984)	X
Ribains	(44.5035/03.4950)	de Beaulieu and Reille (1992b)	X
Samerberg 1973	(47.4500/12.1200)	Grüger (1979a,b)	N
Tenagi Philippon II	(41.1000/24.2000)	Wijmstra (1969)	X
Valle di Castiglione	(41.5330/12.4535)	Follieri et al. (1988) and Follieri et al. (1998)	X
Wladyslawow	(52.0800/18.2800)	Tobolski (1986, 1991)	N
Zgierz-Rudunki	(51.5039/192520)	Jastzebska-Mamelka (1985)	N

Annotation according to the macroremains (Appendix II-IV):

Y - Macroremains existent
N - No macroremains
X - No investigations on macroremains

Appendix IV

List of pollen sites used for the *Abies* maps (Holocene)

(source: European Pollen Database / http://medias.obs-mip.fr/paleo/epd/epd_main.html)

(for contributors' references see Database Meta Information)

Aegelsee (46.3845/07.3236), Aghia Galini (35.0600/24.4100), Ahlenmoor (53.4200/08.4400), Albufera Alcudia (39.4734/03.0709), Algendar (39.5626/03.5731), Altenweiher (48.0048/06.5940), Ampoix (48.1000/02.5600), Amsoldingersee (46.4330/07.3430), Antas (37.1230/-01.4925), Aronde (49.2745/02.4128), Atxuri (43.1500/-01.3300), Banyoles [Girona] (42.0800/02.4500), Barbora JC-6-B (48.5630/14.5600), Beaufort Birkenbach (49.5050/06.0733), Besbog-2 (41.4500/23.4000), Biot (43.4800/07.0600), Biscaye (43.0200/-00.0500), Blato (Zispachy) (49.0230/15.1130), Bledowo lake (52.3300/20.4000), Boehnigsee Goldmoos (46.1533/07.5035), Bolotnoye (51.0300/24.4800), Bolotnya (50.2000/23.5700), Borkovicka Blata (49.1300/14.5400), Brana (48.5700/14.5600), Breidfeld (50.0722/06.0347), Cala Galdana (39.5613/03.5754), Cala'n Porter (39.5214/04.0753), Cervene Blato (48.5100/14.5600), Clapeyret (44.0850/07.1420), Col des Lauzes (45.4609/06.3200), Colfiorito (43.0130/12.5530), Crovani (42.2810/08.4056), Czajkow (50.4700/21.17000), Darzlubie Forest (54.4200/18.1000), Dry Lake II [Rila mountain] (42.0300/23.3200), Dürrenecksee-Moor (47.1000/13.5200), Dvur Ansov (48.4730/16.2315), Edessa (40.4905/21.5709), Etang de Cheylade (45.0524/02.5342), Flögeln (53.4000/-08.4550), Fougères (48.3100/00.5000), Frasne (Doubs) (46.4953/06.0944), Freychinède (42.2800/01.2611), Fuchsschwanzmoos (47.0700/13.5400), Georgenfelder Hochmoor (50.4500/13.4500), Giannitsa B (40.4000/22.1900), Giecz (52.1910/17.2148), Gorno (50.5100/20.5000), Grand Ratz le Pellet (45.2030/05.3630), Grosses Überling Schattseit-Moor (47.1000/13.5400), Halos I (39.1000/22.5000), Hières sur Amby (45.4727/05.1700), Hockham Mere (52.3000/00.5000), Hort Timoner (39.5230/04.0735), Hozelec SK-5-A (49.0300/18.1800), Ioannina (39.3900/20.5500), Ioannina I (39.4545/20.4350), Ioannina II (39.4131/20.5023), Ivano-Frankovskoye (49.5500/23.4600), Jasiel (49.2222/21.5313), Kamenicky (49.4400/15.5800), Kastoria (40.3307/21.1920), Khimaditis Ib (40.3700/21.3500), Khimaditis III (40.3645/21.3510), Kluki (54.4225/17.1705), Kolczewo (53.5500/14.4000), Kopais (38.2900/23.4000), Kulichkovskoye (50.2000/24.7000), Kupena (Western Rhodopes Mts.) (41.5900/24.2000), La Grande Pile (47.4400/06.3014), La Taphanel (45.1628/02.4045), Lac de Creno (42.1203/08.5651), Lac de Lod (45.4800/07.5030), Lac de Siguret (44.4730/06.3300), Lac de Villa (45.4105/07.4540), Lac du Mont de Belier (45.2016/02.3835), Lac Long Inférieur (44.0328/07.2700), Lac Mouton (44.0328/07.2641), Lac Noir (45.2713/02.3738), Lac Saint Léger (44.2512/06.2011), Lade Bank (53.0500/00.0300), Lagaccione (42.3400/11.5100), Lago di Martignano (42.0700/12.2000), Lago di Vico (42.1900/12.1000), Lago Grande di Monticchio (40.5640/15.3600), Lago Padule (44.1755/10.1253), Lake Balaton centre (46.4440/17.2403), Lake Balaton NE (47.0006/18.0615), Lake Balaton SW (46.4906/17.4406), Lake Lednica (52.3325/17.2325), Lake Racze (53.5500/14.4000), Lake Skvzetuszewskie (52.3300/17.2138), Lake Skvzetuszewskie (52.3300/17.2138), Lake Suho Ezero (42.0800/23.2500), Lake Xinias (39.0300/22.1600), Landos (44.5100/03.4930), Le Beillard (48.0424/06.4804), Le Grand Etang de Suze-La-Rousse (44.2100/05.1400), Le Grand Lemps (45.2824/05.2500), Le Jolan (45.0822/02.5133), Le marais de la Perge (sud) (45.2257/-01.0654), Le Monge (43.0300/-00.0100), Les Enfers (47.1500/07.1000), Les Veaux (47.1500/07.1000), L'Estivalet

