Uppermost Limit, Extent, and Fluctuations of the Timberline and Treeline Ecocline in the Swiss Central Alps during the Past 11,500 Years

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Abstract
Pollen and macrofossils were analyzed at two sites above today’s treeline (or tree limit) in the Swiss Central Alps (Gouillé Loéré, 2503 m a.s.l., and Lengi Egga, 2557 m a.s.l.) to test two contrasting hypotheses about the natural formation of timberline (the upper limit of closed forest) in the Alps. Our results revealed that Pinus cembra–Larix decidua forests near timberline were rather closed between 9000 and 2500 B.C. (9600–4000 14C yr BP), when timberline fluctuations occurred within a belt 100–150 m above today’s tree limit. The treeline ecocline above timberline was characterized by the mixed occurrence of tree, shrub, dwarf-shrub, and herbaceous species, but it did not encompass more than 100–150 altitudinal meters. The uppermost limit reached by timberline and treeline during the Holocene was ca. 2420 and 2530 m, respectively, i.e., about 120 to 180 m higher than today. Between 3500 and 2500 B.C. (4700–4000 14C yr BP) timberline progressively sank by about 300 m, while treeline was lowered only ca. 100 m. This change led to an enlargement of the treeline-ecocline belt (by ca. 300 m) after 2500 B.C. (4000 14C yr BP). Above the treeline ecocline, natural meadows dominated by dwarf shrubs (e.g., Salix herbacea) and herbaceous species (e.g., Helianthemum, Taraxacum, Potentilla, Leontodon t., Cerastium alpinum t., Cirsium spinosissimum, Silene exscapa t., and Saxifraga stellaris) have been present since at least 11,000 cal yr ago. In these meadows tree and tall shrub species (>0.5 m) never played a major role. These results support the conventional hypothesis of a narrow ecocline with rather sharp upper timberline and treeline boundaries and imply that today’s treeless alpine communities in the Alps are close to a natural stage. Pollen (percentages and influx), stomata, and charcoal data may be useful for determining whether or not a site was treeless. Nevertheless, a reliable and detailed record of past local vegetation near and above timberline is best achieved through the inclusion of macrofossil analysis.

Introduction
The treeline ecocline is a climatically sensitive transitional zone between closed forests (timberline) and alpine communities characterized by the mixed occurrence of tree, shrub, and herbaceous species, although woody species normally prevail (for the distinction between ecocline and ecotone see, e.g., van der Maarel, 1976). The elevation of the upper boundary reached by tree species in the Alps during the Holocene has recently become a debated topic in alpine ecology and paleoecology (e.g., Theurillat et al., 1998). Conventionally it is assumed that on rather undisturbed slopes tree species formed an upper timberline, separated from alpine vegetation by a narrow treeline ecocline (e.g., Landolt, 1992; Ellenberg, 1996) about 100 (~200) m wide (Ozenda, 1988). According to this hypothesis, herbaceous and dwarf-shrub species are presumed to have formed natural alpine meadows above the treeline ecocline throughout the Holocene (e.g., Lang, 1994). In this alpine belt, tree and tall (>0.5 m) shrub species were uncommon and occurred only in favorable microhabitats (e.g., sheltered by warmed rocks on steep slopes). Most paleoecological studies indicate that the upper treeline never oscillated more than ±100 m from today’s position (Patzelt, 1977; Burga and Perret, 1998, 2001; Haas et al., 1998). Therefore, alpine treeless meadows in the Alps are thought to be natural and more than 10,000 cal yr old.

New charcoal-analytical studies suggest a different scenario. According to Thinon and Talon (1998), Pinus cembra occurred rather densely in the alpine belt of the southern French Alps up to 2900 m a.s.l. Carcailliet et al. (1998) proposed that tree species occurred at least 300 m above today’s tree limit in the Vanoise massif (French western Alps) and postulated that an expanded treeline ecocline (at least 300 altitudinal meters) existed with a mixture of isolated trees or tree groups (mainly Pinus cembra, the Swiss stone pine), shrubs, and herbaceous species on well-drained soils. According to Carcailliet et al. (1998), such a belt has never been described in the Alps by modern ecologists, and the authors therefore proposed that fire and grazing pressure have destroyed it, converting it into the modern treeless alpine meadows approximately 3000 yr ago. Their estimates of the maximum altitude reached by trees is at least 200 m higher than those obtained by palynology, and if compared with the time before 3000 yr BP the modern treeline appears depressed by >300 m according to anthracology (charcoal analysis), but only about 100 m according to palynology (see Carcailliet et al., 1998). Thus these authors questioned the results of palynology and emphasized that vegetative reproduction of woody species may be dominant above timberline. Their interpretation is supported by findings of charred tree remains in the southern French Alps at very high altitudes (2919 m a.s.l.), ca. 200–500 m above today’s tree limit (Talon et al., 1998; Thinon and Talon, 1998).

On the basis of pollen and macrofossil data, other authors (e.g., Lang and Tobolski, 1985; Ponel et al., 1992; Tesserit et al., 1993; Tinner et al., 1996) working in mountain areas with vegetation formed by different belts showed that conventional pollen analysis (percentages) alone may be insufficient for reliable reconstructions of timberline and alpine vegetation history. Lowland vegetation covers wider areas than montaintop vegetation, and its pollen is easily lifted by vertical air-mass occurrences.
movements and deposited at higher altitudes. This pollen movement obscures the local vegetation signal, especially in treeless situations, where local pollen production is low. A way to overcome this difficulty is to use macrofossils to reconstruct the local timberline and alpine vegetation history. No Holocene macrofossil study is available for the area above timberline in the Alps; therefore, a reliable test of the above-mentioned hypotheses has not been possible. In this study two new sites above today’s tree limit were analyzed to test which of the two hypotheses is applicable for the Central Swiss Alps. Aside from its ecological relevance, the main purposes of such a test are (1) to discuss whether the modern alpine belt above treeline is natural (i.e., like that before Neolithic, 5500 B.C.) and hence to estimate how it would evolve if anthropogenic pressure ceased, and (2) to assess whether previous paleoclimatic interpretations of timberline oscillations were based on correct assumptions (i.e., the past presence of an upper sharp boundary of tree species and a narrow treeline ecocline in stability with climate).

