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INVASION OF BEECH AND ESTABLISHMENT OF BEECH FORESTS IN EUROPE

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ABSTRACT - When studying the natural development in the evolution of beechwood forests in Central Europe after the last glaciation, it is necessary to look at the warm periods prior to the last Weichselian glaciation. The Eem interglacial period has already been studied in great detail in Europe; it is evidend with similar climatic conditions as the current Holocene. At that time nearly all of Europe was more or less completely covered with forests. As laminated sediments and datings indicate, the Eem interglacial period lasted from approximately 125000 to 113000 years before today. The types of trees were generally the same as those of the present, except for the beech (*Fagus*) which was missing due to its delayed re-migration and was replaced by the hornbeam (*Carpinus*). It was not until the present time following the glaciation-periods that *Fagus sylvatica* could be found again widespread throughout the woodland vegetation covering Central Europe. The Holocene expansion and re-colonisation of *Fagus sylvatica* from its refuges during the glacial periods will be described in great detail, based on the most recent pollen analytic proofs.

KEY WORDS - *Fagus sylvatica*, beech-woods, Pleistocene refuges, Holocene expansion

INTRODUCTION

Summer-green deciduous forests with beech (*Fagus sylvatica*) form the regional potential natural vegetation of Central Europe; they extend to the coastal evergreen broadleaved zones of the Mediterranean and reappear in the Mediterranean highlands; in the south-east, they border on the Russian steppes and reach in the north up to the boreal coniferous tree zone. The communities of the beech forests dominates over vast expanses of Central Europe as natural forest communities, and the picture presented by the beech forests today is the result of a long evolution in combination with climate, soil and humans. As a rule, there is no natural vegetation coverage, unaffected by the influences of humans here, if we disregard the coastal marsh areas, the steep, inaccessible cliffs, avalanche areas in the mountains as well as former alpine moors and smaller mires and foreststed mires. For the most part, the original natural forest vegetation exists only as remains in aspects altered by cultivation. Even the holocene development of the forests is inextricably linked to the influence of humans.

As pollen-analytical research results reveal, the natural development of vegetation was already disturbed and sometimes even obstructed during the mixed oak forest period, in the Atlanticum by the settlements of the earliest Neolithic people at about 4500 BP (BP = befor present). Neolithic men, who settled the land, worked the fields and cleared the forests did not interfere with a static vegetation state but rather with a dynamic process that had not yet come close to being completed. Beech and hornbeam, for example, had not yet become part of the canopy in the forests at this time in Central Europe and as a result, the formation of these types to beech or mixed beech forests, as they dominate today in the potential forest communities in the central highlands, had not yet begun.

THE BEECH INVASION DURING THE PLEISTOCENE

The quaternary appropriately known as the Pleistocene comprises approximately the last two million years and is marked by extreme changes in climate in Central Europe. This epoch is characterised by gigantic inland ice masses which appeared from Scandinavia to the borders of the central highlands as well as in the south by glaciers in the Carpathian mountains, the Alps and the Pyrenees which advanced to the foothills, whereby the Pleistocene glaciation in the Carpathian mountains was not as extensive as in the Alps. In the meantime the central highlands of Central Europe were subjected to a periglacial climate for long periods of time with occasional deep permafrost, except for the areas which experienced their own periodic glaciation (such as the Harz mountains, the Black Forest in

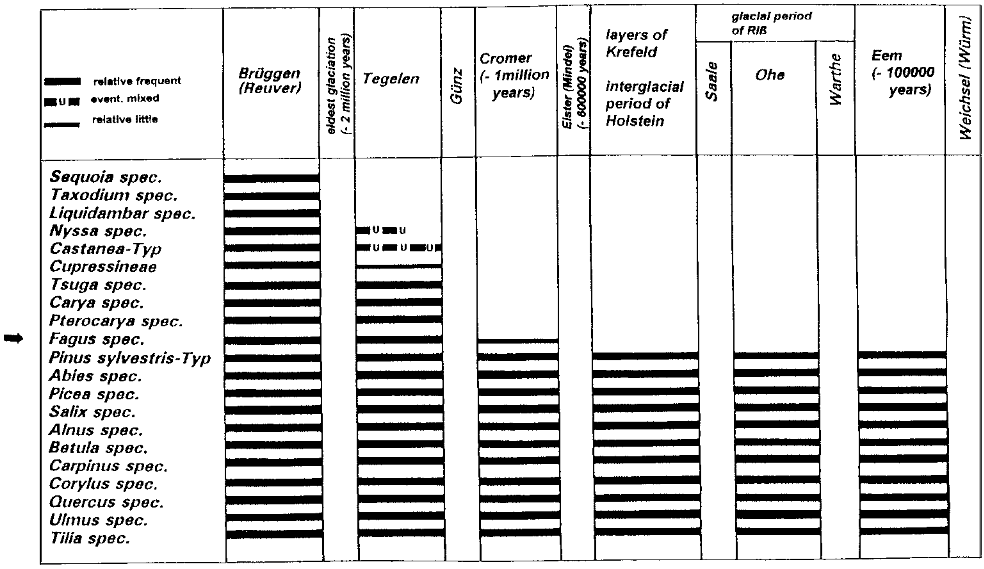


Fig. 1 - Pollenanalytical references of different species since the Pliocene in North-Western Germany (ref. to Rein 1955).

Central Europe). These cold periods were interspersed with the development of temperate periods again and again, the interstadial and the interglacial, including some warmer climatic periods as we experience today. The glacial-interglacial cycles in the Pleistocene with their frequently recurring changes in climate resulted primarily in profound areal changes in plant and animal life. During the cold periods, cold-resistant tundra and steppe plant life took place over large expanses in Central Europe and thermophile woodlands were relegated to single, isolated refuges in the south and south-east of Europe. During several interglacial periods (e.g. Cromer, Holstein, Eem, see fig. 1) there have been always reestablishments of woodland which were quite different in their floral composition in Europe (see de Jong, 1988). In order to study the natural development processes during the holocene in Central Europe it is advisable to take a look at the warm periods preceding the last Vistula glaciation. The Eem interglacial period has been examined in many places in Europe; there were similar climatic conditions as during the present Holocene and as a result there are many good opportunities for comparison (see fig. 2). At that time, almost all of Europe was covered with more or less closed forests. The Eem interglacial period lasted from approximately 125,000 to 113,000 years ago; thus, it lasted a total of only 12,000 years. The types of trees were for the most part the same as today, only the beech (*Fagus*) was missing in places, apparently due to delayed migration, and it was replaced by the hornbeam (*Carpinus*). The natural environment of the European spruce (*Picea*) and the fir (*Abies*) also appears to have extended somewhat further north than in the current holocene period.

Due to climatic changes and the migration sequence of the trees, an initial forest phase with juniper (*Juniperus*) and birch (*Betula*), followed by pine forests with *Pinus sylvestris* can be determined for this interglacial period in Central Europe (see fig. 3). After this, *Ulmus* (div. species), *Quercus* (div. species) and *Fraxinus* appeared, followed by hazel (*Corylus*) and in more wet areas by alder (*Alnus*). The advance of such types as *Taxus* and *Tilia (*div. species) reveals that later the climatic turning point of the interglacial period had been reached. At the end of the Eem interglacial period, hornbeam and European spruce then migrated into these areas dominated by mixed oak forests; they were then dominant until pine and finally birch took over during the climatic decline at the end of the interglacial. Pollen from herbs is conspicuous by its virtual absence, which also confirms the thick forest coverage during the interglacial. With only minor variations, this process repeats itself throughout all of Central Europe and beyond (see fig. 3 and Behre 1966, Beug 1973, Menke & Tynni 1984). An obvious difference in the development of the vegetation in the interglacial period as compared to that during the Holocene is the role played by *Carpinus* and *Fagus*. In the Holstein and the Eem interglacials, the hornbeam (*Carpinus*) prevailed over vast expanses in Europe north of the Alps, in the present Holocene, however, *Fagus* dominates. The beech was not entirely absent from the regions north of the Alps during the Holstein and the Eem interglacial period, but it played a more minor role. Not until the Holocene did *Fagus sylvatica* become dominant in the summer-green deciduous forests of Europe. A cause for this role change could be found partially in the different location of the refuge areas sought out by these species as well as in the new evolutionary development of recent, geographically largely separated and regionally competitive species of *Fagus sylvatica, F. orientalis*, *F. moesiaca* and *F. taurica* from an earlier population from the Eem, while a strong anthropogenic reinforcement of the spreading of *Fagus* is also suspected, particularly in northern Europe (see also Huntley & Birks 1983, Pott 1992, 1997, and Lang 1994). A genetical and biographical analysis of the different beech populations and their forest communities in Europe would be an important and rewarding research project for the future.