(44.5121/03.2308), Liptovsky Jan (49.0230/19.4040), Lobsigensee (47.0155/07.1757), Lomzyca 2 (53.0930/22.0300), Lopatin (50.1300/24.5000), Loras (45.3950/05.1440), Loucky (49.1930/15.3010), Makovich (50.5800/24.1300), Maleshevska Mts (41.4200/23.0200), Malhaire (48.3000/-01.0000), Maly podleski (49.5500/24.1000), Marais de la Perge (45.2351/-01.0037), Mikolajki lake (53.4605/21.2505), Mire Johvika (58.3000/22.2000), Mokre Louky (south) (48.5000/14.5000), Moulin de Prugnolas (45.5059/01.3845), Mutorog - Southern Pirin Mts. (43.3100/23.3700), Naklo near Notec (53.0900/17.3600), Navarrés (39.0600/-00.4100), Olbramovice (48.5930/16.2400), Oltush Lake (51.4148/23.5724), Ospitale (44.0920/10.4648), Palasiny (49.4120/15.2900), Pamerkiai outcrop (54.1850/24.4410), Pecheniya (49.4000/23.5600), Pelléautier (44.3120/06.1100), Peyrelevade (45.4230/02.2300), Plaine Alpe (44.5750/06.3539), Plan du Laus (44.1430/06.4208), Polonichka (50.1600/24.4500), Popovo Ezero (41.4300/23.4000), Pré Rond (44.5508/06.3539), Puerto de Belate (43.0200/-02.0300), Puscizna Rekowianska (49.2900/19.4900), Puy de Pailleret (45.3100/02.4900), Rasna pond (49.1350/15.2215), Regetovka (49.2530/21.1645), Rezabinec (49.1500/14.0700), Rodenbourg Bretzboesh (49.4130/06.1612), Roquetas de Mar (36.4740/-02.3520), Rosle Nowe (52.0800/18.5500), Rotsee (47.0432/08.1932), Sabbion (44.0748/07.2824), Saint Julien de Ratz (45.2100/05.3724), Saint Sixte (45.2530/05.3730), Sanabria Marsh (42.0600/-06.4400), Schwemm (47.3900/12.1800), Selle di Carnino (44.0900/07.4140), Slopiec (50.4700/20.4700), Solokiya (50.2500/24.1000), Steklin (52.5600/18.5900), Stoyanov-1 (50.2300/24.3800), Stoyanov-2 (50.2300/24.3800), Suchedniow (51.0300/20.5100), Svyatoye-2 (51.0600/24.2000), Szymbark (49.3800/21.0600), Tarnawa Wyzna (49.0600/22.5000), Tarnowiec (49.4200/21.3700), Tenaghi Philippon (40.5900/24.4700), Tourbière de Champlong (45.4915/07.4827), Tourbière de la Borde (42.3200/02.0500), Tourbière de Pilaz (45.4901/07.5000), Tourbière de Santa Anna (45.5130/07.3915), Tourves (43.3000/05.5400), Trikhonis 5 (38.3600/21.3000), Trumer Moos (47.5600/13.0400), Tschokljovo marsh (42.2200/22.5000), Vallon de Provence (44.2328/06.2415), Vegoritis 8 (40.4500/21.4500), Vernerovice (50.0600/16.1500), Vitosha mountain (42.5000/23.5000), Voros-mocsar (46.2838/19.1127), Vracov (48.5840/17.1210), Wachel 3 (53.0217/08.0211), Wasenmoos beim Zellhof (47.5900/13.0600), Wiggenhall ST Germans A (52.4100/00.2000), Wolin II (53.5000/14.4000), Zarnowiec peat bog (54.4300/18.0700), Zbudovska Blata (49.5000/14.1950), Zirbenwaldmoor (46.5130/11.0130), Zsombo-swamp (46.2141/19.5939), Zurawiec (54.2500/16.3000), Zvenigorod-Kotsurovskoye (49.4800/24.1400)

Additional pollen sites used for the *Abies* maps (Holocene)

Site name	Latitude/Longitude	Author(s)
Breitenau-Neuhof	(47.5800/08.1200)	Rösch (1989)
Durchenbergried	(47.4400/08.5900)	Rösch (1986, 1990)
Haslacher See	(47.4500/10.4700)	Küster (1986, 1988, 1989)
Hornstaad-Bodensee	(47.4000/09.0100)	Rösch (1992, 1993)
Prato Spilla	(43.5400/11.0408)	Ponel and Lowe (1992)
Rappershausen	(50.2045/10.2540)	Hahne (1991)
Sauborst	(50.1601/12.0438)	Hahne (1992)
Schwarzes Moor	(50.2703/10.0925)	Hahne (1991)
Seelohe (Profil 1+2)	(50.0131/11.4715)	Hahne (1992)
Weissenstadter Forst	(50.0749/11.5258)	Hahne (1992)
Wolfslohe	(49.5323/11.5917)	Hahne (1992)

List of macrofossil sites used for the *Abies* maps (Holocene)

Site name	Latitude/Longitude	Author(s)
Aletschwald	(46.2323/08.0132)	Welten (1982a), van der Knaap and Ammann (1997), Appleby, (unpubl. 1998b), van der Knaap et al. (2000)
Altamira	(43.2241/-04.0705)	Uzquiano (1992a)
Balme de Thuy	(45.5408/06.1624)	Thiébault (1994)
Bedrina, Monte Piottino	(46.2903/08.4626)	Zoller (1960)
Belvis	(42.5018/01.5234)	Vernet (1980)
Bibersee	(47.1225/08.2800)	ALPADABA
Divje babe	(46.0738/13.5926)	Šercelj (1996), Šercelj and Culiberg (1991), Turk et al. (1988-89)
Dolní Věstonice	(48.5255/16.4143)	Klíma (1963), Kneblová (1954), Damblon et al. (1996)
Dourgne	(42.5034/02.0948)	Vernet (1980)
Eggen ob Blatten	(46.2219/07.5926)	Welten (1982a), van der Knaap and Ammann (1997)
Faulenseemoos	(46.4049/07.4141)	Welten (1982a), Lotter et al. (1996)
Forrenmoos	(47.0007/08.1331)	Gehrig (1989), Gehrig (1991)
Gazel	(43.2036/02.2926)	Vernet (1980)
Gola di Lago	(46.0619/08.5757)	Zoller and Kleiber (1971)
Grächen-See	(46.1150/07.5046)	Welten (1982a), van der Knaap and Ammann (1997)
Hobschensee	(46.1510/07.5039)	Ammann (1988), Lang and Tobolski (1985)
La Balma Margineda	(42.2800/01.3000)	Leroyer and Heinz (1992)
Lac Canard Ib	(45.0400/05.5602)	Ponel et al. (1992), Tessier et al. (1993), Hölzer and Hölzer (1987), Couteaux (1982)

Lac de Saint-Léger	(44.2500/06.2000)	Digerfeldt et al. (1997)
Lago di Ganna	(45.5354/08.4939)	Schneider and Tobolski (1985)
Lago di Origlio	(46.0306/08.5642)	Rodmann (1987), Tinner and Conedera (1995)
Les Embreux	(47.1550/07.0706)	Hubschmid and Lang (1985), Matthey (1971), Wegmüller, (1966)
L'Etoile á Nice	(43.4418/07.1709)	Dubar (1986), Damblon et al. (1988)
L'Urgo de Pietra Giordano	(37.5000/14.0300)	Bertolani Marchetti et al. (1984)
Pian di Signano	(46.1553/09.0825)	Zoller (1960)
Pilatussee	(46.5754/08.1149)	Gehrig (1989, 1991)
Pré Rond	(44.5508/06.3539)	Muller et al. (2000)
Rezina marsh	(39.5900/20.4900)	Willis (1992)
Rotsee RL-300	(47.0433/08.1933)	Lotter (1988), Lotter (1991), Lotter et al. (1992)
Šandalja II	(44.5138/13.5024)	Culiberg and Šercelj (1995)
Schwarzmoos L-34	(46.3736/07.2856)	Wegmüller and Lotter (1990)
Sewensee	(47.4829/06.5430)	Schloss (1979), Woillard (1975), Woillard (1978), Juvigne (1977), Janssen (1974)
Soppensee SO89-17	(47.0530/08.0454)	Lotter (1997)
Sopra "Fienile Rossini"	(45.3200/10.1500)	Castelletti and Leoni (1987)
St. Jean de la Porte	(45.3200/06.0800)	unpublished data from Lab Lyon
Suossa	(46.2612/09.1156)	Zoller and Kleiber (1971)
Tschokljovo	(42.2200/22.5000)	Tonkov and Bozilova (1992)
Val Frisal	(46.4814/09.0040)	Zoller et al. (1966)

