Pollen and plant macrofossils at Lac de Fully (2135 m a.s.l.): Holocene forest dynamics on a highland plateau in the Valais, Switzerland

Walter Finsinger[1]* and Willy Tinner[2,3]

([1]Palaeoecology, Institute of Environmental Biology, Utrecht University, Laboratory of Palaeobotany and Palynology, Budapestlaan 4, NL-3584 CD Utrecht, The Netherlands; [2]Paleoecology and Vegetation Dynamics, Institute of Terrestrial Ecosystems, Department of Environmental Sciences, ETH Zurich, CH-8092 Zurich, Switzerland; [3]Section of Palaeoecology, Institute of Plant Sciences, University of Bern, Altenbergrain 21, CH-3013 Bern, Switzerland)

Received 4 April 2007; revised manuscript accepted 19 June 2007

A HOLOCENE RESEARCH PAPER

Abstract: We use pollen, stomata and plant-macrofossil records to infer Holocene timberline fluctuations and changes in forest composition at Lac Supérieur de Fully (2135 m a.s.l.), a small lake located near the modern regional timberline on a highland plateau in the Central Alps. Our records suggest that during the early Holocene vegetation was rather open on the plateau (eg, heaths of *Dryas octopetala*, *Juniperus nana*). The only tree that was able to build major stands was *Betula*. Other timberline trees (eg, *Pinus cembra* and *Larix*) expanded in the catchment of the lake after 8200 cal. BP, when *Abies alba* expanded at lower elevation. The late appearance of these timberline trees contrasts with previous plant-macrofossil records in the region, which show that the timberline had reached elevations up to at least 2350 m already at 11 000 cal. BP. We suggest that local climatic conditions may have delayed the expansion of closed stands of coniferous trees in the catchment of Lac de Fully until *c*. 8200 cal. BP, when climate shifted to more humid and less continental conditions. After *c*. 4600 cal. BP vegetation around the lake primarily responded to human impact, which caused a local lowering of the timberline by at least 150 m.

Key words: Timberline, tree line, abrupt climate change, Alps, pollen, plant macrofossils, Holocene, Valais, Switzerland.

Introduction

The transition between forest and alpine meadows (or treeless tundra) is one of the major and fascinating worldwide ecotonal boundaries, the treeline ecotone (Körner and Paulsen, 2004). The treeline ecotone spans the timberline (ie, the uppermost limit of closed forest) and the tree species limit or krummholz limit (ie, the uppermost limit of isolated and small individuals). Near the treeline (ie, the uppermost limit of isolated groups of tall trees > 2–5 m in height) the growth of plants is limited by climatic conditions (such as the length of the growing season; Körner and Paulsen, 2004). Changes in elevation of the treeline during the past century (eg, Kullman, 2002; Parmesan, 2006 and references therein) unambiguously show how fast plants may respond to climatic change (eg, Menzel and Fabian, 1999) in these harsh environments. This sensitivity has been used to reconstruct Holocene-climatic variability based on changes in treeline elevation inferred from pollen and plant macrofossils in lake sediments (eg, Wick and Tinner, 1997; Haas *et al.*, 1998; Kaltenrieder *et al.*, 2005), from phytolith assemblages in palaeosoils (eg, Carnelli *et al.*, 2004), and from megafossils and dendrochronologically dated subfossil logs (eg, Carrara *et al.*, 1991; Kullman, 1995; Nicolussi *et al.*, 2005). Little is known, however, as to the changes in species composition of timberline forests in response to climatic change, although the present distribution of trees in the Alps (Landolt, 1992) and modelling results (Heiri *et al.*, 2006) indicate the sensitivity of timberline vegetation also to climatic parameters other than growing-season length (eg, amount or seasonal distribution of precipitation).

*Author for correspondence (*e-mail:* w.finsinger@uu.nl)

 10.1177/0959683607082552

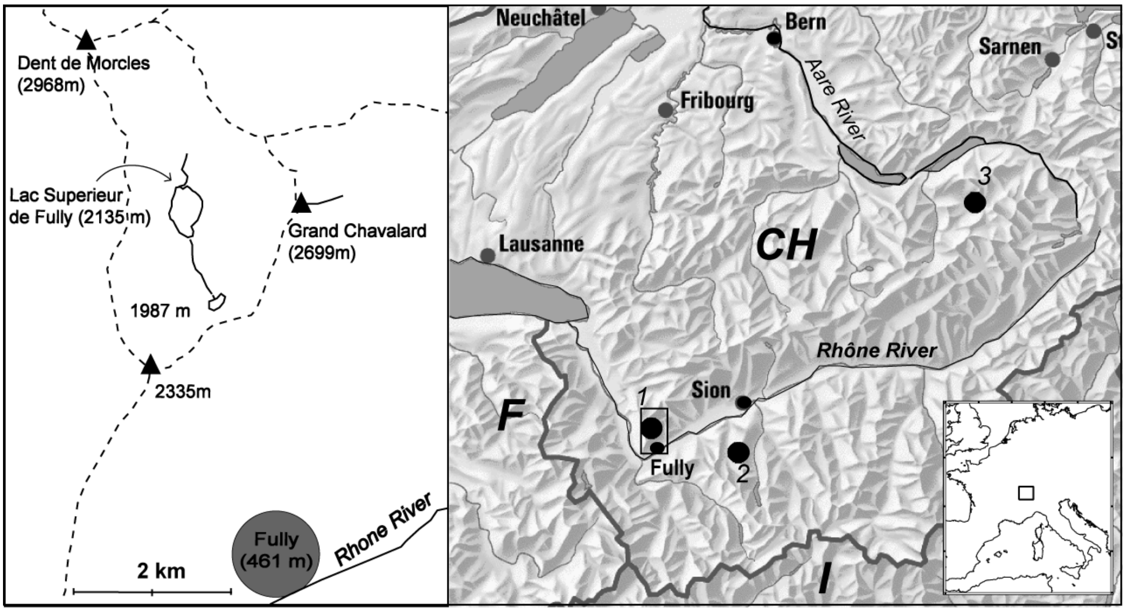

Figure 1 Left: sketch map of the Lac de Fully valley (dotted lines, watersheds; continuous lines, rivers); Right: location of study sites mentioned in the text: 1, Lac de Fully (2135 m a.s.l.); 2, Gouille' Rion (2343 m a.s.l.); 3, Hinterburgsee (1515 m a.s.l.)

Here we report on pollen and plant-macrofossil records to reconstruct the vegetation dynamics at Lac Supérieur de Fully, which is located at 2135 m a.s.l. on a south-facing highland plateau in the Central Alps (Figure 1). Although the lake is located below the modern treeline (which might correspond to the elevation of the potential (natural) timberline at *c.* 2200 m a.s.l.; Landolt, 1992) and near the modern regional timberline (*c.* 2000–2100 m a.s.l.), trees are absent above 1950 m a.s.l. in the lake catchment. We were therefore particularly interested to know if the timberline ever reached the catchment during the warmest phase of the Holocene and how the species composition changed in response to Holocene climatic changes.

