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Holocene biogeography of *Fagus sylvatica* L. and *Carpinus betulus* L. in the Carpathian-Alpine Region

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ABSTRACT. The present distribution of temperate forest types in the Carpathian basin suggests that the direction of forest succession, the order and timing of tree arrival and changes in dominance differed markedly between the eastern and western part of the Carpathian basin and in the adjoining mountain zone. In order to throw light upon the historical aspects of temperate woodland succession in the Carpathian-Alpine Region, we examined in this study the Holocene expansion of two cold temperate tree species, *Carpinus betulus* and *Fagus sylvatica*. Pollen data were extracted from 30 sites, all of which were radiocarbon dated. The dates for the earliest regional appearance and marked *Fagus* and *Carpinus* pollen frequency rises were plotted on maps. Throughout analysis of these maps revealed that *Carpinus betulus* appeared the earliest in the SE Carpathians and in the North Hungarian Middle Mountains, around 8500 cal. BP. We inferred the development of a *Carpinus*-dominated forest belt in this region from ca. 7500 cal. BP. Furthermore, the local expansion of *Carpinus* preceded the spread of *Fagus* in all sites east of the Danube, except above 400 m asl. Local increase of the *Fagus* populations commenced the earliest in Slovenia, around 8000 cal. BP. For *Fagus sylvatica,* a migration route along SW Transdanubia and the Transdanubian Middle Mountains was conceived. Surprisingly early occurrence of *Fagus* and *Carpinus* pollen grains in the joint pollen diagram of Nyíres-tó and Báb-tava suggested that refuges appeared in the nearby piedmont zone of the Eastern Carpathians.

Introduction

Since SMITH'S influential paper on the nature of vegetation responses to particular climate changes (SMITH 1965), several case studies have demonstrated that climate has overriding importance in forcing corresponding vegetation changes (BRADSHAW 1990; PRENTICE *et al.* 1991). Neither migration lag, nor inertia of a vegetation type could be demonstrated to control vegetation rearrangements significantly, and so the individualistic nature of species response to critical climatic thresholds gained stringent support.

Climatic control on the present distribution pattern of several temperate tree species, including *Carpinus betulus* (hornbeam) and *Fagus sylvatica* (beech), was demonstrated by HUNTLEY and co-workers (HUNTLEY *et al.* 1989, 1995; HUNTLEY & PRENTICE 1993) and further improved by the Global System Group (SKYES *et al.* 1996). HUNTLEY compared climatic maps with geographic ranges using the method 'Climate Response Surfaces'. Modern pollen abundance data was fitted to a space determined by the mean January and July temperatures of the data points. A strong positive correlation was found between the climate variables and pollen abundances. Optimum climate of *Fagus sylvatica* for example was given at –1 ºC January, +18 ºC July mean temperatures and 1200 mm annual precipitation (for the climatic limits see Table 1). *Carpinus* proved to be somewhat better adapted to the continentality of the climate; according to SKYES *et al.* (1996) it can tolerate winter mean temperatures as low as –8 ºC, but the summer water deficit is also damaging for its populations (α>0.7).

	min MTCO	max MTCO	min GDD*	optimum MTWA	optimum MTCO	optimum PANN	min α*	Chilling response class
Fagus sylvatica	–3.5 (–11)	6	990	18	–1	1200	0.65	5
Carpinus betulus	–8	5	1100	–	–	–	0.7	5

Table 1 Bioclimatic parameters for *Fagus sylvatica* and *Carpinus betulus* (data extracted from Huntley *et al.* 1989, Skyes *et al.* 1996 and Bartos 1986).
MTCO: coldest-month mean temperature; **MTWA**: warmest-month mean temperature; **GDD***: effective growing degree days (GDD*=GDD-GDD^{o}, where GDD^{o} means degree day that are not used because of the risk of spring frost); **α***: Priestley-Taylor coefficient, the ratio of actual transpiration to equilibrium evapotranspiration evaluated over the total assimilation period for evergreen trees (with temperatures > -4 ^{o}C) and for the growing period in case of deciduous trees (with temperatures > 5^{o}C); **Chilling response class**: early to late spring frost response (1 to 5, low to high)

Forestry and ecological research in the Carpathian basin complement these data in that, by the continental climate of the basin, the distribution of *Fagus* and *Carpinus* is constrained by air-humidity first and foremost (Róth 1935 in Bodor 1986). Forestry handbooks often refer to the climate type suitable for the growth of *Fagus* as 'beech climate', distinguished by the 2 pm mean July air humidity (Májer 1980; Bodor 1986). This value has to be higher than 60%. In the Carpathian basin this is to be expected by about 600–800 mm annual precipitation and 6–8 ºC mean annual temperature (Figure 1).

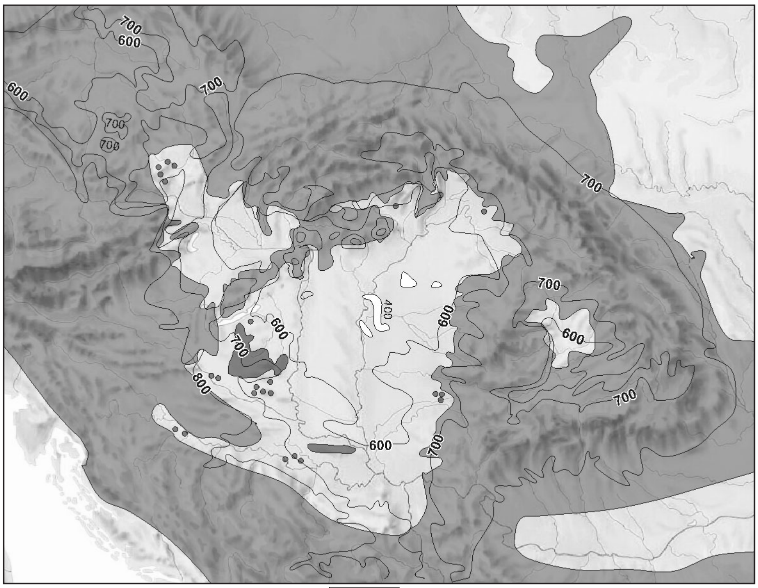

Figure 1 Annual rainfall isopols and the distribution range of *Fagus sylvatica* (beech) in the Carpathian-Alpine Region.

These climatic constraints and the present distribution of *Fagus sylvatica* and *Carpinus betulus* in the Carpathian basin clearly demonstrate that the present warm-temperate continental climate of the Great Hungarian Plain do not favour their growth. The primary reason for this is not temperature, rather the extremely low annual precipitation of the plain (400–500 mm). It is evident, however, that a 50–100 mm increase in annual rainfall and/or a 1–2 °C decline in summer mean temperature would enable the establishment of *Fagus* and *Carpinus*, if not over the entire plain, at least in the northern, eastern and western frontier zones. What follows from this is that in the pollen diagrams of the marginal lowland areas the increase of *Fagus* and *Carpinus* pollen can indicate marked climate changes: decreasing summer temperatures and/or increasing precipitation. Therefore the dates of major population increases can be used for the detection of considerable climate oscillations in the Holocene epoch.

Modern annual rainfall isopols of the Carpathian basin clearly distinguish between the western (Transdanubian) and the eastern continental lowland areas. Moving west of the Danube, annual rainfall increases to 600 mm in a short distance, while the 700 and 800 mm isopols run parallel from SE to NW while approaching the Prealpine zone and the SW Transdanubian Hills (Figure 1). As opposed, annual rainfall in the Great Hungarian Plain declines steeply below 500 mm and in places even below 400 mm. This difference in precipitation can be well explained by the more expressed influence of the Atlantic air masses in the western part of the country. The transition from the relatively mild winter areas to the low-rainfall, cold winter zone is steep. It is enough to move about 50 km to the west from the forest steppe zone of the Great Hungarian Plain to find ourselves in the mixed *Fagus–Carpinus* (Melitti-Fagetum) forests of the Somogy Hills (e.g. József Hill, Figure 2).