Appendix V

List of pollen and macrofossil sites used for the *Picea* maps (Eemian)

Site name	Latitude/ Longitude	Author(s)	Macroremains
Amersfoort 1	(52.0927/05.2322)	Zagwijn (1961) and Cleveringa et al. (2000)	X
Aschenhütte	(51.4036/10.1807)	Ricken and Grüger (1988)	Y
Barendorf 3	(53.1348/10.3121)	Freund et al. (1997)	X
Bispingen	(53.0420/09.5928)	Müller (1974)	X
Bobbitshole	(52.0305/01.0844)	West (1957)	N
Eviijärvi	(63.2600/23.2000)	Eriksson (1993)	X
Fjörsanger	(60.2115/05.1841)	Mangerud et al. (1981)	X
Glówczyn	(52.2915/20.1136)	Niklewski (1968)	Y
Gondiswil-Seilern	(47.0845/07.5220)	Wegmüller (1992)	X
Góra Kalwaria	(51.5831/21.1331)	Sobolewska (1961)	Y
Grabschütz	(51.2826/12.1638)	Litt (1990, 1994) and Mai (1990b)	Y
Grevenhof	(53.0607/10.0220)	Behre (1962)	X
Gröbern	(51.4128/12.2719)	Litt (1990, 1994) and Mai (1990a)	N
Groß Todtshorn	(53.1248/09.4642)	Caspers (1997) and Freund (1997)	N
Helgoland	(54.1117/07.5339)	Behre (1970)	Y
Hollerup	(56.2423/09.5046)	Andersen (1965)	X
Husum	(54.2825/09.0253)	Menke (1985)	X
Imbramowice	(50.2825/16.3342)	Mamakowa (1989)	Y
Jozwin	(52.2340/18.1124)	Tobolski (1991)	Y
Kamphuis	(52.2042/07.0226)	Geel et al. (1986)	Y
Kittlitz	(51.5008/13.5603)	Erd (1973)	X
La Grande Pile	(47.4400/06.3014)	Woillard (1975, 1978) and de Beaulieu and Reille (1992a)	X
Les Echets	(45.5213/04.5455)	de Beaulieu and Reille (1984, 1989)	X
Leveäniemi	(67.3800/21.0100)	Robertson (1991, 1997) and Robertson et al. (1997)	X
Meikirch	(47.0034/07.2205)	Welten (1982b)	X
Mertuanoja	(64.0700/24.3500)	Eriksson, Grölund and Uutela (1999)	X
Mondsee	(47.5107/13.2046)	Klaus (1975), Drescher-Schneider (2000) and Oeggl and Unterfrauner (2000)	Y
Naklo	(53.0925/17.3527)	Noryskiewicz (1978)	N
Neumark-Nord	(50.3929/12.2120)	Litt (1994)	N
Norinkylä 1	(62.3545/22.0107)	Eriksson (1993)	X

Norinkylä 2	(62.3545/22.0107)	Eriksson (1993)	X
Norinkylä 3	(62.3545/22.0107)	Eriksson (1993)	X
Odderade 7	(54.0828/09.1129)	Averdieck (1967)	Y
Oerel	(53.2859/09.0325)	Behre and Lade (1986)	X
Osterwanna II	(53.4437/08.4840)	Behre (1974)	X
Quakenbrück	(52.4030/07.5721)	Hahne et al. (1994a)	N
Rederstall I	(54.1346/09.1219)	Menke and Tynni (1984)	X
Ribains	(44.5035/03.4950)	de Beaulieu and Reille (1992b)	X
Samerberg I	(47.4500/12.1200)	Grüger (1979a,b)	Y
Schönfeld	(51.4930/13.5430)	Erd (1991)	X
Schwindebeck	(52.0730/10.0658)	Behre (1962)	Y
Seitevare	(66.5800/18.3500)	Robertsson (1991)	X
Ukonkangas	(63.5500/25.5200)	Eriksson (1993)	X
Valle di Castiglione	(41.5330/12.4535)	Follieri et al. (1988) and Follieri et al. (1998)	X
Vesiperä A	(64.0603/25.5910)	Eriksson (1993)	X
Vesiperä B	(64.0603/25.5910)	Eriksson (1993)	X
Viitala	(62.3600/25.5910)	Eriksson (1993)	X
Waewa-Ringen	(58.0843/26.1453)	Thomson (1941)	X
Wallensen	(52.0107/09.3716)	Rabien (1953)	Y
Wing	(52.3650/-00.4505)	Hall (1980)	N
Wladyslawow	(52.0800/18.2800)	Tobolski (1986, 1991) and Stankowski (1991)	N
Zgierz-Rudunki	(51.5039/192520)	Jastzebska-Mamelka (1985)	Y

Appendix VI

List of pollen and macrofossil sites used for the *Picea* maps (Brørup)

Site name	Latitude/ Longitude	Author(s)	Macroremains
Amersfoort 3	(52.0927/05.2322)	Zagwijn (1961)	X
Aschenhütte	(51.4036/10.1807)	Ricken and Grüger (1988)	Y
Barendorf 2	(53.1348/10.3121)	Freund et al. (1997)	X
Barendorf 3	(53.1348/10.3121)	Freund et al. (1997)	X
BrØrup	(55.2858/09.0103)	Andersen (1961)	X
Gondiswil-Seilern	(47.0845/07.5220)	Wegmüller (1992)	X
Gröbern	(51.4128/12.2719)	Litt (1990, 1994) and Mai (1990a)	Y
Groß Todtshorn	(53.1248/09.4642)	Caspers (1997) and Freund (1997)	N
Hamburg-Bahrenfeld	(53.3352/09.5547)	Hallik and Kubitzki (1961)	X
Hunteburg	(52.2618/08.1635)	Hahne et al. (1994b)	N
Jammertal	(48.0600/09.4344)	Müller (2000, 2001)	X
Keller	(54.0437/09.2534)	Menke (1970)	X
Kittlitz	(51.5008/13.5603)	Erd (1973)	X
Lac du Bouchet (D)	(44.5500/03.4700)	Reille and de Beaulieu (1990)	X
Lagaccione	(42.3400/11.5100)	Follieri et al. (1998) and Magri (1999)	X
La Grande Pile	(47.4400/06.3014)	Woillard (1975, 1978) and de Beaulieu and Reille (1992a)	X
Les Echets	(45.5213/04.5455)	de Beaulieu and Reille (1984, 1989)	X
Lunteren	(52.0516/05.3722)	Zagwijn (1961)	X
Meikirch	(47.0034/07.2205)	Welten (1982b)	X
Mondsee	(47.5107/13.2046)	Klaus (1975), Drescher-Schneider (2000) and Oeggl and Unterfrauner (2000)	Y
Neheim-Hüsten	(51.2703/07.5800)	Teunissen, Braun and Teunissen-van Oorschot (1972)	N
Neuenhausen-Veldhausen	(52.3112/06.5917)	Freund (1997)	N
Odderade 5	(54.0828/09.1129)	Averdieck (1967)	N
Oerel	(53.2859/09.0325)	Behre and Lade (1986)	X
Osterwanna II	(53.4437/08.4840)	Behre (1974)	N
Pilgrimstad	(62.5800/150100)	Robertson (1988)	X
Quakenbrück	(52.4030/07.5721)	Hahne et al. (1994a)	N
Rederstall I	(54.1346/09.1219)	Menke and Tynni (1984)	X
Ribains	(44.5035/03.4950)	de Beaulieu and Reille (1992b)	X