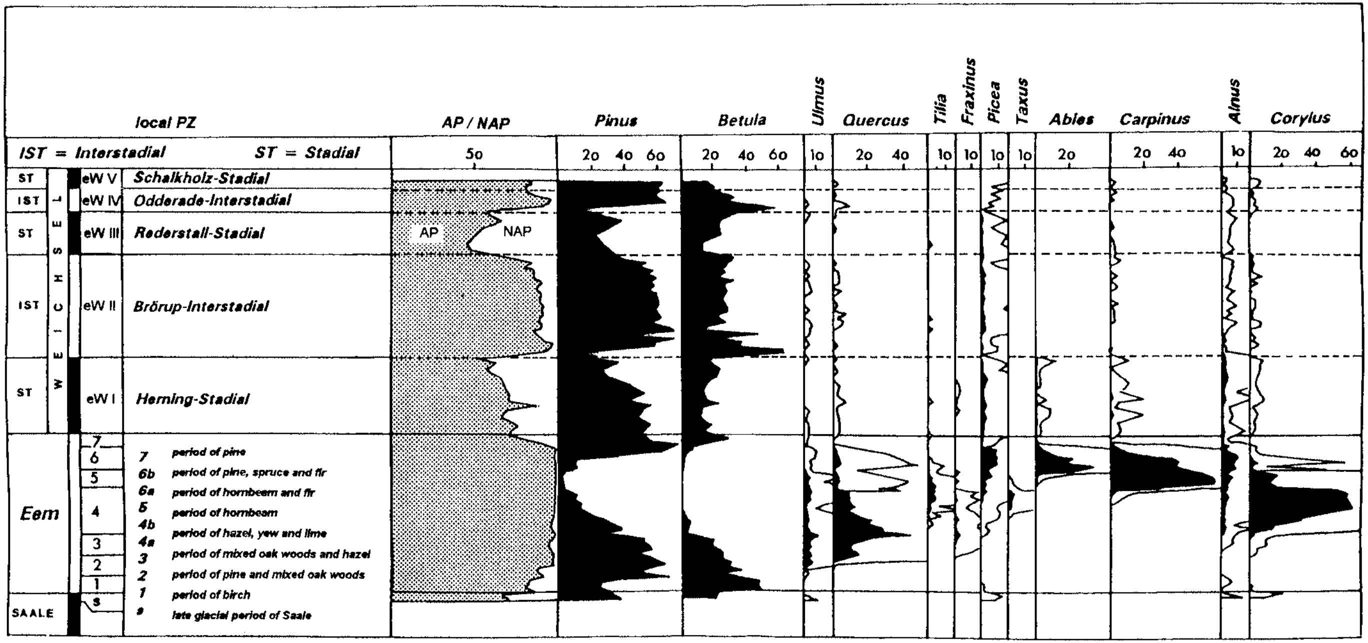


Fig. 2 - Development of vegetation during the Eem-Interglacial and the early Weichselian-Glaciation (time scale from 125000 up to 60000 years before present). Profile from the diagram Gröbern, Elbe-Saale-Region, from Litt (1994).

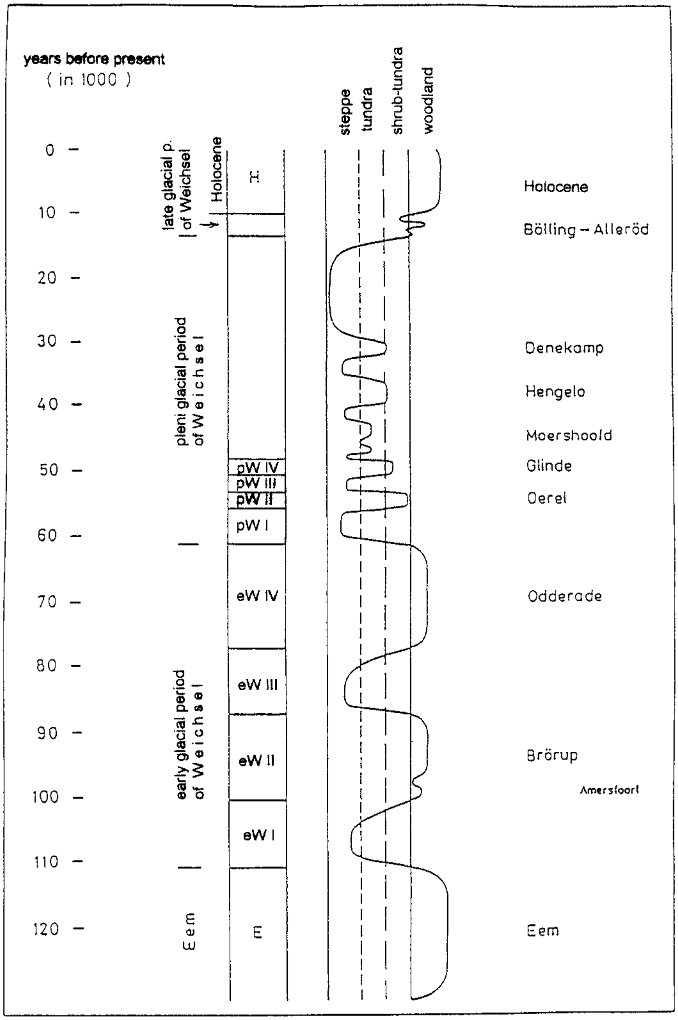


Fig. 3 - Environmental changes of climate and vegetation in Norh Western Germany from the Eem-Interglacial, the Weichselian Glacial (=Vistulian g.) up to the Holocene (from Behre & Lade 1986).

THE INVASION OF THE BEECH IN THE HOLOCENE

The change in the landscape and the change in vegetation in the Pleistocene and during the holocene between and following the glaciation periods is often seen in the context of climatic changes (see fig. 3). As a result, the natural basis of the holocene forest development in Central Europe was triggered and modified by fluctuations in climatic conditions.

Following late and post ice-age improvements in climate, diverse deciduous and coniferous tree types left their refuge areas and returned to our environment (see fig. 4). They advanced in stages, in a very specific sequence, guided by secular climate changes, from the first to the last species to migrate over a period of approximately 9000 years. *Fagus sylvatica* is certain to have spread from different pleistocene refuges in the Mediter-

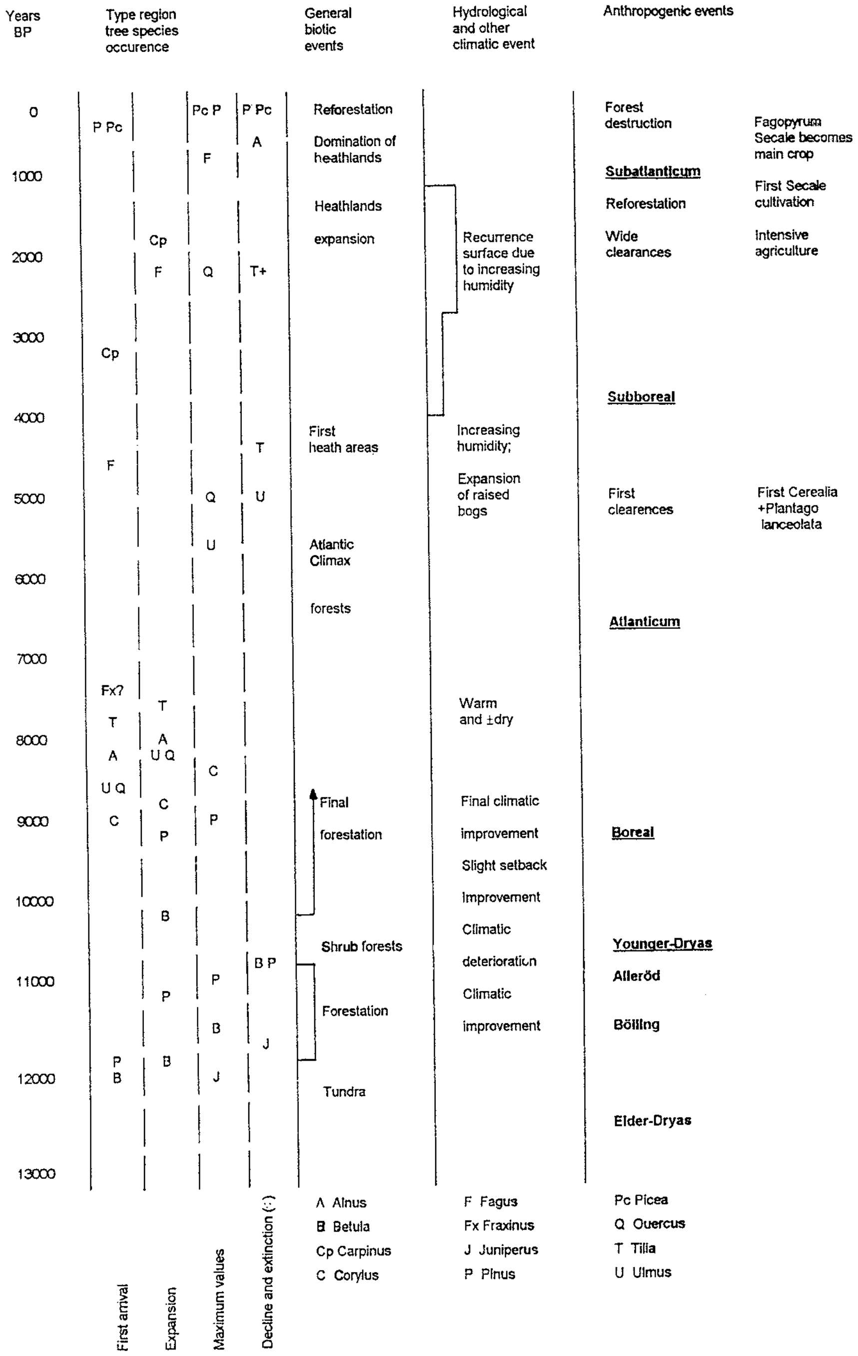


Fig. 4 - Event stratigraphy for the late- and postglacial development and environmental changes in NW-Germany (from Behre *et al.*, 1996).