In this paper we also address the prevailing transport and diffusion mechanisms for macrofossils and macroscopic charcoal particles and discuss the role of fire-generated convection columns in lifting and transporting centimeter-sized plant material. In addition, we briefly address the suitability of pollen-influx methods for tracing past vegetation changes near treeline.

Study Area

The Swiss part of the Rhone valley (Valais, Fig. 1) is characterized by a dry continental climate with precipitation of about 500–700 mm at low altitudes and about 900–1100 mm at 2300 m a.s.l. Near treeline (2300–2350 m), annual mean temperature is about 1°C (July 9°C and January –6°C). The study sites Gouillé Loéré and Lengi Egga are situated at 2503 m a.s.l. and 2557 m a.s.l., respectively. Today’s upper limit of closed forest (timberline) near these sites is situated at about 2100 m, and the limit of open tree groups (height >8 m, potential timberline or presumed natural forest line) is at about 2300 m at Gouillé Loéré and 2200–2250 m at Lengi Egga (see also Eggenberg, 1995). Single, well-developed trees >5 m grow at 2320 m (Gouillé Loéré) and 2250 m (Lengi Egga), whereas individuals of 2 m height (tree limit or treeline sensu Ellenberg [1996] and Körner [1999]) reach about 2350–2400 and 2300–2350 m, respectively. Thus, the study sites are about 100–150 m and 200–250 m above today’s tree limit. The altitudinal position of the tree limit (or treeline) depends on the definition of “tree.” The most commonly used criterion to define “tree” at treeline is a minimum height between 8 and 2 m (see discussions in Arno and Hammerly, 1985; Eggenberg, 1995; Ellenberg, 1996). Although located at the lower end of the definition range, we use the 2-m limit in order to be consistent with previous and current paleoecological timberline studies in the Alps (e.g., Carnelli et al., submitted). The alpine meadows around Gouillé Loéré and Lengi Egga consist mainly of the grass Nardus stricta and the sedge Carex curvula. The geomorphology and geology at Gouillé Loéré and Lengi Egga are comparable, with surficial deposits dominated by glacial sediments of siliceous schist. Late-glacial moraines enclose both basins (Fig. 1). The soils around the lake and the mire are well-drained regosols and are certainly suitable for forest establishment. In the study region timberline and treeline are formed by Pinus cembra and Larix decidua. Because Gouillé Loéré and Lengi Egga are above today’s treeline, two additional sites below and at treeline (Simplon, 2017 m a.s.l., Lang and Tobolski, 1985; Gouillé Rion, 2343 m a.s.l., Tinner et al., 1996; Kaltenrieder, 1999) were also considered in order to compare alpine and subalpine sites (Fig. 1). Gouillé Rion is situated only 870 m from Gouillé Loéré. Simplon is located near an important pollen and macrofossil results: 1 = Gouillé Rion (Tinner et al., 1996), 2 = Simplon (Lang and Tobolski, 1985). Small map on the left: shows the topography around Gouillé Loéré, on the right: the topography around Lengi Egga.

moisture conditions similar to those of Gouillé Loéré and Lengi Egga (for further details, see Lang and Tobolski [1985] and Tinner et al. [1996]).

A slight difference in the hydric continuity (Gams, 1931, 1932) affects the comparison between the sites by approximately 50 m, explaining the different elevations reached by trees today (2350–2400 m at Gouillé Loéré and Gouillé Rion versus 2300–2350 m at Lengi Egga and Simplon). For interpretation of results (especially in regard to the extent of vegetational belts) this effect was not taken into account because it is not clear how much it influenced past vegetation belts. If extrapolated to the past, present differences in continentality would virtually raise the ecological locations of Gouillé Loéré and Gouillé Rion by about 50 m in comparison with Lengi Egga and Simplon.

Material and Methods
CORING, SEDIMENTS, AND RADIOCARBON DATING

The pond Gouillé Loéré has neither a perennial inlet nor an outlet. The hydrological catchment has an area of only 0.09 km². The mean diameter of Gouillé Loéré is 40 m, and during coring its maximum water depth was 75 cm. Two cores with a diameter of 5 cm were taken in 1-m sections from a small platform on rubber boats with a modified Livingstone piston corer. The maximum sediment depth reached was 268 cm. The second site, Lengi Egga, is a mire subdivided by a perennial streamlet (Fig. 1). Its mean diameter is about 170 m, and the area of the hydrological catchment is 2.2 km². The only place suitable for coring was on the southwest end of the mire near the moraine rampart (Fig. 1), where a modified Livingstone piston corer could be used to take 2 cores with a diameter of 8 cm. The maximum sediment depth reached was 191 cm. In the macrofossil diagrams the main components of the sediment are presented according to Troels-Smith (1955). After the sediments were
sieved, AMS (Accelerator Mass Spectrometry) was used to date 4 terrestrial plant macrofossils from the core of Gouillé Loëré (University of Uppsala) and 13 from the core of Lengi Egga (University of Utrecht). In addition to the radiocarbon dates, we can rely on 4 radiocarbon-dated pollen profiles from the study region (1–53 km distant: see Welten, 1982; Tinner et al., 1996). The 14C dates were calibrated as A.D./B.C. by the program Calib version 4.1.2 (Stuiver et al., 1998).

**PALYNOLOGY**

The sediment was sampled in cubes of 1 cm³. Lycopodium tablets were added for estimation of pollen concentration (pollen grains cm⁻³) and pollen influx (pollen grains cm⁻² yr⁻¹). The samples were treated chemically (HCl, KOH, HF, and acetolysis: see Moore et al., 1991) and physically (0.5-mm sieving and decanting) and mounted in fluid glycerine. Pollen grains were identified with a light microscope at 400× magnification with the aid of pollen reference collection of the University of Bern, the key by Moore et al. (1991), and the photo volumes of Reille (1992, 1998). Identification of conifer stomata followed Trautmann (1953). Usually the minimum number of pollen counted was 600 grains. Only pollen of subalpine and alpine upland plant taxa (i.e., growing above 2000 m a.s.l.; for today’s altitudinal ranges of species, see Landolt, 1992) were included in the pollen sum. The diagrams were subdivided into local pollen assemblage zones (LPAZ) by using the zonation method of optimal partitioning (Birks and Gordon, 1985) as implemented in the program ZONE, version 1.2, written by Steve Juggins. To determine the number of statistically significant zones in diagrams, we used the program BSTICK (Bennett, 1996). At Gouillé Loëré the first zone boundary determined as statistically not significant was used to delimit a pollen subzone (boundary LP2a to LP2b). For diagram zonation we used only pollen types included in the pollen sum. Pollen analysis was made by W. Tinner.

