

The expansion of hazel (*Corylus avellana* L.) in the southern Alps: a key for understanding its early Holocene history in Europe?

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Abstract

In Northwestern and Central Europe the Holocene expansion of *Corylus* occurred before or at the same time as that of other thermophilous trees (e.g. *Quercus*). This sequence of expansion has been explained by migrational lag, competition, climatic changes, human assistance, or disturbance by fire. In the southern Alps, however, hazel expanded around 10,500 cal yr BP, more than two millennia after oak had become important. This delayed expansion is in contrast with the rapid expansion often assumed for hazel in central Northern Europe.

We use two well-dated pollen and charcoal records from the southern forelands of the Alps: Lago Piccolo di Avigliana and Lago di Origlio. We conclude that distance of refugia, speed of seed dispersal, and competition cannot sufficiently explain the absence of the hazel expansion prior to the establishment of mixed oak forests in the southern Alps. Instead our records indicate that higher moisture availability and low temperatures inhibited hazel and favoured the establishment of pine and mixed oak forests during the Allerød. The expansion of hazel ~11,000–10,500 cal yr BP was favoured by a combination of high seasonality, summer drought and frequent fires, which helped hazel to out-compete oak in the south as well as north of the Alps.

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1. Introduction

The causes for (a) early Holocene rapid population expansion of *Corylus* (hazel) across Europe and (b) the subsequent hazel maximum have been debated for many years. At present *Corylus* occurs mostly as an understorey shrub in deciduous and conifer forests (Hegi, 1981; Pignatti, 1982), and the dominance of hazel in natural vegetation is an outstanding feature of vegetation history during the Holocene. Much of the debate about *Corylus* expansion and peak abundance has focused on its history in central and northwestern Europe (Firbas, 1949; Smith, 1970; Clark et al., 1989;

Birks, 1993b; Huntley, 1993; Edwards, 1999; Tinner and Lotter, 2001; Tallantire, 2002), where the postglacial hazel population expansion was synchronous with the population expansion of other deciduous trees (e.g. *Ulmus*, *Quercus*, and *Tilia*), or more often preceded it. For these regions, the arguments used to explain the early Holocene sequence of population expansion for hazel and, in particular, its range expansion, were already summarised and discussed by Firbas (1949). He listed the possible (not mutually exclusive) causes as being (i) climatic change, (ii) soil development, (iii) competition with other plants, (v) migrational lag, (vi) human assistance, and (vii) location of refugia.

Between 10,000 and 9000 ¹⁴C yr BP, in response to the climatic warming at the onset of the Holocene, hazel's migration rate (1500 m yr⁻¹) was as much as three times larger than the migration rate of oak (500 m yr⁻¹) (Huntley and Birks, 1983) as a result of

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its earlier age at reproductive maturity (10 years instead of 30), its dispersal capacity (Huntley and Birks, 1983), and/or by a sudden expansion from low-density populations in response to a climatic change in north-western Europe (Tallantire, 2002). Furthermore, Huntley (1993) concluded that “the unique combination of climatic conditions during the early Holocene, perhaps along with the high fire frequency that resulted from these conditions, favoured the rapid spread and high abundance of *Corylus* for several millennia in north-central Europe.” Thus the most likely explanation for the early expansion of *Corylus* would be warm summer conditions, frequent summer water deficits, and the continuing prevalence of cold winter conditions caused by the early Holocene summer radiation maximum and winter radiation minimum (COHMAP Members, 1988) that combined to exclude other ‘thermophilous’ woody taxa (Huntley, 1993).

Instead, in the southern Alps, as well as in other Southern European regions (e.g. the French Pyrenees: Reille and Andrieu, 1995), the Holocene replacement of boreal birch-pine forest by temperate forest included the expansion of oak prior to the increase of hazel populations. Concerning the mechanism triggering the delayed hazel expansion, Zoller (1960b) suggested that the coeval charcoal and hazel maxima (~10,550 calyr BP) indicated that Mesolithic cultures could have played an important role.

In central and northern Europe the sequence of oak preceding hazel is rather uncommon or totally absent in Holocene pollen records. However, it is often recorded in earlier European interglacial pollen records, e.g. in Eemian records of central France (Massif Central of de Beaulieu and Reille, 1992b) and the Vosges (de Beaulieu and Reille, 1992a), in northern Germany at Gröbern (Aalbersberg and Litt, 1998), and in Ipswichian records

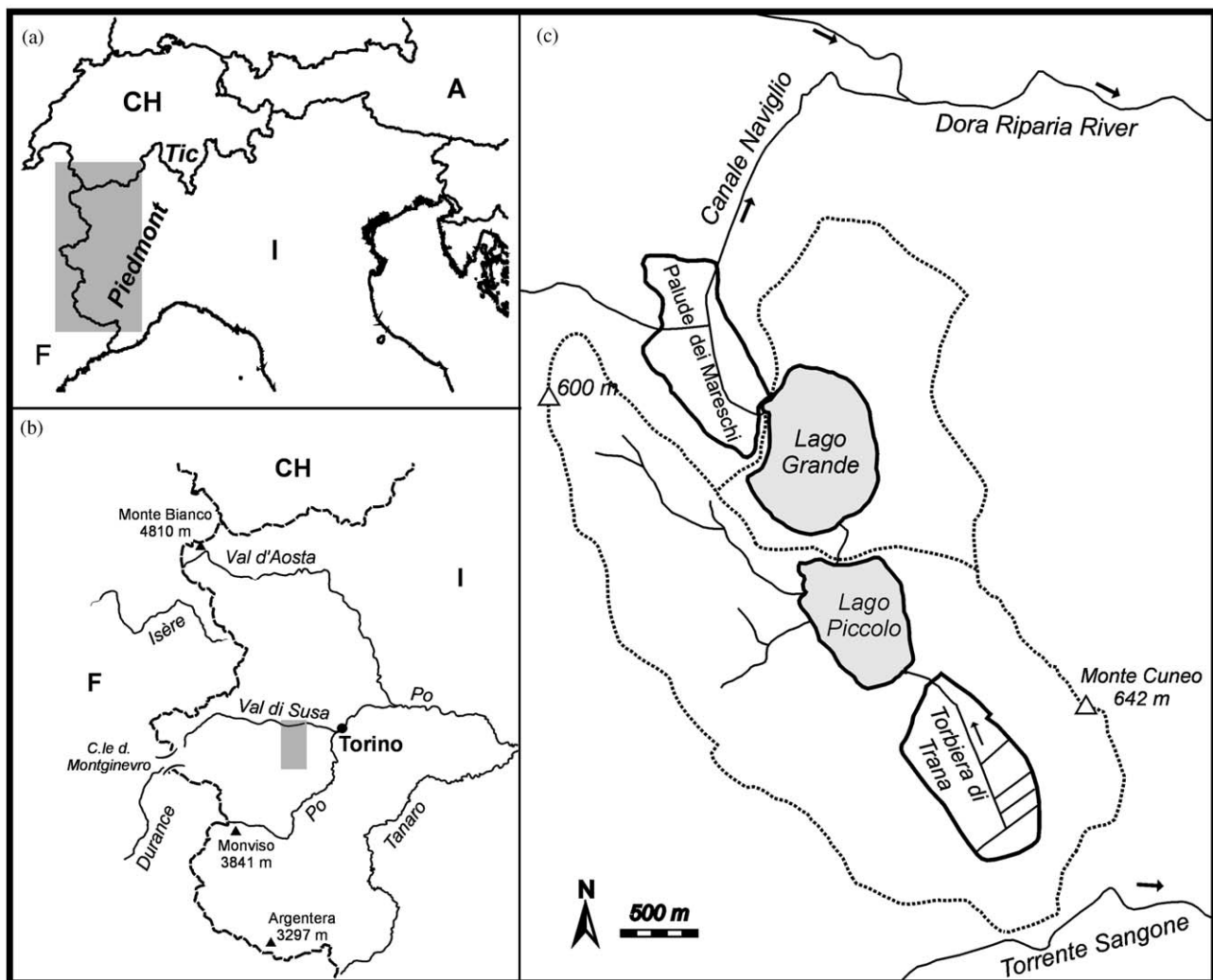


Fig. 1. Map showing (a) the location of Piedmont in northwestern Italy (Lago Piccolo di Avigliana) and Ticino in southern Switzerland (Lago di Origgio), (b) the geographical setting of the Val di Susa, and (c) the local surface hydrology of the Avigliana-lakes catchment (dotted line).

in England (West, 1961; Wright, 1977), when human activities were unlikely to have been a factor. For the early stages of the Eemian Interglacial, when human impact was certainly low, Field et al. (1994) used pollen-based transfer functions to reconstruct a climate with reduced seasonality and greater moisture availability for the *Corylus* phase. In contrast, the application of an extended training-set for the Eemian vegetation record revealed no such temperature variation during that phase (Kühl and Litt, 2003), and illustrated the difficulties in the interpretation of non-analogue pollen assemblages.

The aims of the present paper are (i) to suggest an explanation for the absence of a *Corylus* expansion preceding the establishment of the mixed deciduous oak forest in the southern Alps and (ii) to analyse the causes that may have favoured the expansion of *Corylus*. The answer to these questions may contribute to the understanding of the early Holocene history of hazel in all of Europe.

We use a well-dated Lateglacial and early Holocene lake-sediment record for pollen, plant macrofossil, and microscopic charcoal from the Lago Piccolo di Avigliana. The results obtained are then compared with the record for Lago di Origlio (Tinner et al., 1999), which lies about 200 km east of Lago Piccolo di Avigliana (Fig. 1). These two records are comparable because they are located at similar altitudes in the southern Alps: 353 and 416 m, respectively. Finally, the main factors affecting the spread of *Corylus* and *Quercus* in the southern Alps are reviewed and an integrative model is presented.

2. Materials and methods

2.1. Study site

The Lago Piccolo di Avigliana (353 m a.s.l.; 45°03'N, 07°23'E) is situated in the prealpine fringe of Piedmont (northern Italy) (Fig. 1). The landscape of the Rivoli—Avigliana Morainic Amphitheatre (Sacco, 1887) was built by the Dora Riparia glacier during a series of glacial advances. These innermost moraines were deposited probably during the Last Glacial Maximum (LGM), and since then the area of the lakes has been ice-free. During the Younger Dryas the glaciers were limited to small mountaintop cirques in the Val di Susa valley (Carraro et al., 2002). The lake today is 12 m deep (mean depth 7.7 m) and has an area of 0.58 km², with a catchment area of 8.1 km². The lake is part of a hydrologic system of four basins, the two outer ones being filled (Fig. 1c). It receives its water from the drained overgrown lake, the Torbiera di Trana, where peat was dug out in the 19th century (Sacco, 1887), as well as from two seasonal rivers from the hills. The outlet is connected with the Lago Grande di Avigliana,

from where the water flows north through the Torbiera dei Mareschi into the Dora Riparia River. Metamorphic rocks (calceschists, serpentine, peridotite) occur in the catchment (Petrucci et al., 1970).

The climate is temperate without a dry summer season. The latitudinal oscillations of the polar front can explain why a “transitional Mediterranean precipitation regime” is found here, with separate precipitation maxima in late autumn and in spring (Pinna, 1977). Total annual precipitation is at present ca 880 mm and mean annual temperature 13.0 °C, while mean temperature of the coldest and warmest months are 2.2 °C (January) and 23.9 °C (July), respectively (Biancotti et al., 1998).

The tree and shrub vegetation at present (Tosco, 1975) is dominated by *Alnus glutinosa*, *Ulmus minor*, *Fraxinus excelsior*, *Quercus robur* and *Salix alba* in the flat and humid areas of the lowlands. In the colline zone are *Castanea sativa*, *Q. petraea*, *Corylus avellana*, *F. excelsior* and *Q. pubescens*. On the hills *Q. pubescens* occurs together with other drought adapted species (e.g. *Opuntia vulgaris* and *Celtis australis*) on slopes exposed to the South. At higher altitudes, in the montane belt, *Fagus sylvatica* and *Abies alba* occur.

2.2. Core collection and laboratory methods

The lake-sediment core at Lago Piccolo di Avigliana was collected from a floating platform with a piston corer (Merkt and Streif, 1970) of 8 cm diameter in drives one-meter long. Sediment to 1492 cm below the sediment/water interface was obtained from core AVP1. Results shown in the present work were obtained on only one core (AVP1), while the parallel core (AVP2) was used to double-check core stratigraphy. Sediment components were measured quantitatively by loss on ignition on 1 cm³ samples at 550 °C (4 h) for organic matter content and at 950 °C (2 h) for carbonate content. These exposure times are sufficient to burn all organic matter and to evolve all carbon dioxide from carbonates in mixed sediment types (Heiri et al., 2001). The remaining sediment represents the non-carbonate minerogenic fraction that reflects erosive input from the catchment.

Sediment subsamples (1 cm³) were prepared with chemical (HCL, KOH, HF, acetolysis) and physical treatment (sieving at 500 µm and decanting) and finally mounted on slides with glycerine jelly, following Lotter (1988). For identification of pollen grains, dichotomous keys (Punt, 1976; Moore and Webb, 1978; Punt and Clarke, 1980, 1981, 1984; Punt et al., 1988; Punt and Blackmore, 1991) were used, as well as photographs (Reille, 1992, 1995) and reference material at the Institute of Plant Sciences, Bern. The identification of conifer stomata follows Trautmann (1953). In total 155 pollen types and 12 non-pollen microfossils were identified. Pollen percentages are based on the total of

terrestrial pollen types subdivided into trees, shrubs, herbs, ferns, and aquatics and indeterminate. Pollen analysis was performed on 156 samples (1 cm³ each) distributed over 234 cm of sediment. From 827 to 593 cm the sample interval was 1 or 2 cm in order to record short-lived events. A 1 cm sampling resolution between 712 and 666 cm depth was used for the cross-correlation analysis between pollen and microscopic charcoal time series. A minimum sum of 400 terrestrial pollen grains, excluding aquatic plants, was counted for each sample between 813 and 593 cm, while in the clay rich sediment the pollen sum was generally lower.

Charcoal particles were counted on pollen slides at 250× magnification according to Tinner and Hu (2003) and Finsinger and Tinner (2005).