Samerberg 1973	(47.4500/12.1200)	Grüger (1979a,b)	Y
Stenberget	(55.3129/13.3248)	Berglund and Lagerlund (1981)	X
Tenagi Philippon II	(41.1000/24.2000)	Wijmstra (1969)	X
Valle di Castiglione	(41.5330/12.4535)	Follieri et al. (1988) and Follieri et al. (1998)	X
Wladyslawow	(52.0800/18.2800)	Tobolski (1986, 1991)	N
Zgierz-Rudunki	(51.5039/192520)	Jastzebska-Mamelka (1985)	N

Appendix VII

List of pollen and macrofossil sites used for the *Picea* maps (Odderade)

Site name	Latitude/ Longitude	Author(s)	Macroremains
Gondiswil-Seilern	(47.0845/07.5220)	Wegmüller (1992)	X
Gröbern	(51.4128/12.2719)	Litt (1990, 1994) and Mai (1990a)	Y
Groß Todtshorn	(53.1248/09.4642)	Caspers (1997) and Freund (1997)	Y
Hunteburg	(52.2618/08.1635)	Hahne et al. (1994b)	N
Jammertal	(48.0600/09.4344)	Müller (2000, 2001)	X
Kittlitz	(51.5008/13.5603)	Erd (1973)	X
Lac du Bouchet (D)	(44.5500/03.4700)	Reille and de Beaulieu (1990)	X
Lagaccione	(42.3400/11.5100)	Follieri et al. (1998) and Magri (1999)	X
La Grande Pile	(47.4400/06.3014)	Woillard (1975, 1978) and de Beaulieu and Reille (1992a)	X
Les Echets	(45.5213/04.5455)	de Beaulieu and Reille (1984, 1989)	X
Mondsee	(47.5107/13.2046)	Klaus (1975), Drescher-Schneider (2000) and Oeggl and Unterfrauner (2000)	Y
Neheim-Hüsten	(51.2703/07.5800)	Teunissen, Braun and Teunissen-van Oorschot (1972)	Y
Odderade 5	(54.0828/09.1129)	Averdieck (1967)	N
Oerel	(53.2859/09.0325)	Behre and Lade (1986)	X
Pilgrimstad	(62.5800/150100)	Robertson (1988)	X
Quakenbrück	(52.4030/07.5721)	Hahne et al. (1994a)	N
Rederstall I	(54.1346/09.1219)	Menke and Tynni (1984)	X
Ribains	(44.5035/03.4950)	de Beaulieu and Reille (1992b)	X
Samerberg 1973	(47.4500/12.1200)	Grüger (1979a,b)	Y
Tenagi Philippon II	(41.1000/24.2000)	Wijmstra (1969)	X
Valle di Castiglione	(41.5330/12.4535)	Follieri et al. (1988) and Follieri et al. (1998)	X
Wladyslawow	(52.0800/18.2800)	Tobolski (1986, 1991)	N
Zgierz-Rudunki	(51.5039/192520)	Jastzebska-Mamelka (1985)	N

Annotation according to the macroremains (Appendix VI-VIII):

Y - Macroremains existent
N - No macroremains
X - No investigations on macroremains

Appendix VIII

List of pollen sites used for the *Picea* maps (Holocene)

(source: European Pollen Database / http://medias.obs-mip.fr/paleo/epd/epd_main.html)

(for contributors' references see Database Meta Information)

Abernethy Forest (56.1400/-03.4300), Aegelsee (46.3845/07.3236), Ageröds Mosse (55.5000/13.2500), Ahlenmoor (53.4200/08.4400), Aholami (61.5300/25.1300), Åkerhultagöl [Tomtabaken] (57.2900/14.2800), Akuvaara (69.0730/27.4100), Altenweiher (48.0048/06.5940), Amsoldingersee (46.4330/07.3430), Arkutino lake (42.2200/27.4400), Aronde (49.2745/02.4128), Arsenala-Varna lake (43.1200/27.5000), Barbora JC-6-B (48.5630/14.5600), Beaufort Birkenbach (49.5050/06.0733), Besbog-2 (41.4500/23.4000), Bezdonnoe (62.0200/32.46.00), Bezymiannoe (54.1300/30.0001), Biot (43.4800/07.0600), Bjärsjöholmssjön (55.2700/13.4700), Black Sea South (42.0403/28.2906), Black Sea South-West (42.1103/28.5500), Black Sea SW (42.0403/28.5320), Black Sea West (42.5000/29.5500), Blato (Zispachy) (49.0230/15.1130), Blavasstjonn (64.5500/11.4000), Bledowo lake (52.3300/20.4000), Boehnigsee Goldmoos (46.1533/07.5035), Bolotnoye (51.0300/24.4800), Bolotnya (50.2000/23.5700), Borkovicka Blata (49.1300/14.5400), Brana (48.5700/14.5600), Brede Bridge (50.5600/-00.3600), Breidfeld (50.0722/06.0347), Cervene Blato (48.5100/14.5600), Chernikhovo (53.2500/26.2600), Clapeyret (44.0850/07.1420), Col des Lauzes (45.4609/06.3200), Colfiorito (43.0130/12.5530), Crovani (42.2810/08.4056), Czajkow (50.4700/21.1700), Dags Mosse (58.2000/14.4200), Darzlubie Forest (54.4200/18.1000), Dlinnoe (62.1900/33.5100), Dolgoe (55.1400/28.1100), Dry Lake II [Rila mountain] (42.0300/23.3200), Dürrenecksee-Moor (47.1000/13.5200), Dvur Ansov (48.4730/16.2315), Edessa (40.4905/21.5709), Etang de Cheylade (45.0524/02.5342), Ezerisch (55.5100/30.0000), Färshesjön (56.1000/15.5200), Fjällnas (62.3300/12.1000), Flaatevatn (59.4200/06.1000), Fletnowo (53.3200/18.3900), Flögeln (53.4000/08.4550), Fougères (48.3100/-00.5000), Frasne (Doubs) (46.4953/06.0944), Frengstadsetra (62.3400/10.0800), Fuchsschwanzmoos (47.0700/13.5400), Gel'myazevskoye (49.4000/31.5000), Georgenfelder Hochmoor (50.4500/13.4500), Giecz (52.1910/17.2148), Glubokoe (61.0400/36.0300), Gorno (50.5100/20.5000), Grand Ratz le Pellet (45.2030/05.3630), Grasvatn (63.4200/08.4200), Gretskoe (55.3800/27.4600), Grosses Überling Schattseit-Moor (47.1000/13.5400), Hières sur Amby (45.4727/05.1700), Hirvilampi (60.3730/24.1500), Hoyran Gölü (38.1630/30.5230), Hozelec SK-5-A (49.0300/18.1800), Ilmen Lake (58.1800/31.1400), Imatu mire (59.0800/27.2600), Isokärret (60.1300/22.0800), Ivano-Frankovskoye (49.5500/23.4600), Jasiel (49.2222/21.5313), Kaarkotinlampi (61.2500/25.5200), Kaartlamminsuo (60.4400/24.1300), Kalsa mire (58.1000/27.2700), Kamenicky (49.4400/15.5800), Kanjerjoki [Kuusamo] (66.0700/29.0000), Kassjön (63.5500/20.0100), Kastoria (40.3307/21.1920), Kepskoe (65.0500/32.1000), Kirkkosaari (60.5200/24.3000), Kittilä (65.0130/24.4100), Kluki (54.4225/17.1705), Koldychevo (53.1600/26.0400), Koppalosuo (62.1700/33.3900), Krageholmssjön (55.3000/13.4400), Krugloye (66.2200/37.3500), Kubenskoe Lake (59.4200/39.3000), Kuivajarvi (60.4700/23.5000), Kupena (Western Rhodopes Mts.) (41.5900/24.2000), La Grande Pile (47.4400/06.3014), La Taphanel (45.1628/02.4045), Lac de Lod (45.4800/07.5030), Lac de Villa (45.4105/07.4540), Lac Long Inférieur (44.0328/07.2700), Lac Mouton (44.0328/07.2641), Lac Noir (45.2713/02.3738), Lac Saint Léger (44.2512/06.2011), Ladoga Lake (61.3325/31.2007), Lagaccione (42.3400/11.5100), Lake Balaton centre (46.4440/17.2403), Lake Balaton NE (47.0006/18.0615), Lake Balaton