Site description

The Valais, ie, the Swiss part of the Rhône Valley, is an inner-alpine valley positioned SE–NW (Figure 1) and characterized by a dry climate mainly caused by inner-valley shielding (average annual rainfall of about 600 mm at low elevation (600 m a.s.l.) and about 1000 mm at 2300 m a.s.l.; Heiri *et al.*, 2006). Although the amount of rainfall on the south- and north-facing slopes is similar, vapour-pressure deficit is higher on the south-facing slope because of more intense sunlight. This causes more evaporation and drought stress to plants living there than to plants on the north-facing slope (Zweifel *et al.*, 2006). The different microclimate is reflected in the present vegetation: *Quercus pubescens*, *Pinus sylvestris* and *Juniperus sabina* are abundant on the south-facing slope, while on the north-facing slope the drought-sensitive *Abies alba* forms major stands and thermophilous and drought-adapted *Q. pubescens* is lacking (Steiger, 1995). The natural treeline in the Valais occurs at about 2200–2400 m a.s.l., although only a few forests can be found above 2200 m a.s.l. today (Tinner and Theurillat, 2003; Heiri *et al.*, 2006).

Lac Supérieur de Fully has an area of *c.* 25 ha and is located at the bottom of a former glacier cirque in a local highland of *c.* 10 km^2 area. The site is bordered by mountain chains reaching 2300 to 3000 m a.s.l. towards west, east and north (Figure 1). The bedrock geology at the site is dominated by sedimentary deposits (Carboniferous, Triassic, Jurassic and Cretaceous). The lake has a minor inlet on the north and an outlet on the south. An artificial dam *c.* 100 m long was built AD 1912–1914 to increase the size of the lake. Climatic conditions at these elevations are harsh. Annual mean temperature at 2100 m is *c.* 2°C, July mean temperature *c.* 9°C, and annual precipitation *c.* 1000 mm (linear interpolations and extrapolations from stations in the Valais region).

Materials and methods

A continuous section 268 cm long was taken in late summer 2003 from an open pit at Lac Supérieur de Fully (GPS: 573′372; 113′983; 2135 m a.s.l.). Lake-level was low at that time because the dam had been kept open during the previous year. The section was collected in overlapping segments 50 cm long and stored at +4°C room temperature in the Institute of Plant Sciences (University of Bern). The sediment was subsampled for pollen and plant-macrofossil analyses (1 cm thick slices) avoiding the sand layers (Table 1). For pollen analysis, 64 samples were prepared, but only 62 were analysed because pollen in the clayey sediment at the base of the sequence (ie, 266 cm and 257 cm depth) was virtually absent. *Lycopodium* spores were first added to 1 cm^3 of sediment in order to calculate pollen concentrations, following Stockmarr (1971). Samples were treated physically and chemically, following standard procedures (Moore *et al.*, 1991). The residue was mounted in glycerine on slides and analysed

Table 1 Simplified sediment description of the studied section at Lac Supérieur de Fully

Depth (cm)	Sediment description
0–18	Sand
18–20	Sandy gyttia
20–26	Sand layer (coarsening upward)
26–30.5	Sandy gyttia
30.5–237	Stratified sandy gyttia with distinct sand layers
237–248	Stratified gyttia
248–270	Stratified sandy silt with distinct sand layers

Table 2 Radiocarbon dates and calibrated ^{14}C-ages used to derive the depth–age relationship of the Lac de Fully sediment sequence

Lab. code	Depth (cm)	Macrofossils selected for dating[a]	δ^{13}C (‰ PDB)	^{14}C age (±1σ)	Calibrated ^{14}C age (cal. BP)	2σ range (cal. yr BP)
P-I[b]	44	/	–	1500 ± 100	1400	1690–1190
Poz-10657[c]	43	indet. wood (–bark)	–21.2	5450 ± 40	6247	6310–6186
Dendro-90265[d]	100	*Larix*	–	–	4693	4703–4683
ETH-29190	124	*Larix*	–24.0	4600 ± 55	5316	5470–5054
Poz-10658	138	*Larix* N S, indet. BS	–30.7	5320 ± 40	6097	6266–5956
Poz-10660	171	*Larix* N S, *Betula* BS F, indet. bark	–29.1	6640 ± 40	7525	7581–7441
Poz-10661	191	*J. nana* N, *Larix* N	–32.4	7420 ± 40	8258	8343–8176
Poz-10662	241	*J. nana* N, *Dryas* L, indet. wood (+ bark), *Betula* F	–28.2	9390 ± 50	10 622	10 743–10 550

[a]Abbreviations: N, needle; S, seed; BS, budscale; F, fruit; L, leaf fragment; (+/– bark), with/without bark.
[b]P-I, pollen-inferred age based on the correlation of the Lac de Fully pollen record with the pollen stratigraphy in nearby Gouillé Rion (Tinner *et al.*, 1996).
[c]Rejected ^{14}C date.
[d]Dendrochronologically inferred age (see text for details).

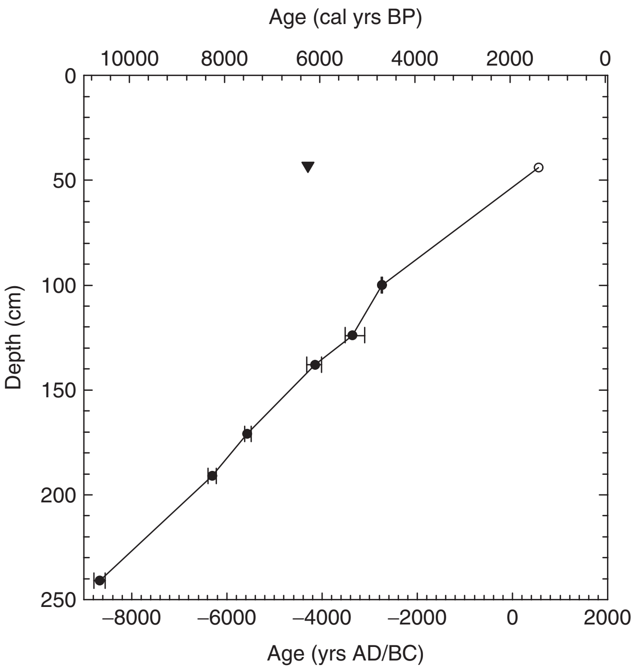

Figure 2 Depth–age relationship of the Lac de Fully sediment sequence. The error bars indicate calibrated 2σ ranges for the calibrated ^{14}C dates. Full circle, calibrated ^{14}C date; empty circle, pollen-inferred age; triangle, rejected ^{14}C date (see text and Table 2 for details)

at × 400 magnification. At least 300 pollen grains were counted for each pollen sample. The pollen key of Moore *et al.* (1991) and the photographic pollen atlas of Reille (1992, 1995) were used. Pollen percentages are referred to the sum of terrestrial pollen, which includes trees, shrubs, herbs and terrestrial ferns. Microcharcoal particles were counted on pollen slides following Tinner and Hu (2003) and Finsinger and Tinner (2005). Conifer stomata were identified following Trautmann (1953).

For plant-macrofossil analysis, 84 sediment samples were taken between 246 cm and 29 cm depth. Sediment volume was measured by water displacement before samples were soaked in pyrophosphate 5% for 1–2 h and washed through a 200 μm sieve. The residue was collected and stored in distilled water at –18°C to avoid contamination with recent carbon (Wohlfahrt *et al.*, 1998). Plant macrofossils were analysed with a binocular 10–50 × magnifications. Plant remains of 13 taxa were identified.

Plant macrofossils collected from five samples (Table 2) were washed twice in distilled water, dried overnight at 60°C, and analysed under the microscope for absence of recent carbon sources (eg, wool, cotton, fibres) before they were sent to the Poznan Radiocarbon Laboratory. In addition to these macrofossils, we used one dendrochronologically inferred age (No. 90265.0, M. Schmidhalter, personal communication, 2004) and one ^{14}C-age (No. 90266.0, M. Schmidhalter, personal communication, 2004), which estimate the age of death of two tree trunks present in the stratigraphy. All ^{14}C ages were calibrated to calendar ages using the Calib5 program and selecting the IntCal04 data set (Reimer *et al.*, 2004). The depth–age relationship was established with a linear interpolation of median probability ages (Figure 2). One ^{14}C age (at 43 cm depth) was rejected from the model because it appeared to be too old and was replaced with a pollen-inferred age estimate based on the first appearance and increase of *Castanea* pollen (Figure 3), which is dated to *c.* 1500 BP in radiocarbon-dated pollen records of that region (Tinner *et al.*, 1996).