For the analysis of plant macrofossils, half-core samples of 1 cm thickness were cut and deep-frozen at −18 °C to avoid contamination (Wohlfahrt et al., 1998). The samples (ca 18 cm³) were then sieved through meshes of 0.2 and 0.1 mm. For radiocarbon dating, macrofossils were picked and cleaned twice with demineralised water and subsequently dried at 50–60 °C overnight. Identifications were made with magnifications from 10 to 50×. The old Linnean name *Betula alba* is used informally for remains of tree birch that cannot be identified to species (Tobolski and Ammann, 2000). Concentrations of macrofossils are given with respect to a standard sediment volume of 50 cm³. Determination of bud scales followed the key of Tomlinson (1985), while for seeds and other remains the reference collection at the Institute of Plant Sciences, Bern, as well as other collected material were used.

2.3. Numerical methods

Cross correlations were calculated for couplets of pollen percentage and microscopic charcoal accumulation rates (CHAR) on 47 contiguous samples between 11,500 and 10,200 cal yr BP (712 and 666 cm). This time interval shows pronounced trends in pollen percentages as well as in CHAR values. Detrending is advisable whenever a stratigraphic time series is significantly correlated with depth (Green, 1981; Bahrenberg et al., 1992). Therefore, a more stationary series was obtained by using the residuals of the data about a fitted linear curve modelling the trend. The 95% confidence interval of the cross-correlation coefficients is estimated by computing ± 1.96 standard errors of the correlation coefficients. The null hypothesis states that the correlation between the two sequences (CHAR and pollen taxa) at the specified match position is zero ($r = 0$, $\alpha = 5\%$, two sided), or that which is expected if the two sequences are independent, random series (Davis, 2002). The median time span of one lag in the cross-correlations is 29 years (span = +8 and −16), being dependent on the inferred deposition time of individual samples.

2.4. Chronology and zonation

The depth-age model is based on radiocarbon dating of terrestrial plant macrofossils as well as the Laacher See Tephra (LST) (Blockley et al., in press; van den Bogaard and Schmincke, 1985) (Table 1). For the depth-age model (Fig. 2a), calibrated ages (CalPal2003 Calibration Curve of CalPal_A, Weninger et al., 2003)

Table 1
Radiocarbon datings on the Lago Piccolo di Avigliana core section discussed in this study

Depth (cm)	Lab. code	Material analysed	Weight (mg)	$\delta^{13}\text{C}$ (‰ PDB)	Age (¹⁴ C yr BP)	Calendar age (cal yr BP)
481	Erl-4802	Leaf fragments of terrestrial plant	5.7	−30.52	5230 ± 51	6020 ± 160
634	Erl-4801	1 <i>Betula</i> fruit, 1 <i>Betula</i> catkin scale, leaf fragments of terrestrial plant	9.1	−30.17	8723 ± 63	9740 ± 260
678–9	Poz-3930	2 <i>Quercus</i> bud scales, 3 <i>Betula</i> fruits, 2 bud scales indet., 1 Coniferous bud scale	1.8	−24.4	9290 ± 50	10,450 ± 280
695	Poz-3918	3 <i>Quercus</i> bud scale, 2 <i>Betula</i> fruits, 2 terrestrial leaf fragments	2.3	−28.5	9320 ± 60	10,500 ± 280
714	Erl-4800	1 Wood indet.	10	−28.05	10,248 ± 64	11,950 ± 600
732–3	Poz-3931	54 <i>Betula</i> fruits, 2 bud scales indet., 1 <i>Betula</i> bud scale, 6 <i>Betula</i> catkin scale, 2 terrestrial leaf fragments, 4 <i>Larix</i> needles, 1 Coniferous bud scale	4.2	−23.3	10,320 ± 50	12,090 ± 560
768	/	LST	/	/	11,000 ^a	12,900 ^b
775	Erl-4799	104 <i>Betula</i> fruits, 9 <i>Betula</i> catkin scales, 2 <i>Quercus</i> bud scales	4.9	−26.77	11,525 ± 80	13,230 ± 120
806	Erl-4798	35 <i>Betula</i> fruits, 5 <i>Betula</i> catkin scales	1.4	−26.28	12,395 ± 102	14,500 ± 660
888	Erl-4797	1 <i>Betula</i> fruit, 1 <i>Alnus</i> seed, Wood indet.	2	−27.82	14,614 ± 111	17,420 ± 260

^aAccording to van den Bogaard and Schmincke (1985).

^bAccording to Baales et al. (2002).

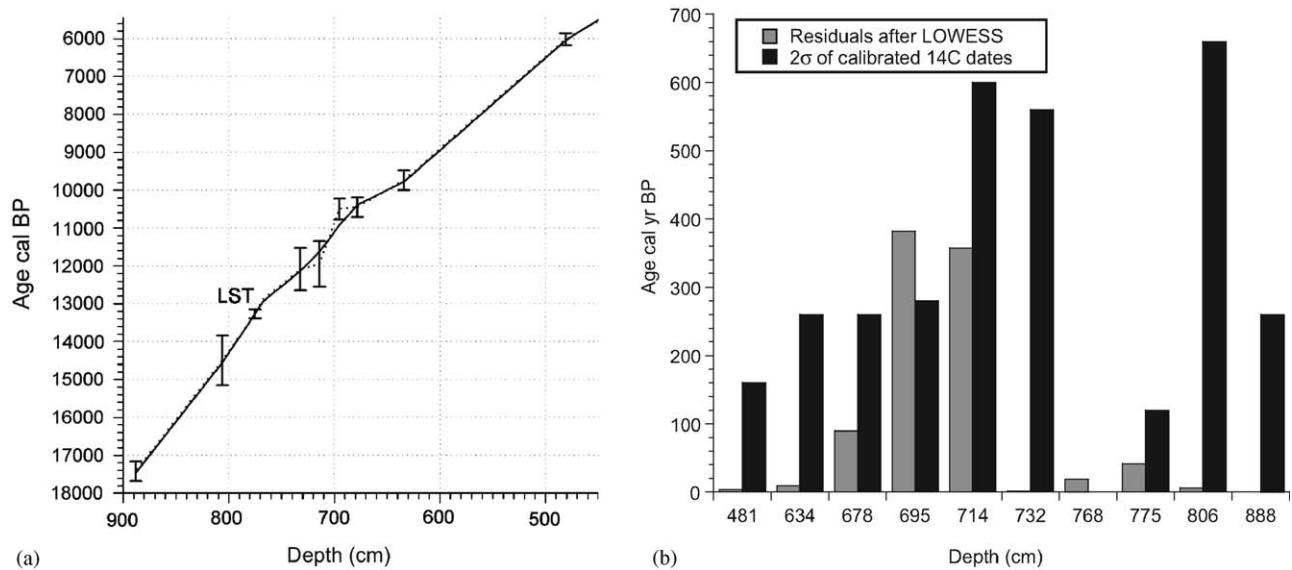


Fig. 2. (a) Depth-age model of the Lago Piccolo di Avigliana core and (b) discrepancy between measured (and calibrated) ^{14}C ages and model-inferred ages.

were corrected with a non-parametric regression technique (LOWESS) (Efron and Tibshirani, 1991). This procedure is conceptually similar to ‘running means’ except that it takes into account the uneven spacing of the independent time variable (Birks, 1998). We then assumed a linear relationship between the LOWESS-smoothed calibrated radiocarbon dates. The LOWESS span (in our case $\alpha = 0.3$), which corresponds to the percentage of values used to establish the locally weighted regression, was chosen by selecting the highest possible smoothing constraining the LOWESS correction to 2σ of the calibrated ^{14}C dates (Fig. 2b). Residuals for the depth-age model obtained exceed the 2σ space only for one date, namely the ^{14}C date at 695 cm, which appears too old (Fig. 2b). As the oldest reliable date in the Lago Piccolo di Avigliana core is at ca 17,500 cal BP, older sediment remains undated.

Zonation of the pollen diagram follows recommendations of Bennett (1996). Numerical zonation was carried out by optimal-sum-of-squares partition, and the number of statistically significant splits was determined with the broken-stick model (MacArthur, 1957). In addition to zone boundaries obtained by the use of this technique (drawn lines in the figures), subzones (dashed lines) have been set where necessary for the diagram’s discussion. The pollen-zone limits were also used to subdivide the macrofossil record of Lago Piccolo di Avigliana.

For regional comparison the local pollen assemblage zones (LPAZ) are referred to as biozones (Schneider, 1985), not to chronozones as defined by Mangerud et al. (1974) (see Ammann et al., 2000).

3. Results

3.1. Lithology and loss on ignition

The sediment from Lago Piccolo di Avigliana consists of stratified blue-grey silt and sand with angular stones from the core bottom up to a depth of ~900 cm. Loss-on-ignition analysis shows that organic content (Fig. 3) first increases slightly at 850 cm to less than 8% in weight and then abruptly between 810 and 790 cm to values around 12%. Inorganic carbonate content shows a first peak at 850 cm, where a Characeae layer occurs, but then increases steadily from 810 cm upwards. Some minor wiggles and a levelling off between 800 and 720 cm interrupt this positive trend. A similar but reversed profile is shown by the non-carbonate minerogenic fraction.

3.2. Vegetation dynamics inferred from pollen analysis

The pollen record at Avigliana shows rapid changes in the percentage diagram during the Lateglacial and the early Holocene (Fig. 4 and Table 2). The most prominent among them are the decrease in *Juniperus* accompanied by a steady increase of *Betula* marking the beginning of afforestation (LPAZ AVP-1b; onset dated at ca 15,700 cal yr BP) and afterwards the expansion of *Pinus sylvestris* in zone AVP-2 (onset dated at ca 14,500 cal yr BP). The local presence of *Juniperus* and *Larix* during zone AVP-1b (Oldest Dryas) is attested by regular findings of stomata. Low pollen percentages of *Quercus* and *Alnus* might be due to long-distance transport (Wick, 1996) or to low-density populations

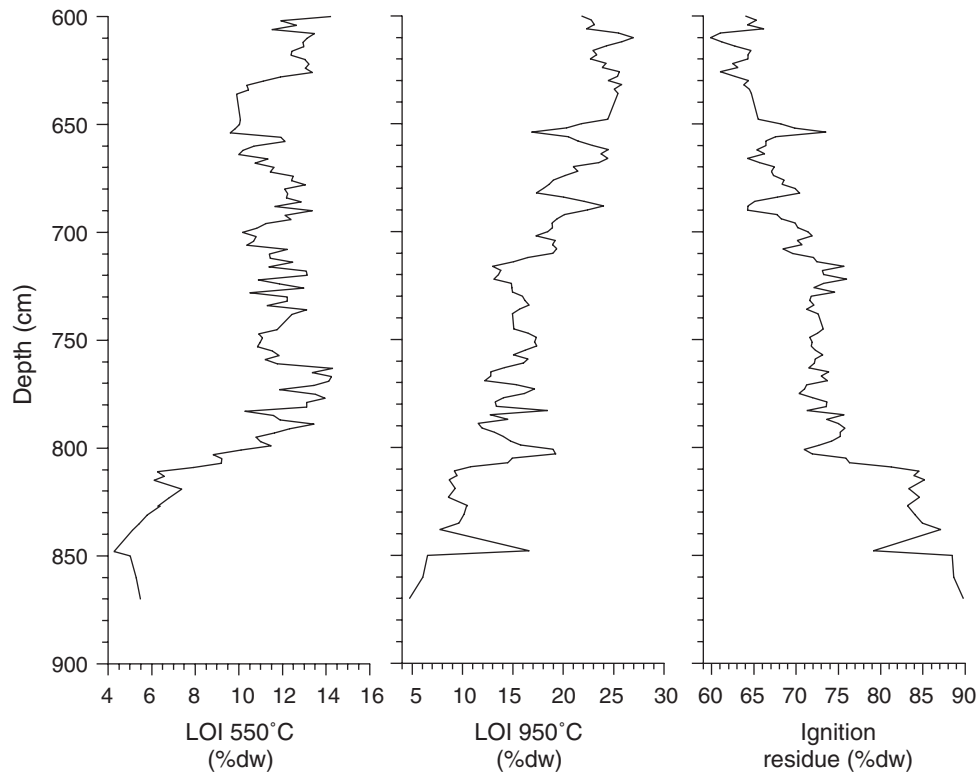


Fig. 3. Loss on ignition of organic matter (550 °C), carbonate content (950 °C) and ignition residue. Values in percentage of dry weight (%dw).

in the catchment (Bennett, 1988). The subsequent ‘*Pinus* phase’ (zone AVP-2; Allerød), i.e. when *Pinus sylvestris* trees became important in the catchment (stomata in our lake sediment core as well as fossil trees in the Val di Susa reported by Friedrich et al., 2001), was interrupted by a short increase in *Artemisia* during subzone AVP-2b (14,150–14,000 cal yr BP) and a decrease of *Pinus*. This pollen pattern likely indicates a brief opening of the landscape. Subsequently in zone AVP-2c (14,000–13,000 cal yr BP), *Quercus*, *Alnus* and *Ulmus* pollen increased slightly, whereas *Fraxinus excelsior* and *Corylus* reached low values. *Juniperus* pollen was very rare, and no stomata of the taxon were recorded.

The steady increase of thermophilous tree pollen allows us to infer population expansions of *Quercus*, *Ulmus* and—though less pronounced—*Tilia* during zone AVP-2d (13,000–12,700 cal yr BP). Herbaceous pollen (e.g. *Artemisia*, Poaceae, Rubiaceae and *Rumex*) and *Betula* decreased. Together with the *Pinus* increase this indicates forest closing. During the following subzone AVP-2e (12,700–12,100 cal yr BP; first part of the YD), lower pollen amounts of thermophilous trees and higher herb and shrub pollen such as *Artemisia*, Chenopodiaceae and *Juniperus*, indicate an opening of the forest cover. *Alnus glutinosa* pollen frequencies increased possibly due to local expansion of riparian forest. The subsequent re-expansion of thermophilous trees occurred in two steps: after a steady increase of only

Quercus in subzone AVP-2f (12,100–11,700 cal yr BP; second part of the YD), *Quercus*, *Fraxinus excelsior* and *Ulmus* increased abruptly at the transition to subzone AVP-3a (~11,700 cal yr BP; ca YD/Holocene transition). Together with the latter increase, *Betula*, *Alnus glutinosa* and *Artemisia* were reduced. At the start of subzone AVP-3a (Preboreal), *Juniperus* pollen was still relatively high, indicating the presence of abundant shrub vegetation. Then *Artemisia* and *Rumex* pollen abruptly increased in subzone AVP-3b (Boreal; ca 11,350–11,200 cal yr BP), while *Quercus* pollen was temporarily reduced. The pattern observed implies that a short cold event occurred. After that, oak recovered again for pollen values level off at ca 30%.