ranean area north to its present-day area, whereby it took at least two different routes to northern and Central Europe. Last glacial evidence of *Fagus sylvatica* exists in Greece (Bottema, 1974; Beug, 1975) in the area of the Adriatic Sea (Gruger, 1975), in the southern Alps (Zoller, 1960; Schneider, 1987) in the southern Apennines (Watson, 1996), in the Cantabrian mountains, the Pyrenees and the Cevennes (Jalut & Delibrias, 1980; de Beaulieu *et al.*, 1984; Rodriguez-Guitian *et al.*, 1996; Reille & Andrieu, 1995; Penalba, 1994; Riuz-Zapata *et al.* 1995; Ramil-Rego, 1993; Ramil-Rego *et al.*, 1996) and testify to the refuge locations (see figs. 5 and 6). There were also glacial refuges for the beech on the southern slopes of the Cantabrian mountains, which have been dated from the period around 7400, or 7500 +/- 70 years before today, particularly by Ramil-Rego (1993), Ruiz-Zapata *et al.*, (1995) in the Portuguese-Galician border

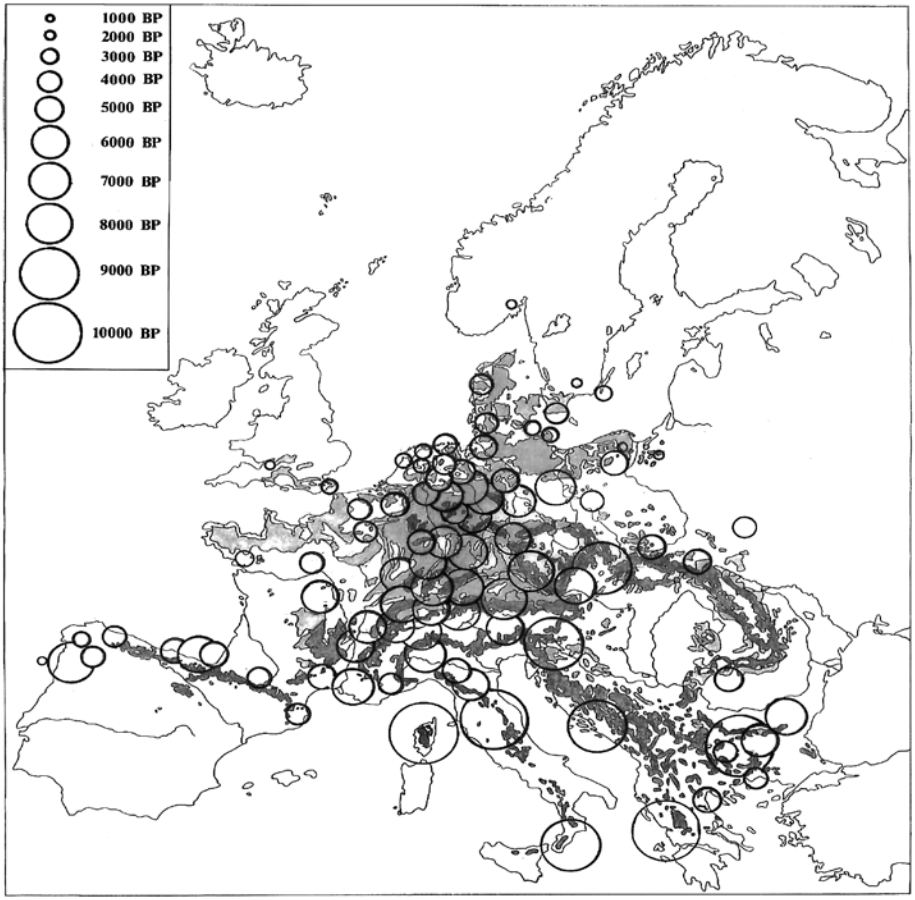


Fig. 5 - Expansion of *Fagus sylvatica* in the Holocene. Chronology of *Fagus* representation indicated by radiocarbon-dated absolute pollen-frequency (first pollen-records and continuity of *Fagus* in pollen-diagrams)

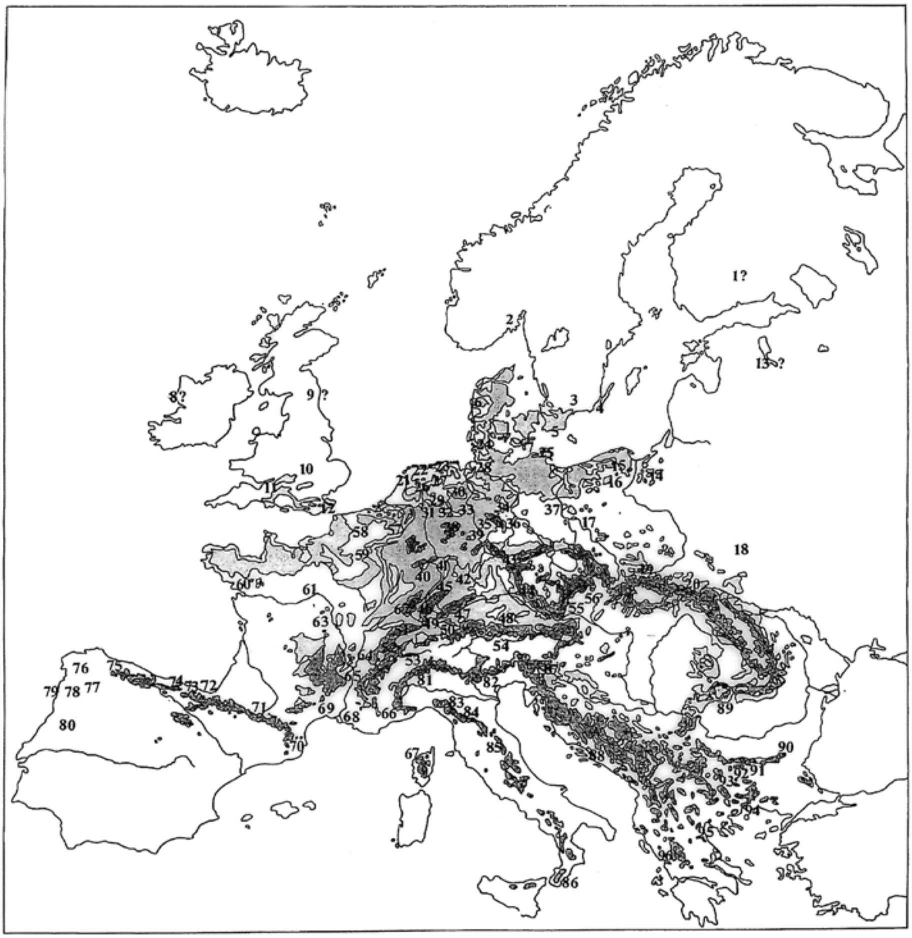


Fig. 6 - Location of the sites investigated pollenanalytically. Expansion of *Fagus sylvatica* in the Holocene.

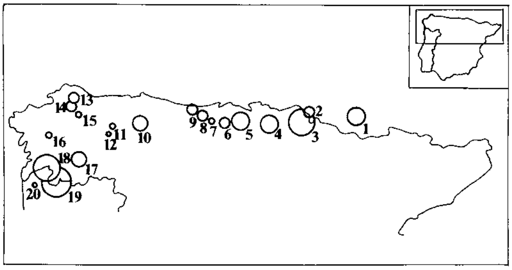
References to the sites investigated pollenanalitically

No.	Location	Bibliography
1	**Finland:** Tanulampi	SAARNISTO 1970
2	**Norway:** Vesterfjöld	FAEGRI u. pers. comm. 1960
	Sweden:	
3	Trummen	DIGERFELDT 1972
	Farskesjön	BERGLUND 1966
4	Torpmosen / Öland	KÖNIGSSON 1968
5	Kragehomlssjön	GAILLARD 1984
	Denmark:	
6	Solso	ODGAARD 1985
7	Holmegaard	ANDERSEN et al. 1983 / AABY 198
		AABY & ODGAARD 1987
8	**Ireland:** Lough Sheeauns	O´CONNELL & BOWLER 1988
	England:	
9	Scaleby Moss	WALKER 1966
10	Diss Mere	PEGLAR & BIRKS 1989
11	Somerset Levels	GODWIN 1960 / BECKETT 1979
		BECKETT & HIBBERT 1989
12	Lodge Road Bog	BAKER et al. 1978
13	**Estonia:** Soitsyarv	KABAILIENE & RAUKAS 1987