The pollen data were zoned numerically with the optimal-sum-of-squares partitioning (Birks and Gordon, 1985). The application of a broken stick model (Bennett, 1996) showed four statistically significant pollen assemblage zones (PAZ). The plant-macrofossil data were zoned visually into five macrofossil assemblage zones (MAZ).

Results and interpretation

Pollen stratigraphy and vegetation history

The lowest pollen assemblage zone (FUY-1; ~11 000–7400 cal. BP; Figure 3) is dominated by *P. sylvestris*, *P. cembra* and *Corylus* pollen. High values of *Ulmus* pollen may suggest that, together with *Corylus*, these trees were fairly abundant on the mountain slopes at lower elevation. *Pinus*, *Larix* and *Juniperus* stomata attest to the presence of these trees and shrub taxa near the lake after *c.* 9000 cal. BP. *Alnus viridis* pollen was present in low amounts, suggesting the local (but rare) presence of the shrub in the area. Based on the pollen assemblages the base of this zone is attributed to the early Holocene.

Zone FUY-2 (*c.* 7400–4700 cal. BP) is characterized by high percentages of *Abies* and *P. cembra*, which were present in the lake catchment as suggested by the continuous presence of conifer stomata in the pollen slides. *Ulmus* percentages decrease during

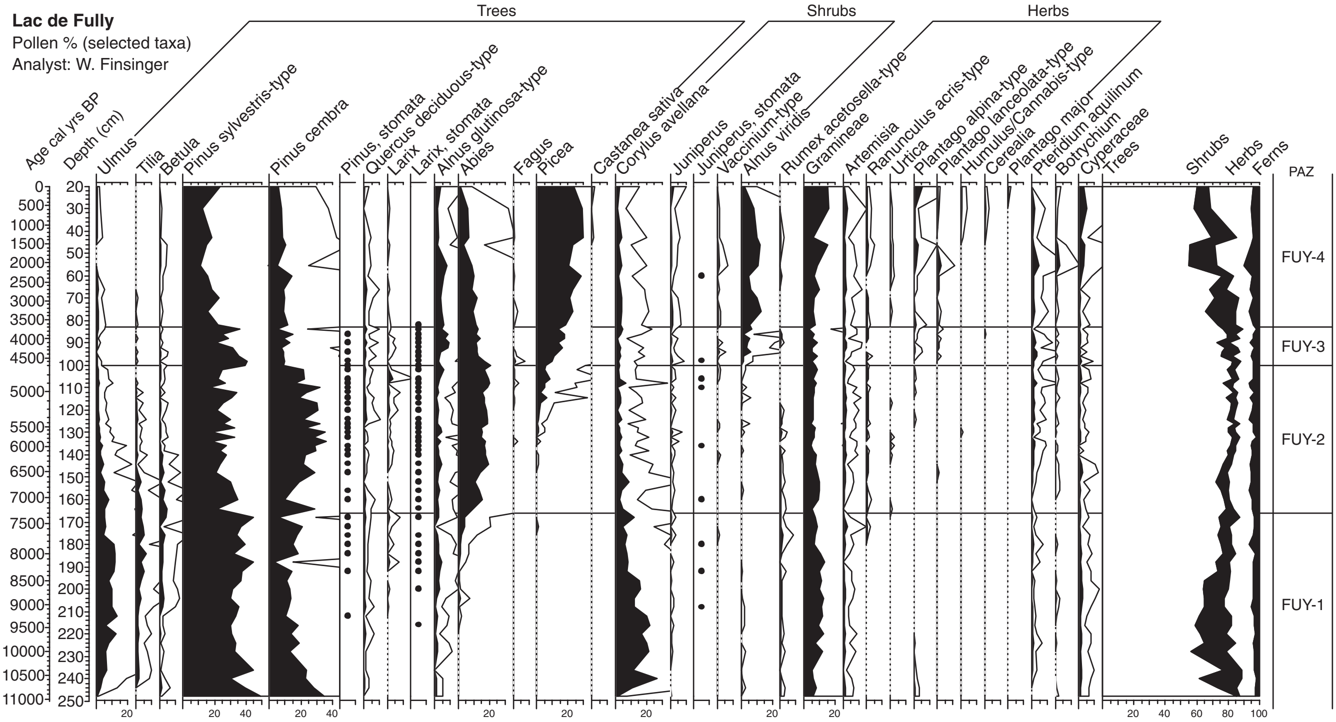

Figure 3 Pollen diagram for Lac de Fully. Only a selection of taxa are shown (the complete records are available from the authors). Zones refer to pollen assemblage zones (PAZ)

this zone, possibly indicating a continued forest reduction at lower altitudes. The presence of *Plantago lanceolata* and *Plantago alpina* pollen, two cultural indicators for agricultural activities (cf. Behre, 1981), may attest to human activities in the valley and possibly near the lake. Discontinuous presence and low percentages of *Urtica* pollen since the onset of this zone might be linked to grazing (cf. Behre, 1981) and nitrogen-rich soils on the mountain slopes, although, just as with *Plantago alpina*, the plant occurs also naturally in the area. In zone FUY-3 (*c*. 4700–3700 cal. BP) pollen values of *Picea* and *A. viridis* increased, while *Abies* and *P. cembra* percentages decreased. The complete collapse of the conifer forest in the lake catchment, however, can be ruled out because of the presence of conifer stomata (*Larix* and *Pinus*) in this zone. Human activities in the valley increased, as inferred from higher percentages of cultural indicators (eg, *P. lanceolata*, *P. alpina*). Zone FUY-4 (3700 cal. BP–present) is characterized by high percentages of *A. viridis* and *Picea*, lower percentages of *Larix* and *Pinus*, and the absence of conifer stomata.