**PLANT MACROFOSSILS**

Plant macrofossils were sieved with a mesh width of 0.2 mm and identified with reference material from the Institute of Plant Sciences and the Botanical Garden at the University of Bern and keys by Schoch et al. (1988) and Tobolksi (1992). Sampling resolution is 2 cm for both sites, whereas sample volume is 30 cm³ for Gouillé Loëré but 90 cm³ for Lengi Egga, owing to the larger core diameter. The diagrams show numbers (e.g., needles, seeds, fruits, leaves) and areas (e.g., bark, wood, and charcoal pieces) of macrofossils per volume of sediment (i.e., 30 and 90 cm³). The diagrams were subdivided into local macrofossil assemblage zones (LMAZ) using the same procedure as with the pollen diagrams. For diagram zonation we excluded all findings not determined to the family, genus, or species level (mainly wood, periderm, and charcoal area measurements as well as unidentified macrofossil fragments). Macrofossil analysis was made by W. Tinner.

**Results and Interpretation**

**THE SEDIMENTS**

Gouillé Loëré shows an undisturbed stratigraphy. Sedimentation rates were very low, especially in silty gyttja. To reach a sufficient temporal resolution, pollen samples were taken in contiguous 1-cm intervals between 231 and 226 cm depth, and the resulting pollen stratigraphy shows all patterns typical for this period (immigration, abandonment, and decline of species) so that the presence of a significant sediment hiatus can be excluded. The formation of silty gyttja probably represents a period when catchment erosion was at a minimum. At Lengi Egga the accumulation of gyttja started earlier and was abruptly interrupted by the deposition of a gravel layer. Apparently this event filled in the lake so that afterward the lake developed into a mire, as shown by the subsequent formation of peat deposits.

**CHRONOLOGY**

The 14C ages are presented in Table 1. If compared with neighboring dates and the biostratigraphy of other radiocarbon-dated sites in the region (e.g., Welten, 1982), the UtC-9528 age appears too old and is rejected. The age-depth curve of Gouillé Loëré was built by linear interpolation of the calibrated 14C dates (Fig. 2), the one of Lengi Egga by smoothing of the calibrated 14C dates with LOWESS (Cleveland, 1981; span 30%, Fig. 2). We applied two different models because linear interpolation is considered to be the most accurate method when only a few dates are available (Gouillé Loëré) and because smoothing usually gives a more probable sediment accumulation-rate curve when numerous dates (Lengi Egga) have to be integrated in an age-depth model (Berglund and Ralska-Jasiewiczowa, 1986). The beginning of the Holocene (10,000 14C yr BP) was determined by comparison with 14C-dated diagrams of the study region (Welten, 1982). The A.D./B.C. age-depth curves were used for a tentative calculation of pollen influx.

**POLLEN RESULTS**

Gouillé Loëré and Lengi Egga have similar pollen stratigraphies, although they have major differences in altitude, geographical location, temporal sample resolution, and sediment properties (Figs. 3, 4). Four major common phases can be summarized as follows: the oldest period, which chronologically corresponds to the Younger Dryas, was characterized by the dominance of nonarboreal pollen (especially Artemisia and Poaceae: see LPAZ LP-1 and EP-1). At the beginning of the Holocene (ca. 9000 B.C., 9600 14C yr BP), Pinus cembra became the predominant pollen type (LP-2a, EP-2). Pinus cembra then reached maximum values and Betula declined (ca. 7000–3000 B.C., LP-2b and EP-3). In the youngest section (after 3000 B.C., LP-3 and EP-4) Pinus cembra pollen was replaced by Picea and Alnus viridis.

Aside from common overall trends, some marked differences are apparent. At Lengi Egga the nonarboreal pollen reached higher percentage values, especially during the early and middle Holocene (EP-2 and 3 in comparison with LP-2). Contemporaneously Pinus cembra reached an average of 40% at Gouillé Loëré but only 20% at Lengi Egga. Concentration of Pinus cembra pollen is also higher at Gouillé Loëré, whereas pollen influx is comparable for both sites (Figs. 3, 4). Pinus stomata were found only at Gouillé Loëré (Fig. 3), and some herbaceous taxa were present in significant numbers only at one of the two study sites (e.g., Plantago alpina at Gouillé Loëré and Cirsium at Lengi Egga). Today meadows with regular presence of Plantago alpina have their upper altitudinal boundary at about 100 m higher than treeline (2500 m), whereas Cirsium spinosissimum is often found in the upper alpine belt below 2800 m (see Landolt, 1992). After 3000 B.C. (LP-3 and EP-4) the nonarboreal pollen subsequently increased at Gouillé Loëré but not at Lengi Egga.

**POLLEN-INFERRED VEGETATION HISTORY**

Pollen percentage results suggest treeline ecocline conditions at Gouillé Loëré, with treeless pioneer vegetation and alpine meadows locally present before 7500 B.C. (8450 14C yr BP) and after 3000 B.C. (4400 14C yr BP). Lengi Egga shows no indication of tree presence throughout the Holocene. However, these results are based on several ecological and palynological assumptions and cannot be derived directly from pollen diagrams. The most decisive criterion is given by the quantity of arboreal pollen (AP, trees and shrubs) in the pollen diagrams. In the diagram of Gouillé Loëré (Fig. 3) AP reached about 70–80% between 7500 and 3500 B.C. Such values are typical for timberline conditions.
TABLE 1
AMS-radiocarbon dates from Gouillé Loére and Lengi Egga

