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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 Thimon and Talon (1998), *Pinus cembra* occurred rather densely in the alpine belt of the southern French Alps up to 2900 m a.s.l. Carcaillet 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 Carcaillet 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 Carcaillet 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; Thimon and Talon, 1998).

On the basis of pollen and macrofossil data, other authors (e.g., Lang and Tobolski, 1985; Pönel et al., 1992; Tessier 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 mountaintop vegetation, and its pollen is easily lifted by vertical air-mass

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 vegetational 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 small 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 pass connecting the central and the southern Alps, 16 km from Lengi Egga. The pass (2005 m a.s.l.) is treeless today, but in nearby more remote areas the present limit of closed forest is also at 2100 m a.s.l. The catchments of Gouillé Rion and Simplon have geology, geomorphology, and soil-

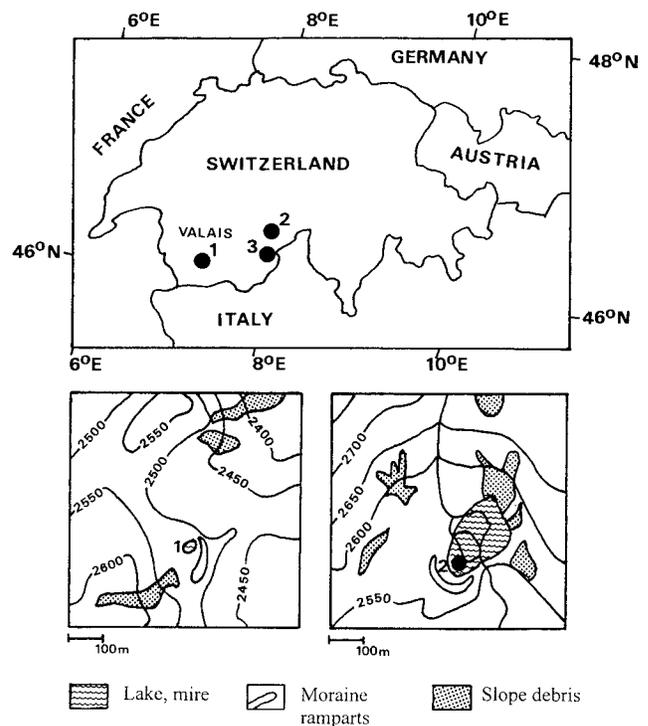


FIGURE 1. Map of the study sites in the Valais, Switzerland. 1 = Gouillé Loéré, 2 = Lengi Egga. Other already published sites with important pollen and macrofossil results: 1 = Gouillé Rion (Tinner et al., 1996), 3 = Simplon (Lang and Tobolski, 1985). Small map on the left: shows the topography around 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 continentality (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 Loéré (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 ^{14}C 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 cm^3 . *Lycopodium* tablets were added for estimation of pollen concentration (pollen grains cm^{-3}) and pollen influx (pollen grains $\text{cm}^{-2}\text{ yr}^{-1}$). 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× or 1000× 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 Loéré 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 Tobolski (1992). Sampling resolution is 2 cm for both sites, whereas sample volume is 30 cm^3 for Gouillé Loéré but 90 cm^3 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 cm^3). 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 Loéré 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, abundance, 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 ^{14}C 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 Loéré was built by linear interpolation of the calibrated ^{14}C dates (Fig. 2), the one of Lengi Egga by smoothing of the calibrated ^{14}C 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 Loéré) 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 ^{14}C yr BP) was determined by comparison with ^{14}C -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 Loéré 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 ^{14}C 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 Loéré but only 20% at Lengi Egga. Concentration of *Pinus cembra* pollen is also higher at Gouillé Loéré, whereas pollen influx is comparable for both sites (Figs. 3, 4). *Pinus* stomata were found only at Gouillé Loéré (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 Loéré 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 Loéré but not at Lengi Egga.