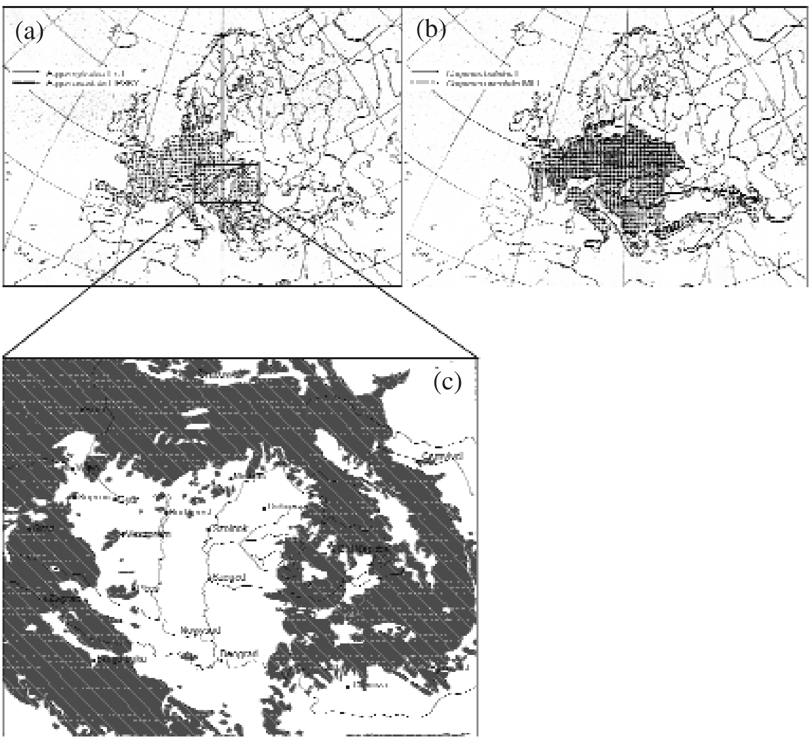

Figure 2 Distribution range of *Fagus sylvatica* and *Carpinus betulus* in Europe (a,b) and in the Carpathian-Alpine Region (c). Redrawn and modified from Meusel *et al.* (1965) and Komlódi (1999). Note that *Carpinus* and *Fagus* occur sporadically out of the range shown in map C, since there only the following main forest types were displayed: Aceri campestri-Quercetum roboris; Dictamno-Tilietum cordatae; Genisto nervatae Pinetum; Fraxino pannonicae-Carpinetum; Querco petraeae-Carpinetum; Querco robori-Carpinetum; Helleboro dumetoro-Carpinetum; Vicio oroboides-Fagetum; Helleboro odoro-Fagetum; Melittio-Fagetum; Abieti-Fagetum; Bazzanio Abietetum (association names according to Simon 1992).

On the basis of the present vegetation of the Carpathian basin we can assume with reason that the directions of forest succession, the order and timing of tree arrival and changes in dominance differed markedly between the eastern and western part of the basin and in the adjoining piedmont zone. This is supported by the available pollen diagrams (e.g. MEDZIHRADSZKY 2001; ZÓLYOMI 1971, 1980, 1987, 1995; NAGY-BODOR *et al.* 1999; WILLIS 1997; JUHÁSZ 2001; MAGYARI 2001, 2002). The pollen record of Lake Balaton for example indicated an early Holocene expansion of *Fagus* (*ca.* 9000 cal. BP), the first frequency peak of which was broadly synchronous with the increase of *Corylus avellana* (hazel) and *Quercus sp.* (oak) in the lowland and eastern middle mountain diagrams (Zólyomi 1984; NAGY-BODOR & JÁRAI-KOMLÓDI 1999). On the other hand, the more continental Eastern Carpathian Mountains (Romania) and the northern fringe of the Great Hungarian Plain showed the early expansion of *Carpinus betulus* that indeed predated the spread of *Fagus sylvatica.* In the Retezat Mountains (SW Romania) for example, an increase in *Carpinus betulus* was discernible from *ca.* 7500 cal. BP (FARCAS *et al.* 1999).

An important question from the point of view of the early Holocene expansion of *Fagus* and *Carpinus* is the position of the full-glacial refuges (DAVIS 1976; CLARK 1997). According to HUNTLEY (1988) *Fagus sylvatica* in Europe was restricted to Italy and the Balkans, and so was *Carpinus betulus*. More recently, however, refuge populations were demonstrated by macrofossil evidence much further north, in the mountain area of the Carpathian-Alpine Region (SERCELJ 1996; WILLIS *et al.* 2000; RUDNER & SÜMEGI 2001). Furthermore, the maps presented by HUNTLEY & BIRKS (1993) show high abundances of the latter species in the Balkan and SE Romania by 6000 uncal. BP, whereas *Fagus* performed better in the Alps and Dinarids.

If we accept the rather south, Italian and Balkan full-glacial refuge populations, then the surprisingly early pollen and plant macrofossil evidences in the North Hungarian Middle Mountains (WILLIS *et al.* 1997; GARDNER 1999; MAGYARI 1999; STIEBER 1969) seek for explanation. Are there links between the Early Holocene dates of appearance in the North Hungarian Middle Mountain and the full glacial refuge population along the foothills of the Carpathians and the eastern Alps, or across Transdanubia? In realty, where were those refuge populations from which the Late Glacial and Holocene expansion of *Fagus* and *Carpinus* started off in the direction of the Carpathian basin? Can we draw up the directions of spread with the aid of radiocarbon dated pollen diagrams along the piedmonts of the Carpathians and eastern Alps? Is it conceivable that some populations of *Fagus* and *Carpinus* survived the last glaciation in mid-altitude areas in the above mentioned mountains? From which directions did *Fagus* and *Carpinus* arrive in the Great Hungarian Plain and what was the reaction of the northern middle-mountain and Transdanubian populations to the changing climate?

These questions led us to collect the available pollen evidence for the onset of the *Fagus* and *Carpinus* rises in the radiocarbon dated pollen diagrams of the Carpathian basin and the neighbouring areas – a zone hereinafter called the Carpathian-Alpine Region (Figure 1).

Data and methods

The maps and diagrams we present are based on a compilation of data from literature and unpublished own sources. Data from the European pollen database was completed by recent publications from Hungary, Romania, Slovakia, the Czech Republic, Austria and Slovenia. Data were extracted for 30 sites, listed in Table 2. and shownin Figure 3. Percentage calculation of *Fagus* *sylvatica* and *Carpinus betulus* pollen types was based on the pollen sum of all terrestrial pollen types. All sites were radiocarbon dated. The timescales were calculated by linear interpolation between dated horizons. All ^{14}C dates were first calibrated using the radiocarbon calibration programme of STUIVER *et al.* (1998), the dates presented in maps are therefore all calibrated BP years.