<table>
<thead>
<tr>
<th>Site</th>
<th>Lab number</th>
<th>Depth (cm)</th>
<th>Conventional radiocarbon date year BP</th>
<th>A.D./B.C. age in diagrams</th>
<th>A.D./B.C. 95% limits</th>
<th>A.D./B.C. age in diagrams</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gouillé Loére</td>
<td>Ua-16259</td>
<td>116–112</td>
<td>1360 ± 100</td>
<td>470–890 A.D.</td>
<td>660 A.D.</td>
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<tr>
<td></td>
<td>Ua-16258</td>
<td>214–212</td>
<td>4900 ± 70</td>
<td>3890–3540 B.C.</td>
<td>3680 B.C.</td>
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<td></td>
<td>Ua-16257</td>
<td>228–226</td>
<td>6690 ± 80</td>
<td>5730–5480 B.C.</td>
<td>5820 B.C.</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Ua-16256</td>
<td>232–230</td>
<td>8290 ± 110</td>
<td>7580–7060 B.C.</td>
<td>7390 B.C.</td>
<td></td>
</tr>
<tr>
<td>Lengi Egga</td>
<td>UIC-9527</td>
<td>17–15</td>
<td>370 ± 30</td>
<td>1440–1640 A.D.</td>
<td>1490 A.D.</td>
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<tr>
<td></td>
<td>UIC-9528a</td>
<td>39–37</td>
<td>3560 ± 50</td>
<td>2030–1740 B.C.</td>
<td>860 B.C.</td>
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<tr>
<td></td>
<td>UIC-9529</td>
<td>49–47</td>
<td>3590 ± 40</td>
<td>2110–1780 B.C.</td>
<td>1930 B.C.</td>
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<td></td>
<td>UIC-9530</td>
<td>57–55</td>
<td>3970 ± 50</td>
<td>2620–2310 B.C.</td>
<td>2400 B.C.</td>
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<td></td>
<td>UIC-9531</td>
<td>81–79</td>
<td>4770 ± 50</td>
<td>3650–3380 B.C.</td>
<td>3560 B.C.</td>
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<tr>
<td></td>
<td>UIC-9532</td>
<td>91–89</td>
<td>5100 ± 50</td>
<td>3980–3780 B.C.</td>
<td>3990 B.C.</td>
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<tr>
<td></td>
<td>UIC-9533</td>
<td>99–97</td>
<td>5580 ± 40</td>
<td>4500–4340 B.C.</td>
<td>4500 B.C.</td>
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<tr>
<td></td>
<td>UIC-9534</td>
<td>107–105</td>
<td>6230 ± 60</td>
<td>5320–5000 B.C.</td>
<td>5090 B.C.</td>
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<td>UIC-9535</td>
<td>117–115</td>
<td>6890 ± 50</td>
<td>5870–5660 B.C.</td>
<td>5650 B.C.</td>
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<td></td>
<td>UIC-9536</td>
<td>123–121</td>
<td>6960 ± 50</td>
<td>5980–5720 B.C.</td>
<td>5870 B.C.</td>
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<td></td>
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<td>6690–6470 B.C.</td>
<td>6650 B.C.</td>
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<tr>
<td></td>
<td>UIC-9538</td>
<td>151–149</td>
<td>8590 ± 60</td>
<td>7750–7540 B.C.</td>
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<td>UIC-9539</td>
<td>159–157</td>
<td>9370 ± 70</td>
<td>9090–8340 B.C.</td>
<td>8570 B.C.</td>
<td></td>
</tr>
</tbody>
</table>

*CALIB 4.1.2. (Stuiver et al., 1998).
*a Excluded from age-depth model.

(e.g., Welten, 1959, 1982; Wick and Tinner, 1997). In contrast values of nonarboreal pollen >30% (lowland trees excluded) may already indicate treeless conditions. However, the use of such threshold values in alpine conditions is not unambiguous (see Lang, 1994). In theory, pollen influx could help to overcome interpretation difficulties caused by percentage diagrams (Lang, 1994), but the method is limited by the major difficulty that reliable pollen-influx calculations require a precise chronology. Nevertheless, we tentatively calculated pollen influx for some of the most important taxa and pollen groups. Figure 5 shows an altitudinal transect from Gouillé Rion (2343 m a.s.l.) to Lengi Egga (2557 m a.s.l.). For Gouillé Rion pollen influx was estimated for two different times: the entire Holocene and the forested period (Tinner et al., 1996). Influx of Pinus cembra shows a marked decrease with altitude, and Larix decidua pollen influx declines to values approaching zero at Gouillé Loére and Lengi Egga. Betula takes an intermediate position between Pinus cembra and Larix; whereas upland herbs show no clear trend (Fig. 5).

It is possible to compare pollen-influx results with modern pollen-influx measurements at timberline (van der Knaap et al., 2001). A transect near Zermatt (Valais, Switzerland) starting in the forest, crossing the timberline, and ending 500 m above timberline shows that pollen influx of Pinus cembra may reach more than 1000 pollen grains cm$^{-2}$ yr$^{-1}$ in forests, about 700 at the timberline ecocline, and about 400 in alpine meadows above timberline. Larix has a more abrupt shift at timberline, for values decrease from over 1000 (forest) to about 150 (ecocline) and to 40 pollen grains cm$^{-2}$ yr$^{-1}$ (alpine meadows). Betula does not occur in the immediate surroundings (<100 m) of the pollen traps, but values steadily decrease from about 200 (forest) to 150 (ecocline) to less than 100 pollen grains cm$^{-2}$ yr$^{-1}$ (alpine meadows). Bortenschlager et al. (1998) obtained similar results for Pinus cembra in western Austria (site Vent). The tree species reached more than 1000 pollen grains cm$^{-2}$ yr$^{-1}$ in forests and only 350–500 above timberline. The total tree influx is also a good diagnostic parameter (e.g., only above timberline was the influx of pollen of herbaceous species significantly higher than that of tree pollen). Tree pollen decreased from about 5000 pollen grains cm$^{-2}$ yr$^{-1}$ in the forests to about 2000 above timberline (Bortenschlager et al., 1998).

The comparison of the average pollen influx values (Fig. 5) with these pollen-trap results suggests that Gouillé Rion was below or at timberline during most of the Holocene. Gouillé Loére and especially Lengi Egga have average influx values very similar to those pollen-trap sites above timberline. However, especially in the case of Pinus cembra, the average pollen influx is not distributed equally through time. During...
the period between 7500 and 3500 B.C. (8500–4700 14C yr BP) *Pinus cembra* reached above-average values of about 400 pollen grains cm\(^{-2}\) yr\(^{-1}\) at both sites (Figs. 3, 4). In the case of Gouillé Lœré the *Pinus cembra*, *Larix*, and total tree pollen-influx values appear too low to sustain the percentage-based interpretation of an ecocline situation.