No.	Location	Bibliography
	Poland:	
14	Woryty	PAWLIKOWSKI et al. 1982
15	Kluki	TOBOLSKI 1987
		LATALOWA & TOBOLSKI 1989
		NORYSKIEWICZ & RALSKA-JASIEWICZOVA 1989
16	Wielkie Gacno	HJELMROOS-ERICSSON 1981 / 82
17	Skrzynka	OKUNIEWSKA-NOWACZYK 1987
18	Lukcze	BALAGA 1982 / 89
19	Slopiec	SZCZEPANEK 1989
20	Puscizna Rekowianska	OBIDOWICZ 1989 / 90
	Tarnawa Wyzna	RALSKA-JASIEWICZOWA 1980
	The Netherlands:	
21	Zuidersee	VAN GEEL et al. 1982 / 83
22	Groningen	VAN ZEIST 1955
	Germany:	
23	Region of the North Sea:	
	Ostfriesland	GROHNE 1975
	Spolsener Moor	O´CONNEL 1986
	Herrenhof	DÖRFLER 1989
	Rehornsmoor	DÖRFLER 1989
	Altes Moor	DÖRFLER 1989
	Swienskuhle	BEHRE & KUCAN 1986
24	Schleswig-Holstein:	
	Süderlügum	KUBITZKI 1961
	Flögeln	BEHRE 1976
	Gr. Plönersee, Poggensee	AVERDIECK et al. 1972
	Großer Segeberger See	AVERDIECK et al. 1972
	Oldesloe	SCHÜTRUMPF 1954
25	Rügen	LANGE / JESCHKE & KNAPP 1986
26	Dutch- / Northwest-German Border:	
	Emmen (The Netherlands)	VAN ZEIST 1959
	Engbertsdijkvenn (Netherl.)	VAN GEEL 1972
		DUPONT & BRENNINKMEIER 1984
	Bathorner Diek, Wielener Moor	ISENBERG 1979
	Klausheide	ISENBERG 1979
	De Borchert	VAN GEEL et al. 1980 / 81
	Gildehäuser Venn, Syen Venn	ISENBERG 1979
	Speller Dose	KRAMM 1978
	Vinter Moor	KRAMM 1978
27	Drenthe (The Netherlands)	CASPARIE 1972
	Geest of North-West Germany:	
	Wietmarscher Moor	ISENBERG 1979 / VAN GEEL 1972
	Hahnenmoor	KRAMM 1978 / MIDDELDORP 1984
	Großes Moor	SCHNEIDER & STECKHAN 1963
	Dümmer	PFAFFENBERG & DIENEMANN 1964
	Weeser Moor	FREUND 1994
	Belmer Bruch	SCHWAAR 1976 / FREUND1994
	Schünebusch	CASPERS 1993
	Hellweger Moor	KUBITZKI 1961
28	Teufelsmoor	OVERBECK 1975
29	Amtsvenn	KUHRY 1985
	Germany:	
30	Wiehengebirge and spurs:	
	Kalkrieser Moor	MOHR 1990
	Nettelstedter Moor	WIERMANN & SCHULZE 1986
	Hücker Moor	FREUND 1994
	Sollingmoore	SCHNEEKLOTH 1967
31	Ruhrgebiet	REHAGEN 1964
	Sterkrade	AVERDIECK in REHAGEN 1964
32	Münsterland:	
	Zwillbrocker Venn	BURRICHTER 1969
	Weißes Venn	REHAGEN 1964
	Nottebrack	TRAUTMANN 1969
	Borkenberge	POTT 1984
	Im Jiewitt	MOHR 1990
	Heppeldüne	BURRICHTER 1982
	Oestinghsn. / Soester Börde	BURRICHTER & POTT 1987
33	Teutoburger Wald	SCHÜTRUMPF 1973
	Hiddeser Bent / Teutob. W.	POTT 1982
	Eggegebirge	TRAUTMANN 1957 / POTT 1985
34	Geest of East Lower-Saxony:	
	Waller Moor	ZICKERMANN 1996
	Bissendorfer Moor	KUBITZKI 1961
	Schierhorn	ZICKERMANN 1996
	Wittenmoor	ZICKERMANN 1996
	Drömling	GOLOMBEK 1980
35	Eichsfeld	CHEN 1988
	Luttersee	CHEN 1988
36	Harz	WILLUTZKI 1962
37	Pechsee, Tegeler See	BRANDE1980, 88
38	Ebbegebirge	POTT 1985
	Lützel / Rothaargebirge	POTT 1985
	Rothaargebirge	POTT 1985, 89
39	Hoher Meißner	STALLING 1983
40	Eifelmaare	STRAKA 1975, 85
41	Hunsrück	FRENZEL 1983 / POTT1989
42	Schwäbische Alb	SMETTAN 1988
43	Fichtelgebirge	FIRBAS et al. 1958
	Germany:	
44	Bayerischer Wald:	
	Bayerischer Wald	STALLING 1987
	Dösinger Ried, Hohenau	STALLING 1987
	Waldviertel	PESCHKE 1972
45	Nordschwarzwald:	
	Nordschwarzwald	RADKE 1972
	Breitnau	RÖSCH 1989
	Horbacher Moor	LANG 1954
46	Schwarzwald	LANG 1983
47	Schleinsee	GEYH, M.M.A. et al. (1971)
48	Auerberg	KÜSTER 1988
	Ammersee	KÜSTER 1984
	Switzerland:	
49	Bodenseegebiet	ROSCH 1983
50	Rotsee	LOTTER 1988
51	Lobsigensee	AMMANN 1989
52	Genfer See	WEGMÜLLER 1966
53	Lac du Mont D´Orge	WELTEN 1982 / BIERI-STECK 1990
	Austria:	
54	Giering	BORTENSCHLAGER 1976
55	Spielberg	PESCHKE 1972
	Czech-Republic:	
55	Kamenicky	RYBNICKOVA & RYBNICEK 1988
56	Vracov	RYBNICKOVA & RYBNICEK 1972
57	**Belgium:** Limburg	JANSSEN 1960
	France:	
58	Fréchencourt	VAN ZEIST & V. D. SPOEL-WALVIUS 1980
59	Marais de Chivres	VAN ZEIST & V. D. SPOEL-WALVIUS 1980
	Silly-la-Poterie	VAN ZEIST & V. D. SPOEL-WALVIUS 1980
60	Saint-Malo-de-Guersac	VISSET 1985
61	La Voise, Coizard-Joches	VAN ZEIST & V. D. SPOEL-WALVIUS 1980
62	Vosges	DE VALK 1981
	Vosges	EDELMANN 1985
63	La Taphanel	DE BEAULIEU, PONS & REILLE 1982
64	Col Luitel	WEGMÜLLER 1977
65	Lac du Bouchet	REILLE & DE BEAULIEU 1988

No.	Location	Bibliography
	France:	
66	Lac de Siguret	DE BEAULIEU 1977 DE BEAULIEU & REILLE 1983
67	Lac de Creno / Corse	REILLE 1975
68	Fos	TRIAT 1975
69	Courthezon	TRIAT-LAVAL 1978
70	Canet-St.-Nazaire / Pyrenees	PLANCHAIS 1985
71	Freychinède / Pyrenees	JALUT et al. 1982 / REILLE 1990
	Estarres / Pyrenees	JALUT et al. 1988
	Spain:	
72	Biscaye	REILLE & ANDRIEU 1995
73	Belate	PENALBA 1989, 94
74	Los Tomos	PENALBA 1989, 94
75	Lago de Ajo	WATTS 1986
76	Chan da Cruz	RAMIL-REGO 1992
	Chan Lamoso	RAMIL-REGO 1992
77	Prada	MALDONADO 1994
	Portugal:	
78	Lagoa do Marinho	RAMIL-REGO 1993
79	Chao da Cheira	RAMIL-REGO et al. 1995
80	Candeeira	VAN DER KNAAP & VAN LEEUWEN 1991
	Italy:	
81	Lago di Ganna	SCHNEIDER & TOBOLSKI 1983, 85
82	Sommersüss	SEIWALD 1980
83	N-Apennine:	
	Casanova	WATSON 1996
	Prato Spilla A	WATSON 1996
	Lago Padule	WATSON 1996
84	Pratignano / N-Apennine	WATSON 1996
85	Lago di Trasimeno	DRESCHER-SCHNEIDER n.p.
86	Canolo Nuovo	SCHNEIDER 1985 / GRÜGER 1977 DRESCHER-SCHNEIDER n.p.
87	**Slovenia:** Ledine	CULIBERG, SERCELJ & ZUPANCIC 1981
88	**Croatia:** Malo Jezero	BEUG 1961, 62 / JAHNS 1990
	Romania:	
89	Cristisor	LUNGU 1971
	Taul Zanogutii	POP, LUPSA & BOSCAIU 1971
	Bulgaria:	
90	Shabla-Ezeretu	FILIPOVA 1985
91	Matnica, Vitosa	FILIPOVITCH 1988
92	Kupena	HUTTUNEN et al. 1992
93	Sucho-Ezero	BOZILOVA, TONKOV & PAVLOVA 1986
	Tschokljovo	TONKOV 1985
	Greece:	
94	Tenaghi Philippon	TURNER & GREIG 1975
95	Litochoro	ATHANASIADIS 1975
96	Ioannina	BOTTEMA 1974

region on the north-west Iberian peninsula (fig. 7). This data contradicts the earlier assumption that the beech came from the west from southern France over the so-called "Via Pirenaico-Cantabrica" to the west to its present-day environment, as can be read in Huntley & Birks (1983) and in Lang (1994), and this confirms the assumption of our Spanish colleagues concerning the auto-perpetuation of the beech in the Cantabrian mountains and the southern edge of the Pyrenees (see particularly Izco, 1987; Izco *et al.*, 1986; Rivas-Martinez, 1987). There might have been further beech refuges near the Carpathian mountains (Ralska-Jasiewiczowa, 1972; 1983). As a result, using