No.	Site name (elevation)	References
1.	Kazarnice (500m)	SERCELJ 1996
2.	Podpesko Jezoro (300m)	GARDNER 1999ab
3.	Jelovica (1100m)	SERCELJ 1996
4.	Balaton, Tó-25 (145 m)	ZÓLYOMI 1994
5.	Keszthely, Úsztató-major (132m)	MEDZIHRADSZKY 2001
6.	Sárrét (104m)	WILLIS *et al.* 1997, 2000
7.	Grosses Überling Schattseit Moor (1730m)	KRISAI *et al.* 1991
8.	Schwemm (664m)	OEGGL 1988
9.	Halleswiessee (781m)	HAHN (*unpublished*), BORTENSCHLAGER *et al.* 1996
10.	Vracov (192m)	RYBNIÈKOVA & RYBNIÈEK 1979, RYBNIÈEK 1983
11.	Svatoborice-Mistrin (175m)	SVODOBOVA 1989
12.	Borkovicka Blata (415m)	JANKOVSKÁ 1980
13.	Kameniczky (624m)	RYBNIÈKOVA & RYBNIÈEK 1979, 1988
14.	Vernerovice (450m)	PEICHLOVA 1979
15.	Liptovsky Jan (660m)	European Pollen Database
16.	Hozelec (685m)	JANKOVSKÁ 1988
17.	Kismohos (394m)	WILLIS *et al.* 1998
18.	Tiszacsermely (102 m)	CSONGOR & FÉLEGYHÁZI 1987
19.	Sirok (200m)	GARDNER 1999ab
20.	Kõris-mocsár (705m)	SZABÓ & FÉLEGYHÁZI 1997
21.	Báb-tava & Nyíres-tó (108m)	MAGYARI *this study*; HARRINGTON 1995
22.	Sarló-hát (90m)	MAGYARI *this study*
23.	Lezerul Calimani (1650m)	FARCAS *et al.* 1999
24.	Taul Zanogitii (1840m)	FARCAS *et al.* 1999
25.	Mohos (1050m)	REILLE *et al.* 2001
26.	Seibersdorf (250m)	WICK & DRESCHER-SCHNEIDER 1999
27.	Bobrov (640 m)	RYBNIÈKOVA & RYBNIÈEK 1996
28.	Trojrohé pleso (1650 m)	HÜTTEMANN & BORTENSCHLAGER 1987
29.	Zlatnická dolina (900 m)	RYBNIÈKOVA & RYBNIÈEK 1996
30.	Panèická louka (1325m)	HÜTTEMANN & BORTENSCHLAGER 1987

Table 2 Site reference list for Figures 3, 4 & 5.

The dates for the earliest regional appearance (no minimum percentage criteria) and for the marked rise in *Fagus* and *Carpinus* pollen values (an optical phenomenon not related to a particular percentage value) were plotted on maps (Figures 6 & 7). We acknowledge that the use of pollen influxes (grains accumulated per square centimetre of sediment surface per year) would have been more advantageous (Davis 1981) in the determination of the reproductive success and the local/regional spread of *Fagus* and *Carpinus*; however, neither pollen concentration nor influx data were available for the majority of the sites. Therefore, by accepting the possible inaccuracy of the percentage calculation, we used the marked percentage increase as an indicator of the local establishment of a species. Examples of changes in pollen frequencies that were considered significant are indicated by arrows on Figure 4. In Figures 6 and 7 grey-filled circles were used for seemingly reliable sites and blank circles for sites at which the dating is uncertain (e.g. one radiocarbon date per sequence or extrapolated date).

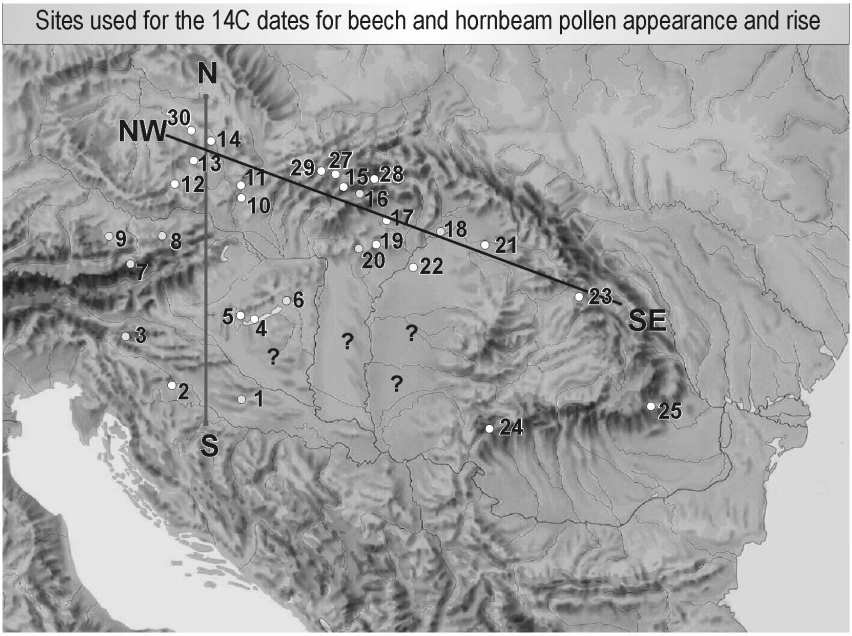

Figure 3 Location of pollen sequences used in mapping the dates of beech and hornbeam pollen appearance and frequency rise. See Table 2 for site numbers and references. Filled circles indicate sites with dates that could be ambiguous because either interpolated or extrapolated from sequences with only one or two radiocarbon age determinations. Map adapted from Zentai (1996).

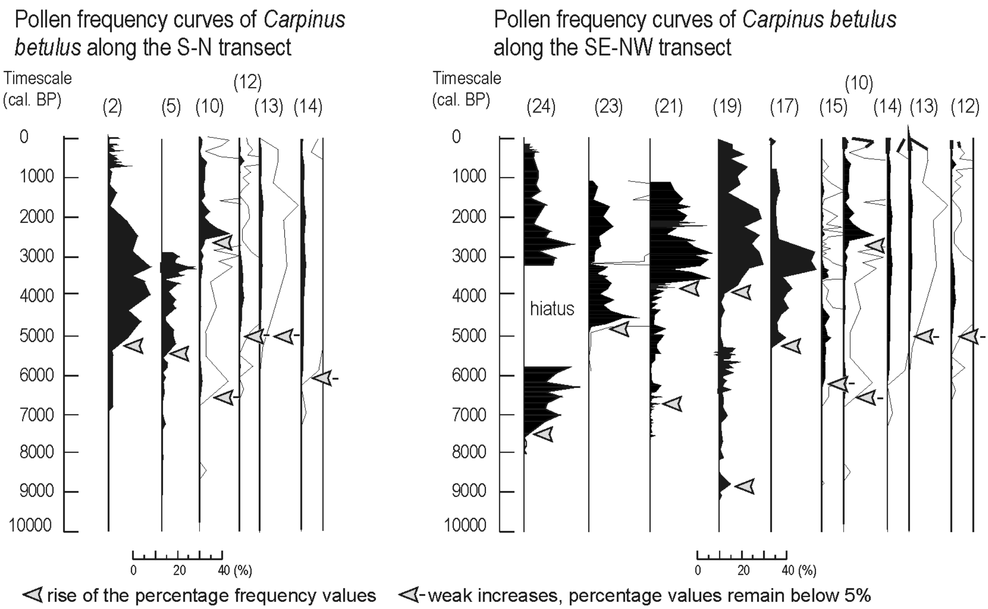

Figure 4 Selected pollen frequency plots of *Crapinus betulus* along the S-E and SE-NW transects in the Carpathian-Alpine Region showing examples of age (cal. BP) readings. For site numbers see Table 2.

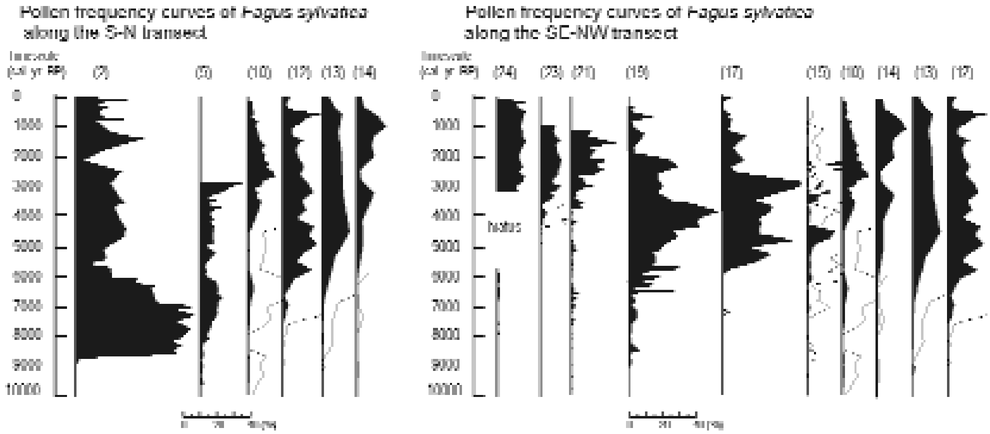

Figure 5 Selected pollen frequency plots of *Fagus sylvatica* along the S-E and SE-NW transects in the Carpathian-Alpine Region. Site numbers are explained in Table 2.