**MACROFOSSIL RESULTS**

In contrast to pollen stratigraphies, the macrofossil stratigraphies of Gouillé Lœré and Lengi Egga have few common features. The early Holocene samples dated 9500 to 8200 B.C. (10,000–9000 14C yr BP) at Gouillé Lœré (LM-1a, Fig. 6) and 9500 to 9000 B.C. (10,000–9600 14C yr BP) at Lengi Egga (EM-1a, Fig. 7), contain very few macrofossils. After 9000 B.C. (9600 14C yr BP), the number of macrofossils found at Lengi Egga gradually increased, reaching maximum values in zone EM-2. At Gouillé Lœré, a similar development is recorded at around 8200 B.C. (9100 14C yr BP, LM-1b), although the total number of macrofossils found is considerably lower. In addition to differences in macrofossil concentrations, Gouillé Lœré had a higher proportion of tree and shrub macrofossils between 8200 and 4300 B.C. (9000–5400 14C yr BP, LM-1b). Moreover, needles of *Pinus cembra* were only found at Gouillé Lœré. At Lengi Egga an abundance of herb and shrub plant remains were preserved in the sediments dating between 7000 and 3600 B.C. (8100–4800 14C yr BP, EM-2) (e.g., *Cirsium spinosissimum*, *Helianthemum*, *Leontodon*, *Potentilla*, *P. aurea* t., *Saxifraga stellaris*, *Silene exscapa* t., *Vaccinium*, and *Juniperus nana*). Aside from the basal samples with very low macrofossil concentrations that predate 9000 B.C. (9600 14C yr BP), the past 5000 yr (LM-2b and 3, EM 3b and 4), show the most similar macrofossil stratigraphies. They were characterized by regular occurrences of alpine plant remains at both sites. However, during this period *Carex* reached high values at Lengi Egga but not at Gouillé Lœré. At Gouillé Lœré remains of alpine-meadow plants (*Loiseleuria procumbens*, *Alchemilla vulgaris*, *Cerastium alpinum* t., *Helianthemum*, *Potentilla aurea* t., *Saxifraga stellaris*, *Silene suecica* t., *Taraxacum* t.) reached maximum values on their first occurrence, whereas at Lengi Egga they were less common than before. During the

**FIGURE 3.** Pollen-percentage diagram (selected taxa) of Gouillé Lœré, Switzerland. Lowland plants, water plants, and ferns are excluded from pollen sum. Concentration (conc.) and influx (infl.) values are given for Betula, Larix, and Pinus cembra. LPAZ = Local pollen assemblage zones. Cult. = cultural indicators. LP-1 to LP-3 = local pollen assemblage zones 1 to 3.

**FIGURE 4.** Pollen-percentage diagram (selected taxa) of Lengi Egga, Switzerland. Lowland plants, water plants, and ferns are excluded from pollen sum. Concentration (conc.) and influx (infl.) values are given for Betula, Larix, and Pinus cembra. LPAZ = Local pollen assemblage zones. Cult. = cultural indicators. EP-1 to EP-4 = local pollen assemblage zones 1 to 4.

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past 3000 yr fossils of shrub and tree (Juniperus nana, Larix) taxa were commonly present only at Gouillé Loére, although less abundantly than meadow species.

MACROFOSSIL-INFERRED VEGETATION HISTORY AT GOUILLE LOÈRE

Before 8200 B.C. (9000 14C yr BP) vegetation was very sparse around Gouillé Loére, and immature soils were probably exposed to erosion. Macrofossil findings point to treeline ecotone conditions at the site between 8200 and 4300 B.C. (9000–5400 14C yr BP, LM-1b). The presence of heliophilous shrubs and herbs (Juniperus nana, Salix, Potentilla, Silene exscapa) shows that the surroundings of the pond were not densely forested. Instead, it is likely that single individuals of Pinus cembra and possibly of Larix decidua grew near the site. The interpretation of macrofossil records is based on the assumption that single findings already indicate the past local presence of a taxon. However, for two macrofossil types (fruits of Betula and needles of Larix) this interpretation may not apply. Indeed, the interpretation of Larix decidua needles is difficult if only small amounts are found. The tree loses its needles every year, so that in the presence of tree species sediment may be very rich in macrofossils (up to 2300 needles/45 cm³; Wick and Tinner, 1997). Moreover, the large number of dry and light needles produced in autumn favors long transport by wind (Wick, 1994) and upward gliding on snow cover (personal observation). A similar problem also occurs for winged Betula fruits, which are very light and easily transported by wind. The local presence of Betula is likely only if fruit scales (bracts) are commonly found (Wick, 1994; Tinner et al., 1996).

FIGURE 5. Pollen influx and mean and standard deviation of selected pollen types and groups along an altitudinal transect during the Holocene. At Gouillé Rion two different times are shown—the whole Holocene and the forested period, according to macrofossil findings (Tinner et al., 1996). GRF = Gouillé Rion forested period, GR = Gouillé Rion Holocene, GL = Gouillé Loére Holocene, LE = Lengi Egga Holocene.

FIGURE 6. Plant-macrofossil concentrations at Gouillé Loére (findings per 30 cm³). LMAZ = Local macrofossil-assemblage zones. Dicot. = dicotyledon, BD = buds, BS = budscales, F = fruits, L= leaves, MS = macrospores, N = needles, RZ = rhizomes, S = seeds, LM-1a to LM-3 = local macrofossil-assemblage zones 1 to 3.
Between 4300 and 3000 B.C. (5400–4400 14C yr BP, LM-2a) total macrofossil concentration decreased, and the taxa still represented are Vaccinium, Juncus triglumis t., and Selaginella selaginoides. Wet soil conditions are indicated by Juncus triglumis, whereas the two other taxa prefer dry to humid soils and can grow at least 200–300 m higher than treeline. Considering that sedimentation became very high only after 1000 B.C. (Fig. 6), it is likely that this macrofossil decrease was not primarily related to increasing sedimentation rates. Instead, it seems that only after 3000 B.C. (4400 14C yr BP, LM-2b and LM-3) were alpine meadows dense enough to produce enough remains to clearly dominate the profile of Gouillé Loéré (Fig. 6). After 3000 B.C. (4400 14C yr BP), Salix herbacea was the most important representative of alpine vegetation at Gouillé Loéré. This species is adapted to very harsh climatic conditions, although it is sensitive to drought and needs snow cover during winter. In the Alps it is very common in areas with snowbeds over siliceous bedrock and in open alpine meadows. Two other important taxa, Saxifraga stellaris and Saxifraga aizoides t., indicate open soils and gravelly and/or rocky environments at Gouillé Loéré after 3000 B.C. (4400 14C yr BP). Alchemilla vulgaris t., Leontodon t., Potentilla, Silene, and Taraxacum suggest the presence of more densely vegetated meadows.