No.	Location	Bibliography	Radiocarbon-Date
1	Biscaye	REILLE & ANDRIEU 1995	5000 BP
2	Atxuri	PENALBA 1989, 94	3000 BP
3	Belate	PENALBA 1989, 94	7000 BP !
4	Saldropo	GARCIA et al. 1989	4500 BP
5	Los Tomos	PENALBA 1989, 94	5000 BP
6	Estacas de Trueba	MARISCAL 1995	3000 BP
7	Pico Sertal	MARISCAL 1986	2000 BP
8	Cueto de la Avellanosa	MARISCAL 1983	3000 BP
9	Llano Ronanzas	MARY et al. 1973	3000 BP
10	Lago de Ajo	WATTS 1986	4000 BP
11	Caspedosa I	MUNOZ et al. 1995	2000 BP
12	Suarbol	MUNOZ et al. 1995	1000 BP
13	Chan Lamoso	RAMIL-REGO 1992	3000 BP
14	Chan da Cruz	RAMIL-REGO 1992	3000 BP
15	Lagoa de Cospeito	RAMIL-REGO 1992	2000 BP
16	Brins I	VAN MOURIK 1986	2000 BP
17	Prada	MALDONADO 1994	4000 BP
18	Lagoa do Marinho	RUIZ ZAPATA et al. 1995	7000 BP !
19	Lagoa do Marinho	RAMIL-REGO 1993	7500 BP !
20	Chao da Cheira	RAMIL-REGO et al. 1995	1000 BP

Fig. 7 - Holocene expansion of *Fagus sylvatica* on the North-West Iberian Peninsula.

the pollen diagrams available up to now, it is easy to identify the late glacial and Holocene migration of *Fagus sylvatica* from the south and south-west of Europe to the north and north-west: the invasion of the beech advanced along two main routes. The easterly route led from the Balkan peninsula to the north-west through the Dinaric Alps to the eastern Alps and from there through the Danube valley and the Bohemian central highlands to the northern German and Polish lowlands and further over the Baltic Sea to southern Sweden (see fig. 8). The western route led from the southern Apennine peninsula to the western Alps and on the Iberian peninsula from northern Portugal (Serra de Estrela) and from Galicia separately into the Pyrenees, into the French Massif Central and throughout north-west France to southern England and Wales (Lang, 1994). The migration of the beech with its western and eastern sources met in the northern foothills of the Alps (cf. also Kral, 1979; Kuster, 1986), and from there, *Fagus* reached the central highland regions of the Vosges mountains, the Black Forest, in the Swabian Alb and in the Bavarian Forest by approximately 5000 B.C. (fig. 8).

Since the mid-Atlanticum, *Fagus sylvatica* is also present in the corresponding deposits of large mires; between 5000 and 4500 B.C., the beech reached its lime and loess locations in the northern central highlands (fig. 9) from the south-east at approximately the same time; from there it most probably spread to the neighbouring silicate locations as well as the higher montane regions.

During the subboreal period around 1800 B.C. *Fagus* finally reached the northern edge of the geest in NW Europe on the border to the coastal marsh of the North Sea as well as the limy end moraines close to the coast of the Baltic Sea. Recent C-14 dating from the mires of the Elbe-Weser river basins (Kubitzki, 1961; Casparie, 1972; Behre, 1976) or from the mires in East Frisian (Grohne, 1957; Kucan, 1973) confirm the synchronous subboreal spreading phases of the beech. Pollen analyses with standard diagrams of the larger mires also indicate that closed beech curves with one and more percent proportions, measured against the sum of all of the tree pollen, appear almost at the same time in the north-western European lowlands upon examination of a larger area. A discontinuous and delayed propagation of the beech took place only in small areas where the beech-conducive mixed sandy soil changed to moist and wet moor locations or in the direct vicinity of river and coastal marshes where the beech cannot grow in any case. In the west Frisian coastal marsh region and in the area around the Dutch Isselmeer, the first evidence of beech trees can be found on small, island-like geest layers from about 850 B.C. or 500 B.C. (see fig. 9 and van Zeist, 1955; van Geel *et al.,* 1982/83).

FACTORS INFLUENCING THE ESTABLISHMENT OF THE BEECH

As pollen-analytical results show, the former vegetation were first subjected to a natural change of vegetation stages affected by climate and succession. This often includes the supposition that woodlands always settled in their potential areas, where they always reacted to climatic change immediately. Based on more recent studies however, we know that there is a basic, direct connection between the development of climate as the basis for forest development in Central Europe, while in reality this evolution must be modified considerably and put in the context

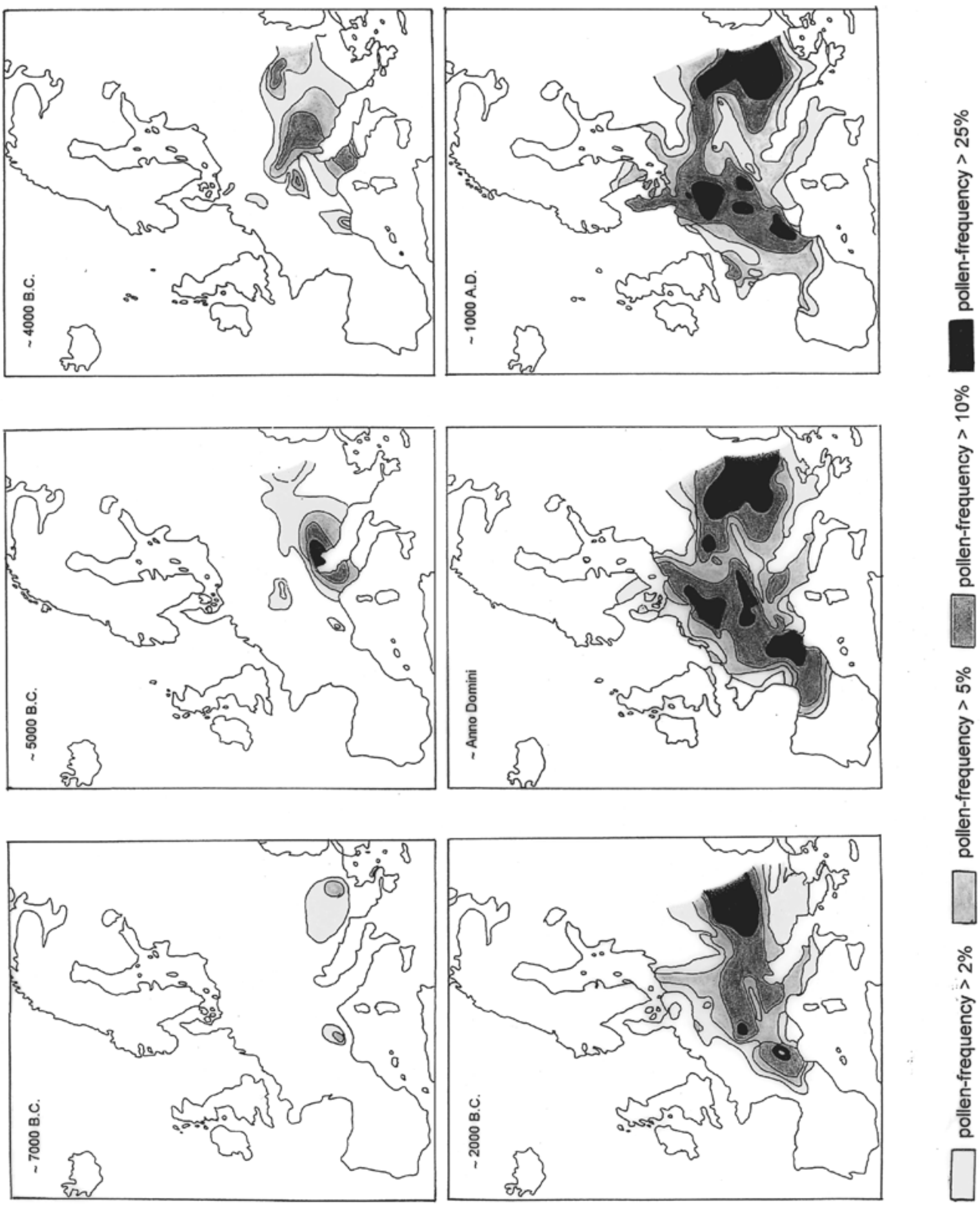


Fig. 8 - Holocene distribution and expansion of *Fagus sylvatica* from the glacial refugees to Central Europe. Region of identical pollen frequency demonstrate the successive formation of the European beach-area spread from its glacial refuges. The different colours remark pollen-density on pollen diagrams (from Pott, 1993).