POLLEN-INFERRED VEGETATION HISTORY

Pollen percentage results suggest treeline ecocline conditions at Gouillé Loéré, with treeless pioneer vegetation and alpine meadows locally present before 7500 B.C. (8450 ^{14}C yr BP) and after 3000 B.C. (4400 ^{14}C 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 Loéré (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 Loéré and Lengi Egga

Site	Lab number	Depth (cm)	Conventional	A.D./B.C.	A.D./B.C.
			radiocarbon date year BP	95% limits ^a	age in diagrams
Gouillé Loéré	Ua-16259	116–112	1360 ± 100	470–890 A.D.	660 A.D.
	Ua-16258	214–212	4900 ± 70	3890–3540 B.C.	3660 B.C.
	Ua-16257	228–226	6690 ± 80	5730–5480 B.C.	5620 B.C.
	Ua-16256	232–230	8290 ± 110	7580–7060 B.C.	7390 B.C.
Lengi Egga	UtC-9527	17–15	370 ± 30	1440–1640 A.D.	1490 A.D.
	UtC-9528 ^b	39–37	3560 ± 50	2030–1740 B.C.	860 B.C.
	UtC-9529	49–47	3590 ± 40	2110–1780 B.C.	1930 B.C.
	UtC-9530	57–55	3970 ± 50	2620–2310 B.C.	2400 B.C.
	UtC-9531	81–79	4770 ± 50	3650–3380 B.C.	3560 B.C.
	UtC-9532	91–89	5100 ± 50	3980–3780 B.C.	3990 B.C.
	UtC-9533	99–97	5580 ± 40	4500–4340 B.C.	4500 B.C.
	UtC-9534	107–105	6230 ± 60	5320–5000 B.C.	5090 B.C.
	UtC-9535	117–115	6890 ± 50	5870–5660 B.C.	5650 B.C.
	UtC-9536	123–121	6960 ± 50	5980–5720 B.C.	5870 B.C.
	UtC-9537	137–135	7780 ± 50	6690–6470 B.C.	6650 B.C.
	UtC-9538	151–149	8590 ± 60	7750–7540 B.C.	7650 B.C.
	UtC-9539	159–157	9370 ± 70	9090–8340 B.C.	8570 B.C.

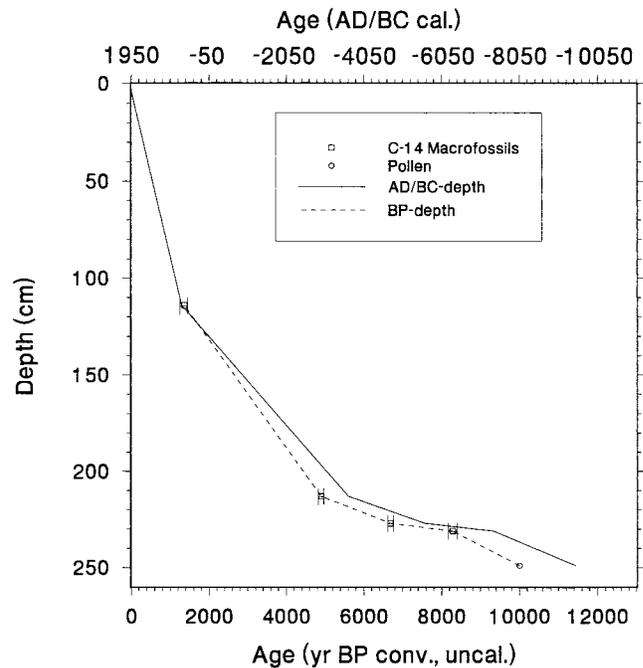
^a CALIB 4.1.2. (Stuiver et al., 1998).^b Excluded from age-depth model.