**MACROFOSSIL-INFERRRED VEGETATION HISTORY AT LENGI EGGa**

At Lengi Egga moss fragments indicate pioneer vegetation before 9000 B.C. (9600 14C yr BP, Fig. 7, EM-1a). Only after 9000 B.C. do macroscopic remains of higher plants (Salix herbacea, Potentilla aureat, Caryophyllaceae) document the establishment of more closed alpine plant communities (EM-1b). After 7000 B.C. (8100 14C yr BP) alpine vegetation became progressively more diverse (EM-2), reaching a maximum between 6200 and 5100 B.C. (7400–6200 14C yr BP). After 2300 B.C. (3850 14C yr BP) macrofossil transport and preservation mechanisms changed with lake conversion into a mire. It is likely that this contributed significantly to the decrease in macrofossil findings and diversity (EM-3). However, this change allowed Carex to expand. Trees are represented by regular single-needle occurrences of Larix decidua, fruits of Betula “alba,” and one needle finding of Picea, although some more charred needles of Picea and Larix were found in zones EM-3 and EM-4 (Fig. 7). In comparison with the quantity of alpine macrofossils found, tree remains are of marginal importance and are probably best explained by wind transport from lower vegetation belts or a few arboreal (krummholz-like) individuals growing near the site. The dominance of alpine taxa suggests that the site was above treeline throughout the Holocene. The lack of Pinus cembra needles supports this interpretation, considering that one of the largest modern stands of the Alps (Aletschwald, 3 km away) has been growing near the site since at least 7000 B.C. (8000 14C yr BP; Welten, 1982).

The major vegetation changes found in the pollen diagrams of Gouillé Loéré and Lengi Egga have no unambiguous correspondence in the macrofossils, indicating that the signal was primarily derived from forests below the sites. A better agreement between pollen and macrofossil records is found for minor taxa. For example, microspores and macrospores of Selaginella selaginoides show very similar curves at Gouillé Loéré and Lengi Egga, and at Lengi Egga, Cirsium (spinosissimum) reaches a maximum in pollen and macrofossil diagrams around 6000 B.C. (7200 14C yr BP).

**Discussion**

**THE HOLOCENE ALTITUDINAL RANGE OF TREES**

The interpretation of percentage diagrams near treeline is based on several ecological and palynological assumptions. Despite this, a verification of Welten’s (1982) pollen-based results by macrofossil analysis (Tinner et al., 1996) showed that pollen interpretations at treeline are consistent with macrofossil results for the dominant tree species. As shown by the computation of pollen influx, absolute pollen analysis may help to interpret pollen results in a more direct way. As done in Scandinavia, the most promising way would be to define pollen analogues for different vegetation types based on both influx and percentage values (e.g., Hicks, 1994). Unfortunately, such a systematic comparison has not yet been attempted for the Alps, although it is likely that apparent contradictions between the interpretation of pollen percentage and influx data (e.g., Gouillé Loéré between 7500 and 3500 B.C., 8500 and 4700 14C yr BP) could be avoided.

The potential of pollen-influx analysis at timberline can be illustrated by the case of Larix decidua. The contrast in pollen influx between alpine and forested sites is even more evident than the differences observed in the macrofossil data (Figs. 3–7). This points to a very clear difference in...
pollen accumulation rates between sites where Larix was locally present or not, which is in agreement with modern pollen-influx studies (van der Knaap et al., 2001).

Macrofossil analysis is thought to be the most reliable tool for reconstructing vegetation history at and above timberline (e.g., Lang, 1994). Transport of macroscopic particles depends on saltation (driven through strong winds) and in part on (melt) water transport. Because they are not usually transported very far from their point of origin (Birks and Birks, 1980), macrofossil results have a high (meter to decimeter) spatial resolution. Stomata found in pollen slides can be used as proxies for macrofossils. At the present time, classification and determination of stomata is restricted to a few coniferous tree and shrub taxa (Trautmann, 1953; Ammann and Wick, 1993; Hansen, 1994), and taxonomic resolution is lower than for macrofossils. Although the method certainly provides valuable information for interpretation of pollen diagrams from treeline sites with coniferous species, the uppermost Holocene tree limit and the transition to alpine vegetation can be traced only tentatively, since it is not possible to unambiguously infer the presence of alpine vegetation from the absence of conifer stomata. However, macrofossil analysis can document the presence of past alpine vegetation, if plant remains are deposited and preserved in the sediments. In the diagrams of Gouillé Loéré and Lengi Egga the stomata results are in agreement with the macrofossil data for Pinus and Juniperus (stomata findings of Pinus and Juniperus at Gouillé Loéré, Juniperus at Lengi Egga) but not for Larix (no stomata findings in either Figure 3 or 4).

To illustrate how sharply and unambiguously past forest-alpine transitions can be traced by macrofossil analysis, we computed macrofossil percentage values along a virtual transect starting at about 200 m below (2017 m) and ending at about 200–250 m above today’s treeline lower boundary (2557 m, Fig. 8). The decreasing importance of tree species with altitude is documented for the whole Holocene, and the lowering of timberline after 3000–2500 B.C. (4000 $^{14}$C yr BP) as well as the intermediate position of Gouillé Loéré between two forested sites (Simplon, Gouillé Loéré until 2500 B.C.) and an alpine site (Lengi Egga, Fig. 8) is shown. Our results imply that during the maximum timberline position (9000–3000 B.C.) the natural Holocene treeline ecocline was rather narrow (100–150 m). The lower limit of the ecocline, corresponding to timberline, was at ca. 2530 m (average between Gouillé Loéré and Lengi Egga). Thus, maximum timberline and treeline positions were ca. 120–180 m higher than today (2300 vs. 2420 m, and 2350 vs. 2530 m, respectively).