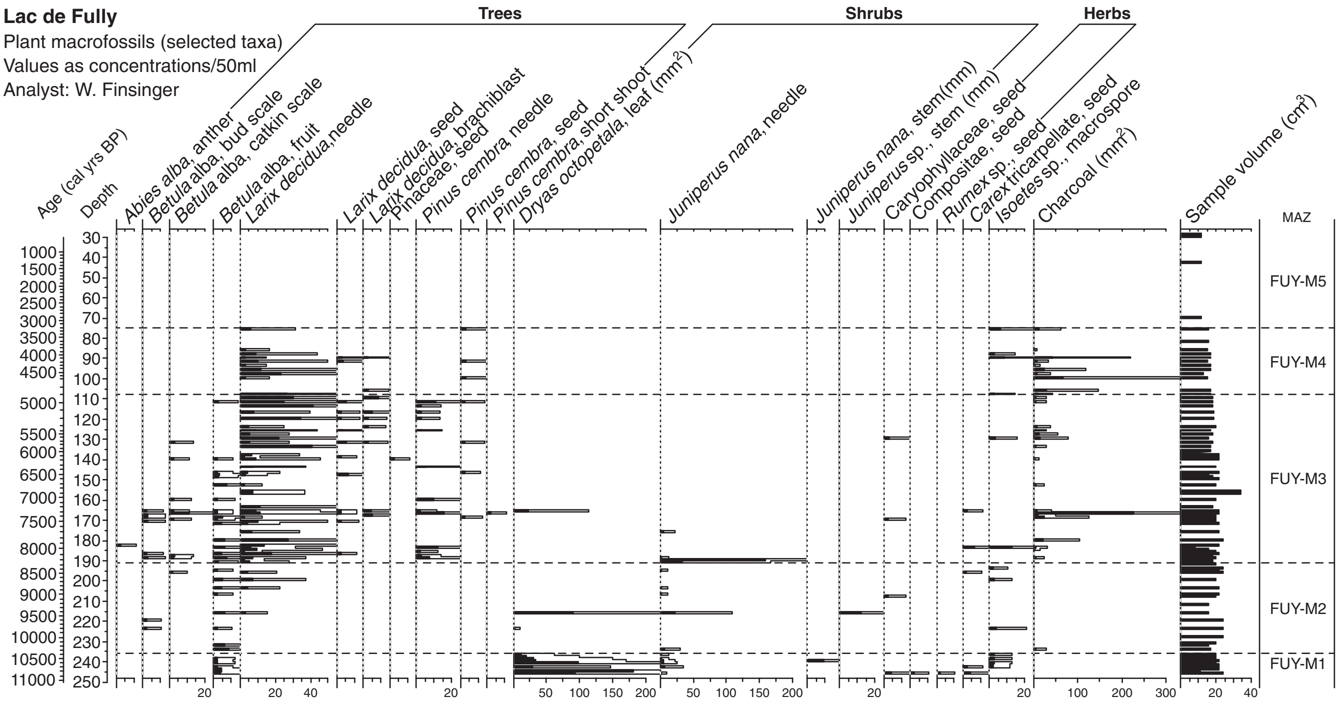

Figure 4 Macrofossil diagram for Lac de Fully. Only a selection of taxa are shown (the complete records are available from the authors). Zones refer to macrofossil assemblage zones (MAZ). Results are given as plant-macrofossil concentrations in 50 cm³

Macrofossil stratigraphy and local vegetation history

The first macrofossil zone (FUY-M1; 11 000–10 300 cal. BP) is initially dominated by alpine dwarfshrubs and shrubs (*Dryas octopetala* and *Juniperus nana*) and by tree birches (*Betula* ('*alba*')) (Figure 4), suggesting the presence of light-demanding trees, shrubs and heaths around the lake. In the second zone (FUY-M2; 10 300–8300 cal. BP), *Larix decidua* needles indicate stands of this coniferous tree near the lake. Macroscopic charcoal fragments are absent in all samples. After 8300 cal. BP (onset of FUY-M3) the macrofossil assemblage is dominated by remains of coniferous trees (*P. cembra*, *Larix*) and *Betula* ('*alba*'), indicating the establishment of rather closed forests around the lake. At the onset of this zone high concentrations of *J. nana* needles occur, suggesting that the establishment of forests was preceded by the formation of rather dense *J. nana* heaths around the lake. Macroscopic charcoal fragments are present in many samples, and three of them were identified as *Larix*/*Picea* (166 cm and 180 cm) and *P. cembra* (167 cm), indicating that local forest fires occurred around the lake. Because of the virtual absence of *Abies* macrofossils, we infer that this species never really played a major role in the forest vegetation at the elevation of Lac de Fully. The only evidence for the presence of *Abies* near the lake is given by one single anther (identified through its pollen content), which could have been transported by wind. Zone FUY-M4 (4900–3200 cal. BP) is characterized by high concentrations of *Larix* and charcoal fragments, the absence of *Betula* remains and only few *P. cembra* seeds, suggesting that heliophilous *Larix* stands or forests prevailed around the lake. Plant macrofossils such as leaves, needles and fruits are lacking in the uppermost zone (FUY-M5; < 3200 cal. BP), and the wood fragment at 43 cm depth (as inferred from the ^{14}C date, Table 2) might be so old because of the longer terrestrial residence time of wood.

Discussion

In mountain regions pollen spectra at high altitude also contain pollen grains produced by plants growing in vegetation belts at lower elevations and thus do not reflect the local vegetation accurately. Therefore, inferences on changes in vegetation composition and treeline elevation are substantially improved by considering plant macrofossils (Birks and Birks, 2000; Tinner and Theurillat, 2003). In the Lac Supérieur de Fully record, however, pollen, stomata and plant macrofossils of *Betula*, *Larix* and *P. cembra* show similar changes in their abundances (Figure 5). We may therefore infer that changes in pollen percentages of these timberline species were not primarily influenced by changes in pollen productivity (Autio and Hicks, 2004) but by changes in population densities of the timberline forests, which is in agreement with recent modelling results (Heiri *et al.*, 2006).

Vegetation response to long-term climate change

The general trend observed at many high-elevation sites (> 1600–1800 m a.s.l.) in the Alps involves afforestation at the beginning of the Holocene and a subsequent decline of the timberline by several 100 m at *c.* 5000 cal. BP (Burga and Perret, 1998). It resulted mainly from climatic changes that were probably coupled to changes in summer and winter insolation (Tinner and Kaltenrieder, 2005) as well as from human disruption of forests, which led to an artificial lowering of the timberline after *c.* 5000 cal. BP (Tinner and Theurillat, 2003). This long-term trend is also reflected in the pollen and macrofossil record from Lac de Fully (Figures 3, 4 and 5): an open alpine vegetation dominated by shrubs (*Dryas octopetala* and *J. nana*) was followed by an open treeline condition with shrubs and sparse trees (*Betula* and *Larix*) since 9500 cal. BP. Then, at *c.* 8300 cal. BP, *P. cembra* and *Larix* expanded in the catchment, indicating the maximum expansion of timberline, which dominated the local vegetation and the highland plateau until *c.* 3500 cal. BP.