(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 Loéré 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 treeline 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 400 (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 Loéré and especially

Dating Gouillé Loéré



Dating Lengi Egga

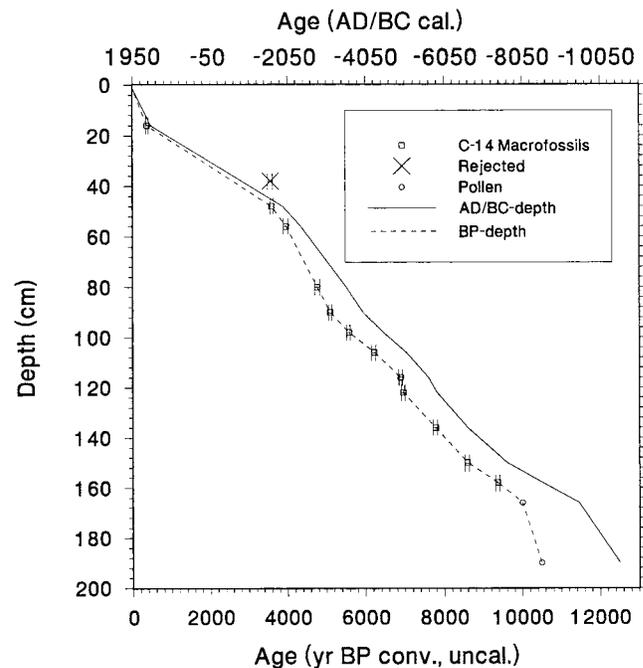


FIGURE 2. Radiocarbon dating of the sediments of Gouillé Loéré and Lengi Egga. The A.D./B.C. and the BP scales are interdependent (i.e., they cannot be linked together). The open squares indicate ¹⁴C-AMS dates (terrestrial plant macrofossils), the black circles pollen-stratigraphical ages derived from comparison with radiocarbon-dated pollen diagrams of the region.

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

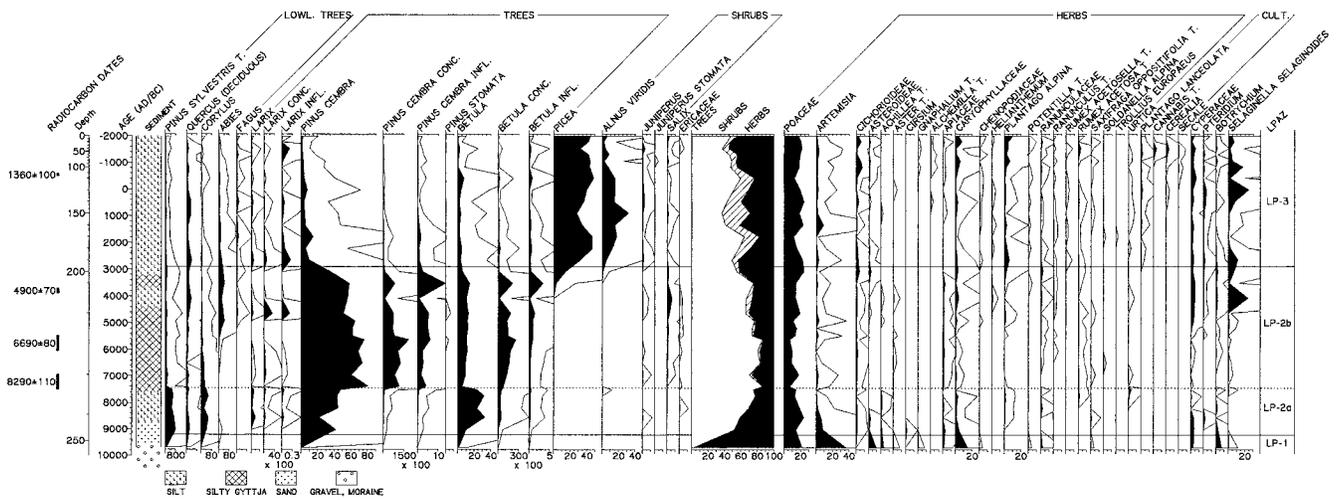


FIGURE 3. Pollen-percentage diagram (selected taxa) of Gouillé Loéré, Switzerland. Lowland plants, water plants, and ferns are excluded from pollen sum. Concentration (conc.) and influx (infl.) values are given for Betula, Larix, and Pinus cembra. LPAZ = Local pollen assemblage zones. Cult. = cultural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