We infer a gradual population expansion of *Corylus* from the steady increase of *Corylus* pollen between 11,200 and ca 10,400 cal yr BP (subzone AVP-3c), that culminated ~10,000 cal yr BP (zone AVP-4; Boreal) with a maximum abundance of ~15%. Between 10,400 and 9700 cal yr BP (zone AVP-4), *Corylus* pollen reached maximum values and Poaceae pollen increased. Forest openings or disturbances are further indicated by *Pteridium* spores, which were regularly found in this zone. Later, *Corylus* pollen was only slightly reduced when *Alnus glutinosa* expanded at ca 9700 cal yr BP (onset of zone AVP-5; Atlantic). *Pteridium* spores were still present and *Vitis* pollen appeared in the diagram.

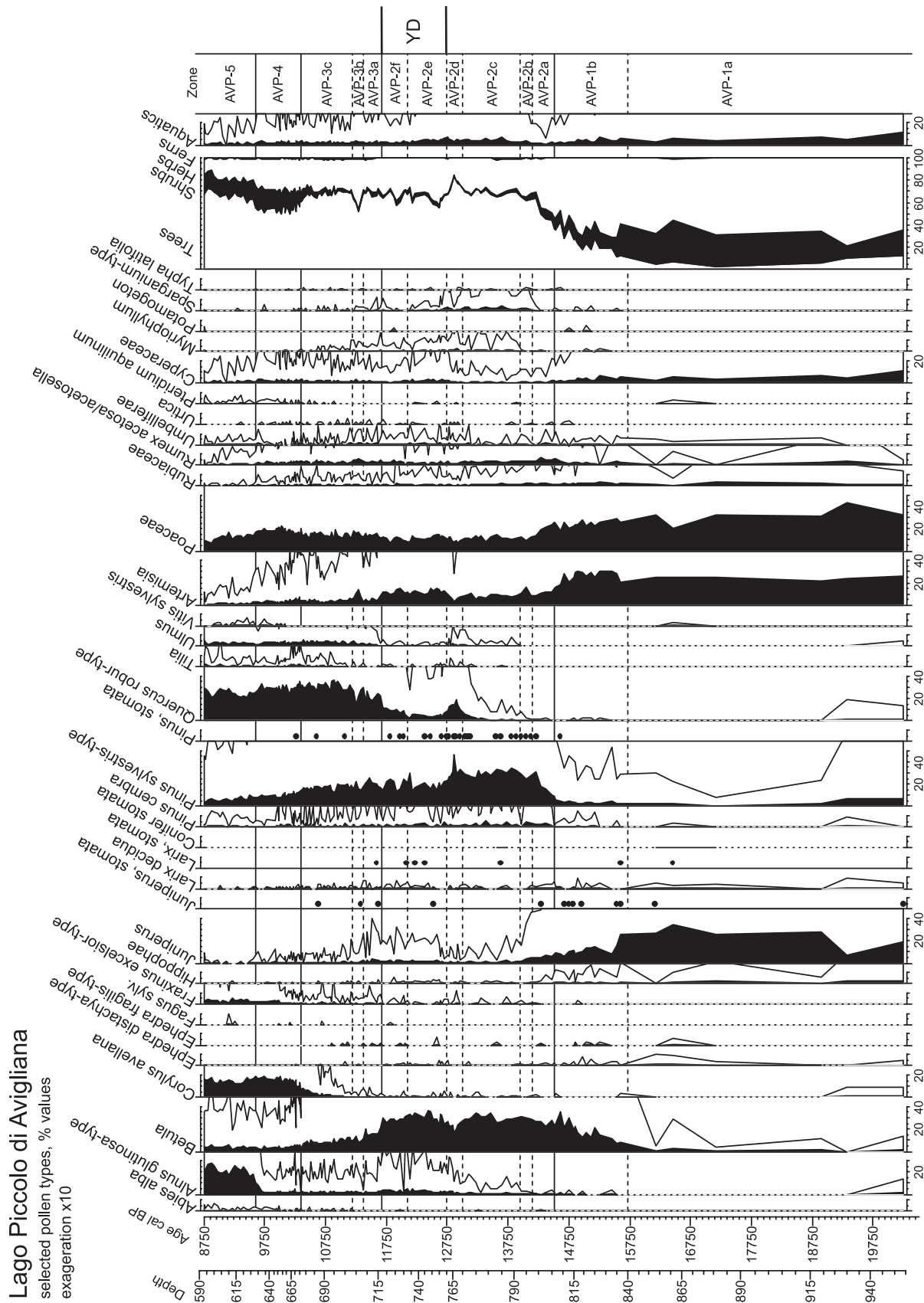


Fig. 4. Lago Piccolo di Avigliana pollen % diagram with selected taxa. Local Pollen Assemblage Zones as discussed in the text. Full horizontal lines show statistically significant limits; dashed lines for other limits.

Table 2
Chrono- and biostratigraphy of Lago Piccolo di Avigliana

Lago Piccolo di Avigliana LPAZ	Depth/age model inferred (cal BP) for the onset of LPAZ	Event marking the onset of LPAZ at Lago Piccolo di Avigliana	Inferred vegetation change	Correlation to biozones
AVP-5	9700	▲ <i>Alnus glutinosa</i> -type	Development of alder carr in flat areas	Atlantic
AVP-4	10,400	Abrupt ▲ <i>Corylus</i> , ▲ <i>Fraxinus</i> and Poaceae	Persisting disturbance	Boreal
AVP-3c	11,200	Abrupt ▲ <i>Quercus</i> , regular presence of <i>Pteridium</i> and gradual ▲ <i>Corylus</i> ; gradual ▼ <i>Betula</i> , abrupt ▼ <i>Artemisia</i>	▲disturbance and opening of deciduous forest	Preboreal
AVP-3b	11,400	▲ <i>Artemisia</i> and <i>Rumex</i> ; ▼ <i>Quercus</i>	Opening of deciduous forest	
AVP-3a	11,670	▲ <i>Quercus</i> , <i>Ulmus</i> , <i>Fraxinus</i> , <i>Corylus</i> ; ▼ <i>Betula</i> , <i>Artemisia</i> , <i>Alnus</i>	Further ▲mixed deciduous oak forest	
AVP-2f	12,100	Gradual ▲ <i>Quercus</i> and ▼ <i>Betula</i> ; still high values of <i>Artemisia</i> and <i>Juniperus</i>	▲mixed deciduous oak forest	Younger Dryas
AVP-2e	12,750	▲ <i>Betula</i> , <i>Artemisia</i> , <i>Juniperus</i> , <i>Alnus</i> ; ▼ <i>Quercus</i> , <i>Ulmus</i> , <i>Fraxinus</i>	▼mixed deciduous oak forest	
AVP-2d	13,000	▲ <i>Quercus</i> and <i>Pinus</i> , ▼ <i>Betula</i>	▲mixed deciduous oak forest	Allerød
AVP-2c	14,000	Regular presence of <i>Quercus</i> , <i>Ulmus</i> , <i>Fraxinus</i> , <i>Corylus</i> ? <i>Betula</i> still abundant	Establishment of mixed deciduous oak forest	
AVP-2b	14,150	▲ <i>Artemisia</i>	Opening of boreal forest	
AVP-2a	14,500	▲ <i>Pinus sylvestris</i> , ▼ <i>Artemisia</i>	Closing of boreal forest	
AVP-1b	15,700	▲ <i>Betula</i> with ▼ <i>Juniperus</i>	Start of the afforestation	Bølling

▲ and ▼ equal ‘increase of’ and ‘decrease of’, respectively.

Aquatic plants, scarcely present during subzone AVP-1b, increased first with *Sparganium* in subzone (AVP-2b) and then with *Myriophyllum* (subzone AVP-2c). *Typha latifolia* never reached high values but is recorded after zone AVP-2.

3.3. Plant macrofossils at Lago Piccolo di Avigliana

Concerning presence or absence of species in the catchment, the macrofossil record confirms the pollen-inferred vegetation reconstructions (Fig. 5).

During subzone AVP-1a (> 15,700 cal yr BP), macrofossils show the local presence of tree *Betula* and *Larix*. Surprisingly, *Betula* fruits and catkin scales were found already at a depth of 885 cm, where pollen values are extremely low (<5%). The presence of *Betula nana*, rarely found during the Lateglacial in the southern Alps and their forelands (Schneider and Tobolski, 1985) and extinct today in the Italian Peninsula (Caccianiga, pers. comm.), is here confirmed. At 850–848 cm, the high abundance of *Chara oregonia* possibly indicates a short phase of low lake level. During subzone AVP-1b (15,700–14,500 cal yr BP) an assemblage similar to that in the previous subzone is found, but with higher abundance of *Betula alba* macrofossils, implying a gradual increase of importance of tree birch. In the following subzone (AVP-2a; 14,500–14,150 cal yr BP),

bud scales of conifers (possibly *Pinus sylvestris*) were present, while *Betula alba* concentrations decreased and *Betula nana* fruits disappeared, mirroring the expansion of pine and birch forests. At the top of subzone AVP-2c (14,000–13,000 cal yr BP), after a sudden increase of *Betula alba* fruits and catkin scales, the first macrofossil of *Quercus* unambiguously documents its presence in the lake catchment area. One single oak bud scale was found during the Younger Dryas, where *Betula alba* and *Larix* concentration increased, and where the first *Alnus glutinosa* fruit testifies to the local presence of this tree. Although we cannot be sure that oak persisted during the entire Younger Dryas at the southern foothills of the Alps, relatively high pollen percentages and one oak bud scale speak in favour of an oak population present in the catchment of the Lago Piccolo di Avigliana.

During the Holocene, leaf fragments of deciduous trees or shrubs were frequent, possibly documenting the abundance of deciduous trees. Concentration of *Betula alba* macrofossils decreased steadily to minimum values, while *Larix* needles were still present.

The macrofossil record as well as the *Pinus* stomata (Fig. 4) unequivocally indicate that between ca 17,500 and ca 8750 cal yr BP Lago Piccolo di Avigliana was continuously below timberline. The Lago Piccolo di Avigliana macrofossil record corroborates the presence of forest-steppe vegetation, as often proposed (Beug,

Lago Piccolo di Avigliana

Plant macrofossils

Analyst: W. Finsinger

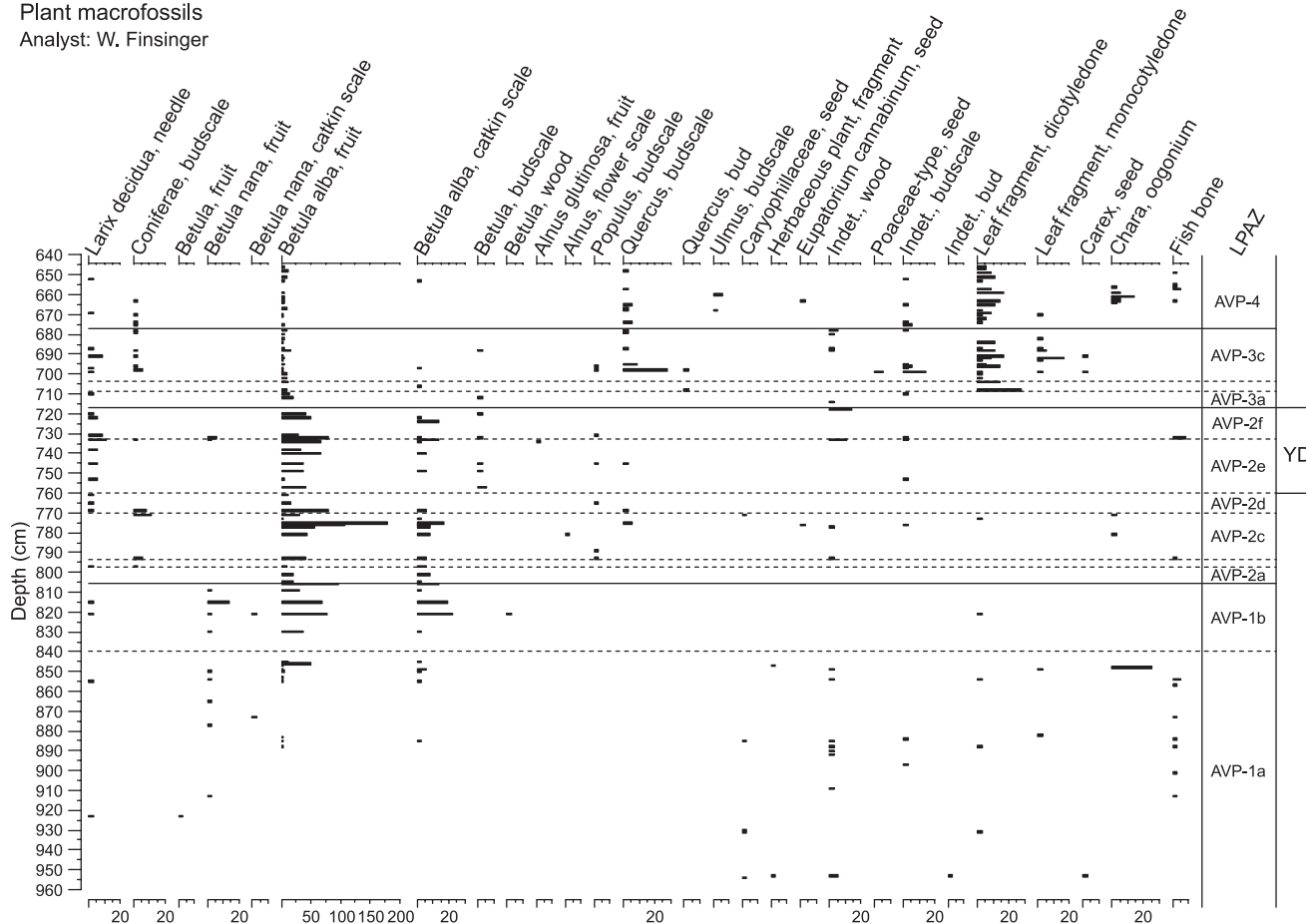


Fig. 5. Lago Piccolo di Avigliana macrofossil diagram. Concentration referred to standard volume of 50 cm³. Zones are taken from pollen diagram.