Results

The timing of the first detection and local/ regional expansion of *Carpinus betulus*

Before entering into a detailed interpretation of Figure 6, it should be anticipated that the data presented on these maps are somewhat uncertain, since they represent the first and often very few pollen grains of *Carpinus betulus* without a particular percentage criterion (Figure 6a). Apart from an extralocal/regional source, these grains could also arrive into the basins via long distance transport or sediment reworking. One argument in favour of the extra-local/regional source would be the size-range of the examined basins that suggests a predominantly local and extra-local pollen sources with the exception of Lake Balaton (Jacobson & Bradshaw 1981). Therefore, in our view, the sporadic appearance of *Carpinus betulus* and *Fagus sylvatica* pollen likely indicate the establishment of reproductive trees in these regions.

Taking into account these difficulties, we can say from Figure 6 that *Carpinus* most probably appeared the earliest in the SE Carpathians. In this region the pollen diagram of Taul Zanogutii (Farcas *et al.* 1999) showed the first appearance of *Carpinus* about 8000 cal. BP despite the high altitude of the site (1840 m asl). Moreover, *Carpinus* frequencies were increasing here as early as 7500 cal. BP and reached 20–25% indicating that *Carpinus*-rich forests have formed a distinctive vegetation belt in the SE Carpathians from the middle Holocene. In the pollen diagram of the lower lying mires of Sirok (200 m) in NE Hungary and Halleswielle in the NW Alps (781m), the first *Carpinus* pollen grains were encountered at *ca*. 8800 and 8530 cal. BP, however the steady increase of the frequency curves was delayed and only commenced at 4000 and 4400 cal. BP. Since we have no radiocarbon data from the lower regions of the SE Carpathians, it is impossible to say whether these very early appearances indicate refuge populations in the north, or in case of the North Hungarian Mountains we have to reckon with the early Holocene expansion of *Carpinus* from the SE Carpathians. The only Upper Weichselian macrofossil data in favour of the survival of *Carpinus* in the North Hungarian Mountains of Hungary originates from the Tokaj Hill where Rudner found *Carpinus betulus* charcoal dated to 26962+/– 657

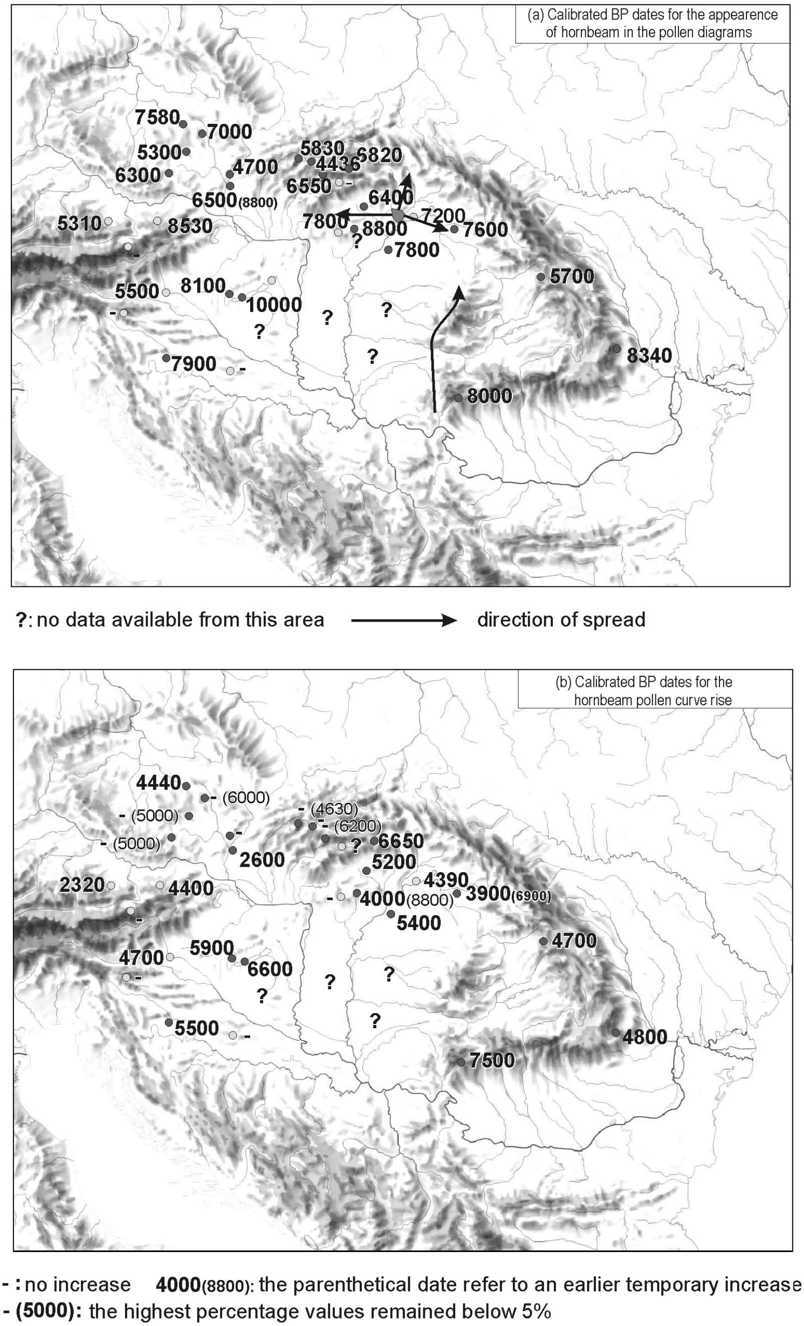

Figure 6 Calibrated radiocarbon ages (cal. BP) for the appearance (a) and first pollen frequency increase (b) of hornbeam (*Carpinus betulus*) in the Carpathian-Alpine Region. Sites with multiply radiocarbon dates are marked with filled circles; blank circles distinguish sites with poor chronology (1 or 2 radiocarbon dates). Sites are shown in Figure 3 and Table 2.

uncal. BP (Willis *et al.* 2000; Rudner & Sümegi 2001). In the sediments of Lake Balaton *Carpinus* pollen appeared uninterruptedly from *ca.*10000 cal. BP. Since the pollen source area of this lake encompasses Transdanubia including the foothills of the Alps, we can only surmise that its early occurrence indicate the establishment of reproductive populations in the SE hilly region, in Serbia or in the hills directly north of the lake. This is at the same time indicative of the proximity of the glacial refuges.

In the Northern Carpathians, Morva Lowland and Bohemian Basin the dates for the first appearance of *Carpinus* pollen are all younger than 7000 cal. BP. We can thus assume that the expansion of *Carpinus* appeared from the south and east. Unfortunately no radiocarbon data was available from the middle and southern part of the Great Hungarian Plain for the first occurrence of *Carpinus*. The two pollen diagrams discussed in this paper (Báb-tava, Sarló-hát) represented the northern and north-eastern margins of the lowland, and indicated the relatively early appearance of *Carpinus* pollen, at *ca.* 7900 and 7800 cal. BP. However, the marked increase of the frequency curves commenced only between 5400 and 3900 cal. BP (Figure 6b).