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 Loéré 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 Loéré 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 Loéré (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 Loéré, 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 Loéré 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 Loéré. 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 Loéré. At Gouillé Loéré remains of alpine-meadow plants (*Loiseleuria procumbens*, *Alchemilla vulgaris*, *Cerastium alpinum* t., *Helianthemum*, *Potentilla aurea* t. *Saxifraga stellaris*, *Saxifraga aizoides* t., *Silene suecica* t., *Taraxacum* t.) reached maximum values on their first occurrence, whereas at Lengi Egga they were less common than before. During the

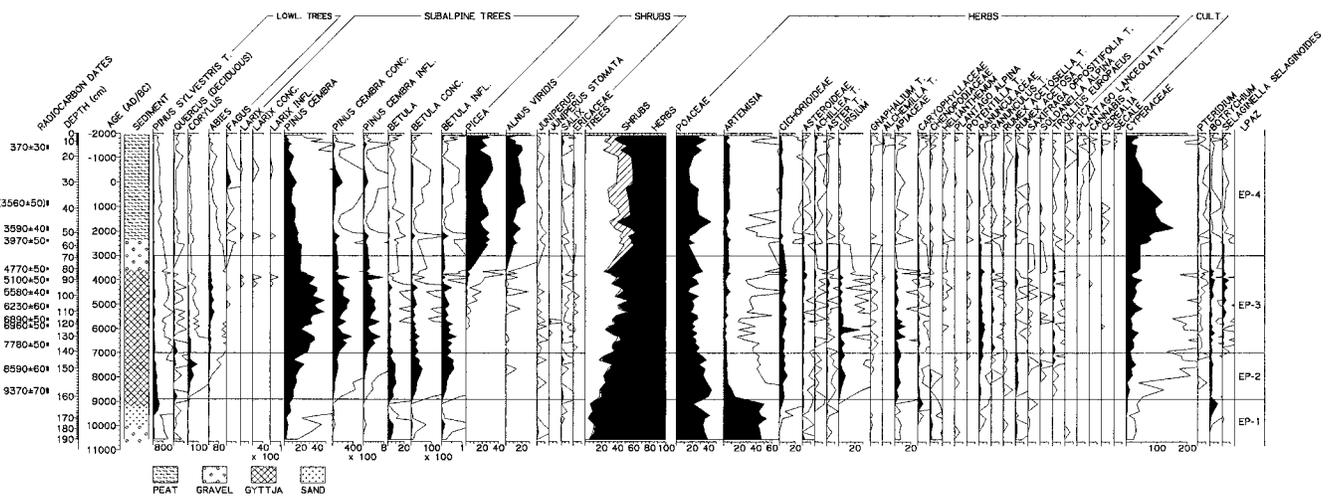


FIGURE 4. Pollen-percentage diagram (selected taxa) of Lengi Egga, Switzerland. Lowland plants, water plants, and ferns are excluded from pollen sum. Concentration (conc.) and influx (infl.) values are given for Betula, Larix, and Pinus cembra. LPAZ = Local pollen assemblage zones. Cult. = cultural indicators.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