SW (46.4906/17.4406), Lake Beloslav-Poveljanovo (43.1200/27.5000), Lake Duranunlak (43.4000/28.3300), Lake Ermistu (58.2200/23.5800), Lake Flarken (58.3500/13.4000), Lake Glubelka (54.5700/26.2500), Lake Karujarv (58.2300/22.1200), Lake Kolmilaträsk (60.1700/20.0900), Lake Kvarnträsk (60.2100/19.5900), Lake Lednica (52.3325/17.2325), Lake Maardu (59.2600/25.0000), Lake Nero (57.1100/39.2705), Lake Sambösjön (57.0800/12.2500), Lake Shabla-Ezeretz (43.3500/28.3300), Lake Skvzetuszewskie (52.33.00/17.2138), Lake Solso (56.0800/08.3800), Lake Srebarna (44.0500/27.0700), Lake Suho Ezero (42.0800/23.2500), Lake Trummen (56.5200/14.5000), Lake Xinias (39.0300/22.1600), Lalaxkärret (60.0900/21.5200), Landos (44.5100/03.4930), Landruchie Mire (61.0000/39.0000), Landshaftnoe (64.3400/30.3200), Le Beillard (48.0424/06.4804), Le Grand Etang de Suze-La-Rousse (44.2100/05.1400), Le Grand Lemps (45.2824/05.2500), Le Jolan (45.0822/02.5133), Le Marais St Boetien (49.3700/03.4900), Leikishke bog (54.3200/23.3200), Les Enfers (47.1500/07.1000), Les Veaux (47.1500/07.1000), L'Estivalet (44.5121/03.2308), Liivjarve Bog (59.1300/27.3500), Lilla Gloppsjön (59.4816/14.3740), Liptovsky Jan (49.0230/19.4040), Lobsigensee (47.0155/07.1757), Lochinskoe (53.3300/28.3600), Lomzyca 2 (53.0930/22.0300), Long Lough (54.2500/-05.5200), Lopatin (50.1300/24.5000), Loras (45.3950/05.1440), Loucky (49.1930/15.3010), Lough Henney (54.2600/-05.5400), Maanselänsuo (65.3700/29.3600), Makovich (50.5800/24.1300), Maleshevska Mts (41.4200/23.0200), Malhaire (48.3000/-01.0000), Masehjavri (69.0300/20.5900), Mayralampi (62.2000/26.1400), Mezhgornoe (66.2200/30.4200), Mikolajki lake (53.4605/21.2505), Mire Garvan (44.0701/26.5700), Mire Johvika (58.3000/22.2000), Mire Pelisoo (58.2800/22.2300), Mire Petrolivo (56.0000/31.5900), Mire Saviku (58.2400/27.1400), Mire Sosvyatskoe (56.1200/32.0000), Mokre Louky (south) (48.5000/14.5000), Moossalmmoor (47.4500/13.3100), Moskovskiy Bobrik (50.3300/34.3000), Mossen (60.0700/21.3600), Moulin de Prugnolas (45.5059/01.3845), Mukkavaara (68.5500/21.0000), Mustusuo (61.4820/33.3000), Mutorog - Southern Pirin Mts. (43.3100/23.3700), Naroch (54.4900/26.4500), Nemino (62.4500/34.3500), Nenazvannoe (61.4820/33.2900), Nosuo (64.3400/30.5000), Novolsky (56.4600/26.1100), Nowy Gutiski (50.1600/26.5000), Ödenseemoor (47.3700/13.3800), Olbramovice (48.5930/16.2400), Oltush Lake (51.4148/23.5724), Onego Lake (61.4300/34.5500), Osoyevka (50.5400/35.1300), Osvea (56.0300/28.0500), Påidre (58.1600/25.3800), Palasiny (49.4120/15.2900), Pamerkiai outcrop (54.1850/24.4410), Pannel Bridge, East Sussex (50.5400/00.4100), Peat bog Ivanovskoye (56.4900/38.4600), Pecheniya (49.4000/23.5600), Pelléautier (44.3120/06.1100), Peschanoe (51.5900/25.2900), Peyrelevade (45.4230/02.2300), Pinarbasi (37.2800/30.0300), Plaine Alpe (44.5750/06.3539), Plan du Laus (44.1430/06.4208), Plesheevo Lake (56.4500/38.3000), Polonichka (50.1600/24.4500), Popovo Ezero (41.4300/23.4000), Pré Rond (44.5508/06.3539), Ptichje (66.2100/30.3400), Puscizna Rekowianska (49.2900/19.4900), Puy de Pailleret (45.3100/02.4900), Raigastvere lake (58.3600/26.4000), Ran Viken (56.1700/14.1800), Rasna pond (49.1350/15.2215), Rattuvarri (69.2100/20.1900), Redmere (52.2600/00.2600), Regetovka (49.2530/21.1645), Rezabinec (49.1500/14.0700), Rodenbourg Bretzboesh (49.4130/06.1612), Rödschitzmoor (47.3300/13.5400), Rotsee (47.0432/08.1932), Roztoki (49.4300/21.3500), Rudushskoe Lake (56.3000/27.3300), Rugozero (64.0500/32.3800), Rukatunturi (66.1000/29.0900), Rybachiy (69.3800/32.2200), Ryönänsuo (60.2600/24.1000), Sabbion (44.0748/07.2824), Saint Julien de Ratz (45.2100/05.3724), Saint Sixte (45.2530/05.3730), Sandvikvatn (59.1700/05.3000), Särkikangas (65.5500/29.1200), Schwemm (47.3900/12.1800), Selle di Carnino (44.0900/07.4140), Shepeta bog (55.4700/25.1000), Siikasuo (61.1800/22.0400), Sipola (65.0300/24.4730), Slopiec (50.4700/20.4700), Sögüt Gölü (37.0300/29.5300), Solnechnoe (65.5000/34.2000), Solokiya (50.2500/24.1000), Stoyanov-1 (50.2300/24.3800), Stoyanov-2 (50.2300/24.3800), Stupino (52.1500/39.5000), Suchedniow (51.0300/20.5100), Suovalampi