Considering the dates of the main population increases, we can say that, in the SE Carpathians, the expansion of *Carpinus* started already at *ca.* 7500 cal. BP, considerably earlier than in all other sites in the region. We can infer the formation of a distinctive vegetation belt in the SE Carpathians formed by *Carpinus*-dominated forests. In southern Transdanubia, the expansion started about one thousand years later, between 6600 and 5900 cal. BP suggesting that, in the forests of the Middle Holocene, *Carpinus* was an important canopy tree in this region.

As a summary of the above discussion, we can conclude that the local expansion of *Carpinus* preceded the spread of *Fagus* in all sites east of the Danube (Figure 6 and 7) except above 400 m asl. in the northern Carpathian Mountain Range (including Nagymohos (17), and Kõris-mocsár (20)). This contrast in the Holocene vegetation development of the two areas can probably be explained by the differences in summer precipitation and winter minimum temperatures (i.e. continentailty). These values are definitely lower at present in the eastern sector and the relative differences must have been subsisted thorough the Holocene. The local and regional population increases are very difficult to establish at some Hungarian sites (e.g. Sirok and Báb-tava), since *Carpinus* frequencies display a first increase relatively early (Sirok: 8800 cal. BP; Báb-tava: 7800 cal. BP). However, the relative frequencies remain low (< 5%) until *ca.* 3900 cal. BP. These values indicate that *Carpinus* was a constant admixture in the middle Holocene forests of NE Hungary, but only became the dominant tree consequent upon climatic deterioration commencing around 5400 cal. BP. A further conspicuous difference between the E and NW Carpathians is the early regional appearance but low frequency of *Carpinus* pollen in the latter area (Figure 4). Sites 12, 13, 14 and 15 for example displayed constant but low percentages (regional component) thorough the Holocene suggesting that *Carpinus* did not play a decisive role in the Holocene forest succession there. On the other hand, *Carpinus* has been an important element of the woodlands in the SE Carpathians since the early Holocene (from *ca.* 7500 cal. BP).

The timing of the first detection and local/ regional expansion of *Fagus sylvatica*

Along the S-N transect we found a definite trend in the first appearance of *Fagus sylvatica* pollen with younger dates in the north (Figure 7a). It is also notable that the eastern and western parts of the investigated area differentiate in respect of the regional establishment and first increase. The pollen diagrams of Transdanubia are characterised by an early appearance (e.g. 11400, 9300, 82000 cal. BP), and the first maxima cluster around 8000–6000 cal BP. By contrast, the relatively early (e.g. 91000 cal. BP) regional establishment of *Fagus* in the North Hungarian Mountains was not followed by an immediate rise, which was hampered until *ca.* 5400 cal. BP.

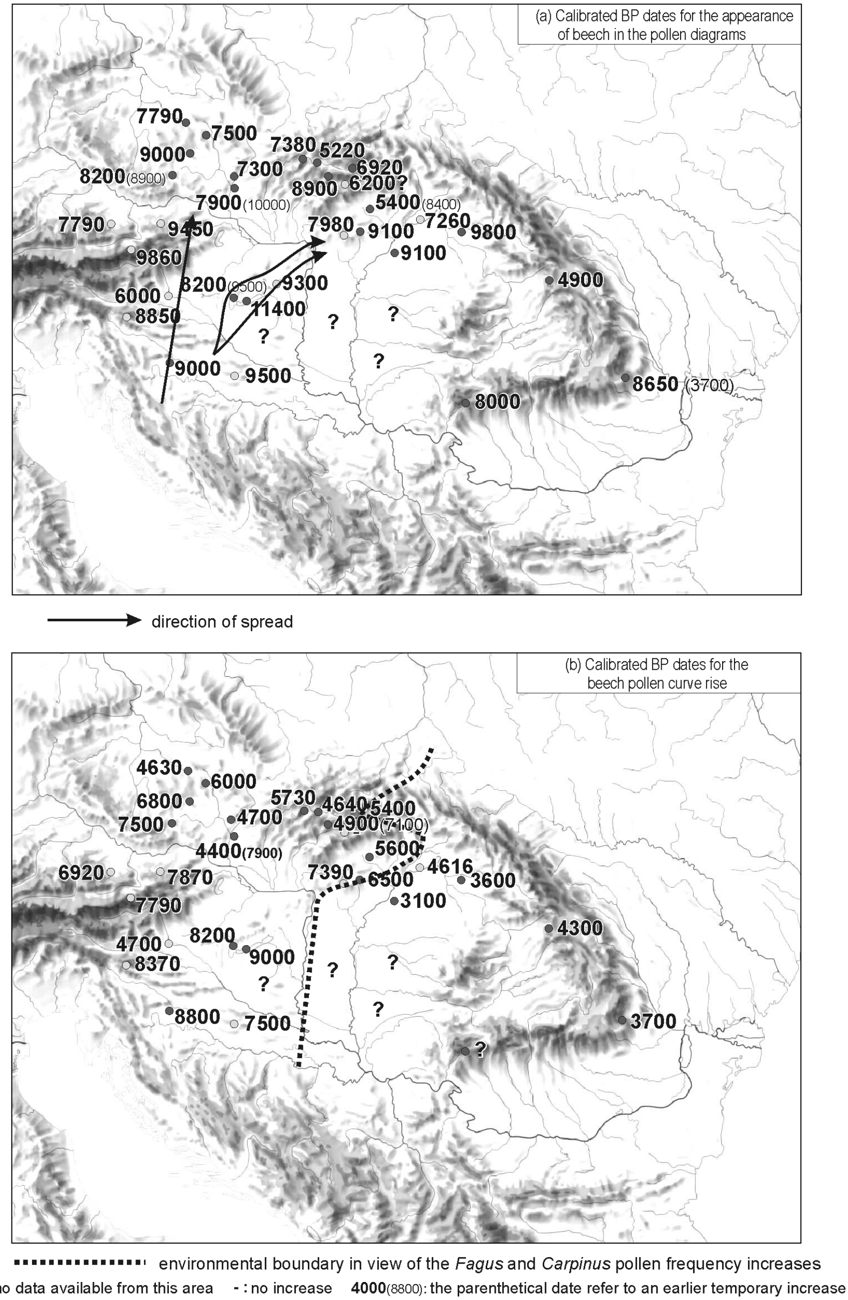

Figure 7 Calibrated radiocarbon dates (cal. BP) for the appearance (a) and first pollen curve rise (b) of beech (*Fagus sylvatica*) in the Carpathian-Alpine Region. Sites with multiply radiocarbon dates are marked with filled circles; blank circles distinguish sites with poor chronology (1 or 2 radiocarbon dates). Sites used for the [14]C dates are shown in Figure 3 and Table 2.

Considering the local increase of the *Fagus* populations, it is evident from the maps (Figure 7b) that it took place much earlier in the mountains (7390–4900 cal. BP) than in the lowlands (3600–3100 cal. BP). Similarly to *Carpinus*, along the SE-NW transect, no clear trend is seen in the dates of the regional arrival and spread. For example, some sites in the North Hungarian Middle Mountains show a surprisingly early regional signal and population increase (Figure 7b) hinting at the survival of *Fagus* nearby, e.g. along the piedmont of the Northern Carpathians.

Finally, we note that the dates for the local spread of *Fagus* and *Carpinus* suggest that the Holocene climatic conditions and their changes on a millennial timescale led to a remarkably diverse pattern of vegetation succession in the various parts of the Carpathian-Alpine Region. The principal point in respect of the late middle Holocene climatic deterioration is that the onset of the *Fagus* and *Carpinus* rise lagged 2000 to 3000 years in the lowland areas indicating that a marked precipitation increase commenced between 4600 and 3400 cal. BP and was possibly coupled with the lowering of the summer mean temperatures. The climate change was however a gradual process, and depending on the local conditions, the mountain and more western areas inevitably tipped the balance earlier, allowing for the competitive growth of *Fagus* and *Carpinus* against the mixed-oak forest elements.

Discussion

What trees did *Fagus* and *Carpinus* replace?