1975; Ammann et al., 1983; Ammann and Tobolski, 1983) for the time interval between the ~full glacial (outside the LGM-moraines) and the very early Lateglacial (at Avigliana ca 17,500 to ca 15,000 cal yr BP).

3.4. Regional fire history and ecology between Piedmont and Ticino

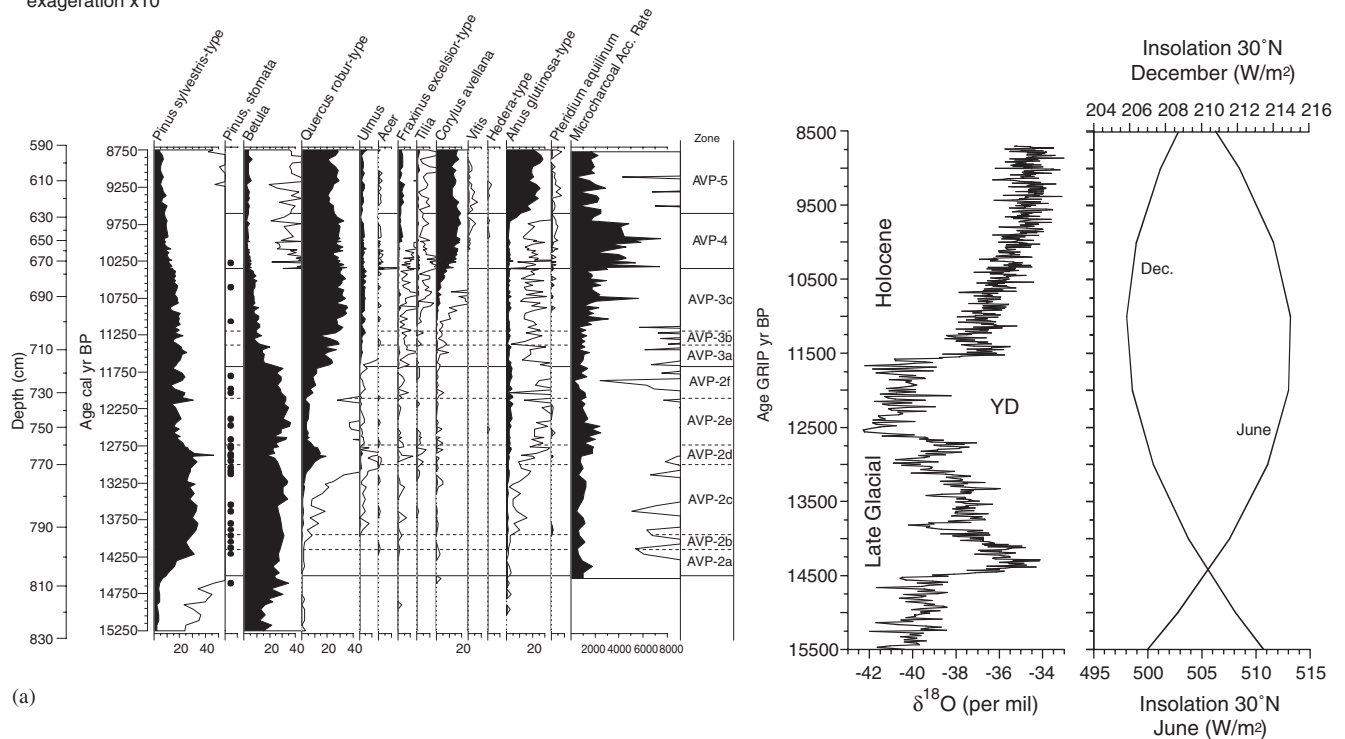
At Lago Piccolo di Avigliana (Fig. 6a), microscopic CHAR was relatively low during the entire Lateglacial, except for a slight increase during the first part of the Younger Dryas (subzone AVP-2e). From increased CHAR values we infer that regional fire frequency increased abruptly during the early Holocene after 11,200 cal yr BP (subzone AVP-3c). Subsequently, it rapidly decreased to low values around 9700 cal yr BP (zone AVP-4), when *Alnus glutinosa* expanded. In this time interval of ca 600 years, microscopic CHAR values were more than double the Lateglacial values.

Pteridium aquilinum, a fire-adapted taxon (Tinner et al., 2000), was recorded in the pollen records after ~11,000 cal yr BP and after 10,600 cal yr BP at Lago

Piccolo di Avigliana and at Lago di Origlio, respectively (Fig. 6a and b).

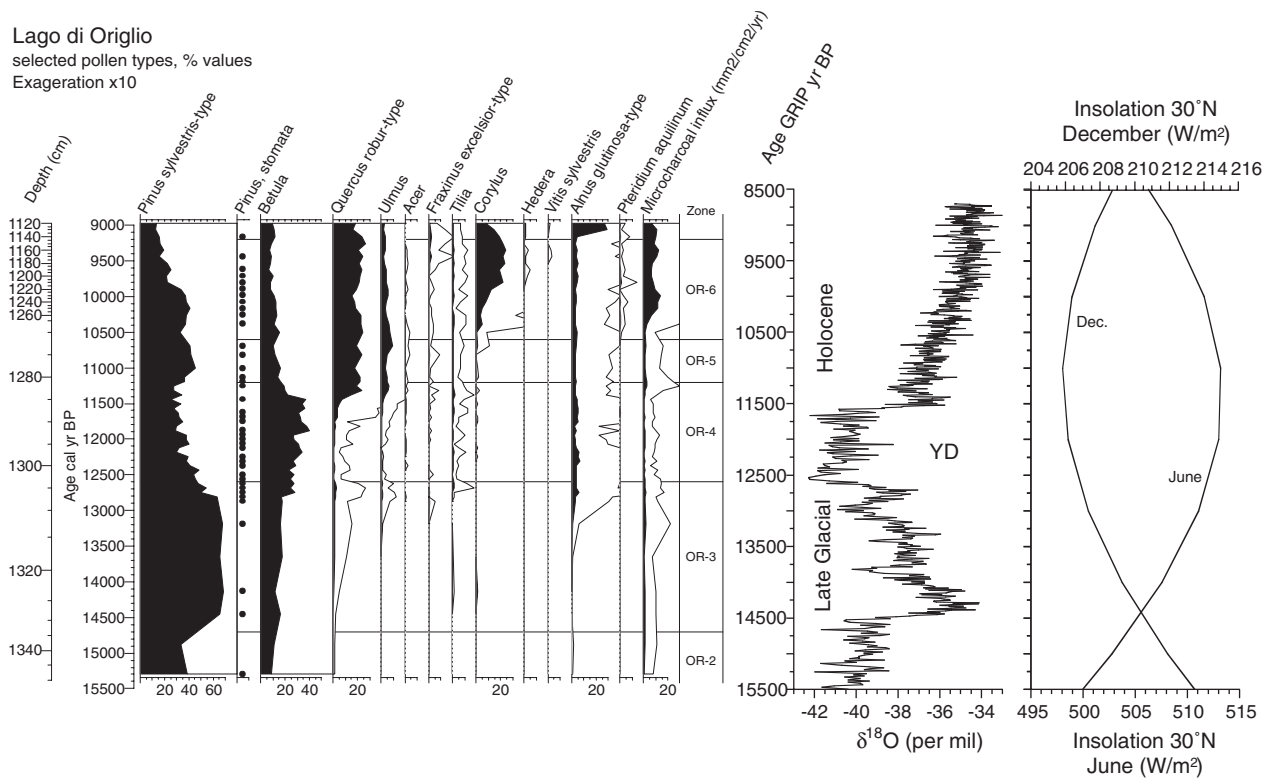
To analyse the statistical significance of short-term correlation between vegetation (e.g. *Corylus*) and inferred fire activity in the southern Alps, we calculated cross-correlations for the Lago Piccolo di Avigliana record (Fig. 7). Cross correlograms show that some taxa are positively correlated with CHAR peaks, suggesting a relationship between their occurrence and forest-fire activity. *Pteridium* spores and *Cirsium* pollen show a positive correlation at time lag +1, indicating that fire might have favoured their expansion. CHAR and *Fraxinus* pollen are also significantly correlated. The highest positive correlation is reached approximately 60 years after a fire (time lag +2). Surprisingly, *Corylus* is positively correlated with charcoal peaks at time lag –1, possibly showing that fires occurred in response to *Corylus* increases. Previous studies showed that *Corylus* pollen percentages can increase after fires (Clark et al., 1989; Tinner et al., 1999). Since the correlation coefficient is low, these results would need a confirmation by other records. However, cross-correlations of undetrended data led to a significant positive correlation

Lago Piccolo di Avigliana
selected pollen types, % values
exageration x10



(a)

Lago di Origgio
selected pollen types, % values
Exageration x10



(b)

Fig. 6. (a) selected pollen types and microscopic CHAR of Lago Piccolo di Avigliana (this study) and (b) selected pollen types and microscopic CHAR of Lago di Origgio (Tinner et al., 1999). Zonation of Lago Piccolo di Avigliana follows LPZ discussed in the text; Lago di Origgio zonation follows Tinner et al. (1999); $\delta^{18}\text{O}$ (‰ SMOW) record from the GRIP deep ice-core (middle) (Dansgaard et al., 1993; Johnsen et al., 1992) between 15.5 and 8.5 ka GRIP yr BP (ss09 chronology); insolation curves (right) were taken from Berger and Loutre (1991).

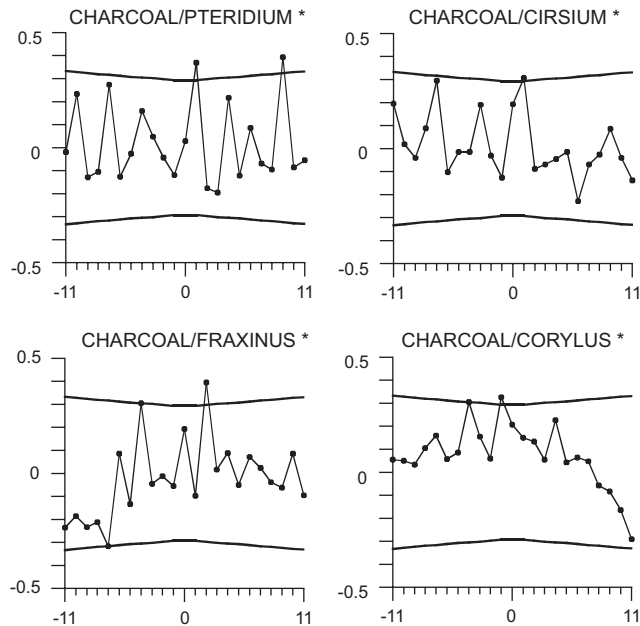


Fig. 7. Cross-correlation plots between microscopic CHAR values and selected pollen types. x-axis = lag point of cross-correlations; y-axis = coefficient of correlation; horizontal bow-lines = limits of statistical significance.

at time lag 0 (Spearman correlation coefficient = 0.789), which is probably the result of a strong common trend.

4. Discussion

4.1. The hazel population expansion north and south of the Alps

The expansions of oak before the Younger Dryas and of *Corylus* during the early Holocene at the Lago Piccolo di Avigliana were not exceptional for the southern forelands of the Alps. In fact, similar though less pronounced records showing these regional features have been observed, e.g. Lago di Origlio (Fig. 6b and 8).

At Lago Piccolo di Avigliana (Fig. 4), *Corylus* pollen was continuously present since 13,700 cal yr BP (with percentages around 1–2%). Then, at around 10,400 cal yr BP, the hazel population expanded gradually in the catchment of the Lago di Avigliana and was only slightly reduced after the subsequent expansion of *Alnus* at 9,700 cal yr BP (Atlantic biozone).

In central and northern Europe, population expansions of *Corylus* took place under circumstances different from those in the southern Alps. In the first area, hazel expanded during the early Holocene decline of *Pinus* and *Betula*, while other thermophilous deciduous trees expanded only later. On the Swiss Plateau, hazel spread around 11,000 cal yr BP at Soppensee (Lotter, 1999), at Lobsigensee (subzone CHb-5a, Boreal

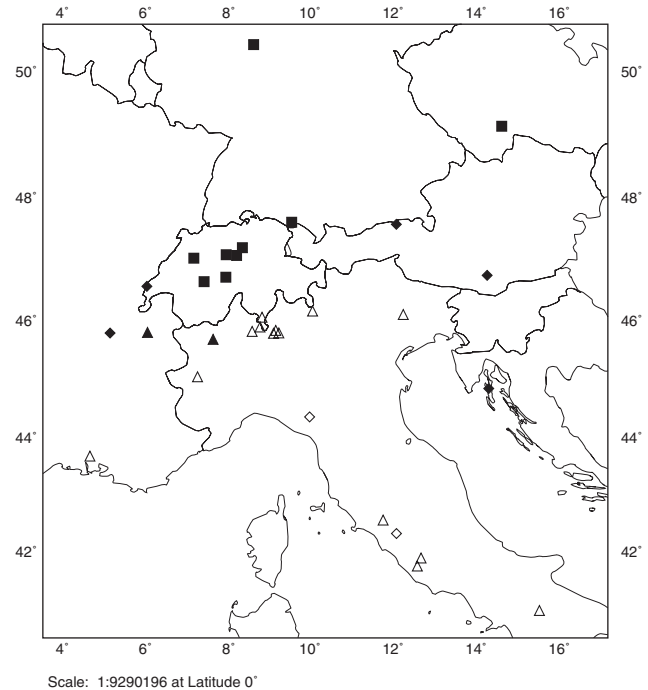


Fig. 8. Map showing the geographic pattern of *Corylus* and *Quercus* population expansions. A clear north-south division appears, with oak expanding first in the south and hazel expanding first in the north of the Alps. Δ = *Quercus* expansion before *Corylus* during the Lateglacial; \blacktriangle = *Quercus* expansion before *Corylus* during the Holocene; \blacksquare = *Corylus* expansion before *Quercus* during the Holocene; \diamond and \blacklozenge = synchronous expansion during the Lateglacial and the Holocene, respectively.

biozone) (Ammann et al., 1996), and at Bibersee (Beckmann, 2003). In central-west Germany, *Corylus* expanded around 10,700 cal yr BP (Bos and Urz, 2003). In northwestern Europe, hazel's expansion is not older than 9600 ^{14}C yr BP, i.e. around 10,500 cal yr BP (Tallantire, 2002). At Lago Piccolo di Avigliana and at Lago di Origlio, the expansion took place around 10,400–10,200 cal yr BP. Therefore hazel expanded almost synchronously during the early Holocene north and south of the Alps or possibly even earlier north of the Alps.