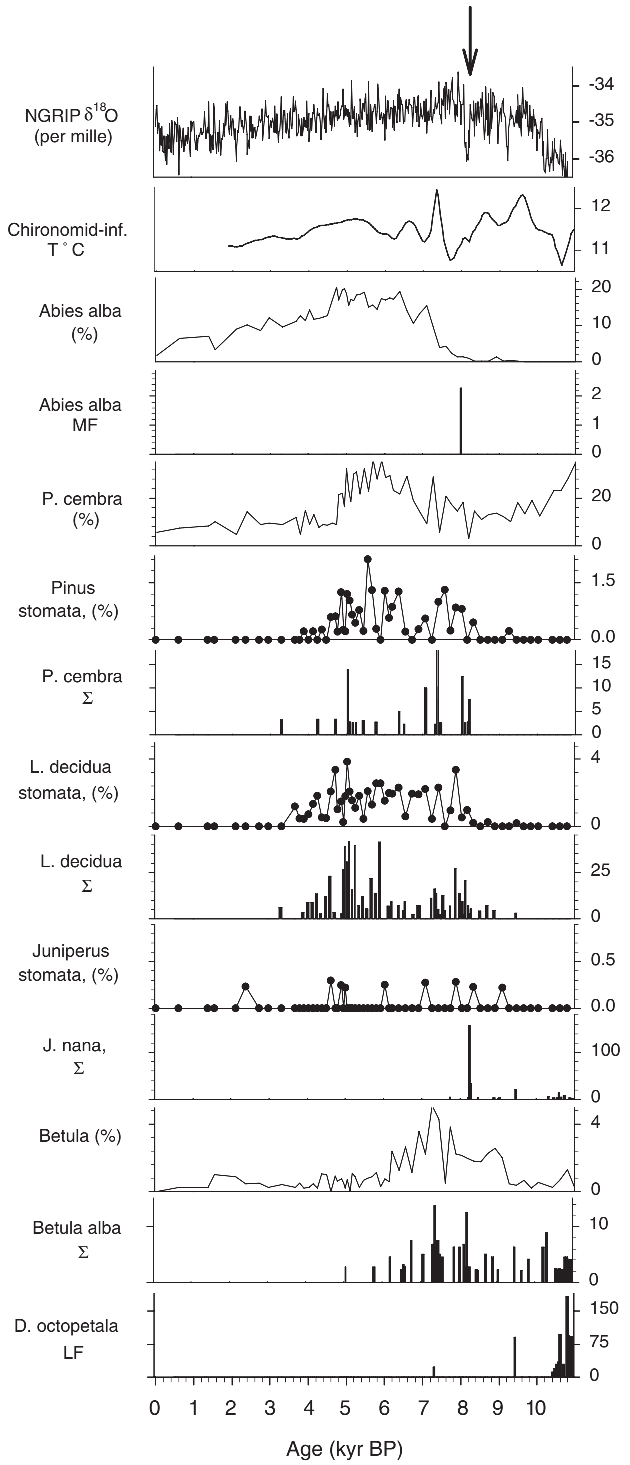

Figure 5 Comparison between early and middle Holocene forest dynamics at Lac de Fully, a proxy record for summer air temperature in the Alps (Heiri *et al.*, 2004), and δ^{18}O in Greenland (Rasmussen *et al.*, 2006). Plant macrofossils (histograms), pollen (line), stomata (line with solid circles) of selected taxa. Arrow (top) indicates the 8.2 ka event in the ice-core record

Vegetation response to the abrupt climate change at 8.2 ka

Superimposed on the long-term millennial climatic trend, which primarily resulted from variations in the Earth's orbit, centennial-scale abrupt climatic changes occurred. Among these abrupt climate changes, the '8.2 ka event' (Wick and Tinner, 1997; Alley *et al.*, 1997; Rohling and Pälike, 2005) stands out as being one of the most pronounced and probably therefore most studied abrupt climatic changes that occurred during the Holocene. The existence of a unique event at *c*. 8200 cal. BP around the North Atlantic is no longer in question, but there remain uncertainties about how widespread the anomalies were and how well the length, duration and character of the event can be characterized (Alley and Àgust-dòttir, 2005; Rohling and Pälike, 2005; Nesje *et al.*, 2006). The currently favoured hypothesis is that these anomalies were related to a transient change in the North Atlantic overturning circulation (Came *et al.*, 2007), possibly triggered by the final drainage of Lake Agassiz (eg, Nesje *et al.*, 2004). The isotope data suggest a climate cooling of ~1.7°C in mean-annual air temperature in Central Europe (von Grafenstein *et al.*, 1998). In the Alps a chironomid-inferred July air-temperature decrease of ~1°C at high elevation shows a close temporal agreement with the 8.2 ka event in the Greenland ice-core records, but suggests that the cooling in the Alps may have been protracted by several centuries (Heiri *et al.*, 2003, 2004; Figure 5). A similar feature is indicated also in a speleothem $\delta^{18}O$ record of the Spannagel Cave (Vollweiler *et al.*, 2006), where the greatest positive $\delta^{18}O$ anomaly (possibly indicating colder temperatures) occurred after 8000 cal. BP and was followed by a rapid climate warming.

The abrupt climate change at 8200 cal. BP had important effects in the shaping of vegetation in Central Europe during the Holocene (Tinner and Lotter, 2001), and it caused an unambiguous lowering of the timberline in the Central Alps (Wick and Tinner, 1997; Haas *et al.*, 1998; Tinner and Kaltenrieder, 2005). On the basis of the macrofossil record, it seems likely that at Lac de Fully the short-term increase of *J. nana* and collapse of the open *Larix* forest at *c*. 8200 cal. BP may indicate the response of local vegetation to the abrupt climate change at 8.2 ka that was very soon followed by the expansion of *P. cembra* and *Larix* near the site. A similar pattern has been observed at Gouillé Rion (2343 m a.s.l.), where the collapse of *Larix* occurred at *c*. 8400–8300 cal. BP (Tinner and Kaltenrieder, 2005). The subsequent expansion of *P. cembra* that led to the dominance of the species at Gouillé Rion took place at *c*. 8300–8200 cal. BP (Tinner and Kaltenrieder, 2005).

In contrast to other records in the Valais, early Holocene afforestation at Lac de Fully was delayed by several millennia: *Larix* remains are absent until 9500 cal. BP and *P. cembra* remains are absent until 8300 cal. BP, while at Gouillé Rion (2343 m a.s.l.) alpine grasslands were afforested by *Larix* and *J. nana c*. 11 000 cal. BP and *P. cembra* expanded at *c*. 10 000 cal. BP (Tinner and Kaltenrieder, 2005). Also at lower elevation, macrofossil-inferred afforestation occurred earlier than at Lac de Fully: at Böhnigsee (*c*. 2100 m a.s.l.; Markgraf, 1969) and at Simplon (*c*. 2050 m a.s.l.; Lang and Tobolski, 1985) timberline rose above these lakes around 11 000 cal. BP (Tinner and Theurillat, 2003). It is highly unlikely that the difference in the timing of afforestation by *P. cembra* and *Larix* depended on the low speed of spread of these species (see discussion in Tinner and Kaltenrieder, 2005) or on climatic gradients producing shorter growing-season lengths at Lac de Fully. Instead, the late expansion of *Larix* and *P. cembra* may be explained by the local climatic conditions involving either higher drought stress or shorter growing-season length at Lac de Fully that inhibited their growth in the catchment of the lake. The late appearance of *P. cembra* might be related to its higher drought-stress intolerance than *Larix*, *Dryas* and *J. nana. Larix* sheds its needles in winter, and the two shrubs take advantage of the thermal insulation of snow in late winter, while *P. cembra* needles are fully exposed to late winter drought stress (Körner, 1999; Tinner and Kaltenrieder, 2005). However, slope contrasts may come into play in low-stature plant cover, when oceanicity, snow pack or general moisture gradients are important, as was shown for subarctic-birch treelines and as can be seen in some very dry parts of central Asia or northern Chile (Körner and Paulsen, 2004). Alternatively, cold-air retention at the bottom of the former glacier cirque might have caused lower soil temperatures, which have a negative influence on tree growth (Körner and Paulsen, 2004; Körner and Hoch, 2006).

Surprisingly, tree-species that had established at the timberline and at lower elevation after 8200 cal. BP were significantly different from those that were growing there before. Thus, synchronously with the expansion of *P. cembra* and *Larix* at the timberline, *Abies* expanded at lower elevation (Figure 5). We suggest that the expansion of *Abies*, as inferred from the Lac de Fully pollen record, may indicate that drought stress in the Central Alps was lower after 8200 cal. BP. In effect, it is likely that *Abies* (and *Fagus*) in Central Europe were at their physiological drought limit during the early Holocene (Tinner and Lotter, 2001), when negative precipitation anomalies occurred (< −400 mm annual precipitation in comparison with today; Guiot *et al.*, 1993) and seasonality was enhanced because of higher summer insolation and lower winter insolation (Kutzbach and Webb, 1993). The successful expansion of *A. alba* and *Fagus* in the lowlands of Central Europe further suggests that after 8200 cal. BP climatic conditions did not return to the early Holocene mode with its frequent (summer) droughts and (spring) frosts, which favoured the abundance of *Corylus* (Tinner and Lotter, 2001; Finsinger *et al.*, 2006).