In the previous section we have demonstrated that the Holocene expansion of *Carpinus betulus* preceded *Fagus sylvatica* in the area east of the Danube, and in the mountain areas commenced as far back as 8800 cal. BP. The increase of *Carpinus* pollen frequencies in the lowland and mountain diagrams was accompanied by a decline in *Corylus avellana* (hazel) in the first place, and in *Ulmus* (elm), *Tilia* (lime), *Acer* (maple) and *Fraxinus* (ash) species subordinately. On the other hand, *Quercus* (oak) pollen types retained relatively high abundance, or rather increased with *Carpinus*. This is clearly indicative of a change from sparse park forests of average height and typical light-demanding species to denser, well structured (lower and higher canopy plus shrub layers) forests made up of *Carpinus betulus* and *Quercus* species above all. High altitude pollen diagrams in Romania suggest that a forest belt dominated by *Carpinus* in the higher canopy developed by *ca.* 7000 cal. BP in the SE-Carpathians and survived without appreciable change until *ca.* 2250 cal. BP. The elevation range of this *Carpinus* forest must have been strongly connected with fluctuation in the elevation range of *Picea abies* (Norway spruce) and *Fagus sylvatica*. Judging from the continuous pollen record of lezerul Calimani (Farcas *et al.* 1999), contraction of the *Carpinus* forest has been gradual since *ca.* 3500 cal. BP (Figure 6); however, in the Eastern Carpathians, mixed oak-*Carpinus* and *Carpinus-Fagus* forests have survived up to present (Soó 1953). By the joint interpretation of the pollen diagrams and maps presented in Figures 6 and 7 we can draw up an approximate borderline east of which the Holocene expansion of *Carpinus* preceded *Fagus*, whereas to the west and north of which *Fagus* expanded and reached high abundance first. Interesting to see the position of the North Hungarian Middle Mountains on this map. Characteristics of the Holocene vegetation development clearly connect the Great Hungarian Plain, and especially its eastern frontier zone, with the Eastern

Carpathians, whereas the North Hungarian Middle Mountain joins with Transdanubia and the Northern Carpathians in respect of the Holocene expansion of *Fagus* and *Carpinus* (see e.g. Sirok (No. 19) and Kismohos (No. 17) in Figures 6 and 7). An exception to this rule is the Vysoké Tatra Mountain in the N Carpathians from where the pollen diagram of Trojrohé pleso (1600 m asl) was mapped (No. 28; HÜTTEMANN & BORTENSCHLAGER 1987). Although the lake lies near to the present tree limit, it receives a great quantity of pollen from lower altitudes carried by upwelling air masses, therefore the pollen spectra give us a broad picture of the vegetation changes in the neighbouring slopes and valleys. According to HÜTTEMANN & BORTENSCHLAGER (1987), *Fagus* occurred earlier in this area. However, the population of *Carpinus* has started to grow earlier, together with *Picea*, since *ca.* 6650 cal. BP, whilst *Fagus* increased together with *Abies alba* (silver fir) about a thousand year later at the expense of spruce. The pollen record hint at the development of an oak-hornbeam dominated forest zone below the spruce forests in the middle Holocene that slightly resembled to the middle Holocene altitudinal zonation of the Eastern Carpathians.

Taul Zanogutii, a crevasse lake in the SE Carpathians, is situated about 200 m higher than Trojrohé pleso (FARCAS *et al.* 1999). Despite the high altitude of the site, the pollen diagram indicated the earliest increase of *Carpinus* among the mapped records. Pollen frequencies attained 15–20% (see curve No. 24 in Figure 4), on the basis of which FARCAS *et al.* (1999) inferred the early development of *Carpinus* dominated forests at lower altitudes, but possibly reaching 1000 m asl.

Comparing the two above discussed diagrams, it seems reasonable to surmise that *Carpinus betulus* may not formed an independent forest belt in the Vysoké Tatra Mountain, the *Picea* belt must have been rather underlain by a mixed *Quercus-Picea-Acer-Ulmus-Fraxinus* forest (mountain mixed forest). On the strength of the nearby Bobrov pollen record (Table 2, Figure 3), we can estimate the lower boundary of the spruce belt around 600 m asl. Silver fir-beech forests (Abieto-Fagetum) similar to the present could have developed by *ca.* 5500 cal. BP in this area.

Let us now examine the forest communities *Fagus* invaded successfully. East of the borderline shown in Figure 7b, *Fagus* penetrated and gradually took over Carpinetum and Querco-Carpinetum forests, added to which Piceetum forests in the mountains become replaced partially by *Fagus sylvatica* and *Abies alba* from *ca.* 6200 cal. BP. Increasing abundance of *Fagus* counterbalanced a simultaneous decline in *Quercus*, *Corylus*, *Picea* and in part *Carpinus* frequencies. This rather simplistic situation, however, was much diverted in Transdanubia, in the SE Alps and in the NW Carpathians. According to the latest pollen analytical investigations in Slovenia for example, *Fagus* surely survived the last glacial maximum in the Dinaric Range (HOBBOM 1999; SERCELJ 1996).

From among the Slovenian and Croatian pollen sequences, the earliest increase in *Fagus* was found in Podpesko Jezero (No. 2, 300 m asl). Here the early Holocene *Corylus* maximum directly superseded a marked increase in *Fagus* pollen. Simultaneously with the *Fagus* pollen rise, the percentages of *Corylus avellana* declined markedly together with *Ulmus*, *Tilia* and *Quercus*. We can therefore conclude that similarly to its eastern expansion history, *Fagus* has invaded and occupied hazel scrubs and relatively low-built mixed oak forests in the lowland and middle mountain areas of Slovenia.

In the Transdanubian pollen spectra, *Fagus* frequency plots usually have dual maxima. This has some important implications from biostartigraphical point of view. Although the example in Figure 7 (curve No. 5: MEDZIHRADSZKY 1998, 2001) shows damped *Fagus* frequency rises as a consequence of the overrepresentation of local wetland trees, a great number of pollen spectra from Lake Balaton (not displayed in Figure 5 because of unreliable dating control) displayed high amplitude fluctuation in *Fagus sylvatica* frequencies with maxima between *ca.* 8000–6000 and 5000–2800 cal. BP. The first expansion of *Fagus*, similarly to the Slovenian territories, affected hazel populations in the first place; in the regional pollen diagram of Lake Balaton oak pollen types declined as well, but frequencies remained relatively high together with beech. We can therefore say that the first wave of *Fagus* advance in S Transdanubia and in the Transdanubian Middle Mountains (Figure 1) was damaging for the populations of hazel, oak and lime that had formed scrub woodlands antecedently. These forest associations most likely receded to talus slopes and rocky surfaces with limited fertility (poor soils), whilst according to FEKETE and ZÓLYOMI (1966) beech-dominated forests formed a separate belt, directly surmounting oak forests in the Transdanubian Middle Mountains by *ca.* 8000 cal. yr. BP. This structure of forest zonation altered to some extent at the second advance of *Fagus* that was accompanied by an increase in *Carpinus* as well. The present pattern of altitudinal zonation developed in this period, about 5000 cal. yr. BP. Mixed oak-hornbeam forests (Querco-Carpinetum) intercalated between the *Fagus* and oak dominated forest belts, whilst the Submediterranean scrub-forests rich in hazel receded even further.