In spite of the near-synchronism of the hazel expansion, oak and other thermophilous trees (e.g. *Ulmus*, *Fraxinus*, and *Tilia*) show a time delay of several millennia in the north. Their expansion did not take place before 11,000 cal yr BP on the Swiss Plateau (Ammann et al., 1996; Beckmann, 2003; Lotter, 1999). Instead, south of the Alps (e.g. at Lago Piccolo di Avigliana and at Lago di Origlio) the first oak expansion took place before the Younger Dryas (i.e. \sim 13,000 cal yr BP). The pattern shown here based on only four sites, however, is not a local one. It reflects the standard sequence of expansions north and south of the Alps (Fig. 8). According to available pollen records in the surroundings of the Alps, in the south and in the southwest oak expanded before hazel (before the

Younger Dryas), whereas in the north hazel expanded decades to centuries before oak.

4.2. Potential reasons for differences in timing of expansion of *Corylus* and *Quercus*

In our comparison on the different behaviour of *Corylus* and *Quercus*, we considered only one species for *Corylus* (*C. avellana* L.) but four species of *Quercus* (*Q. petraea* (Mattuschka) Liebl., *Q. pubescens* Willd., *Q. robur* L. s.s., and *Q. cerris* L.), although at present more species of this genus occur south of the Alps, e.g. *Q. pyrenaica* (Val di Susa), *Q. dalechampii*, and *Q. virgiliana* (Pignatti, 1982).

Differences in timing of expansion for thermophilous species may be caused by (1) distance of refugia (Birks and Line, 1993), (2) ecology and speed of seed dispersal and thus also differential migration rates (Iversen, 1960), (3) competition among species (Birks, 1986) under a given climate, (4) influence of disturbances such as fire (Bennett, 1988), and (5) climate (Webb, 1986).

Given these possible causes, it is conceivable that hazel did not expand during the Allerød in the southern Alps because (i) its refugia were too far away, whereas oak's refugia were nearer, (ii) its migrational speed was not so fast as north of the Alps, (iii) hazel immigrated together with oak but was not able to expand due to competition with other arboreal taxa, (iv) hazel was not sustained by disturbance factors, e.g. fires, that provided competition advantages for *Corylus*, (v) unsuitable climate inhibited hazel, or (vi) a complex combination of these factors.

To assess the reasons for the nearly synchronous expansion of hazel north and south of the Alps under different ecological conditions, it is necessary to address these hypotheses in more detail.

4.2.1. Distance of refugia

The term 'refugium' is often used informally to refer to an area of any size in which a taxon persisted, at any population density, during a cold stage (Bennett et al., 1991). Two independent lines of evidence for the detection of oak and hazel refugia may be used: pollen records and chloroplast DNA.

Low and continuous amounts of hazel pollen since ~13,000 cal yr BP (subzone AVP-2d) might testify to the local presence of low-density populations in the surroundings of Lago Piccolo di Avigliana (Fig. 6a) and since 11,300 cal yr BP (zone OR-5) at Lago di Origlio (Fig. 6b). Generally speaking, at other sites in northern Italy the sequence of expansion is the same (Schneider, 1985; Schneider and Tobolski, 1985; Wick, 1996; Gobet et al., 2000).

Intuitively with a simple tree-migration model, taxa that did first increase in frequency may have been those closest to the various sites during the intervening cold

periods (Huntley and Birks, 1983). *Corylus* expanded in Italy together with *Quercus* and before the Younger Dryas at Lago di Vico (Zone V1-18) in Central Italy (Magri and Sadori, 1999). However, at other sites in Central Italy it expanded after *Quercus* but again before the Younger Dryas at Lagaccione (Magri, 1999), Valle di Castiglione (Follieri et al., 1988), and Lago di Albano (Lowe et al., 1996), as well as in southern Italy at Lago di Monticchio (Allen et al., 2000) and in the northern Appennines at Prato Spilla 'C' (Lowe, 1992). Therefore the palaeobotanical evidences would suggest that in Italy refugia of *Corylus* were not more distant than those of *Quercus* and other thermophilous taxa (*Tilia*, *Ulmus*, and *Fraxinus*). However, for some reason hazel always expanded later than oak in the forelands of the southern Alps and at some sites on the Italian Peninsula (Fig. 8).

Molecular studies have the potential to reveal lineages whose modern distribution could help identify refugia (Hewitt, 1999). Analyses of present tree populations in Europe have been made for both *Quercus* and *Corylus*. For *Corylus*, Palmé and Vendramin (2002) argue that western and northern Europe is at present inhabited by one single haplotype, and most of the diversity is found in southeastern Europe (Italy and the Balkans). Their data exclude Italy and the Balkans as possible origins for the postglacial recolonisation of hazel into northern Europe and, in combination with pollen data, suggest for northern European hazel populations either a western origin or an expansion from several scattered refugia. For southern European populations they suggest a southern origin.

For *Quercus*, the analysis of chloroplast DNA shows clear evidence for refugia in the Italian Peninsula (Fineschi et al., 2002; Petit et al., 2002). In addition there is evidence that trees were able to cross the apparently significant obstacle of the southern Alps, migrating from Italy westward to southwestern France and northeastern Spain (Fineschi et al., 2002; Petit et al., 2002) as well as to Switzerland (Matyàs and Sperisen, 2001) during the early Holocene.

In conclusion, refugia for both tree genera were present in the Italian Peninsula. It seems that the distance to refugia from our sites was not different for the two genera. However, the expansions may have taken place from single and separated refugia or even from scattered trees and shrubs. The most unequivocal evidence for the simultaneous presence of oak and hazel in refugia areas would be provided by macrofossils, as these can unambiguously provide evidence for past local vegetation (Birks, 1993a; Birks and Birks, 2000), but unfortunately such data are still sparse in Italy.

4.2.2. Ecology (and speed) of seed dispersal and resulting differential migration rates

Migration speed depends on seed-dispersal velocity and on the age of first reproduction (Lang, 1994). Both

genera (oak and hazel) produce big and heavy seeds. Being not adapted for wind dispersal, they are dependent on the activity of caching animals, mainly birds and rodents (e.g. European jays, squirrels, carrion crows). At present *Quercus petraea* L. is dispersed to a similar amount by rodents and jays, whereas dispersal by rodents is clearly more important for *Corylus* (Kollmann and Schill, 1996). The large nutrient reserves of nuts not only attract animal dispersers but also permit seedlings to establish a large photosynthetic surface or extensive root system, making them especially competitive in semi-arid environments (e.g. dry mountains, Mediterranean climates) (Vander Wall, 2001). Recent observations on the effectiveness of seed dispersal for *Quercus petraea* and *Corylus avellana* show that, when compared with wind-dispersed species, their seeds are sometimes hidden in the soil, whereas most seeds of wind-dispersed species have little chance of penetrating vegetation and litter, in turn increasing mortality of wind-dispersed seeds (Kollmann and Schill, 1996). The nutcracker (*Nucifraga caryocatactes*), living today in the subalpine belt in the Alps, is able to transport seeds regularly up to 15 km. It not only collects *Pinus cembra* seeds but also seeds of *Corylus*, *Quercus*, and *Fagus* (Bonn and Poschod, 1998). Therefore, if oak was already present at the southern foot of the Alps before or during the Younger Dryas, the distance of 100 km separating the two regions could have been crossed by seed transport within at most 100–150 years by *Quercus* and <50 years by *Corylus*, excluding major relevant lags of migration. As Clark (1998) showed with the ‘fat-tail model’, rare events of very long-distance dispersal may explain rapid migration. If birds are more important vectors than rodents for *Quercus* (compared to *Corylus*), one may expect faster migration of oak. However this is not supported for Central Europe (Huntley and Birks, 1983). Therefore if caching animals are available the difference in timing of expansion between hazel and oak cannot depend on the dispersal mechanism, but rather possibly on germination speed or on survival of the plant after germination.

Regarding age of first reproduction, hazel should attain faster migration speed because it produces seeds already after 10 years while oak reaches maturity only after ca 30 years (Firbas, 1949; Lang, 1994). Under the assumption of stepwise migration from pioneer trees for further seed dispersal by means of dispersal agents, hazel could be potentially three times as fast as oak, which is not the case in the southern Alps. Thus, given the assumption of equal distance of refugia or local presence of low-density populations, the hypothesis of migrational lag is inadequate to explain the absence of hazel expansion during the Lateglacial. Hypothetically, however, it might be a determining factor for the earlier expansion of hazel north of the Alps, although the

observed time lag for oak’s expansion in the north does not fit with the dispersal mechanism.

Survival in the early stages of plant ontogeny might be more important. For example, *Corylus* seems to be more sensitive to drought than *Quercus petraea*. Higher water permeability of the husks of hazel nuts and their smaller embryo are suggested as the most likely explanations for lower germination rate of hazel (Kollmann and Schill, 1996). Moreover, germination rates in dry grassland sites are higher for *Quercus* than for *Corylus* seeds buried in the soil. On the surface, germination was low in both oak and hazel (Kollmann and Schill, 1996).

4.2.3. Competition among species under a given climate

Over most of its range today *Corylus avellana* is an understorey species (1–5 (20) m height) in deciduous and conifer forests (Hegi, 1981; Pignatti, 1982). Pure stands of *Corylus* may occur, apparently as the natural woodland cover, on some areas in western Britain and Ireland, as well as on some very exposed areas of the western coasts of the British Isles (Huntley, pers. comm.) and on scree (Hegi, 1981). In Piedmont pure stands usually occur on siliceous or carbonatic scree and on abandoned pastures and fields (Mondino et al., 1981). Its ecological behaviour in Central Europe shows indifference concerning soil moisture, soil acidity and lime content (Ellenberg et al., 1992). *Corylus* reaches peak abundance earlier during succession than do species that are normally components of the canopy, by which it is overtopped within <100 years (Huntley and Birks, 1983). During the early Holocene, however, *Corylus* pollen percentages remained high for several millennia both north and south of the Alps. We therefore infer that ordinary succession alone cannot explain the observed patterns.

4.2.4. Disturbances, especially fires

Long-term studies (Clark et al., 1989; Tinner et al., 1999) have shown a greater fire advantage for hazel than for oak. So too have recent observations in which *Corylus* increased after forest fires because it can sprout well after fire (Delarze et al., 1992). Hazel pollen production is enhanced when vegetation is opened by disturbance (Aaby, 1986; Bégeot, 1998). If the fire activity inferred from microcharcoal analysis was low during the Allerød, then it is likely that hazel was not able to expand in forested environments that included thermophilous taxa. Our data show (Fig. 7) that *Corylus* and *Pteridium* are significantly correlated with microcharcoal. Moreover, at both sites (Lago Piccolo di Avigliana and Lago di Origlio) *Pteridium* accompanies the hazel rise. We thus conclude that it is likely that forest fires supported the population spread of hazel, potentially contributing to maintain a high population density once the species had expanded.

Forest fires might have been set by Mesolithic people (Smith, 1970; Zoller, 1960b). If so, then the ubiquity of the hazel spread would suggest that Mesolithic people with similar strategies were everywhere in Europe at around the same time (~10,500 cal yr BP). In northern Europe the evidence for forest fires during the expansion of *Corylus* is often missing (Clark et al., 1989; Edwards, 1999; Beckmann, 2003). However, in central-west Germany a positive correlation between the number of charcoal particles and percentages of *Pteridium* spores was recorded during the early Holocene (Bos and Urz, 2003). Similarly, in the southern Netherlands *Pteridium* and *Corylus* also seem to appear together (Van Leeuwarden (1982), cited in Bos and Urz, 2003). Nevertheless, additional studies are needed to test the validity of this mechanism to other regions of northern and central Europe.

4.2.5. The possible role of climate

Competition disadvantages of hazel compared to oaks and other thermophilous trees may explain the absence of a hazel mass expansion during the Allerød in the southern Alps. However, they do not explain why the mass expansion of hazel occurred 2000–1500 years later than the expansion of oak and why hazel expanded at around the same age across the Alps, in central and northwestern Europe. Rudolph (1930) suggested that, in general, climatic triggers are the best explanation for synchronous changes in forest composition over wide areas. Although no radiocarbon dates were available at that time, he postulated that hazel expanded nearly synchronously over northern and central Europe. The study by Tallantire (2002) showed this assumption to hold in northern Europe. Our comparison between Southern Alpine and Northern Alpine sites confirms synchronicity for our study region.

The effects of climatic change might depend on differential ecological tolerances of oak and hazel. According to Huntley (1993), *Corylus* shows a greater overall climatic tolerance than either *Ulmus* or the north European *Quercus* species. It is more tolerant of seasonal drought, cold winters, and relatively cool summers than the other taxa and finally is also fire-tolerant (Huntley, 1993). If temperature would be the only relevant factor during the gradual Lateglacial and Holocene climatic warming, hazel would be expected to expand first, which was not the case in the southern Alps.