The interpretation of pollen and macrofossil results presented here is supported by soil biosequences in the study area of Gouillé Ron and Gouillé Loéré (Tinner et al., 1996). Biosequences based on soil-development models are probably the most systematic way to analyze variation in soils due to potential or actual vegetation (e.g., Ugolini and Edmonds, 1983; Birkeland, 1999). Various features (horizons, texture, skeleton, structure, color—for methodology and interpretation see Tinner et al., 1996) in 26 soil profiles indicate that closed forests reached 2400–2450 m a.s.l. (i.e., 100–150 m higher than today’s potential timberline, and about 50–100 m above today’s tree limit) during the Holocene. According to soil biosequences the treeline ecocline (and hence the regular occurrence of single trees) encompassed 50–100 altitudinal meters, reaching 2450–2500 m a.s.l. It is striking how closely the macrofossil-inferred maximum position of Holocene timberline (ca. 2420 m) coincides with a marked change in soil properties as evidenced by soil biosequences (ca. 2410 m; Tinner et al., 1996). Soils above 2470 m present the same properties as alpine soils between 2500 and 2600 m. This suggests a sparse presence of trees in the upper treeline ecocline. Carnelli et al. (submitted) reached the same conclusion for the Lengi Egga site.

The timberline position as indicated by macrofossil findings and soil biosequences is slightly higher than suggested in previous pollen and stomata-based estimates (see Lang, 1994: 2300–2400 m). In our records no evidence could be found for a conspicuous presence of krummholz-like Pinus cembra and Larix above tree limit (i.e., the upper boundary of the treeline ecocline, 2530 m). Because net biomass productivity in subalpine forests is about four to five times higher than in alpine meadows (800–1000 g m$^{-2}$ yr$^{-1}$ vs. 200 g m$^{-2}$ yr$^{-1}$; Ellenberg, 1996; Strasser et al., 1991), the average values of tree species remains at Lengi Egga (about 5%, see Fig. 8) and G. Loéré (30%) probably overestimate the effective tree-cover, even if we assume that all tree macrofossils derived from individuals growing in situ.

Our results do not support the hypothesis of a broad treeline ecocline, as proposed by Carcailllet et al. (1998) and Thimon and Talon.
(1998) for the southwestern (Vanoise massif) and southern French Alps (Queyras and Ubaye). However, the results of these studies do not contradict our results. Today’s potential timberline is located at around 2400–2450 m a.s.l. and 2500–2550 m a.s.l. in the Vanoise massif and in Queyras and Ubaye, respectively. If our results are extrapolated to the French Alps (the French and Swiss sites have similar climatic and ecological conditions), timberline may have reached 2520–2570 m a.s.l. in the Vanoise and 2620–2670 m in Queyras and Ubaye (+120 m), respectively. The uppermost treeline positions were probably 100–180 m higher, i.e., at 2620–2750 m in the Vanoise and 2720–2850 m in Queyras and Ubaye. This estimation is in accordance with the charcoal-analytical results for Vanoise (2600–2700 m a.s.l.; Carcaillet et al., 1998) as well as for Queyras and Ubaye (2800–2900 m a.s.l.; Thimon and Talon, 1998).

At Lengi Egga, a recent charcoal-analytical study (Carnelli et al., submitted) estimates the maximum positions of timberline and treeline at about 2400 m a.s.l. and 2500 m a.s.l., respectively. These estimates are very close to ours (2420 and 2530 m a.s.l., respectively). Therefore it seems that paedoanthracological, pollen, soil, and macrofossil studies lead to similar estimates of uppermost timberline and treeline. However, if compared with macrofossil analysis, palynological and anthracological studies are affected by a considerable spatial fuzziness. It is well known that the pollen of trees and shrubs is easily lifted by winds and transported far above timberline. Similarly, field observations show that high-intensity wildfires usually transport millimeter- and centimeter-sized particles vertically hundreds of meters (or more), so that plant material can then land several kilometers (or more) ahead of the main fire (McArthur, 1967; Anderson, 1968; Pisaric, 2002; SALTUS, 2001; Colin and Cabaret, unpubl. data; Ellis, pers. comm. 2002). Most of the plant debris is charred, but uncharred material is transported as well (e.g., Anderson, 1968; Pisaric, 2002). These observations appear in contrast to experimental studies, which assert that mm-sized particles are not transported far away by fires (e.g., Ohlson and Tryterud, 2000) but are in agreement with other empirical investigations and theoretical estimations or predictions (Garstang et al., 1997; Clark et al., 1998; Benedict, 2002). Thus, there are good reasons to doubt that every single charcoal particle found in soils >0.4–1 mm is really derived from vegetation burned in situ, although from a statistical point of view most macroscopic charcoal of this size are certainly deposited within small distances from the fire (Clark, 1988; Tinner et al., 1998). Since it is plausible that during fires most charcoal is deposited within the burned forests, the past altitudinal limit may be reconstructed by interpreting changes in charcoal-mass concentration along altitudinal transects (e.g., in particles per 100 cm³ or in mg kg⁻¹; see Carcaillet and Talon, 2001; Benedict, 2002; Carnelli et al., submitted), instead of just evaluating the presence or absence of a taxon. The capacity of convection columns and vortex processes to transport uncharred cm-sized plant material (e.g., needles) for several kilometers (e.g., Anderson, 1968; Pisaric, 2002) challenges the assumption that macrofossils are not transported very far from their point of origin. Care should be taken in the interpretation when only a few macrofossils are present and if there is evidence of past forest fires (e.g., through the sedimentary record of charred plant remains; see discussion in Pisaric, 2002). In this sense we cannot exclude the possibility that some macrofossils were transported by forest fires for long distances. In fact, 75% of the Picea needles and 22% of the Larix needles contained in the sediments of Lengi Egga were charred (see Fig. 7). However, no charred needles were found at Gouillé Loére (Fig. 6) and Gouillé Rion (Tinner et al., 1996; Kaltenrieder, 1999). Thus, it is likely that at Lengi Egga (the highest site) forest fires were the predominant mechanism of transport for Picea macrofossils. Conversely, no unambiguous clue is given for forest-fire transport of needles or other uncharred remains at Gouillé Loére and Gouillé Rion. This interpretation implies that it is important to distinguish between charred and uncharred macrofossil findings, because they may originate from different source areas.