What do the buried macrocharcoals tell us about the history of *Fagus* and *Carpinus?*

The analysis of charred wood fragments has a great past in Hungary (HOLLENDONNER 1938; GREGUSS 1940; STIEBER 1969; VALKÓ 1970). There are numerous sites, especially caves, from where Weichselian and Holocene macrocharcoals were recovered, most often in connection with prehistoric hearths. At the time of these investigations opportunities for radiocarbon dating were limited, therefore the age of the sediments was chiefly determined using the accompanying archaeological material. From the standpoint of *Fagus* and *Carpinus* expansion, the most important analysis in the North Hungarian Middle Mountains was carried out by STIEBER (1969) on the sediments of the Rejtek Rock Shelter (Figure 1). Although this sequence has not yet been dated with absolute techniques, sophisticated matching with the well-established Late Glacial and Holocene microvertebrate and malacostratigraphies (Kordos 1985, 1991; FÛKÖH 1993, 1995) suggests that the first macrocharcoals of *Fagus sylvatica* and *Carpinus betulus* occurred around the Late Glacial/Holocene boundary and were present up to the top of the sequence (middle Holocene). Whilst Stieber's data bear evidence for early Holocene occurrence, the loess-charcoal analysis of RUDNER in the vicinity of Tokaj (Figure 1) provides radiocarbon dated evidence for the Upper Weichselian survival of *Carpinus betulus* on the Tokaj Hill (WILLIS *et al.* 2000; RUDNER & SÜMEGI 2001).

We can infer from these data that the full glacial survival of *Fagus* in the North Hungarian Middle Mountains is unlikely, whereas *Carpinus* survived in microclimatic shelters with great certainty (WILLIS *et al.* 2000). In the Holocene NE Hungarian cave sediments *Fagus* and *Carpinus* charcoals are significant constituents (STIEBER 1969), therefore the early appearance suggested by the pollen spectra can be unambiguously confirmed by the anthracological record.

North of the Carpathian basin, macrofossil analysis of the travertine deposits of Gánóc near Poprád were published by PAX (1925). Although the age of these travertine deposits is even more uncertain, PAX identified *Carpinus betulus* macrofossils in the early Holocene layers, and called our attention to the surprisingly early appearance of this species in the Northern Carpathians.

The pollen sequence of JANKOVSKA from the Lyptovsky Mountain of the Tatra Range (Lyptovsky Jan, 660 m asl) is situated about 40–50 km to the east of Gánóc. In this diagram, the first occurrence of *Carpinus betulus* pollen was dated to *ca.* 6550 cal. BP, i.e. much later than suggested by the macrofossils. On the other hand, the macrofossil findings were from much lower altitudes, therefore the discrepancy between the dates seems consistent with the difference in elevation. Moreover, KULLMAN provided excellent evidence from Sweden for that, in case of small populations, the pollen spectra fail to record the presence of thermophilous deciduous taxa even though macrofossils are present (KULLMAN 1998).

We have discussed in the introduction that, in our opinion, the mid-late Holocene population increase and further expansion of *Fagus* and *Carpinus* refer to lessening continentality and gradual increase in available moisture (α^x). In the northern and north-eastern frontier zone of the Great Hungarian Plain we have dated the onset of this change to *ca.* 5400 cal. yr. BP (MAGYARI 2002). *Fagus* and *Carpinus* pollen were found in several mid-lowland sequences as well (e.g. Alpár-Tõserdõ, Petõfi-tó, Bócsa; JÁRAI-KOMLÓDI 1966, 1995; BORSY *et al.* 1991), albeit in low frequencies (<5%). These pollen spectra are not shown in our maps (Figures 6 and 7) since they lack absolute timescales, even though some are supplied with one or two radiocarbon dates. The approximate age for the occurrence of *Fagus* and *Carpinus* pollen was estimated to *ca*. 4000–5000 cal. BP in these sequences. The detected low pollen abundances can however represent far-distance populations, therefore we considered it especially important to explore what the archaeological excavations tell us about the utilisation, and so likely local occurrence of *Fagus* and *Carpinus* in the Great Hungarian Plain. The most detailed investigation in this field was carried out by VALKÓ & STIEBER (1969). They examined the charred wood material of the Bronze Age tell in Békés-Várdomb (Figure 1; Perjamos and Hatvan Cultures). Out of the 837 specimens, only one piece was identified with *Fagus sylvatica*, whilst 40 fragments belonged to *Carpinus betulus*. The dominant charcoals were however *Quercus petraea* and *Q. robur*. The obvious inference from all these was that in the floodplain forests of the Körös river near Békés, *Carpinus* was surely present as an admixture, and according to VALKÓ (1970) formed Querco-Carpinion forests in the high-floodplain zone similar in species composition to the present Querco robori-Carpinetum (SOÓ & PÓCS 1957 *em*. SOÓ 1980) association (BORHIDI & SÁNTA 1999). *Fagus* was, however, most likely missing from these forests or was present sporadically.

To the west of Békés, in the middle of the Great Hungarian Plain, the charred wood material of the Bronze Age settlement of Tószeg has been investigated by HOLLENDONNER (1926), SÁRKÁNY & STIEBER (1952). Among the identified macrocharcoals, *Carpinus betulus* was listed, albeit in small quantity. It is therefore likely that in the very middle of the plain the climate change favoured the establishment of *Carpinus* in well-drained fertile soils, however, *Fagus* trees did not appear. If *Fagus* had been established in the central areas of the lowland, its valuable timber must have been used by the Bronze Age settlers that however could not be demonstrated so far.

Moving away the central areas of the plain, the charcoal findings of several Bronze Age excavations demonstrate that *Fagus* and *Carpinus* were relatively frequent in the lowland frontier zone (e.g. Pesterzsébet, Füzesabony: GREGUSS 1940), even though they are missing from the recent flora of these sites. These findings are also supported by two lowland fringe pollen records, Csaroda (No. 21) and Sarló-hát (No. 22), and altogether point to the late

Holocene prevalence of oak-hornbeam forests with the possible admixture of beech. On the basis of the pollen records, *Carpinus betulus* reached its maximum distribution and abundance in the Great Hungarian Plain between *ca.* 4000 and 3000 cal. BP, whereas *Fagus* was the most frequent between *ca.* 3500 and 2000 cal. BP.

Directions of spread and possible northern refuges

Since the geographical distribution of the pollen records shown in maps (Figure 3) is rather uneven, moreover the proposed refuge areas has not been included in this study, our aim was first of all to examine the existing data points and infer tendencies in the timing of tree arrivals and population increases, for example time-transgressive spreads along the S-N and SE-NW transects. We set out from the idea that along these transects, dates of pollen arrival and percentage frequency increase may show some irregularities not interpretable in terms of elevation difference; e.g. a pollen sequence located in the middle of an axis has glaringly early date of first appearance. In a case like that the area of first detection can be expected as a possible glacial refuge.

Throughout examination of the maps and pollen diagrams let us to draw the following inferences:

1) The regional pollen diagrams of Lake Balaton indicate that *Fagus sylvatica* established productive populations in Transdanubia as early as *ca.* 11400 cal. BP. However, this early regional pollen load was not demonstrable in any of the so far examined smaller sedimentary basins with predominantly local and extralocal pollen-source areas. The dates of first detection do not show a distinct trend. The earliest occurrence in Slovenia was around 9500 cal. BP that was however preceded by an Austrian site, Grosses Überling Schattseit Moor (1730 m asl). Here the first *Fagus* pollen was found around 9860 cal. BP. Disregarding the regional diagram of Lake Balaton, the earliest date of major population increase was found in Slovenia, at Podpesko Jezero (No. 2). Here a massive increase in *Fagus* pollen abundances started as early as *ca.* 8800 cal. BP, whereas all sites north of Podpesko showed this increase later with the dates decreasing from south to north (Figure 7).

Judging from the radiocarbon dates, the North Hungarian Middle Mountains most likely populated from the direction of Transdanubia, since the dates of first detection are older in every instance here (Figure 7).

2) Surprisingly early occurrence of *Fagus* and *Carpinus* pollen grains in the joint pollen diagram of Nyíres-tó and Báb-tava (No. 21) suggests that refuges appeared in the nearby piedmont zone of the Eastern Carpathians; alternatively, the northward expansion of *Fagus* and *Carpinus* from the Balkan refuges commenced already in the Late Glacial period along a well-defined route stretching south to north in the foothill zone. In lack of sufficient data, this assumption can be tested by systematic pollen and plant macrofossil analyses along the hypothetical dispersion route.