(69.3500/28.5000), Svencele bog (55.2943/21.1732), Svitjaz (53.2600/25.5500), Svyatoye-2 (51.0600/24.2000), Swienskuhle DAH III (53.4000/08.4330), Syrjälänsuo (61.1300/28.0700), Szymbark (49.3800/21.0600), Tarnawa Wyzna (49.0600/22.5000), Tarnowiec (49.4200/21.3700), Tenaghi Philippon (40.5900/24.4700), The bog Liman (49.4400/37.4000), Tondi (59.2800/24.5500), Tourbière de Champlong (45.49.15/07.4827), Tourbière de la Borde (42.3200/02.0500), Tourbière de Pilaz (45.4901/07.5000), Tourbière de Santa Anna (45.5130/07.3915), Trikhonis 5 (38.3600/21.3000), Trollvatnet (69.5230/23.2800), Trumer Moos (47.5600/13.0400), Tschokljovo marsh (42.2200/22.5000), Tullerinsuo (61.2000/21.5700), Tytuvenu tyrelis (55.3500/23.1800), Vallon de Provence (44.2328/06.2415), Vasikkasuo (64.4000/27.5200), Vegoritis 8 (40.4500/21.4500), Vernerovice (50.0600/16.1500), Vishnevskoe Lake (60.3008/29.3101), Vitosha mountain (42.5000/23.5000), Vôhma mire (59.0300/27.2000), Voros-mocsar (46.2838/19.1127), Vracov (48.5840/17.1210), Wachel 3 (53.0217/08.0211), Wasenmoos beim Zellhof (47.5900/13.0600), Welney Washes (52.3100/00.1500), Willingham Mere (52.2000/-02.1900), Wolin II (53.5000/14.4000), Ylimysneva (62.0800/22.5200), Zalozhtsy-2 (49.4500/25.2700), Zapovednoe (65.0700/32.3800), Zaruckoe (63.5400/36.1500), Zirbenwaldmoor (46.5130/11.0130), Zsombo-swamp (46.2141/19.5939), Zurawiec (54.2500/16.3000), Zvenigorod-Kotsurovskoye (49.4800/24.1400)

List of macrofossil sites used for the *Picea* maps (Holocene)

Site name	Latitude/Longitude	Author(s)
Åreskutan 1	(63.2600/13.0600)	Kullman (2001)
Åreskutan 2	(63.2500/13.0400)	Kullman (2001)
Akkisvaara	(68.1300/21.4200)	Kullman (2001)
Aletschwald	(46.2323/08.0132)	Welten (1982a), van der Knaap and Ammann (1997), Appleby (unpubl. 1998b) and van der Knaap et al. (2000)
Alsberget	(64.4000/17.3900)	Kullman (2001)
Anhovo	(46.0030/13.3515)	Šercelj (1996)
Arka	(48.3000/21.3000)	Vértes (1964), Vogel and Waterbolk (1964) and Willis et al. (2000)
Aurafreida II	(46.2245/10.0553)	Burga (1987)
Bachlern I and II	(49.0655,5/12.5526,2)	Stalling (1987)
Ballasviken	(66.2800/16.3200)	Kullman (2001)
Barbora	(49.0031/14.4558)	Jankovská (1980)
Barfredhågna	(62.0300/12.2400)	Kullman (2001)
Berg (Moor "Berg")	(46.3855/08.2929)	Zoller et al. (1966)
Besko	(49.3311/21.5928)	Koperowa (1970) and Środoń (1990)
Bivio	(46.2912/09.3947)	Heitz (1975)
Björnmyran	(64.4000/17.4500)	Kullman (2001)
Bláto	(49.0300/15.1200)	Rybníček and Rybníčková (1968)
Blåhammarfjället	(63.1200/12.1100)	Kullman (2001)
Bodrogkeresztúr	(48.1107/21.2202)	Krolopp (1977) and Willis et al. (2000)
Böhnigsee ob Bürchen	(46.1555/07.5058)	Markgraf (1969) and van der Knaap and Ammann (1997)
Bór na Czerwonem	(49.2753/20.0158)	Obidowicz (1990)
Borkovická blata	(49.1600/14.3600)	Jankovská (1980)
Branná	(49.0031/14.4558)	Jankovská (1980)
Brno	(49.1000/16.3800)	Rybníček, Dickson and Rybnicková (1998)
Bromossen	(63.1000/12.2300)	Kullman (2001)
Bromyran	(63.0400/16.4900)	Kullman (2001)
Cavloccio	(46.2431/09.4213)	Kleiber (1974)
Chüealp	(46.4235,5/09.5534,5)	Matthey (1985)
Col di Val Bighera	(46.1618/10.2208)	Gehrig (1997)
Cosautsi	(48.1300/28.1603)	Haesaerts, Borziak, van der Plicht and Damblon (1998)
Czajków	(50.0500/21.1900)	Środoń (1970) and Szczepanek (1971)
Dobra	(49.4300/20.1500)	Środoń (1968)
Dolní Věstonice	(48.5255/16.4143)	Kneblová (1954), Klíma (1963) and Damblon et al. (1996)