Although some proxies of climatic change do not show a significant difference in climatic conditions before and after the 8.2 ka event (eg, the $\delta^{18}O$ record of Greenland ice-cores, Figure 5), indications for the onset of warmer climatic conditions after 8200 cal. BP can be derived from chironomid-inferred temperatures (Heiri *et al.*, 2003; Figure 5), from a stalagmite record in the Central Alps (Vollweiler *et al.*, 2006) and from the elevation of treeline as inferred from dendrochronologically dated subfossil logs in the Austrian Alps (Nicolussi *et al.*, 2005). In the Northern Alps, based on the evidence of a more temperate aquatic fauna at Bachalpsee, Lotter *et al.* (2006) suggest that warmer and/or longer summers could have favoured the expansion of *Abies* at 8400 cal. BP below timberline. A change towards a different climate regime around 8200 cal. BP has been suggested for Fennoscandia (Seppä and Birks, 2001; Seppä *et al.*, 2005) by means of pollen-based summer temperature reconstructions and from $\delta^{18}O$ records of lake carbonates. Seppä *et al.* (2005) suggested that the maritime climate mode that dominated until 8200 cal. BP in Fennoscandia was followed by a stable 'Holocene thermal maximum', which was characterized by higher annual temperatures and by markedly drier conditions. This enduring climatic change in Scandinavia may have been coupled to a shift towards oceanic and wetter conditions in Central Europe (Tinner and Lotter, 2006).

Despite the wealth of palaeobotanical data for change in vegetation composition at low elevation in Central Europe (Tinner and Lotter, 2001) and for timberline fluctuations in the Alps (eg, Tinner *et al.*, 1996; Haas *et al.*, 1998; Heiri *et al.*, 2004), little is known concerning vegetation dynamics below timberline in response to abrupt climate changes. Results of modelling studies indicate that forests just below the treeline seem to be in a continuous state of change, involving dieback of trees in response to temperature decreases, after which more cold-adapted species can take advantage of reduced competition (Heiri *et al.*, 2006). The time-resolution of the pollen and macrofossil records at Lac de Fully is probably not sufficiently high to reflect the reforestation succession in response to a centennial-scale temperature decrease. On the other hand, our results may indicate that vegetation near the modern timberline and below this elevation responded rapidly to the climate warming after *c*. 8200 cal. BP, allowing the observed expansions of *Abies alba* and *Pinus cembra*. It suggests also that moisture and/or local

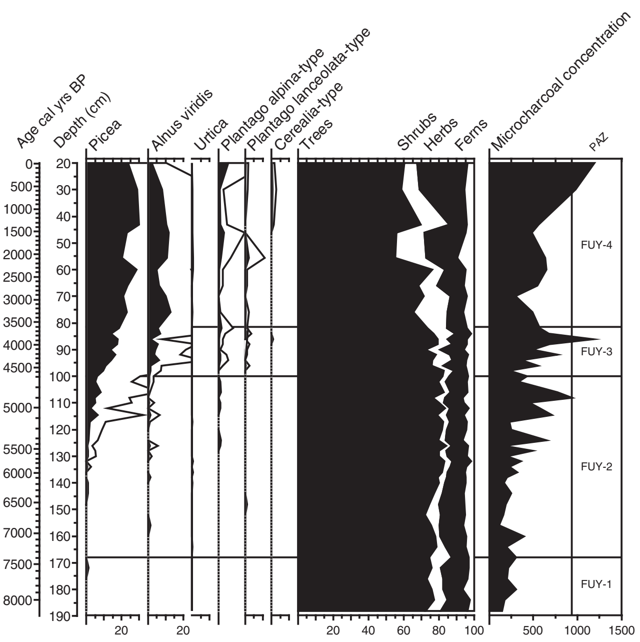

Figure 6 Selected pollen taxa and microcharcoal concentration (no. charcoal fragments/cm^3) for Lac de Fully

topography may play an important role in vegetation dynamics at timberlines in mountain regions.

The demise of timberline forests as a result of human impact at Lac de Fully

The first regular appearance of Cerealia t. pollen at lower elevation in the Valais is dated to 7000 cal. BP (Welten, 1982; van der Knaap and Ammann, 1997). However, unambiguous archaeological evidence for Neolithic land use was found in Sion and is dated to *c*. 7450 cal. BP (Stöckli, 1995). First signs of human activities in the Lac de Fully pollen record are provided by pollen of cultural indicators that are present starting from ~7300 cal. BP (*Urtica* pollen), though land use became intensive only at around *c*. 4500 cal. BP (Figures 3 and 6). This finding is in agreement with other pollen records from the Valais (eg, Welten, 1982; Tinner *et al.*, 1996), which suggest that agricultural activities intensified at the time of the Neolithic/Bronze Age transition at high elevation in the Valais region and elsewhere in the Alps (eg, Gobet *et al.*, 2003; Lotter *et al.*, 2006).

Pollen and macrofossils indicate that until 3500 cal. BP timberline forests were not disrupted by human impact. However, the forest at the timberline started to be opened around 4700 cal. BP (Figure 5), and the tree population decreased abruptly around 3500 cal BP at Lac de Fully. This pattern is typical for the Valais region, where the timberline lowered by about 300 m at 4700 cal. BP and was below 2100 m at *c*. 4000 cal. BP (Tinner and Theurillat, 2003). Palaeoecological and modelling evidence (Heiri *et al.*, 2006) suggest that human impact was the primary cause of this timberline collapse. In contrast, treeline remained more or less stable, and it decreased by about only 100 m after 4700 cal. BP (Tinner and Theurillat, 2003). At Lac de Fully *Picea*, a subalpine tree, was more abundant after 4500 cal. BP than before, which is in agreement with other findings in the Valais (eg, Tinner *et al.*, 1996). Spruce forests were probably placed at altitudes < 2000 m a.s.l., and it has been hypothesized that spruce was able to expand in response either to climatic change or to human impact (eg, Markgraf, 1970; Heiri *et al.*, 2006).

Based on the pollen record, three distinct phases of human impact were distinguished. Between 3700–2600 cal. BP treeline was below Lac Supérieur de Fully, *A. viridis* expanded and grazing indicators (eg, *P. alpina*) were reduced. This might indicate a lessening of human impact and a reoccupation of abandoned areas by *A. viridis* that was later followed by *Picea*. However, it has been also hypothesized that the widespread expansion of *A. viridis* in the Valais was a consequence of land-use change and increased fire frequencies (cf. Welten, 1982; Tinner *et al.*, 1996; Gobet *et al.*, 2003). In agreement, microcharcoal values increased towards the top of this zone, indicating increasing regional fire activity (Figure 6). A second and clearer phase of human impact is indicated by higher percentages of *P. alpina*, *P. lanceolata* and *Urtica* pollen from *c*. 2000 to 1500 cal. BP. Also the higher abundance of *Botrychium* spores suggests more open ground near the lake (Figure 3). In addition, an opening of the spruce forest at lower elevation may be inferred from the decrease of *Picea* pollen and the increase of *Vaccinium* and *A. viridis* pollen. The last human-impact phase (younger than 1500 cal. BP) is characterized by Cerealia and *Humulus/Cannabis* pollen, which attest to the expansion of agriculture at lower altitudes. Timberline during this phase was further decreased, as can be inferred from lower *A. viridis*, *Picea*, *Abies* and *P. cembra* and increasing amounts of herb pollen. The increase of microscopic charcoal towards the top of the sequence (Figure 6) probably indicates that forest disruptions were partly caused by fire.