Surprisingly, parameters of climate tolerance for these species in spatially explicit models of vegetation dynamics, e.g. DiscForM (Lischke et al., 1998), are similar for the two genera. On the other hand, Fassl (1996) found marked differences in temperature limits between deciduous oak and *Corylus avellana* L. in Europe and Asia, showing a slightly greater tolerance of *Quercus robur* L. for cold winters. Its minimal temperature conditions for the coldest month lie at -15°C ,

while maximum temperature for the warmest month is at $+26^{\circ}\text{C}$ today. For *Corylus avellana* L., these values are -14 and $+31^{\circ}\text{C}$, respectively, showing the strong adaptation of the species to hot and dry summers (e.g. in Mesopotamia). Solantie (1983, in Tallantire, 2002) took into account the length of the growing season, obtaining a climatic limit for hazel at 163 days with mean air temperature above 5°C , whereas for oak the estimate gave 144 days.

This would imply that *Corylus* could not expand in the southern Alps either because winter temperatures or summer temperatures were too low. Indeed, winter insolation was at its minimum during the early Holocene (Figs. 6a and b), when hazel was successful and the inferred seasonality was at its maximum (COHMAP Members, 1988), thus falsifying the first hypothesis. Huntley (1993) suggested that the unique character of early Holocene climatic conditions, with high seasonality, possibly in combination with a higher fire frequency, might have sustained the high hazel abundance recorded in pollen diagrams across north-central Europe. However, neither Clark et al. (1989) nor Tinner and Lotter (2001) could detect a convincing correlation between their charcoal records and the high early Holocene abundance of *Corylus* in Central Europe. Therefore, Tinner and Lotter (2001) concluded that the correlation over hundreds of years between *Corylus* pollen values and oxygen isotopes provides direct evidence that the high hazel pollen abundance was caused by climatic conditions rather than other factors, such as human assistance and fire, which may have played a marginal role. In these studies, however, the Mediterranean region was not taken into account.

To develop and thus to influence significantly vegetation, forest fires depend on the availability of dry woody biomass, which in turn increases (seasonally) with dry climate. During the Last Glacial Interglacial Transition (LGIT, ca 14–9 ka ^{14}C yr BP), the general pattern of climatic changes recorded in the North Atlantic region (Eicher and Siegenthaler, 1976; Björck et al., 1998; Lowe, 2001; Yu and Eicher, 2001) is also reflected in the peri-Adriatic region (Asioli et al., 1999). Oxygen-isotope data from the GRIP ice-core show a gradual increase in $\delta^{18}\text{O}$ values, implying a gradual warming during the early Holocene, levelling-off around 9500 cal yr BP (Figs. 6a and b). The gradual nature of climate change in the early Holocene is also evidenced by the Cariaco Basin record, which shows that during the Preboreal the Intertropical Convergence Zone (ITCZ) shifted progressively to a northern position, reaching its northernmost position during the Holocene ‘thermal maximum’ (Haug et al., 2004).

Summer insolation gradually increased during the LGIT, reaching its maximum during the early Holocene around 11,000 cal yr BP, while winter insolation decreased symmetrically (Berger and Loutre, 1991) (Figs. 6a and b), thus increasing overall Northern Hemisphere seasonality.

Palaeoclimatic simulations indicate that around 11,000 cal yr BP the increased insolation caused summer temperatures to be higher than at present in Eurasia by 2–4 °C (COHMAP Members, 1988). Proxy records from the Central Alps show that treeline altitude was at its maximum after ~10,000 cal yr BP (Tinner and Theurillat, 2003), glacier activity was virtually absent since ~10,500 cal yr BP (Leemann and Niessen, 1994), and July air temperatures were higher than today after the end of the Younger Dryas to 8200 cal yr BP (Heiri et al., 2003a). Records in the Northern Hemisphere confirm that warmest summer temperatures occurred during the early Holocene. In northern Sweden, chironomid-based temperature reconstructions from three sites indicate maximum temperature for the early Holocene (Larocque and Hall, 2004). In southern-central Norway, grain-size and loss-on-ignition analyses showed that the ‘Erdalen Event’ (Dahl et al., 2002) was followed by a prolonged period (between ~10,200 and ~7500 cal yr BP) with no glaciers in the catchment (Lie et al., 2004). Sea-surface temperatures in the North Atlantic and Mediterranean Sea were at a maximum around 9000 years BP and decreased through the Holocene, as indicated by the alkenone method (Marchal et al., 2002). In northern British Columbia, Canada (Spooner et al., 2002) and in northeastern Siberia (Porinchu and Cwynar, 2002) chironomid-inferred summer temperatures show maximum temperatures between 9000 and 10,000 yr BP. Finally, a summary of selected Holocene temperature reconstructions shows that the highest summer temperatures occurred in the early Holocene and that the overall Holocene temperature decline was apparently a response to orbital forcing (declining boreal summer insolation) (Bradley, 2000).

We suggest that increased early Holocene seasonality with high summer temperatures and pronounced seasonal drought (Kutzbach and Webb, 1993) may have favoured the expansion of *Corylus* ~11,000–10,500 cal yr BP in our region. This was reinforced by increased forest-fire activity as a consequence of these dry weather conditions. The quasi-synchronicity of the hazel expansion north and south of the Alps might therefore be explained by drought stress (COHMAP Members, 1988) and higher fire frequency.

Corylus-pollen abundance increased possibly because warm temperatures and drought stress inhibited other thermophilous trees from growing on exposed slopes (see discussion in Tinner and Lotter, 2001). In comparison with sites in Central Europe, the hazel maximum in the southern Alps is much less pronounced or, as suggested by Zoller (1960a), completely absent. With a maximum of ca 20% in the south, *Corylus* pollen percentages attain less than half the percentage values reached north of the Alps (e.g. 55% at Lobsigensee (Ammann et al., 1996) and 60% at Soppensee (Lotter, 1999)). It might be that in the southern Alps a different species of *Quercus* was present than in the north,

possibly with higher resistance to drought (e.g. *Quercus cerris* or *Quercus pubescens*, which are more tolerant of seasonal drought) while oak populations in the north were more affected by those special climatic conditions.

Therefore, we suggest that Huntley’s (1993) climatic hypothesis might also apply to the southern Alpine region. Better drought-adapted evergreen trees, such as *Q. ilex* or *Q. suber* (Pignatti, 1982; Pigott and Pigott, 1993), on the other hand, might have been absent because of too low winter temperatures. In this respect, the unique character of the early Holocene palaeoenvironment accounted for the earlier population expansion of *Corylus avellana* than of *Quercus* as well as its relative abundance at this time north of the Alps. It also triggered the synchronous expansion of the shrub south of the Alps, where thermophilous trees had expanded ~2000 years before during a period with less pronounced drought events and lower fire frequencies. Thus the late expansion of hazel south of the Alps corroborates the explanation suggested by Huntley (1993) for northwestern and central Europe. In addition to climate, fire may have contributed to sustain hazel’s population establishment and maintenance.

5. Conclusion

In this study we show that central and northern European long-term plant sequences are not transferable to the southern Alpine area, where an inverse long-term succession of hazel and oak shows that as in other regions and as in previous interglacials *Quercus* expanded without a preceding hazel phase in the Holocene. We conclude that hazel could not expand its populations during the Allerød because trees taller than hazel were more competitive under the climatic conditions at that time. The delayed population expansion of hazel might have been sustained by openings in the vegetation as a consequence of drought and higher frequency of forest fires. The marked influence of fires on *Corylus* in the southern Alps is documented by our microscopic charcoal record as well as by the synchronous expansion of fire-adapted *Pteridium* in the pollen diagrams of Lago Piccolo di Avigliana and Lago di Origlio. It is not plausible that fires were set by Mesolithic hunters and gatherers since similar patterns of vegetation history were observed also during previous Interglacials (West, 1961; Wright, 1977; de Beaulieu and Reille, 1992a).

The evident quasi-synchronicity (~11,000–10,500 cal yr BP) of the hazel expansion north and south of the Alps might therefore be explained with a non-linear response of vegetation to inferred drought stress (COHMAP Members, 1988). This special palaeoenvironmental character of the early Holocene was mainly caused by the high summer insolation, which in turn increased summer temperatures and diminished moisture availability (COHMAP Members, 1988; Kutzbach

and Webb, 1993). In this respect, Huntley's (1993) hypothesis is supported by our palaeoenvironmental reconstruction in the southern Alpine region that offers a plausible explanation for the virtual absence of pure *Corylus* stands in the present vegetation.

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Appendix A

Locations (in decimal degrees), altitude (m a.s.l.), and references for sites used in Fig. 8.

Position		Altitude (m a.s.l.)	Site name	Reference
Lat °N	Long °E			
46.6458	7.54333	989	Aegelsee	Wegmüller and Lotter (1990)
47.2041	8.46666	429	Bibersee	Beckmann (2003)
45.7908	5.2833	410	Hières sur Amby	Clerc (1988)
46.718	8.068	1510	Hinterburgsee	Heiri et al. (2003b)
45.800	6.1833	445	Lac d'Annecy	David et al. (2001)
43.033	−0.0833	430	Lac de Lourdes	Reille and Andrieu (1995)
45.6847	7.76111	820	Lac de Villa	Brugiapaglia (1996)
42.5667	11.8500	355	Lagaccione	Magri (1999)
45.833	9.267	374	Lago del Segrino	Gobet et al. (2000)
41.7467	12.6733	293	Lago di Albano	Lowe et al. (1996)
45.7868	9.21427	260	Lago di Alserio	Wick (2000a)
45.7927	9.34318	226	Lago di Annone	Wick (1996)
45.052	7.38833	353	Lago di Avigliana Piccolo	This study
45.817	8.700	239	Lago di Biandronno	Schneider (1977)
45.8917	8.89	460	Lago di Ganna	Schneider and Tobolski (1985)
46.055	8.93833	416	Lago di Origlio	Tinner et al. (1999)
46.100	12.333	250	Lago di Revine	Wick (2000b)
42.328	12.170	510	Lago di Vico	Magri and Sadori (1999)
51.433	23.55	165	Lake Perespilno	Goslar et al. (1999)
46.750	14.350	548	Längsee	Schmidt et al. (1998)
47.032	7.299	514	Lobsigensee	Ammann (1989)
43.69	4.8	2	Marais des Baux	Andrieu-Ponel et al. (2000)
43.050	−0.0319	394	Monge	Reille and Andrieu (1995)
40.944	15.6083	656	Monticchio	(Allen et al. 2000)
50.418	8.735	143	Oppershofen 3	Bos (2001)
46.1583	10.1516	1350	Pian di Gembro	Pini (2002)
44.366	10.083	1350	Prato Spilla 'C'	Lowe (1992)
46.5667	6.1708	1040	Praz-Rodet	Mitchell et al. (2001)
47.0755	8.32555	419	Rotsee	Lotter (1988)
47.617	9.650	474	Schleinsee	Clark et al. (1989)
47.583	12.1667	664	Schwemm	Oeggl and Eicher (1989)
47.0883	8.07567	596	Soppensee	Lotter (1999)
49.150	14.700	412	Švarcenberk	Pokorný (2002)
41.8917	12.7597	44	Valle di Castiglione	Follieri et al. (1988)
44.853	14.389	10	Vransko Jezero	Schmidt et al. (2000)