Macrofossil and pollen data suggest that alpine meadows prevailed during the entire Holocene at the Lengi Egga site. This implies that today’s alpine communities in the study region are close to a natural state, although some dominant species like Nardus stricta may have been favored by summer pasturing. Thus, it is likely that (assuming constant climatic conditions), modern meadow communities would persist and not be invaded by tree species if anthropogenic pressure ceased.

**ALPINE VEGETATION RESPONSE TO HOLOCENE CLIMATIC OSCILLATIONS**

Pollen-percentage fluctuations (sum of tree pollen, Pinus cembra, Betula) at Lengi Egga and Gouillé Rion coincide with Holocene glacier and lake level oscillations in the Alps (Tinner and Ammann, 2001) and are best explained by several conspicuous Holocene tree diebacks in the subalpine forests of the region. At Lengi Egga pollen oscillations occurred at ca. 9100 B.C. (minimum of Betula pollen), 7200 B.C., 5850 B.C., 3800 B.C., 1600 B.C., 400 B.C., A.D. 1400, and A.D. 1800 (minimum of tree pollen; see Fig. 4 and Tinner and Ammann, 2001 for comparison with glacier oscillations). Surprisingly, despite the registration of these events by subalpine forests of the central Alps, these climatic coolings did not clearly affect the local alpine vegetation at Lengi Egga (Fig. 7). It is likely that the meadows were not severely disturbed because presently most alpine species are far below their altitudinal limits at Lengi Egga, so that local vegetation appears well buffered against climatic coolings. The paradox that climatic reversals were revealed by plant species not growing at the site emphasizes again the relevance of regional pollen transport in the Alps across different vegetation belts.

Figure 9 summarizes the altitudinal limits of the main vegetational belts during the past 13,000 cal yr as well as the temporal and altitudinal position of timberline fluctuations. Gouillé Rion was densely forested between 9000 and 2500 B.C. (9600–4000 ¹⁴C yr BP, Tinner et al., 1996, and Fig. 8). Since closed forests (timberline) never reached Gouillé Loére, the maximum range of timberline fluctuations can be estimated to be less than 160 m. After 2500 B.C. (4000 ¹⁴C yr BP) the range of vegetational oscillations is difficult to ascertain, although several key taxa (Juniperus nana, Alnus viridis, and Picea) show that they occurred within the treeline ecocline (Wick and Tinner, 1997, and Fig. 4).

The striking expansion of the treeline ecoclone after 2500 B.C. (4000 ¹⁴C yr BP, Fig. 9) was probably caused by both climate change and human disturbance. In the study region the Bronze Age began at 2200 B.C. (3850 ¹⁴C yr BP, Hochuli et al., 1998). The results of Tinner et al. (1996) indicate that this transition was the onset of a new and more intensive land-use system based on alpine summer farming. However, since similar Holocene treeline trends as in Figure 9 could be found elsewhere in Europe and on other continents where anthropogenic influence was negligible (Bradley, 1999), it is likely that human impact amplified the effect of climatic changes by lowering timberline—but not treeline—by about 200 additional meters. In this sense, the Holocene treeline history in the study region roughly mirrors the general long-term climatic trend of the Northern Hemisphere and especially, if compared with today, the prevalence of warm and dry summers raising treeline during the early and middle Holocene (see summer insolation curve: Kutzbach and Webb, 1993).

The lower temporal resolution at Gouillé Loére probably impedes a clear capture of the climatic signals, although Gouillé Rion (which recorded climatic oscillations in both the pollen and the macrofossil records) is only 800 m away. This shows the significance of well-dated high-resolution pollen analysis for reconstructing short- to middle-term vegetational oscillations.
Conclusions

The data presented in this article support the conventional hypothesis of a more or less sharp Holocene: comparative study in the Aletsch region, Val d’Arpette and Forêt Méditerranéenne, Aix-en-Provence, France) for information on air transport of plant material during fires. Corrections of the manuscript by H. E. Wright Jr. and E. Gobet are gratefully acknowledged. We are grateful to M. Reasoner and B. Talon for many valuable suggestions on the manuscript.

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Berglund, B. E., and Ralska-Jasiewiczowa, M., 1986: Pollen analysis of fossil stomata in the central Swiss Alps during the past 13,000 cal yr. The limits of the vegetational belts are placed between the sites recording the presence of the respective vegetative type as inferred by macrofossil analysis. The chronology relies on AMS-dating of terrestial macrofossils at Gouillé Rion, Gouillé Loëre, and Lengi Egga, while at Simplon and Böhnigsee the original chronology published by the authors is supported by radiocarbon dating of gyttja samples (see van der Knaap and Ammann, 1997). For Böhnigsee no macrofossil data are available. Therefore stomata frequencies were used to reconstruct local vegetation (see Ammann and Wick, 1993). S = Simplon (Lang and Tobolski, 1985), B = Böhnigsee (Markgraf, 1969), R = Gouillé Rion (Tinner et al., 1996), L = Gouillé Loëre (this study), E = Lengi Egga (this study).

The data presented in this article support the conventional hypothesis of a more or less sharp Holocene upper forest boundary (timberline) at most 100–150 m higher than today’s potential timberline (2420 vs. 2300). The treeline ecocline had an extension of about 100–150 m. The treeline upper limit was at most 150–200 m higher than today’s tree limit (2530 vs. 2350) between 9000 and 2500 B.C. (9600–4000 14C yr BP). During this period timberline fluctuations occurred between the two sites Gouillé Loëre and Gouillé Rion (Fig. 9). However, these conclusions are based on just four subalpine and alpine macrofossil profiles. Although they are supported by pollen, anthracological, and soil investigations, there is an urgent need for additional macrofossil analyses of sites below, at, and above treeline. Further paleoecological methods (e.g., pedoanthracology, soil biosequences, phytoliths, paleoentomology) may also contribute to tracing former treeline positions. To exclude misinterpretations, the proof of the past local presence of tree species should not be based on the presence/absence of charred remains alone, as large organic fragments can be lifted for hundreds of meters in the convective columns of fires. Since timberline in the Alps is formed by different species as determined by climate, sites in the southern and northern Alps should be studied as well.