Conclusions

Pollen, stomata and plant-macrofossil analyses at Lac Supérieur de Fully (2135 m a.s.l.) indicate that the lake was located below the timberline from *c*. 9200 to 3500 cal. BP and that after, at latest, 4700 cal. BP vegetation around Lac Supérieur de Fully primarily responded to human impact. Maximum forest cover occurred after 8200 cal. BP, when *P. cembra*, *Larix* and *Abies* forests expanded on the south-exposed highland plateau or below. In comparison with other records in the Central Alps, at Lac Supérieur de Fully initial afforestation was delayed by several millennia. It is suggested that this change in vegetation was a response to the onset of a different climate mode, which began after *c*. 8200 cal. BP and involved less frequent droughts and spring frosts than during the early Holocene (Tinner and Lotter, 2001; Finsinger *et al.*, 2006). Possibly local factors such as the position on a south-facing and the kettle-shaped highland plateau played a role by inhibiting, because of increased drought stress, the establishment of trees until 8200 cal. BP at Lac de Fully. It is noticeable that the late early-Holocene afforestation at Lac Supérieur de Fully was only recognized because of earlier studies in nearby regions. Thus, a network of well-studied and well-dated sites is important for studying spatial patterns of population expansion and noticing local climatic effects.

Acknowledgements

We wish to thank Philippe Curdy, Oliver Heiri and Lukas Zimmermann for discussions, Martin Schmidthalter for dendro-dating, Florencia Oberli for preparing the pollen samples and Herb Wright Jr for linguistic improvements. Financial support from the Musée Cantonal d'Histoire Naturelle (Sion, Valais; WF) is greatly acknowledged. We are further indebted to Hilary Birks and an anonymous reviewer for fruitful comments. This is Netherlands Research School of Sedimentary Geology no. 2007.06.04.

References

Alley, R.B. and **Àgustdòttir, A.M.** 2005: The 8k event: cause and consequences of a major Holocene abrupt climate change. *Quaternary Science Reviews* 24, 1123–49.

Alley, R.B., Mayewski, P.A., Sowers, T., Stuiver, M., Taylor, K.C. and **Clark, P.U.** 1997: Holocene climatic instability: a prominent, widespread event 8200 yr ago. *Geology* 25, 483–86.

Autio, J. and **Hicks, S.** 2004: Annual variations in pollen deposition and meteorological conditions on the fell Aakenustunturi in northern Finland: potential for using fossil pollen as a climate proxy. *Grana* 43, 31–47.

Behre, K.-E. 1981: The interpretation of anthropogenic indicators in pollen diagrams. *Pollen et Spores* 23, 225–45.

Bennett, K.D. 1996: Determination of the number of zones in a biostratigraphical sequence. *New Phytologist* 132, 155–70.

Birks, H.H. and **Birks, H.J.B.** 2000: Future uses of pollen analysis must include plant macrofossils. *Journal of Biogeography* 27, 31–35.

Birks, H.J.B. and **Gordon, A.D.** 1985: *Numerical methods in Quaternary pollen analysis*. Academic Press.

Burga, C.A. and **Perret, R.** 1998: *Vegetation und Klima der Schweiz seit dem Jüngeren Eiszeitalter*. Ott Verlag.

Came, R.E., Oppo, D.W. and **McManus, J.F.** 2007: Amplitude and timing of temperature and salinity variability in the subpolar North Atlantic over the past 10 k.y. *Geology* 35, 315–18. doi: 10.1130/G23455A.1.

Carnelli, A.L., Theurillat, J.-P., Thinon, M., Vadi, G. and **Talon, B.** 2004: Past uppermost tree limit in the Central European Alps (Switzerland) based on soil and soil charcoal. *The Holocene* 14, 393–405.

Carrara, P.E., Trimble, D.A. and **Rubin, M.** 1991: Holocene treeline fluctuations in the northern San-Juan Mountains, Colorado, USA, as indicated by radiocarbon-dated conifer wood. *Arctic and Alpine Research* 23, 233–46.

Finsinger, W. and **Tinner, W.** 2005: Minimum count sums for charcoal-concentration estimates in pollen slides: reliability and potential errors. *The Holocene* 15, 293–97.

Finsinger, W., Tinner, W., van der Knaap, W.O. and **Ammann, B.** 2006: The expansion of hazel (*Corylus avellana* L.) in the southern Alps: a key for understanding its early Holocene history in Europe? *Quaternary Science Reviews* 25, 612–31.

Gobet, E., Tinner, W., Hochuli, P.A., van Leeuwen, J.F.N. and **Ammann, B.** 2003: Middle to Late Holocene vegetation history of the Upper Engadine (Swiss Alps): the role of man and fire. *Vegetation History and Archaeobotany* 12, 143–63.

Guiot, J., Harrison, S. and **Prentice, I.C.** 1993: Reconstruction of Holocene precipitation patterns in Europe using pollen and lake-level data. *Quaternary Research* 40, 139–49.

Haas, J.N., Richoz, I., Tinner, W. and **Wick, L.** 1998: Synchronous Holocene climatic oscillations recorded on the Swiss Plateau and at timberline in the Alps. *The Holocene* 8, 301–309.

Heiri, C., Bugmann, H., Tinner, W., Heiri, O. and **Lischke, H.** 2006: A model-based reconstruction of Holocene treeline dynamics in the Central Swiss Alps. *Journal of Ecology* 94, 206–16. doi: 10.1111/j.1365-2745.2005.01072.x.

Heiri, O., Lotter, A.F., Hausmann, S. and **Kienast, F.** 2003: A chironomid-based Holocene summer air temperature reconstruction from the Swiss Alps. *The Holocene* 13, 477–84.

Heiri, O., Tinner, W. and **Lotter, A.F.** 2004: Evidence for cooler European summers during periods of changing melt-water flux to the North Atlantic. *Proceedings of the National Academy of Sciences of the United States of America* 101, 15 285–88.

Kaltenrieder, P., Tinner, W. and **Ammann, B.** 2005: Long-term vegetation history at timberline in the Swiss Alps (Alpe d'Essertse, VS). *Botanica Helvetica* 115, 137–54.

Körner, C. 1999: *Alpine plant life*. Springer.

Körner, C. and **Hoch, G.** 2006: A test on treeline theory on a montane permafrost island. *Arctic, Antarctic, and Alpine Research* 38, 113–19.

Körner, C. and **Paulsen, J.** 2004: A world-wide study of high altitude treeline temperatures. *Journal of Biogeography* 31, 713–32.

Kullman, L. 1995: Holocene tree-limit and climate history from the Scandes-Mountains, Sweden. *Ecology* 76, 2490–502.

—— 2002: Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. *Journal of Ecology* 90, 68–77.

Kutzbach, J.E. and **Webb, T., III** 1993: Conceptual basis for understanding late-Quaternary climates. In Wright, H.E.J., Kutzbach, J.E., Webb, T., III, Ruddiman, W.F., Street-Perrott, F.A. and Bartlein, P.J., editors, *Global climates since the Last Glacial Maximum.* University of Minnesota Press, 5–11.

Landolt, E. 1992: *Unsere Alpenflora*. Gustav Fisher.

Lang, G. and **Tobolski, K.** 1985: Hobschensee – Late-Glacial and Holocene environment of a lake near the timberline. In Lang G., editor *Swiss lake and mire environments during the last 15,000 years*. Dissertationes Botanicae. J. Cramer, 209–28.

Lotter, A.F., Heiri, O., Hofmann, W., van der Knaap, W.O., van Leeuwen, J.F.N., Walker, I.R. and **Wick, L.** 2006: Holocene timberline dynamics at Bachalpsee, a lake at 2265 m a.s.l. in the northern Swiss Alps. *Vegetation History and Archaeobotany* 15, 295–307.