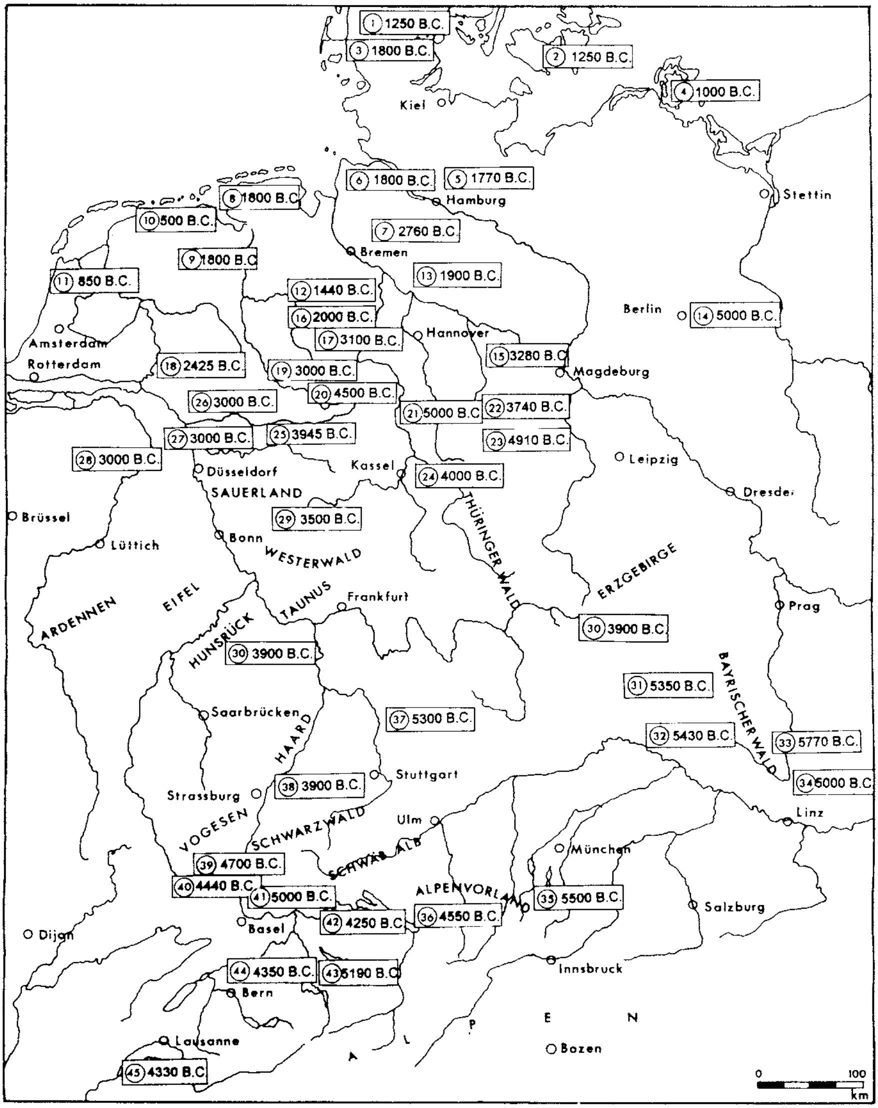


Fig. 9 - Holocene expansion of *Fagus sylvatica* based on radiocarbon-dated pollen diagrams (from Pott, 1993).

of other parameters effecting change in the environment. Vegetation is not static. It changes when new plants migrate into a landscape or when such environmental conditions change as the climate, the soil or human influence. Many types of animals can react to changes in their environment by moving to new living territories, but plants cannot. In pollen diagrams, the most important sources of vegetation history, the changes in vegetation and landscapes over thousands of years are recorded. The following factors come into question as causes for the sequence of woodland development in general and the specific beechwood-establishment with different speeds of migration and establishment of the individual tree types:

- the different warmth requirements for individual species, at first particularly cold-resistant species were able to expand, for example; the different *Betula*-species and *Pinus sylvestris* as pioneers.
- the refuges located at different distances (warmth-requiring species, i.e. most of our deciduous trees survived the glacial periods in the south Mediterranean regions, others further north);
- the successive biological process of soil maturation as well as the settlement of pioneer species, whereby the first forest species of birch and pine still appear as pioneer woodland trees;
- the different establishment opportunities for species depending on their seeds and fruits, whereby anemophilous species have a definite advantage; according to current information on the spreading of the beech to the north we must assume transport by animals, whereby particularly animals for long-distance-transport play an important role (e.g. bears who can carry the cupulae of the beech as beech-nuts caught in their fur), or birds as well (e.g. jay-birds, s. Johnston & Webb, 1989). Long-distance spreading via rivers cannot be overlooked because the fruit and seeds of the beech tree are able to float.
- the different fertility conditions for tree species. Birch trees, for example, attain the age of fertility relatively early at 10 years (Straka, 1975), beech trees on the other hand considerably later when they have reached the age of 40 and they are fructifying only every 6-7 years on average; *Fagus sylvatica* required approximately 10-20 seed generations to spread throughout Central Europe from the south to the north-west;
- the different competitive factors (e.g. phytogenic competition) or the masking of natural development due to the modifying influence of mankind. Prehistoric man's selection of settlement sites in Central Europe was limited almost everywhere to locations conductive to beech growth. As a result, *Fagus sylvatica* was never able to settle its potential area in Central Europe and particularly in the north-west European Pleistocene lowlands (cf. van Zeist, 1959; 1981; Burrichter, 1976; Burrichter *et al.,* 1988; Pott, 1981; 1982; 1985a; 1985b).
- considering well dated pollen diagrams we must think of small elm declines and subsequent changes in the forest composition with beech-spreading, being also closely related to Mesolithic and Neolithic impact (see for example Pott, 1982; Lotter, 1988; Rösch, 1993; Liese-Kleiber, 1993; Richoz, *et al*. 1994; Haas, 1996).
- for this reason, we can assume that the potential distribution of the beech is higher on the Pleistocene young and old moraines and that the potential natural beech-oak forest would have claimed more space than the current oak-birch forests in NW-Europe if there had been no human settlement activity.

Consequently, man's prehistoric influence since the Neolithic period about 5500 BC within the period of Atlanticum did not affect a static vegetation state, but rather a dynamic process; since the earlier Atlanticum, then, we can no longer speak of large-scale natural woodland vegetation.

With the exception of soils low in nutrients or affected by ground water, beech attained absolute dominance in the environment of the Central European highlands on different substrates. Due to its edaphic and climatic competitive advantages, it also developed its enormous superiority in spite of small-scale differences, allowing a rough division in thirds of the current beech, mixed beech and beech-free forests.

The ecological amplitude of the beech is so large that under current climatic conditions it occupies a closed area from the lowlands to the montane regions, where its main emphasis lies, from Sicily to southern Sweden - with the exception of regions which are arid in summer. As a sub-Atlantic-sub-Mediterranean geo-element, beech is even able to form the forest border in Atlantic-tinged mountains such as the Cevennes and the Vosges mountains (see also explanations in Carbiener, 1963; Pott, 1988; 1993; 1996). The so-called maritime timberline is found where the average July temperature reaches approximately 10°C.

Consequently, *Fagus sylvatica* finds a place in virtually all altitudes ranging from lowlands to the alpine regions in the north-west European central highlands. The beech forests reach the furthest outposts on limestone and loess in the flatlands of the northern environment in the central highlands. They are already typically developed in altitudes of 50 m above sea-level, while the horn-beam-beech forests on silicate stone formations do not reach any lower than 160 m above sea-level, whereby they can often be considered as transitional types between beech-oak forests and pure beech forests at these altitudes. This phenomenon clearly indicates the superior competitive strength of the beech on better sites (cf. also Leuschner *et al*., 1993). On the geest plains in the north-west German flatlands beech appears only as a mixed wood with durmast and pedunculate oak particularly in *Lonicero periclymeno-Fagetum* (*=Fago-Quercetum)*, as well as in *Stellario-Carpinetum*; local domains for lowland beech forests from the complex of the *Maianthemo-Fagetum* (*=Milio-Fagetum)* continue to form the loess-clay borders and loess substrates in the loess-border landscapes. This small-scale differentiation dates back to the time of the first appearance of the beech in these areas.

C-14 DATA ON THE HOLOCENE DISTRIBUTION OF THE BEECH IN THE CENTRAL HIGHLAND ENVIRONMENT OF NORTH-WEST EUROPE

During the Atlanticum in north-west Europe, closed mixed oak forests initially formed following the massive spreading of the *Ulmus, Quercus, Tilia, Fraxinus* and *Acer*, which revealed natural deviations in their vegetation composition in loess landscapes, geest- or central highland landscapes. In the area of north-west German, Dutch and Danish geest and loess landscapes, the mixed oak forest is characterised by an abundance of linden trees on better soils at least during the later period of the Atlanticum. The marshy flatland areas of sandy geest are taken over by alder trees, and in the hilly to mountainous locations, mixed oak forests with many linden trees also determine the vegetation with a probably significant amount of *Corylus avellana* in the undergrowth.

In figure 9, only those radio-carbon dated pollen diagrams which include up to approximately 1,000 tree pollen samples are evaluated as a comparison of the invasion of the beech in the central highland environment with the Pleistocene geest landscape. Comparing pollen diagrams from different authors can be a problem because closed curves drawn for reference sizes of 200 tree pollens, for example, will look much different to those drawn for 1000 tree pollens. In the last case, the closed beech curve will appear much earlier. A differentiated study of beech migration and spread in a relatively limited area will indicate the gradual emigration phases of the beech from its primary lime and loess locations in the central highland regions to the geest plains in the old moraine landscape.