POLLEN INFLUX NEAR TIMBERLINE

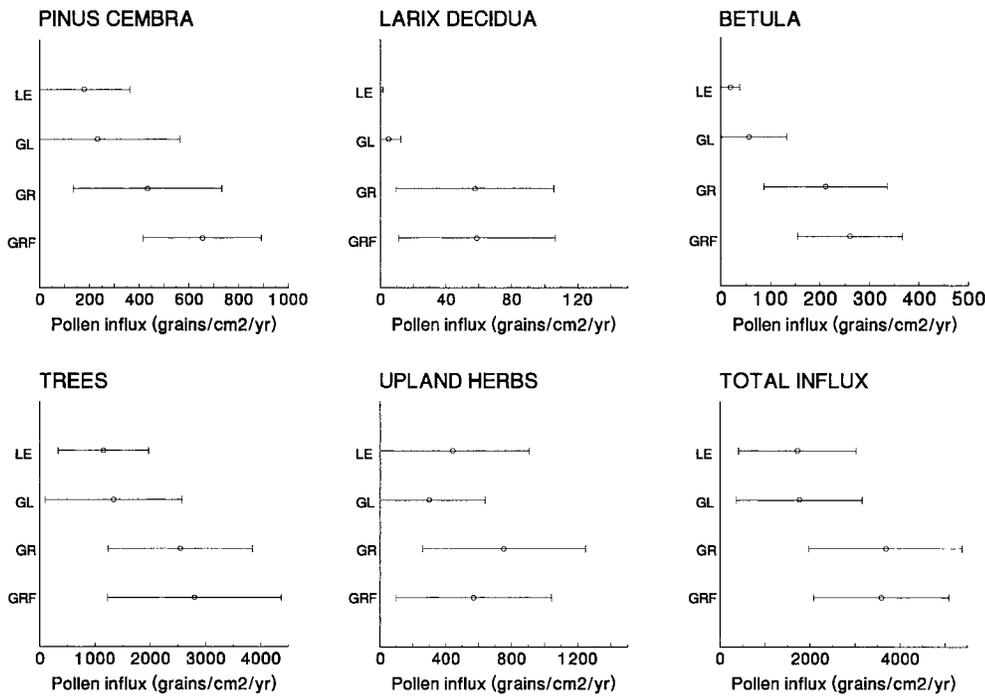


FIGURE 5. Pollen influx and mean and standard deviation of selected pollen types and groups along an altitudinal transect during the Holocene. At Gouillé Rion two different times are shown—the whole Holocene and the forested period, according to macrofossil findings (Tinner et al., 1996). GRF = Gouillé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

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

MACROFOSSIL-INFERRED VEGETATION HISTORY AT GOUILLE LOERE

Before 8200 B.C. (9000 ¹⁴C yr BP) vegetation was very sparse around Gouillé Loéré, 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* t.) 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.,

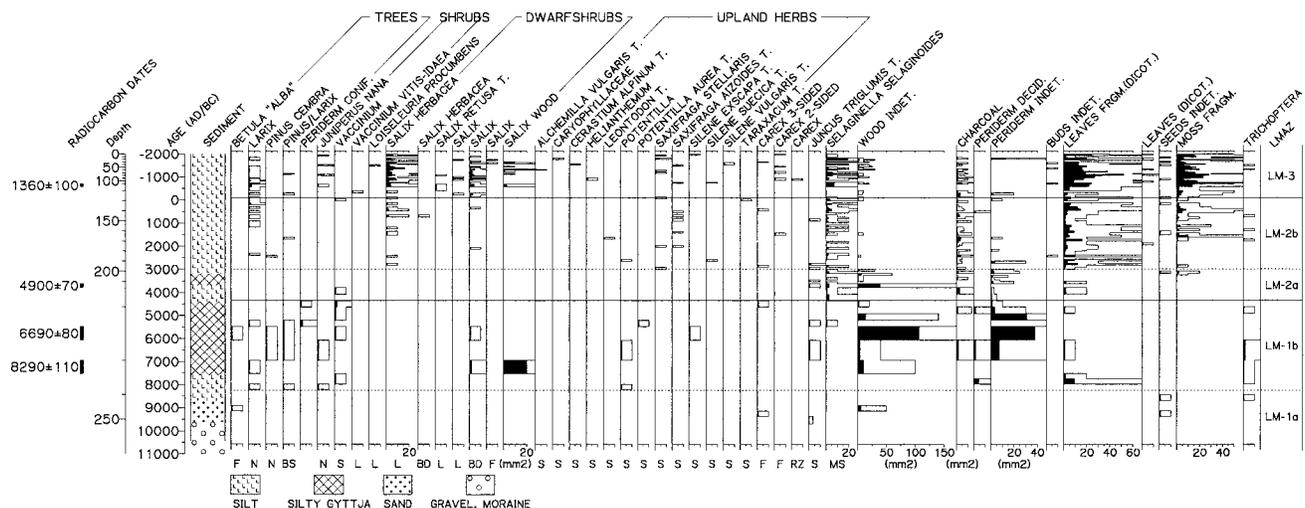


FIGURE 6. Plant-macrofossil concentrations at Gouillé Loéré (findings per 30 cm³). LMAZ = Local macrofossil-assemblage zones. Dicot. = dicotyledon, BD = buds, BS = bud scales, F = fruits, L = leaves, MS = macrospores, N = needles, RZ = rhizomes, S = seeds, LM-1a to LM-3 = local macrofossil-assemblage zones 1 to 3.