Markgraf, V. 1969: Moorkundliche und vegetationsgeschichtliche Untersuchungen an einem Moorsee and der Waldgrenze im Wallis. *Botanische Jahrbücher* 89, 1–63.

—— 1970: Palaeohistory of the Spruce in Switzerland. *Nature* 228, 249–51.

Menzel, A. and **Fabian, P.** 1999: Growing season extended in Europe. *Nature* 397, 659.

Moore, P.D., Webb, J.A. and **Collinson, M.E.** 1991: *Pollen analysis*. Blackwell Science Ltd.

Nesje, A., Dahl, S.O. and **Bakke, J.** 2004: Were abrupt Lateglacial and early-Holocene climatic changes in northwest Europe linked to freshwater outbursts to the North Atlantic and Arctic Oceans? *The Holocene* 14, 299–310.

Nesje, A., Bjune, A.E., Bakke, J., Dahl, S.O., Lie, O. and **Birks, H.J.B.** 2006: Holocene palaeoclimate reconstructions at Vanndalsvatnet, western Norway, with particular reference to the 8200 cal. yr BP event. *The Holocene* 16, 717–29. doi:10.1191/0959683606hl954rp.

Nicolussi, K., Kaufmann, M., Patzelt, G., van der Plicht, J. and **Thurner, A.** 2005: Holocene tree-line variability in the Kauner Valley, Central Eastern Alps, indicated by dendrochronological analysis of living trees and subfossil logs. *Vegetation History and Archaeobotany* 14, 221–34.

Parmesan, C. 2006: Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics* 37, 637–69, doi: 10.1146/annurev.ecolsys.37.091305.110100.

Rasmussen, S.O., Andersen, K.K., Svensson, A.M., Steffensen, J.P., Vinther, B.M., Clausen, H.B., Siggaard-Andersen, M.-L., Johnsen, S.J., Larsen, L.B., Dahl-Jensen, D., Bigler, M., Röthlisberger, R., Fischer, H., Goto-Azuma, K., Hansson, M.E. and **Ruth, U.** 2006: A new Greenland ice core chronology for the last glacial termination. *Journal of Geophysical Research* 111, D06102, doi:10.1029/2005JD006079.

Reille, M. 1992: *Pollen et spores d'Europe et d'Afrique du nord*. Laboratoire de Botanique Historique et Palynologie.

—— 1995: *Pollen et spores d'Europe et d'Afrique du Nord – supplement 1*. Laboratoire de Botanique Historique et Palynologie.

Reimer, P.J., Baillie, M.G.L., Bard, E., Bayliss, A., Beck, J., Bertrand, C.J.H., Blackwell, P.G., Buck, C.E., Burr, G.S., Cutler, K.B., Damon, P.E., Edwards, R.L., Fairbanks, R.G., Friedrich, M., Guilderson, T.P., Hogg, A.G., Hughen, K.A., Kromer, B., McCormac, G., Manning, S., Ramsey, C.B., Reimer, R.W., Remmele, S., Southon, J.R., Stuiver, M., Talamo, S., Taylor, F.W., van der Plicht, J. and **Weyhenmeyer, C.E.** 2004: IntCal04 terrestrial radiocarbon age calibration, 0–26 cal kyr BP. *Radiocarbon* 46, 1029–58.

Rohling, E.J. and **Pälike, H.** 2005: Centennial-scale climate cooling with a sudden cold event around 8,200 years ago. *Nature* 434, 975–79.

Seppä, H. and **Birks, H.J.B.** 2001: July mean temperature and annual precipitation trends during the Holocene in the Fennoscandian treeline area: pollen-based climate reconstructions. *The Holocene* 11, 527–39.

Seppä, H., Hammarlund, D. and **Antonsson, K.** 2005: Low-frequency and high-frequency changes in temperature and effective humidity during the Holocene in south-central Sweden: implications for atmospheric and oceanic forcings of climate. *Climate Dynamics* 25, 285–97.

Steiger, P. 1995: *Wälder der Schweiz*. Ott Verlag.

Stöckli, W.E. 1995: Geschichte des Neolithikums in der Schweiz. In Stöckli, W.E., Niffeler, U. And Gross-Klee, E., editors, *Die Schweiz vom Paläolithikum bis zum frühen Mittelalter – Neolithikum*. Schweizerische Gesellschaft für Ur- und Frühgeschichte, 19–52.

Stockmarr, J. 1971: Tablets with spores used in absolute pollen analysis. *Pollen et Spores* 13, 615–21.

Tinner, W. and **Hu, F.S.** 2003: Size parameters, size-class distribution and area–number relationship of microscopic charcoal: relevance for fire reconstruction. *The Holocene* 13, 499–505.

Tinner, W. and **Kaltenrieder, P.** 2005: Rapid responses of high-mountain vegetation to early Holocene environmental changes in the Swiss Alps. *Journal of Ecology* 93, 936–47.

Tinner, W. and **Lotter, A.F.** 2001: Central European vegetation response to abrupt climate change at 8.2 ka. *Geology* 29, 551–54.

—— 2006: Holocene expansions of *Fagus silvatica* and *Abies alba* in Central Europe: where are we after eight decades of debate? *Quaternary Science Reviews* 25, 526–49.

Tinner, W. and **Theurillat, J.-P.** 2003: Uppermost limit, extent, and fluctuations of the timberline and treeline ecotone in the Swiss Central Alps during the past 11,500 years. *Arctic, Antarctic, and Alpine Research* 35, 158–69.

Tinner, W., Ammann, B. and **Germann, P.** 1996: Treeline fluctuations recorded for 12,500 years by soil profiles, pollen, and plant macrofossils in the Central Swiss Alps. *Arctic and Alpine Research* 28, 131–47.

Trautmann, W. 1953: Zur Unterscheidung fossiler Spaltöffnungen der mitteleuropäischen Coniferen. *Flora* 140, 523–33.

van der Knaap, W.O. and **Ammann, B.** 1997: Depth–age relationships of 25 well-dated Swiss Holocene pollen sequences archived in the Alpine Palynological Data-Base. *Revue de Paléobiologie, Genève* 16, 433–80.

Vollweiler, N., Scholz, D., Mühlinghaus, C., Mangini, A. and **Spötl, C.** 2006: A precisely dated climate record for the last 9 kyr from three high alpine stalagmites, Spannagel Cave, Austria. *Geophysical Research Letters* 33, L20703, doi: 10.1029/2006GL027662.

von Grafenstein, U., Erlenkeuser, H., Müller, J., Jouzel, J. and **Johnsen, S.** 1998: The cold event 8200 years ago documented in oxygen isotope records of precipitation in Europe and Greenland. *Climate Dynamics* 14, 73–81.

Welten, M. 1982: Vegetationsgeschichtliche Untersuchungen in den westlichen Schweizer Alpen: Bern-Wallis. *Denkschrift der Schweizerischen Naturforschenden Gesellschaft* 95, 1–104.

Wick, L. and **Tinner, W.** 1997: Vegetation changes and timberline fluctuations in the Central Alps as indicators of Holocene climatic oscillations. *Arctic and Alpine Research* 29, 445–58.

Wohlfahrt, B., Skog, G., Possnert, G. and **Holmquist, B.** 1998: Pitfalls in the AMS radiocarbon-dating of terrestrial macrofossils. *Journal of Quaternary Science* 13, 137–45.

Zweifel, R., Zimmermann, L., Zeugin, F. and **Newbery, D.M.** 2006: Intra-annual radial growth and water relations of trees: implications towards a growth mechanism. *Journal of Experimental Botany* 57, 1445–59.