At the turn of the Atlanticum, there is a remarkable change in the forest, whereby there are obvious correlations between the spreading of the beech and the usually reciprocal behaviour of the pollen spectrum with reductions in the proportions of *Tilia-, Ulmus-, Quercus-* as well as *Corylus*. Reasons for this might include:

- beech forests have formed in several stages following climatic changes and successive biological phenomena (see above) at the expense of the oak forests. Elm and linden trees dropped gradually following a slow deterioration of the climate over a long period of time so that after the competition of the linden no longer threatened the beech, its growth thickened and it was able to develop into the prevailing tree;
- as a shade tree element, *Fagus sylvatica* displaced the light-requiring deciduous trees, particularly the heliophiluous *Corylus avellana*; as shade trees, beech and linden have similar habitat requirements so that after *Fagus* has first established itself on the better soils, the linden is inferior as competitor in the long run.
- the reduction of linden and elm spectrums in the pollen diagrams could also be the result of local causes influenced by competitive factors or even setbacks due to infections with the fungus *Graphium ulmi*, which could explain the secular fluctuations of elm and linden values in the Atlanticum before the appearance of the beech or before the advance of human settlements;
- during the spread of the beech, the first stronger influences of late Neolithic or Bronze-Age man were felt in the central highlands and particularly in the loess regions; the number of linden and elm pollen producers dropped while the number of settlements rose, which could have been caused by the openings in the forest created by the land clearing process, the creation of new locations and anthropogenic influences (e.g. pruning, utilisation of linden bark).
- some pollen-diagrams of southern Germany and Switzerland show small charcoal peakes of elm reductions and subsequent *Fagus*-rising. Some charcoal-pieces recovered on a Mesolithic site in Southern Germany, dated to approximatively 6250 BC can also be considered as a record of the local presence of *Fagus* tree in the Older Atlantic period of Central Europe (see Schweingruber 1978). Later, as described above, *Fagus* was taking advantage of vegetation disturbances for ist own spreading.
- the natural environment as well is temporally and regionally different in the vicinity of the north-west European highlands. Farmers belonging to early Neolithic band ceramian groups were the first to prefer limy soils, particularly in areas with loess in the growth region of today’s potential *Maianthemo*-(*Milio) Fagetum* around 5500-4500 B.C. (see also fig. 10).
- following pollen-analytical and archaeological findings, the geest areas are likely to have been settled by Neolithic-Megalithic cultures by approximately 3000 B.C. or in places even earlier, whereby partial areas of today’s beech-oak forests were already sacrificed for cultivation or farmland in prehistoric times.

In general the reduction of atlantic mixed forests and the spreading of beech in Central Europe is very probably due to the natural succession processes related to climatic trends in the Atlantic period. But as proposed, above these forest succession processes were probably accelerated and influenced by human impact during the Early and Middle Neolithic period (see for example Pott, 1993; Haas, 1996).

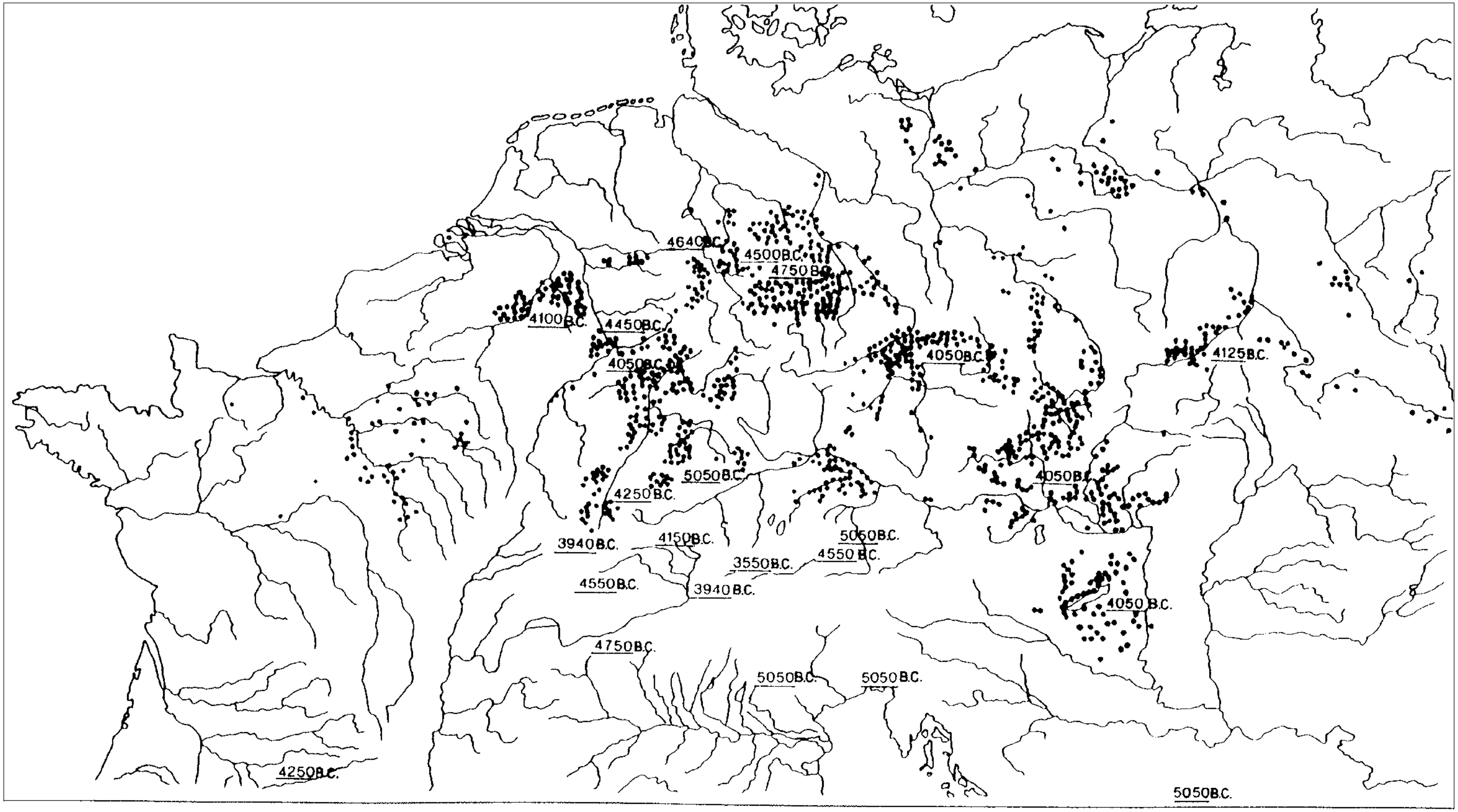


Fig. 10 - Distribution and expansion of early neolitic agriculture in Central-Europe after radiocarbon-dated first cereals (from Pott, 1993).

At almost the same time at the beginning of the sub-Atlanticum around 1000 B.C., there was a stronger development of beech in all areas of geest, loess landscapes and in the mountains, which must be considered as the start of the final formation of the beech- forest in Europe (fig. 11). In the northern flatlands, the culmination of the spreading of the beech was delayed compared with the mountainous areas by more than 1.000 years, beginning in 800 B.C. and continuing up until the 4th and 5th centuries A.D. (fig. 9). At the time of the culminating human migrations, when many cultivated areas in potential beech-oak forests had to be abandoned by humans or were only worked partially, it was possible for beech trees to take over these areas for the first time as well (cf. also Behre, 1988).

If we consider this forest and vegetation development, which was obviously not abrupt but rather gradual in nature, affecting areas differently depending on local conditions, we must assume a natural and simultaneously anthropogenic multifactorial complex of effects which made an initial spreading of the *Fagus sylvatica* possible.

At the end of the Atlanticum approximately 7000 years ago, Central Europe was covered by virtually endless forests: these reached from the Alps to the North and Baltic Sea as well as from western France to far into Russian territory. The forest did not look the same all over, the composition of the tree types for each region had changed since the preceding millennia: in Central Europe, other forest trees in addition to the beech such as the European spruce (*Picea abies*), the fir (*Abies alba*) and the hornbeam (*Carpinus betulus*) had taken over new areas. The fir came from the west, more exactly from the western Alps. Starting from its refuges south of the Alps, the European spruce (*Picea abies*) had spread out in the east to the alpine regions and from there also became acclimatised in regions lying further west. The spruce infiltrated the boreal pine forests and after a time, grew taller than the pines, which were then robbed of light in the shade of the first and dropped in number in that area. The spruce only spread to areas where hazel bushes from *Corylus avellana* had prepared the soil. As a result, the spruce made its first appearance in Central Europe in the eastern Alps, on the northern fringe of the Alps, up to the Bohemian Forest and northwards to the Erzgebirge through the Thuringian Forest to the Harz mountains, into Sauerland and even up to the northern Lüneburg Heath (s. also Küster, 1995; Pott, 1995; 1996). The hornbeam (*Carpinus betulus*) found its glacial refuge near the Carpathian mountains and on the Balkan; it advanced towards Central Europe very slowly; these species which arrived relatively late could only assert themselves gradually against the already firmly established forest communities (see also fig. 4).

The locational conditions of the earlier mountain elm forests of the Atlanticum on the north edge of the Alps and in the central highlands were conducive to the growth of the beech and the fir; gradually the beech claimed more and more land where mountain elms (*Ulmus glabra*) had stood previously. The elm forests were pushed back to unstable, steep cliffs which were regularly subjected to earth slides where the beech and fir could not grow. This is where the steep-cliff and canyon forests of *Tilio platyphylli-Acerion pseudoplatani* group can still be found today. Similarly, we find today the hornbeam forests with *Carpinus betulus* in Central Europe only where the beech cannot grow because of too much soil moisture(e.g. *Stellario-Carpinetum* as an azonal forest type in Central Europe); or where the beech cannot follow because of the continental climate (e.g. *Galio-Carpinetum* and