References

- Aaby, B., 1986. Trees as anthropogenic indicators in regional pollen diagrams from eastern Denmark. In: Balkema, A.A. (Ed.), *Geological survey of Denmark*, Copenhagen.
- Aalbersberg, G., Litt, T., 1998. Multiproxy climate reconstruction for the Eemian and Early Weichselian. *Journal of Quaternary Science* 13, 367–390.
- Allen, J.R.M., Watts, W.A., Huntley, B., 2000. Weichselian palynostratigraphy, palaeovegetation and palaeoenvironment; the record from Lago Grande di Monticchio, southern Italy. *Quaternary International* 73/74, 91–110.
- Ammann, B., 1989. Late-quaternary palynology at Lobsigensee. *Dissertationes Botanicae* 137, 157.
- Ammann, B., Tobolski, K., 1983. Vegetational development during the Late-Würm at Lobsigensee (Swiss Plateau). *Studies in the late Quaternary of Lobsigensee* 1. *Revue de Paléobiologie* 2, 163–180.
- Ammann, B., Chaix, L., Eicher, U., Elias, S.A., Gaillard, M.-J., Hofmann, W., Siegenthaler, U., Tobolski, K., Wilkinson, B., 1983. Vegetation, insects, molluscs and stable isotopes from late Würm deposits at Lobsigensee (Swiss Plateau). *Studies in the late Quaternary of Lobsigensee* 7. *Revue de Paléobiologie* 2, 221–227.
- Ammann, B., Gaillard, M.-J., Lotter, A.F., 1996. Switzerland. In: Berglund, B.E., Ralska-Jasiewiczowa, M., Wright, H.E. (Eds.), *Palaeoecological events during the Last 15,000 Years: Regional Syntheses of Palaeoecological Studies of Lakes and Mires in Europe*. Wiley, New York.
- Ammann, B., Birks, H.J.B., Brooks, S.J., Eicher, U., von Grafenstein, U., Hofmann, W., Lemdahl, G., Schwander, J., Tobolski, K., Wick, L., 2000. Quantification of biotic responses to rapid climatic changes around the Younger Dryas—a synthesis. *Palaeogeography Palaeoclimatology Palaeoecology* 159, 313–347.
- Andrieu-Ponel, V., Ponel, P., Jull, A.J.T., de Beaulieu, J.L., Bruneton, H., Leveau, P., 2000. Towards the reconstruction of the Holocene vegetation history of Lower Provence: two new pollen profiles from Marais des Baux. *Vegetation History and Archaeobotany* 9, 71–84.
- Asioli, A., Trincardi, F., Lowe, J.J., Oldfield, F., 1999. Short-term climate changes during the Last Glacial-Holocene transition: comparison between Mediterranean records and the GRIP event stratigraphy. *Journal of Quaternary Science* 14, 373–381.
- Baales, M., Jöris, O., Street, M., Bittmann, F., Wiethold, J., 2002. Impact of the Late Glacial Eruption of the Laacher See Volcano, Central Rhineland, Germany. *Quaternary Research* 58, 273–288.
- Bahrenberg, G., Giesse, E., Nipper, J., 1992. *Statistische Methoden in der Geographie*, vol. 2. Teubner, Stuttgart.
- Beckmann, M., 2003. Pollenanalytische Untersuchungen der Zeit der Jäger und Sammler und der ersten Bauern an zwei Lokalitäten des Zentralen Schweizer Mittellandes: Umwelt und erste Eingriffe des Menschen in die Vegetation vom Paläolithikum bis zum Jungneolithikum. *Dissertationes Botanicae* 390, 1–186.
- Bégeot, C., 1998. Pollen behaviour of Hazelnut (*Corylus avellana*), an indicator of human impacts? One example along a transect in Southern French Jura. *Acta Botanica Gallica* 145, 271–279.
- Bennett, K.D., 1988. Post-glacial vegetation history: Ecological considerations. In: Huntley, B., Webb, III, T. (Eds.), *Vegetation History*. Kluwer Academic Publishers, Dordrecht.
- Bennett, K.D., 1996. Determination of the number of zones in a biostratigraphical sequence. *New Phytologist* 132, 155–170.
- Bennett, K.D., Tzedakis, P.C., Willis, K.J., 1991. Quaternary refugia of North European trees. *Journal of Biogeography* 18, 103–115.
- Berger, A., Loutre, M.F., 1991. Insolation values for the climate of the last 10 million years. *Quaternary Science Reviews* 10, 297–317.
- Beug, H.-J., 1975. Changes of climate and vegetation belts in the mountains of Mediterranean Europe during the Holocene. *Bulletin of Geology* 19, 101–110.
- Biancotti, A., Bellardone, G.S.B., Cagnazzi, B., Giacomelli, L., Marchisio, C., 1998. Regional distribution of rainfalls and temperatures. *Climatological studies in Piedmont* 1, 1–80.
- Birks, H.J.B., 1986. Late-Quaternary biotic changes in terrestrial and lacustrine environments, with particular reference to north-west Europe. In: Berglund, B.E. (Ed.), *Handbook of Holocene Palaeoecology and Palaeohydrology*. Wiley, New York.
- Birks, H.H., 1993a. The importance of plant macrofossils in late-glacial climatic reconstructions—an example from Western Norway. *Quaternary Science Reviews* 12, 719–726.
- Birks, H.J.B., 1993b. Precision, concepts, controversies: Alan Smith's contribution to vegetational history and palaeoecology. In: Chambers, F.M. (Ed.), *Climate Change and Human Impact on the Landscape*. Chapman & Hall, London.
- Birks, H.J.B., 1998. Numerical tools in palaeolimnology—progress, potentialities, and problems. *Journal of Paleolimnology* 20, 307–332.
- Birks, H.H., Birks, H.J.B., 2000. Future uses of pollen analysis must include plant macrofossils. *Journal of Biogeography* 27, 31–35.
- Birks, H.J.B., Line, J.M., 1993. Glacial refugia of European trees—a matter of chance? *Dissertationes Botanicae* 196, 283–291.
- Björck, S., Walker, M.J.C., Cwynar, L.C., Johnsen, S., Knudsen, K.-L., Lowe, J.J., Wohlfahrt, B., INTIMATE Members, 1998. An event stratigraphy for the Last Termination in the North Atlantic region based on the Greenland ice-core record: a proposal by the INTIMATE group. *Journal of Quaternary Science* 13, 283–292.
- Blockley, S.P.E., Pyne-O'Donnell, S.D.F., Lowe, J.J., Matthews, I.P., Pollard, A.M., Turney, C.S.M., Molyneux, E.G., in press. A new and less destructive laboratory procedure for the physical separation of distal glass tephra shards from sediments. *Quaternary Science Reviews*: doi:10.1016/j.quascirev.2004.12.008.
- Bonn, S., Poschlod, P., 1998. *Ausbreitungsbiologie der Pflanzen: Grundlagen und kulturhistorische Aspekte*. Quelle & Meyer Verlag, Wiesbaden.
- Bos, J.A.A., 2001. Lateglacial and Early Holocene vegetation history of the northern Wetterau and the Amöneburger Basin (Hessen), central-west Germany. *Review of Palaeobotany and Palynology* 115, 177–212.
- Bos, J.A.A., Urz, R., 2003. Late Glacial and early Holocene environment in the middle Lahn river valley (Hessen, central-west Germany) and the local impact of early Mesolithic people—pollen and macrofossil evidence. *Vegetation History and Archaeobotany* 12, 19–36.
- Bradley, R.S., 2000. Past global changes and their significance for the future. *Quaternary Science Reviews* 19, 391–402.
- Brugiapaglia, E., 1996. *Dynamique de la végétation Tardiglaciaire et Holocene dans les Alpes Italiennes Nord-Occidentales*. PhD Thesis, Université de Saint-Jerome, Marseille.
- Carraro, F., Cadoppi, P., Castelletto, M., Sacchi, R., Baggio, P., Giraud, V., Bellardone, G., 2002. Note Illustrative della Carta Geologica d'Italia alla scala 1:50 000, Foglio 154—Susa. Regione Piemonte, Torino.
- Clark, J.S., 1998. Why trees migrate so fast: confronting theory with dispersal biology and the paleorecord. *American Naturalist* 152, 204–224.
- Clark, J.S., Merkt, J., Müller, H., 1989. Post-glacial fire, vegetation, and human history on the northern alpine forelands, south western Germany. *Journal of Ecology* 77, 897–925.
- Clerc, J., 1988. *Recherches pollenanalytiques sur la paléo-écologie Tardiglaciaire et Holocene du Bas-Dauphiné*. Ph.D. Thesis, Université St. Jérôme, Marseille.
- COHMAP Members, 1988. Climatic changes of the last 18,000 years: observations and model simulations. *Science* 241, 1043–1052.
- Dahl, S.O., Nesje, A., Lie, Ø., Fjorheim, K., Matthews, J.A., 2002. Timing, equilibrium-line altitudes and climatic implications of two

- early Holocene glacier readvances during the Erdalen Event at Jostedalsgreen, western Norway. *The Holocene* 12, 17–25.
- Dansgaard, W., Johnson, S.J., Clausen, H.B., Dahl-Jensen, D., Gundestrup, N.S., Hammer, C.U., Hvidberg, C.S., Steffensen, J.P., Sveinbjörnsdóttir, A.E., Jouzel, J., Bond, G., 1993. Evidence for general instability of past climate from a 250-kyr ice-core record. *Nature* 364, 218–220.
- David, F., Farjanel, G., Jolly, M.P., 2001. Palyno- and chronostratigraphy of a long sequence from Lac d'Annecy (northern outer Alps, France). *Journal of Paleolimnology* 25, 259–269.
- Davis, J.C., 2002. *Statistics and Data Analysis in Geology*. Wiley, New York.
- de Beaulieu, J.L., Reille, M., 1992a. The last climatic cycle at La-Grande Pile, Vosges, France. a New Pollen Profile. *Quaternary Science Reviews* 11, 431–438.
- de Beaulieu, J.L., Reille, M., 1992b. Long Pleistocene pollen sequences from the Velay Plateau (Massif Central, France). *Vegetation History and Archaeobotany* 1, 233–242.
- Delarze, R., Calderari, D., Hainard, P., 1992. Effects of fire on forest dynamics in southern Switzerland. *Journal of Vegetation Science* 3, 55–60.
- Edwards, K.J., 1999. Palynology and people: observations on the British record. *Quaternary Proceedings* 7, 531–544.
- Efron, B., Tibshirani, R.J., 1991. Statistical data analysis in the computer age. *Science* 253, 390–395.
- Eicher, U., Siegenthaler, U., 1976. Palynological and oxygen isotope investigations on Late Glacial sediment cores from Swiss lakes. *Boreas* 5, 109–117.
- Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W., Paulissen, D., 1992. Indicator values of plants in Central Europe. *Scripta Geobotanica* 18, 1–258.
- Fassl, K., 1996. Die Bewertung von Zeigerarten in europäischen Pollendiagrammen für die Rekonstruktion des Klimas im Holozän. In: Frenzel, B. (Ed.), *Paläoklimaforschung*. Gustav Fischer Verlag.
- Field, M.H., Huntley, B., Müller, H., 1994. Eemian climate fluctuations observed in a European pollen record. *Nature* 371, 779–783.
- Fineschi, S., Turchini, D., Grossoni, P., Petit, R.J., Vendramin, G.G., 2002. Chloroplast DNA variation of white oaks in Italy. *Forest Ecology and Management* 156, 103–114.
- Finsinger, W., Tinner, W., 2005. Minimum count sums for charcoal-concentration estimates in pollen slides: reliability and potential errors. *The Holocene* 15, 293–297.
- Firbas, F., 1949. Spät- und nacheiszeitliche Waldgeschichte Mitteleuropas nördlich der Alpen, I. Gustav Fischer, Jena.
- Follieri, M., Magri, D., Sadori, L., 1988. 250,000-year pollen record from Valle di Castiglione (Roma). *Pollen et Spores* 30, 329–356.
- Friedrich, M., Kromer, B., Kaiser, K.F., Spurk, M., Hugen, K.A., Johnsen, S.J., 2001. High-resolution climate signals in the Bølling-Allerød Interstadial (Greenland Interstadial 1) as reflected in European tree-ring chronologies compared to marine varves and ice-core records. *Quaternary Science Reviews* 20, 1223–1232.
- Gobet, E., Tinner, W., Hubschmid, P., Jansen, I., Wehrli, M., Ammann, B., Wick, L., 2000. Influence of human impact and bedrock differences on the vegetational history of the Insubrian Southern Alps. *Vegetation History and Archaeobotany* 9, 175–187.
- Goslar, T., Balaga, K., Arnold, M., Tisnerat, N., Starnawska, E., Kuzniarski, M., Chrost, L., Walański, A., Wieckowski, K., 1999. Climate-related variations in the composition of the Late Glacial and early Holocene sediments of Lake Perespilno (eastern Poland). *Quaternary Science Reviews* 18, 899–911.
- Green, D.G., 1981. Time series and postglacial forest ecology. *Quaternary Research* 15, 265–277.
- Haug, G.H., Hugen, K.A., Sigman, D.M., Peterson, L.C., Röhl, U., 2004. Southward migration of the intertropical convergence zone through the Holocene. *Science* 293, 1304–1308.
- Hegi, G., 1981. *Illustrierte Flora von Mitteleuropa*. Paul Parey Verlag, Berlin.
- Heiri, O., Lotter, A.F., Lemcke, G., 2001. Loss on ignition as a method for estimating organic and carbonate content in sediments: reproducibility and comparability of results. *Journal of Paleolimnology* 25, 101–110.
- Heiri, O., Lotter, A.F., Hausmann, S., Kienast, F., 2003a. A chironomid-based Holocene summer air temperature reconstruction from the Swiss Alps. *The Holocene* 13, 477–484.
- Heiri, O., Wick, L., van Leeuwen, J.F.N., van der Knaap, W.O., Lotter, A.F., 2003b. Holocene tree immigration and the chironomid fauna of a small Swiss subalpine lake (Hinterburgsee, 1515 m asl). *Palaeogeography Palaeoclimatology Palaeoecology* 189, 35–53.
- Hewitt, G.M., 1999. Post-glacial re-colonization of European biota. *Biological Journal of the Linnean Society* 68, 87–112.
- Huntley, B., 1993. Rapid early Holocene migration and high abundance of hazel (*Corylus avellana* L.): alternative hypotheses. In: Chambers, F.M. (Ed.), *Climate change and human impact on the landscape*. Chapman & Hall, London.
- Huntley, B., Birks, H.J.B., 1983. *An Atlas of Past and Present Pollen Maps for Europe: 0–13,000 years ago*. Cambridge University Press, Cambridge.
- Iversen, J., 1960. Problems of the Early Post-Glacial forest development in Denmark. *Geological Survey of Denmark. IV Series* 4, 5–32.
- Johnsen, S.J., Clausen, H.B., Dansgaard, W., Fuhrer, K., Gundestrup, N., Hammer, C.U., Iversen, P., Jouzel, J., Stauffer, B., Steffensen, J.P., 1992. Irregular glacial interstadials recorded in a New Greenland Ice Core. *Nature* 359, 311–313.
- Kollmann, J., Schill, H.P., 1996. Spatial patterns of dispersal, seed predation and germination during colonization of abandoned grassland by *Quercus petraea* and *Corylus avellana*. *Vegetatio* 125, 193–205.
- Kühl, N., Litt, T., 2003. Quantitative time series reconstruction of Eemian temperature at three European sites using pollen data. *Vegetation History and Archaeobotany* 12, 205–214.
- Kutzbach, J.E., Webb III, T., 1993. Conceptual basis for understanding late-Quaternary climates. In: Wright, H.E.J., Kutzbach, J.E., Webb III, T., Ruddiman, W.F., Street-Perrott, F.A., Bartlein, P.J. (Eds.), *Global Climates since the Last Glacial Maximum*. University of Minnesota Press, Minneapolis.
- Lang, G., 1994. *Quartäre Vegetationsgeschichte Europas. Methoden und Ergebnisse*. G. Fischer, Jena.
- Larocque, I., Hall, R.I., 2004. Holocene temperature estimates and chironomid community composition in the Abisko Valley, northern Sweden. *Quaternary Science Reviews* 23, 2453–2465.
- Leemann, A., Niessen, F., 1994. Holocene glacial activity and climatic variations in the Swiss Alps: reconstructing a continuous record from proglacial lake sediments. *The Holocene* 4, 259–268.
- Lie, O., Dahl, S.O., Nesje, A., Matthews, J.A., Sandvold, S., 2004. Holocene fluctuations of a polythermal glacier in high-alpine eastern Jotunheimen, central-southern Norway. *Quaternary Science Reviews* 23, 1925–1945.
- Lischke, H., Löffler, T.J., Fischlin, A., 1998. Aggregation of individual trees and patches in forest succession models: capturing variability with height structured, random, spatial distributions. *Theoretical Population Biology* 54, 213–226.
- Lotter, A.F., 1988. *Paläoökologische und Paläolimnologische Studie des Rotsees bei Luzern*. *Dissertationes Botanicae* 124, 1–187.
- Lotter, A.F., 1999. Late-Glacial and Holocene vegetation history and dynamics as shown by pollen and plant macrofossil analyses in annually laminated sediments from Soppensee, central Switzerland. *Vegetation History and Archaeobotany* 8, 165–184.