Dossaccio, Bormio	(46.2814/10.2014)	Welten (1982a) and van der Knaap and Ammann (1997)
Draga	(45.3760/14.4000)	Levanič and Čufar (1997)
Dunaszekesö	(46.0459/18.4439)	Krolopp (1977) and Willis et al. (2000)
Etang d'y Cor	(46.1842/07.2845)	Welten (1982a) and van der Knaap and Ammann (1997)
Faulenseemoos	(46.4049/07.4141)	Welten (1982a) and Lotter et al. (1996)
Finsterauer Filz	(48.5635,3/13.3440,2)	Stalling (1987)
Flatruet	(62.4600/12.4600)	Kullman (2001)
Forrenmoos	(47.0007/08.1331)	Gehrig (1989, 1991)
Fuschlsee	(47.4800/13.1600)	Voigt (1996)
Gevsjöflon	(63.2200/12.4200)	Kullman (2001)
Glunersee	(46.5136,1/09.4303)	Wegmüller (1976)
Goce Delchev	(41.3443/23.4326)	Stefanova (1997)
Göscheneralp	(46.3846/08.2908)	Zoller et al. (1966)
Gondo-Alpjen	(46.1242/08.0648)	Welten (1982a) and van der Knaap and Ammann (1997)
Grächen-See	(46.1150/07.5046)	Welten (1982a) and van der Knaap and Ammann (1997)
Greicheralp, Riederalp	(46.2247/08.0149)	Welten (1982a) and van der Knaap and Ammann (1997)
Grossmossen	(60.4400/13.2800)	Kullman (2001)
Grünsee ob Alp Straßberg	(46.5126/09.4717,6)	Wegmüller (1976)
Haidmühle	(48.4918,5/13.4513,2)	Stalling (1987)
Helfenberg/Afiesl	(48.3515/08.0840)	Felber (1980)
Hobschensee	(46.1510/07.5039)	Lang and Tobolski (1985) and Ammann (1988)
Högsvedjeberget	(63.0800/18.2500)	Kullman (2001)
Höhenbiel	(46.3415/08.2946)	Küttel (1990)
Hojkov	(49.2519/15.3556)	Rybníčková (1974)
Horgen Scheller	(47.1547/08.3553)	Favre and Jacomet (1998)
Horní Pole	(49.1755/15.2930)	Rybníčková (1974)
Jedlicze	(49.4330/21.3930)	Pazdur et al. (1983)
Kamasjåkka	(68.0500/19.5100)	Kullman (2001)
Kameničky	(49.4400/16.0300)	Rybníčková and Rybníček (1988)
Kamionka/Szymbark	(49.3730/21.0600)	Środoń (1983, 1990) and Gil et al. (1974)
Karino	(58.3500/50.1500)	Cherdyntsev et al. (1968)
Kemi (Tervola)	(66.2435/24.5145)	Reynaud and Tobolski (1974)
Kępa	(49.3744/21.4938)	Gerlach et al. (1972) and Środoń (1990)
Klockamyren	(63.1800/12.2900)	Kullman (2001)
Kostienki 14	(52.5144/33.0803)	Damblon et al. (1996)
Krabbfjällnäset 1	(66.0700/14.3700)	Kullman (1998)
Kulz	(49.2312,6/12.2620,3)	Stalling (1987)

La Pila cave	(43.2560/-04.0100)	Uzquiano (1992b)
Lac Canard Ib	(45.0400/05.5602)	Ponel et al. (1992) and Tessier et al. (1993)
Lac d'Ai	(46.2153/07.0020)	van der Knaap et al. (2000)
Lac de Bretaye	(46.1938/07.0424)	van der Knaap et al. (2000)
Lac de Joux	(46.3921/06.1856)	Wegmüller (1966)
Lago Basso	(46.2627/09.1745)	Wick and Tinner (1997)
Lake Mondsee	(47.4900/13.2500)	Felber (1974)
Lake Panichishte	(42.0760/23.0760)	Marinova and Tonkov (2003)
Lake Suho Ezero	(42.0400/23.3500)	Bozilova et al. (1986) and Bozilova (1995)
Ledsageren	(61.4500/10.3800)	Nydal, Gulliksen, Lövseth and Skogseth (1985)
Les Embreux	(47.1550/07.0706)	Wegmüller (1966), Matthey (1971) and Hubschmid and Lang (1985)
Lethikumpu	(67.1600/21.0500)	Kullman (2001)
Litlevola	(62.3700/11.5000)	Kullman (2001)
Lörmoos	(46.5902/07.2448)	Zwahlen (1985)
Lutnermayok	(67.4100/33.1700)	Kremenetski et al. (1999)
Madaras	(46.0327/19.1615)	Dobosi (1967) and Willis et al. (2000)
Malmflon	(63.5300/15.4300)	Kullman (2001)
Maloja-Dorf	(46.2431/09.4213)	Kleiber (1974)
Maloja-Riegel I	(46.2423/09.4127)	Kleiber (1974)
Meierei bei St. Moritz	(46.2952/09.5048)	Kleiber (1974)
Mende	(47.2623/19.2639)	Geyh, Schweitzer, Vértes and Vogel (1969), Krolopp (1977) and Willis et al. (2000)
Mörsil	(63.1900/13.4500)	Kullman (2001)
Mokré Louky b. Trebon	(49.0100/14.4600)	Jankovská (1987)
Mt. Getryggen 1	(63.1100/12.2200)	Kullman (1996)
Mt. Storsnasen 14	(63.1300/12.2200)	Kullman (1996)
Mt. Storsnasen 15	(63.1400/12.2400)	Kullman (1996)
Mt. Storsnasen 16	(63.1400/12.2200)	Kullman (1996)
Mt. Storsnasen 30	(63.1300/12.2500)	Kullman (2001)
Mt. Storsnasen 31	(63.1400/12.2100)	Kullman (2001)
Mt. Storsnasen 32	(63.1400/12.2500)	Kullman (2001)
Mt. Storsnasen 33	(63.1400/12.2100)	Kullman (2001)
Mt. Storsnasen 34	(63.1400/12.2500)	Kullman (2001)
Mt. Storsnasen 35	(63.1600/12.1900)	Kullman (2001)
Mt. Storsnasen 36	(63.1600/12.2000)	Kullman (2001)
Mt. Storsnasen 9	(63.1500/12.2000)	Kullman (1995)
Mt. Sylarna 1	(63.0200/12.2000)	Kullman (1998)