3) Interpretation of the network of radiocarbon dates for *Carpinus betulus* resulted in less fruitful inferences as far as the directions of spread are concerned. We lack pollen sequences from the Tokaj Hills where Rudner & Sümegi (2001) found *Carpinus* macrocharcoals dated to the Upper Weichselian (26962+/– 657 uncal. BP). As a refuge population was clearly demonstrated here, it most probably played a role in the early re-population of several other middle mountain sites (e.g. Kismohos and Sirok). Apart from Lake Balaton (regional signal), *Carpinus* pollen grains were first detected (>1%) at Sirok that is situated in the northern part

of the investigated area, and so provides a good example of surviving deciduous tree populations at much northern latitudes then assumed earlier (Bennett *et al.* 1992). These northern refuges can also explain the apparent disarray in the radiocarbon data that did not give us a clue for the reconstruction of dispersion routes.

The role of humans in the expansion and population increase of *Fagus* and *Carpinus*

There are several palaeobotanists (Iversen 1973; Aaby 1983; Andersen *et al.* 1983; Björkman 1996) who argue climatic determinism in the present and past distribution of the temperate arboreal flora, and indeed demonstrate that human disturbance did facilitate the establishment of *Fagus* and *Carpinus* in areas that were covered by dense oak woodlands antecedently (Küster 1997). An influential critique of the 'climate school' was presented by Küster (1997). He doubted the role of climate in the mid-Holocene expansion of *Fagus* and *Carpinus* in the lowland areas of Germany. His reasoning built around the difference between the natural disturbance regime of the lowland and mountain areas. According to Küster, in the mountains, there is higher biodiversity due to considerable variation in slope, aspect, soil type and other local features (Küster 1997). Consequently, natural openings occur more frequently than in lowland situations and in regions with gently rolling topography. These natural openings are especially favorable for invasion by new taxa, such as *Fagus sylvatica* and *Carpinus betulus*. Opportunities for the penetration of new tree species in the closed-canopy lowland areas are however much more limited, since natural openings are relatively infrequent (Küster 1997). In such stable environment, a considerable disturbing agent is formed by human settlements.

In Germany, prehistoric farmers appeared in the lowland areas in the fifth millenium BC, concurrently with the onset of the *Fagus* and *Carpinus* rises. This simultaneity led Küster to conclude that human disturbance alone was responsible for the successful establishment of *Fagus* and *Carpinus*, moreover rejected the possibility of a simultaneous climatic change.

If we refer the argumentation of Küster to the Great Hungarian Plain, several points in the reasoning become assailable. First of all, the majority of the lowland pollen diagrams in the Carpathian basin point to the existence of naturally open vegetation types throughout the Holocene, that is to say, some loess and sand areas have never become forested (Magyari 2002). Consequently, the absence of natural openings could not hamper the establishment of *Fagus* and *Carpinus*. The most important landscape units for the penetration of new woody taxa were most likely forest-edges, since light, soil and water conditions were the most favorable in these places for the seedlings. We must furthermore add that the seedlings of *Fagus* grow better under a canopy, whilst *Carpinus* seedlings are light-demanding and so prefer openings (Májer 1980). If climatic conditions favor their regeneration, both species can dominate in climax associations, but clearly *Carpinus* can also take part in secondary successions as pioneer tree (Gardner & Willis 1998).

In light of these data we can conclude that the reasoning according to which the lack of natural openings put a stop to the establishment of *Fagus* and *Carpinus* in the Great Hungarian Plain is erroneous. There was no need of human disturbance to find suitable growing space, therefore the German lowland closed-forest obstacle did not prevail in the Carpathian basin. Notwithstanding, the frequency increase of *Fagus* and *Carpinus* was coupled with a gradual decline in total arboreal pollen percentages in all NE Hungarian lowland pollen diagrams (see e. g. Figure 8), albeit arboreal pollen concentrations increased. It is therefore demonstrable that the increasing population of the Great Hungarian Plain started on a massive forest clearance that could in part be held responsible for the overall increase in arboreal pollen concentrations and influxes (Hicks 2000). On the other hand, sedimentation rates declined dramatically in several oxbow lakes simultaneously with the *Fagus* and *Carpinus* rises (Figure 8), thus the increase in pollen concentrations does not necessarily mean that the arboreal pollen influxes got higher. At present, the number of radiocarbon dates is insufficient to resolve this uncertainty, however the stepwise and parallel increase in total pollen concentrations at Báb-tava and Sarló-hát (Figure 8) infer a common factor acting upon the sediment accumulation rate of these two distant lakes. Taking into account their different morphology, age and succession, the most likely explanation is **climatic change** that has affected the flood regime, thereby blocking the major sediment source.

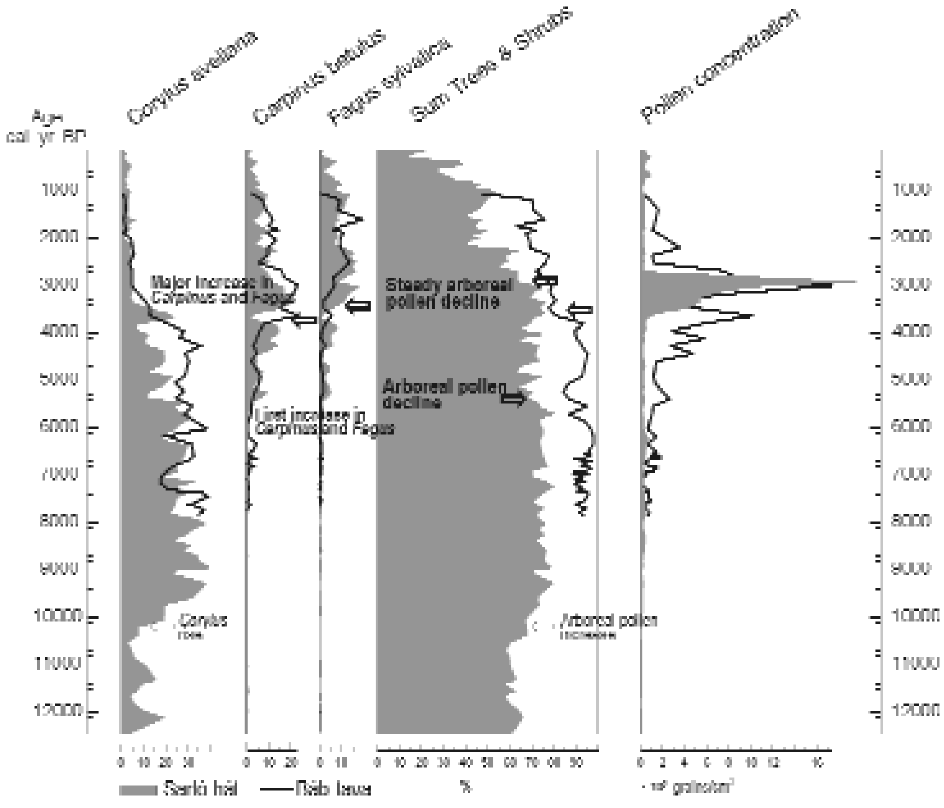

Figure 8 Selected percentage frequency pollen curves and terrestrial pollen concentrations for Sarló-hát and Báb-tava, NE Hungary. For the location of sites see Figure 3 and Table 2.

We can see from these data that the Carpathian basin has a specific environment hardly comparable to the main lowland areas of Central Europe. In this study, we demonstrated via pollen and plant macrofossil data that the Holocene population dynamism of beech and hornbeam in the Carpathian-Alpine Region has been unusually entangled. The number of data is enough to conclude that the expansion of beech and hornbeam was not simply from the south to the north, however, insufficient to demonstrate all major dispersion routes and refuges, especially for *Carpinus betulus*.

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