- Lowe, J.J., 1992. Lateglacial and early Holocene lake sediments from the northern Apennines, Italy—pollen stratigraphy and radiocarbon dating. *Boreas* 21, 193–208.
- Lowe, J.J., 2001. Climatic oscillations during the Last Glacial Cycle—Nature, causes and the case for synchronous effects. *Proceedings of the Royal Irish Academy* 101B, 19–33.
- Lowe, J.J., Accorsi, C.A., Bandini Mazzanti, M., Bishop, A., van der Kaars, S., Forlani, L., Mercuri, A.M., Rivalenti, C., Torri, P., Watson, C.S., 1996. Pollen stratigraphy of sediment sequences from lakes Albano and Nemi (near Rome) and from the central Adriatic, spanning the interval from oxygen isotope Stage 2 to the present day. *Memorie dell'Istituto Italiano di Idrobiologia* 55, 71–98.
- MacArthur, R.H., 1957. On the relative abundance of bird species. *Proceedings of the National Academy of Sciences of the United States of America* 43, 293–295.
- Magri, D., 1999. Late Quaternary vegetation history at Lagaccione near Lago di Bolsena (central Italy). *Review of Palaeobotany and Palynology* 106, 171–208.
- Magri, D., Sadori, L., 1999. Late Pleistocene and Holocene pollen stratigraphy at Lago di Vico, central Italy. *Vegetation History and Archaeobotany* 8, 247–260.
- Mangerud, J., Andersen, S.T., Berglund, B.E., Donner, J.J., 1974. Quaternary stratigraphy of Norden, a proposal for terminology and classification. *Boreas* 3, 109–128.
- Marchal, O., Cacho, I., Stocker, T.F., Grimalt, J.O., Calvo, E., Martrat, B., Shackleton, N., Vautravers, M., Cortijo, E., van Kreveld, S., Andersson, C., Koc, N., Chapman, M., Saffi, L., Duplessy, J.C., Sarnthein, M., Turon, J.L., Duprat, J., Jansen, E., 2002. Apparent long-term cooling of the sea surface in the northeast Atlantic and Mediterranean during the Holocene. *Quaternary Science Reviews* 21, 455–483.
- Matyás, G., Sperisen, C., 2001. Chloroplast DNA polymorphisms provide evidence for postglacial re-colonisation of oaks (*Quercus* spp.) across the Swiss Alps. *Theoretical and Applied Genetics* 102, 12–20.
- Merkt, J., Streif, H., 1970. Stechrohr-Bohrgeräte für limnische und marine Lockersedimente. *Geologische Jahrbücher* 88, 137–148.
- Mitchell, E.A.D., van der Knaap, W.O., van Leeuwen, J.F.N., Buttler, A., Warner, B.G., Gobat, J.M., 2001. The palaeoecological history of the Praz-Rodet bog (Swiss Jura) based on pollen, plant macrofossils and testate amoebae (Protozoa). *The Holocene* 11, 65–80.
- Mondino, G.P., De Biaggi, E., Grisoni, F., Dalmasso, G., Della Beffa, G., Salandini, R., 1981. I boschi e la Carta Forestale del Piemonte. Guida Editori, Napoli.
- Moore, P.D., Webb, J.A., 1978. *An illustrated Guide to Pollen Analysis*. Hodder and Stoughton, London.
- Oeggl, K., Eicher, U., 1989. Pollen-isotope and oxygen-isotope analyses of lateglacial and postglacial sediments from the Schwemm raised bog near Walchsee in Tirol, Austria. *Boreas* 18, 245–253.
- Palmé, A.E., Vendramin, G.G., 2002. Chloroplast DNA variation, postglacial recolonization and hybridization in hazel, *Corylus avellana*. *Molecular Ecology* 11, 1769–1779.
- Petit, R.J., Brewer, S., Bordacs, S., Burg, K., Cheddadi, R., Coart, E., Cottrell, J., Csaikl, U.M., van Dam, B., Deans, J.D., Espinel, S., Fineschi, S., Finkeldey, R., Glaz, I., Goicoechea, P.G., Jensen, J.S., König, A.O., Lowe, A.J., Madsen, S.F., Matyas, G., Munro, R.C., Popescu, F., Slade, D., Tabbener, H., de Vries, S.G.M., Ziegenhagen, B., de Beaulieu, J.L., Kremer, A., 2002. Identification of refugia and post-glacial colonisation routes of European white oaks based on chloroplast DNA and fossil pollen evidence. *Forest Ecology and Management* 156, 49–74.
- Petrucchi, F., Bortolami, G.C., Dal Piaz, G.V., 1970. Ricerche sull'Anfiteatro morenico di Rivoli-Avigliana (Provincia di Torino) e sul suo substrato cristallino. *Memorie della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano* 18, 95–168.
- Pignatti, S., 1982. *Flora d'Italia*. Edagricole, Bologna.
- Pigott, C.D., Pigott, S., 1993. Water as a determinant of the distribution of trees at the boundary of the Mediterranean zone. *Journal of Ecology* 81, 557–566.
- Pini, R., 2002. A high-resolution Late-Glacial–Holocene pollen diagram from Pian di Gembro (Central Alps, Northern Italy). *Vegetation History and Archaeobotany* 11, 251–262.
- Pinna, M., 1977. *Climatologia. Manuali di Geografia*, vol. 5. UTET, Torino.
- Pokorný, P., 2002. A high-resolution record of Late-Glacial and Early Holocene climatic and environmental change in the Czech Republic. *Quaternary International* 91, 101–122.
- Porinchu, D.F., Cwynar, L.C., 2002. Late-Quaternary history of midge communities and climate from a tundra site near the lower Lena River, Northeast Siberia. *Journal of Paleolimnology* 27, 59–69.
- Punt, W., 1976. *Northwest European Pollen Flora*, vol. 1. Elsevier, Amsterdam.
- Punt, W., Blackmore, S., 1991. *Northwest European Pollen Flora*, vol. 6. Elsevier, Amsterdam.
- Punt, W., Clarke, G.C.S., 1980. *Northwest European Pollen Flora*, vol. 2. Elsevier, Amsterdam.
- Punt, W., Clarke, G.C.S., 1981. *Northwest European Pollen Flora*, vol. 3. Elsevier, Amsterdam.
- Punt, W., Clarke, G.C.S., 1984. *Northwest European Pollen Flora*, vol. 4. Elsevier, Amsterdam.
- Punt, W., Blackmore, S., Clarck, G.C.S., 1988. *Northwest European Pollen Flora*, vol. 5. Elsevier, Amsterdam.
- Reille, M., 1992. *Pollen et spores d'Europe et d'Afrique du nord*. Laboratoire de Botanique Historique et Palynologie, Marseille.
- Reille, M., 1995. *Pollen et Spores d'Europe et d'Afrique du Nord—Supplement 1*. Laboratoire de Botanique Historique et Palynologie, Marseille.
- Reille, M., Andrieu, V., 1995. The late Pleistocene and Holocene in the Lourdes Basin, Western Pyrénées, France: new pollen analytical and chronological data. *Vegetation History and Archaeobotany* 4, 1–21.
- Rudolph, K., 1930. *Grundzüge der nacheiszeitlichen Waldgeschichte Mitteleuropas*. Beihefte zum Botanischen Centralblatt 47, 111–176.
- Sacco, F., 1887. L'anfiteatro morenico di Rivoli: studio del Dott. Federico Sacco. *Bollettino del Reale Comitato Geologico d'Italia* 8, 141–180.
- Schmidt, R., Wunsam, S., Brosch, U., Fott, J., Lami, A., Löffler, H., Marchetto, A., Müller, H.W., Prazáková, M., Schwaighofer, B., 1998. Late and Post-Glacial history of meromictic Längsee (Austria), in respect to climate change and anthropogenic impact. *Aquatic Sciences* 60, 56–88.
- Schmidt, R., Müller, J., Drescher-Schneider, R., Krisai, R., Szerocynska, K., Baric, A., 2000. Changes in lake level and trophy at Lake Vrana, at large karstic lake on the Island of Cres (Croatia), with respect to palaeoclimate and anthropogenic impacts during the last approx. 16,000 yrs. *Journal of Limnology* 59, 113–130.
- Schneider, R., 1977. Pollenanalytische Untersuchungen zur Kenntnis der spät- und postglazialen Vegetationsgeschichte am Südrand der Alpen zwischen Turin und Varese (Italien). *Botanische Jahrbücher für Systematik* 100, 26–109.
- Schneider, R., 1985. Palynological research in the southern and southeastern Alps between Torino and Trieste. *Dissertationes Botanicae* 87, 83–103.
- Schneider, R., Tobolski, K., 1985. Lago di Ganna—Late-Glacial and Holocene environments of a lake in the Southern Alps. *Dissertationes Botanicae* 87, 229–271.

- Smith, A.G., 1970. The influence of Mesolithic and Neolithic man on British vegetation: a discussion. In: Walker, D., West, R.G. (Eds.), *Studies in the Vegetational History of the British Isles*. Cambridge University Press, Cambridge.
- Spooner, I.S., Mazzocchi, D., Osborn, G., Gilbert, R., Larocque, I., 2002. A multi-proxy holocene record of environmental change from the sediments of Skinny Lake, Iskut region, northern British Columbia, Canada. *Journal of Paleolimnology* 28, 419–431.
- Tallantire, P.A., 2002. The early Holocene spread of hazel (*Corylus avellana* L.) in Europe north and west of the Alps: an ecological hypothesis. *The Holocene* 12, 81–96.
- Tinner, W., Hu, F.S., 2003. Size parameters, size-class distribution and area-number relationship of microscopic charcoal: relevance for fire reconstruction. *The Holocene* 13, 499–505.
- Tinner, W., Lotter, A.F., 2001. Central European vegetation response to abrupt climate change at 8.2 ka. *Geology* 29, 551–554.
- Tinner, W., Theurillat, J.-P., 2003. Uppermost limit, extent, and fluctuations of the timberline and treeline ecotone in the Swiss Central Alps during the past 11,500 years. *Arctic, Antarctic, and Alpine Research* 35, 158–169.
- Tinner, W., Hubschmid, P., Wehrli, M., Ammann, B., Conedera, M., 1999. Long-term forest fire ecology and dynamics in southern Switzerland. *Journal of Ecology* 87, 273–289.
- Tinner, W., Conedera, M., Gobet, E., Hubschmid, P., Wehrli, M., Ammann, B., 2000. A palaeoecological attempt to classify fire sensitivity of trees in the southern Alps. *The Holocene* 10, 565–574.
- Tobolski, K., Ammann, B., 2000. Macrofossils as records of plant responses to rapid Late Glacial climatic changes at three sites in the Swiss Alps. *Palaeogeography Palaeoclimatology Palaeoecology* 159, 251–259.
- Tomlinson, P., 1985. An aid to the identification of fossil buds, bud-scales and catkin-bracts of British trees and shrubs. *Circaea* 3, 45–130.
- Tosco, U., 1975. Carta della vegetazione dell'Anfiteatro morenico di Rivoli (Torino, Basse Alpi Cozie e Graie). *Documents de Cartographie Ecologique* 16, 97–112.
- Trautmann, W., 1953. Zur Unterscheidung fossiler Spaltöffnungen der mitteleuropäischen Coniferen. *Flora* 140, 523–533.
- van den Bogaard, P., Schmincke, H.-U., 1985. Laacher See Tephra: a widespread isochronous late Quaternary tephra layer in central and northern Europe. *Geological Society of America Bulletin* 96, 1554–1571.
- Vander Wall, S.B., 2001. The evolutionary ecology of nut dispersal. *Botanical Review* 67, 74–117.
- Webb III, T., 1986. Is vegetation in equilibrium with climate? How to interpret late-Quaternary pollen data. *Vegetatio* 67, 75–91.
- Wegmüller, S., Lotter, A.F., 1990. Palynostratigraphische Untersuchungen zur spät- und postglazialen Vegetationsgeschichte der nordwestlichen Kalkvoralpen. *Botanica Helvetica* 100, 37–73.
- Weninger, B., Jöris, O., Danzeglocke, U., 2003. CalPal. Radiocarbon Laboratory, Köln.
- West, R.G., 1961. Interglacial and interstadial vegetation in England. *Proceedings of the Linnean Society of London* 172, 81–89.
- Wick, L., 1996. Late-Glacial and early Holocene palaeoenvironments in Brianza, northern Italy. *Il Quaternario*, 653–660.
- Wick, L., 2000a. Lago di Alserio. In: Wick, L. (Ed.), XXIV. Moorexkursion—Exkursion Guide, Southern Alps. Institute of Plant Sciences, University of Bern, pp. 29–31.
- Wick, L., 2000b. Lago di Revine—Late Glacial. In: Wick, L. (Ed.), XXIV. Moorexkursion—Exkursion Guide, Southern Alps. Institute of Plant Sciences, University of Bern, pp. 99–102.
- Wohlfahrt, B., Skog, G., Possnert, G., Holmquist, B., 1998. Pitfalls in the AMS radiocarbon-dating of terrestrial macrofossils. *Journal of Quaternary Science* 13, 137–145.
- Wright Jr., H.E., 1977. Quaternary vegetation history—some comparison between Europe and America. *Annual Reviews of Earth and Planetary Sciences* 5, 123–158.
- Yu, Z., Eicher, U., 2001. Three Amphi-Atlantic century-scale cold events during the Bolling-Allerod warm period. *Géographie Physique et Quaternaire* 55, 171–179.
- Zoller, H., 1960a. Die wärmezeitliche Verbreitung von Haselstrauch, Eichenmischwald, Fichte und Weisstanne in den Alpenländern. *Bauhinia* 1, 189–207.
- Zoller, H., 1960b. Pollenanalytische Untersuchungen zur Vegetationsgeschichte der insubrischen Schweiz. *Denkschrift der Schweizerischen Naturforschenden Gesellschaft* 83, 45–156.