Mt. Sylarna 2	(63.0200/12.1500)	Kullman (2001)
Mt. Sylarna 3	(63.0300/12.1700)	Kullman (2001)
Mullfjället	(62.2500/12.5600)	Kullman (2001)
Myrvang	(63.0400/11.2600)	Kullman (2001)
N. Tväråklumpen 1	(63.1200/12.2300)	Kullman (1996)
N. Tväråklumpen 6	(63.1200/12.2300)	Kullman (2001)
N. Tväråklumpen 8	(63.1100/12.2100)	Kullman (2001)
N. Tväråklumpen 9	(63.1200/12.2200)	Kullman (2001)
Näcksjön	(62.3600/12.2600)	Kullman (2001)
Niställingen	(60.4300/13.2100)	Kullman (2001)
Ö. Bunnerstöten 1	(63.0800/12.3900)	Kullman (2001)
Ö. Bunnerstöten 2	(63.0800/12.3900)	Kullman (2001)
Ö. Bunnerstöten 3	(63.0800/12.3900)	Kullman (2001)
Ö. Bunnerstöten 4	(63.0800/12.3900)	Kullman (2001)
Öje	(60.4800/13.5100)	Kullman (2001)
Ollsta	(63.2800/15.1300)	Kullman (2001)
Ovčja jama	(45.4643/14.1249)	Osole (1963) and Šercelj (1996)
Oxberget	(64.3300/17.3500)	Kullman (2001)
Palù near Edolo	(46.1013/10.1937)	Gehrig (1997)
Palughetto basin	(46.0825/12.1248)	Avigliano et al. (2000)
Pechoraya Bay	(65.0760/57.1360)	Khotinskiy (1984)
Pian di Signano	(46.1553/09.0825)	Zoller (1960)
Pichozero	(61.4700/37.2500)	Wohlfarth et al. (2004)
Piilonsuo	(60.4600/24.3900)	Koponen and Nuorteva (1973)
Pilatussee	(46.5754/08.1149)	Gehrig (1989, 1991)
Pillon, Gsteig-Diablerets	(46.2135/07.1155)	Welten (1982a) and van der Knaap and Ammann (1997)
Plancklacke/Sankt Jakob Defreggen	(46.5145/12.1726)	Oeggl and Wahlmüller (1994, 1997)
Plankenalm	(47.3012/13.4808)	Drescher-Schneider (1997, 1999)
Plansena	(46.2333/10.0631)	Burga (1987)
Preluca Tiganului	(47.4883/23.3191)	Björkman et al. (2002)
Przymiarki	(49.2652/19.5537)	Obidowicz (1990)
Puscizna Rekowianska	(49.2900/19.4900)	Obidowicz (1990)
Řásná	(49.1400/15.2300)	Rybníčková (1974)
Roztoki A	(49.4442/21.3648)	Harmata (1987) and Środoń (1990)
S. Stadsberget	(63.2200/17.1800)	Kullman (2001)
Sägistalsee	(46.4053/07.5839)	van der Knaap et al. (2000)
Safárka	(48.5255/20.3430)	Jankovská et al. (2002)

Ságvár	(46.5000/17.4500)	Gábori-Csánk (1960), Vogel and Waterbolk (1964) and Willis et al. (2000)
Schöpfenwaldmoor	(46.4441/07.5055)	Appleby (unpubl. 1998a) and van der Knaap, van Leeuwen, Fankhauser and Ammann (2000)
Schwarzmoos L-34	(46.3736/07.2856)	Wegmüller and Lotter (1990)
Schwarzmoos Q-45	(46.3736/07.2856)	Wegmüller and Lotter (1990)
Schwarzsee/Reschenscheideck	(46.5215/10.2850)	Gaillard (1984) and van der Knaap and Ammann (1997)
Semenic (Banat Mountains)	(45.0900/22.0500)	Rösch and Fischer (2000)
Simplon-Hopschensee	(46.1512/08.0126)	Küttel (1979), Welten (1982a), van der Knaap and Ammann (1997) and van der Knaap et al. (2000)
Simplon/Gampisch-Alter Spittel	(46.1354/08.0045)	Welten (1982a)
site 6	(47.3965/21.2250)	Willis et al. (2000)
site 7	(47.2937/19.2700)	Willis et al. (2000)
site 8	(47.2958/21.2850)	Willis et al. (2000)
site 9	(47.3461/21.1170)	Willis et al. (2000)
site 10	(47.4825/21.0810)	Willis et al. (2000)
site 12	(47.3147/21.1950)	Willis et al. (2000)
site 14	(47.3944/21.1740)	Willis et al. (2000)
site 17	(47.3440/19.1260)	Willis et al. (2000)
site 19	(47.2518/21.2250)	Willis et al. (2000)
Sivárňa	(49.1900/20.3600)	Jankovská (1994)
Skidsjön	(65.0200/16.0600)	Kullman (2001)
small kettlehole (KH1)	(59.4000/25.4500)	Koff and Kangur (2003)
Smerek III	(49.1100/22.2700)	Ralska-Jasiewiczowa (1980)
Solymár	(47.3633/18.5652)	Geyh, Schweitzer, Vértes and Vogel (1969), Krolopp (1977) and Willis et al. (2000)
Steregoiu	(47.4848/23.3241)	Björkman et al. (2002)
Storlien	(63.1900/12.0500)	Kullman (2001)
Stormyran	(64.1300/17.3100)	Kullman (2001)
Storulvåfjället 13	(63.0900/12.2100)	Kullman (2001)
Storvallen	(63.1700/12.0900)	Kullman (2001)
Stråten 3	(63.1100/12.2500)	Kullman (2001)
Stråten 4	(63.1100/12.2600)	Kullman (2001)
Stugudal	(62.5500/11.5600)	Kullman (2001)
Suchdol	(49.0714/15.1153)	Rybníčková (1974)
Suossa	(46.2612/09.1156)	Zoller and Kleiber (1971)
Sur	(46.3147/09.3747)	Heitz (1975)
Svappavaara	(67.4000/21.0100)	Kullman (2001)

Švarcenberk	(49.1135/14.4212)	Jankovská (1980)
Tandövarden	(60.5000/13.1100)	Kullman (2001)
Tápiósüly	(46.5917/18.5541)	Geyh, Schweitzer, Vértes and Vogel (1969), Pécsi (1975), Krolopp (1977) and Willis et al. (2000)
Tarnowiec E	(49.4200/21.3700)	Harmata (1987) and Środoń (1990)
Tokaj	(48.0841/21.2453)	Geyh, Schweitzer, Vértes and Vogel (1969), Krolopp (1977) and Willis et al. (2000)
Trogenmoos	(46.4543/07.5150)	Rybníček and Rybníčková (1977) and van der Knaap et al. (2000)
Tuolluvuoma	(67.5100/20.2200)	Kullman (2001)
Val Caltea	(46.0406/12.3529)	Fuchs (1970) and Ravazzi (2002)
Val Frisal	(46.4814/09.0040)	Zoller et al. (1966)
Veiem	(64.2800/12.0700)	Nydal, Gulliksen, Lövseth and Skogseth (1985)
Veszprém	(47.0551/17.5449)	Geyh, Schweitzer, Vértes and Vogel (1969), Krolopp (1977) and Willis et al. (2000)
Visokata Ela	(41.5006/23.2918)	Stefanova (1997)
Weiberhemd-Moor	(51.1239/09.5622)	Stalling (1983)
Willendorf II	(48.1912/15.2408)	Damblon et al. (1996) and Haesaerts et al. (1996)
Zalaegerszeg	(46.5053/16.5049)	Geyh, Schweitzer, Vértes and Vogel (1969) and Krolopp (1977)
Zeneggen-Hellelen A	(46.1659/07.5039)	Welten (1982a) and van der Knaap and Ammann (1997)
Zlarin	(43.4030/15.5220)	Srdoč, Sliepčevic, Obelic and Horvatinčic (1979)
Županov spodmol	(45.4643/14.1249)	Osole (1976) and Šercelj (1996)