FIGURE 8. Macrofossil-percentage diagrams of four sites in the central Swiss Alps (Simplon: Lang and Tobolski [1985] modified; Gouillé Rion: Tinner et al. [1996] and Kaltenrieder [1999] modified; Gouillé Loéré and Lengi Egga: this study, Figures 6 and 7). Today's treeline is at about 2350 m a.s.l., i.e., near Gouillé Rion. Aquatic plants, Cyperaceae, and area measurements were excluded from macrofossil sum, and only taxa that could be unambiguously attributed to trees (indicating forests), shrubs (shrublands), and dwarf shrubs and upland herbs (alpine meadows) were considered for percentage calculation. The diagrams were subdivided in eleven 1000 radiocarbon-year steps.

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 decameter) 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 ¹⁴C 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. 2420 m (average between Gouillé Rion

and Gouillé Loéré), and the upper limit, corresponding to treeline, 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 Rion 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; Strassburger 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 Carcaillet et al. (1998) and Thion 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.; Thion and Talon, 1998).

At Lengi Egga, a recent charcoal-analytical study (Camelli 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 pedoanthracological, 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 charcoals 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 Loéré (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 Loéré 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 (minima 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 Loéré, 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 ecocline 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 Loéré 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.

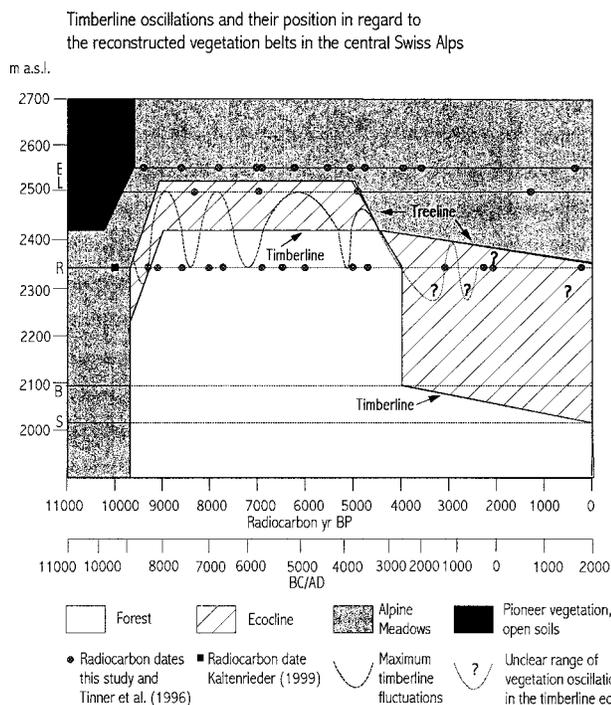


FIGURE 9. Diagram showing the altitudinal ranges of the main vegetational belts in the central Swiss Alps during the past 13,000 cal yr. The limits of the vegetational belts are placed between the sites recording the presence of the respective vegetation type as inferred by macrofossil analysis. The chronology relies on AMS-dating of terrestrial macrofossils at Gouillé Rion, Gouillé Loéré, and Lengi Egga, while at Simplon and Böhningsee the original chronology published by the authors is supported by radiocarbon dating of gyttja samples (see van der Knaap and Ammann, 1997). For Böhningsee 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 = Böhningsee (Markgraf, 1969), R = Gouillé Rion (Tinner et al., 1996), L = Gouillé Loéré (this study), E = Lengi Egga (this study).

Conclusions

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 ^{14}C yr BP). During this period timberline fluctuations occurred between the two sites Gouillé Loéré 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.

Acknowledgments

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