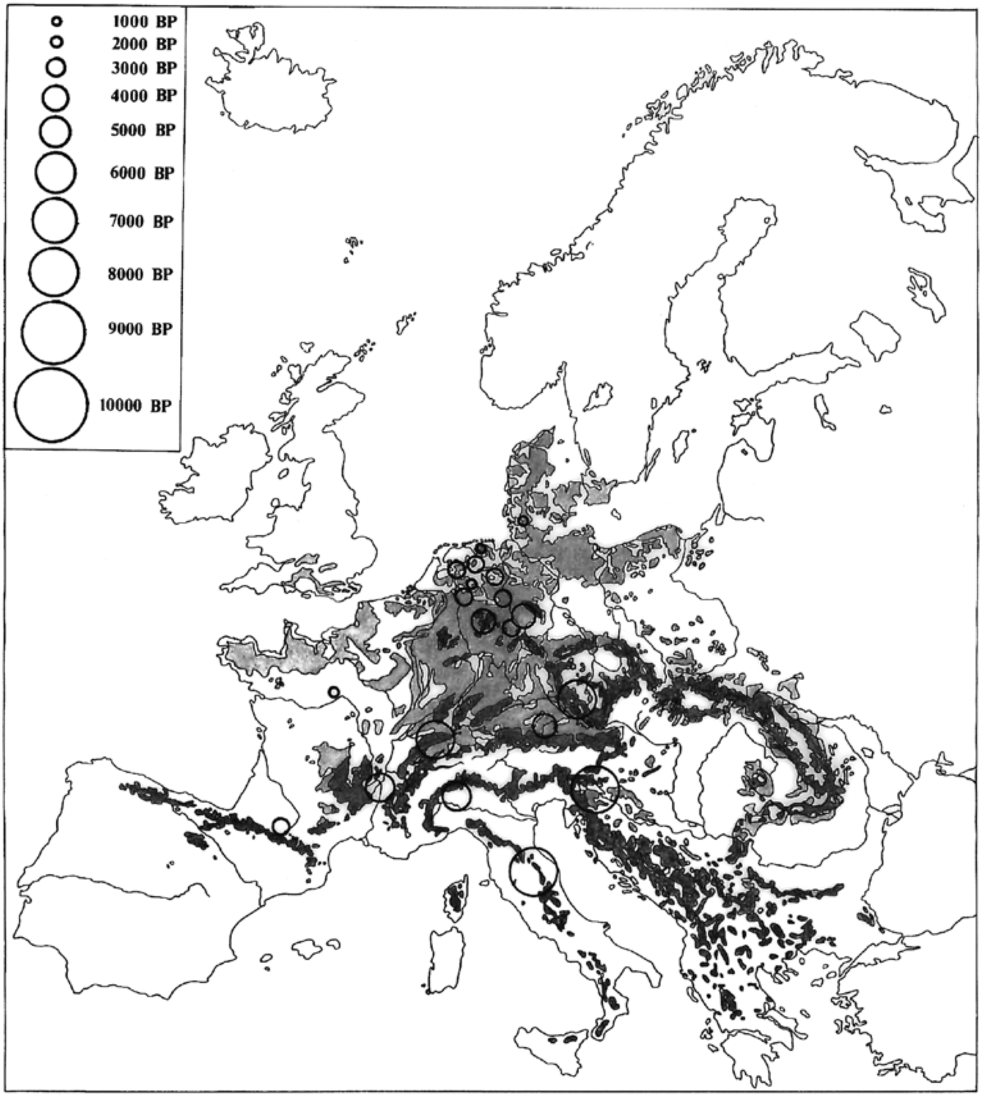


Fig. 11 - Expansion and establishment of *Fagus sylvatica* based on pollen diagrams with a pollen-frequency of more than 5 % AP.

Tilio-Carpinetum as climate-zonal forests in Central and Eastern Europe, or the *Quercetalia-pubescentis* communities and *Carpinus* in southern Europe). Even the extremely nutrient-poor, Pleistocene quartz-sandy soils in north-western Europe are largely free of beech; here it was possible for the oak-birch forests of the *Quercetea roboris* to develop as endemic vegetation types. All of the other regions belong to the domain of the beech.

THE BEECH FOREST COMMUNITIES

The sociological structure and species framework of the natural beech forests with their large ecological amplitude depends primarily on edaphic conditions. In addition, the path of the water through the soil and the exposition as well as the inclination of the mountain slopes can also be important. In the majority of Central European forests, the *Fagus sylvatica*, a shade tree, also plays an important role in the existence or absence of other types of trees. As already mentioned, the beech attains optimum growth in our climate, because not only can it produce more shade, it can also tolerate more shade than its competitors. With its fan-shaped limbs with many branches and leaves which fill in the gaps, the beech can take in a great deal of light with relatively little foliage. Just a small percentage of the incoming sunlight suffices for the so-called shade leaves on its lower branches to carry on photosynthesis. An average of only three per cent of each part of the light spectrum needed to perform photosynthesis is able to penetrate the leafy crown of the beech to reach the forest floor (Leuschner, 1994). Using this ability to throw a lot of shade and to make do with little light if necessary, the beech was and is able to assert itself on the sandy mixed soil of the geest which affords sufficient nutrients. As a result, the beech is superior to all other types of trees on not too wet, not too dry and not to nutrient-poor soils. The forester says: “The beech needs a moist head and dry feet”, i.e. it prefers the sub-Atlantic-sub-Mediterranean climate but avoids the moist soils. With the exception of warmth-requiring beech forest communities of the *Cephalanthero-Fagenion* group, such as the sedge-beech forest (*Carici-Fagetum*) and the blue grass-beech forest (*Seslerio-Fagetum*), which settle in small-scale special locations, the pure beech forests can be divided into different series from the lowlands to the montane regions:

- Series of the *Luzulo-Fagenion* group on nutrient-poor and acidic silicate rock with the central associations of the acidopytic beech forest (*Luzulo-Fagetum*) and the *Periclymeno-Fagetum* (syntaxonomic version according to Pott, 1995),
- Series on alkaline rock rich in minerals with the woodruff-beech forest (*Galio odorati-Fagetum*) and the basiphytic beech forest (*Hordelymo-Fagetum*) as the central associations in the *Galio-odorati-Fagenion* group,
- Between both, as it were, there is the neutrophytic beech forest (*Maianthemo-Fagetum = Milio-Fagetum*) as a linking element,
- Series of the pre-alpine beech forests of the *Lonicero-alpigenae-Fagenion* sub-montane and montane regions in the foothills of the Alps with many regional associations and the central *Lonicero alpigenae-Fagetum,*
- Series of beech forest rich in coniferous trees such as fir and spruce of the *Galio-Abietenion* group whereby the fir (*Abies alba*) on the north edge of the Alps and in the foothills of the Alps only grows best in those regions today where the forest floor was already prepared with leaf mould by the mixed forests with *Acer pseudoplatanus* during the Atlanticum so that apparently only *Abies alba* was able to gain a foothold here when the montane beech-fir-spruce mixed forests in the subboreal region.
- Series of the high montane to sub-alpine cripple beech forests of the *Aceri-Fagenion* group on the maritime timberline of the Atlantic central highlands, in the Swiss Jura and in the western Alps. The *Aceri-Fagetum* comprises the local existence limit of the beech forests there starting from approximately 1000 meters in altitude.

These potential natural forest types form the starting point or reference basis for anthropogenic intervention also represent the reference level for forest utilisation with their natural potential. Today's coppices, for example, no longer consist of mostly beech in their combination of species, but rather of oak and birch due to habitat changes and the process of selection in the case of perpetual tree-cutting by coppicing on a silicate base; on a lime base, on the other hand, the role of the beech is largely taken over by the hornbeam and oak, whereby in the latter particularly *Carpinus betulus* is reinforced by its vitality (hornbeam effect Pott, 1981).

Permanent forest destruction with irreversible habitat changes, such as anthropogenically initiated drift sand deposits and dune formation, earlier sod cultivation and secondary podzolisation took place for centuries in north-west German old moraine flatlands at the expense of the beech. The clear settling preferences in the growth areas of today's potential *Maianthemo-Fagetum* region of loess landscapes or in *Luzulo-Fagetum* areas of the geest regions have remained largely consistent during the pre-historic and historic periods. It was exactly here that earlier potential *Lonicero periclymeno-Fagetum* areas were secondarily covered by drift sand as a result of earlier extensive cultivation, particularly heath cultivation, and belong today to the *Betulo-Quercetum* region. The growth areas of the *Maianthemo-Fagetum* were the preferred areas for settlement and land cultivation from the earliest Neolithicum until today, that means over a period of approximately 7,500 years. As a result, the near-natural beech forests exist for the most part in unfavourable locations only as small-scale remainders.

RESUMÉ

L'étude des processus d'évolution naturelle relatifs à la consitution des forêts de hêtres d'Europe centrale aprés la période phase glaciaire, il suppose l'impérative prise en considération des phases de réchauffement précédant la derniére glaciation, dite de la Vistule. L'interglaciaire Eemien est en Europe l'objet de nombreuses études de détail, et ces conditions climatiques sont considérées comme comparables à celles de l'Holocène actuel. Le territoire de l'Europe était à cette période interglaciaire dans sa quasi totalité couvert de forêts constituant des ensambles plus ou moins fermés. Selon les datations des sédiments stratigraphiques, l'interglaciaire Eemien est compris entre 125.000 et 113.000 ans avant notre ère. Les espèces arborées caractéristiques étaient pendant cette phase sensiblement les mêmes qu'aujourd'hui, à l'exception du hêtre (*Fagus),* qui, absent en raison du retard de sa recolonisation, était remplacé par le charme *(Carpinus).* C'est seulement pendant la période postglaciaire contemporaine que le *Fagus sylvatica* (Hêtre des bois) réapparaît dans la végétation forestière d'Europe centrale sous forme d'ensembles couvrant des surfaces homogènes. L'expansion et la réintégration du *Fagus sylvatica* pendant l'Holocène à partir de ses refuges des phases glacières font l'objet d'une description détaillée sur la base des nouvelles méthodes d'analyse des pollens.

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