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ORIGINAL ARTICLE

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Holocene timber-line dynamics at Bachalpsee, a lake at 2265 m a.s.l. in the northern Swiss Alps

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Abstract Palaeobotanical analysis and radiocarbon dating of lake sediments from Bachalpsee (2265 m a.s.l.), a small lake above the present-day timber-line in the northern Swiss Alps reveals that the region was already deglaciated during the Younger Dryas. The sediment record is dominated by long-distance transported pollen that originates from lowland vegetation but the plant macrofossils give evidence of the local vegetation development. Comparison with palaeobotanical results from three sites along an altitudinal transect permits the reconstruction of the regional timber-line history. Throughout the entire Holocene the catchment of Bachalpsee consisted of a mosaic of open meadows and dwarf shrubs (*Salix, Vaccinium, Rhododendron*). Chironomid and cladoceran assemblages suggest that the early to mid-Holocene was the warmest interval at Bachalpsee. Comparison of the palaeobotanical results with those from the mire "Feld" (2130 m a.s.l.) in the vicinity of Bachalpsee showed that during the mid-Holocene the timber-line was formed by *Pinus cembra* and *Picea abies* with some scattered *Abies alba* trees and was situated close to Bachalpsee but never reached its catchment. The maximum timber-line in the Northern Alps was reached between 6000 and 3000 cal B.P. which is several millennia later than in the Central Alps. The species composition of the tree-line (*Abies alba, Pinus cembra* and the absence of *Larix decidua*) points to less continental and moister climatic conditions compared with the central Alps during the early to mid-Holocene. From 3000 cal B.P. onwards the timber-line was lowered by human deforestation with the most intense pulses of human impact occurring since the Middle Ages. The catchment of Bachalpsee has been used as alpine pasture since the Bronze Age.

Keywords Tree-line fluctuations · Holocene · Northern Swiss Alps · Palaeolimnology · Plant macrofossils

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Introduction

The Alps are characterised by steep climatic gradients and as a consequence many different ecosystems can be encountered in a short geographical distance. The transitions between these ecosystems are typical elements in such mountainous landscapes. The most conspicuous landscape boundary in the Alps is certainly the tree-line ecotone (i.e. the limit of individual tree occurrence) that separates the sub-alpine coniferous forest from the open alpine dwarf-shrub heaths and grasslands. The tree-line and timber-line (i.e. the upper limit of closed forest) location is closely related to the length of the growing season, usually correlated with temperatures reaching more than 5 °C during 100 days (Ellenberg 1996; Körner 1999). For palaeoclimate studies based on biotic proxies, sites close to ecotonal situations are considered ideal as comparatively minor climatic shifts may produce a large biotic response, for example an uphill or downhill displacement of the ecotone (Faegri and Iversen 1989).

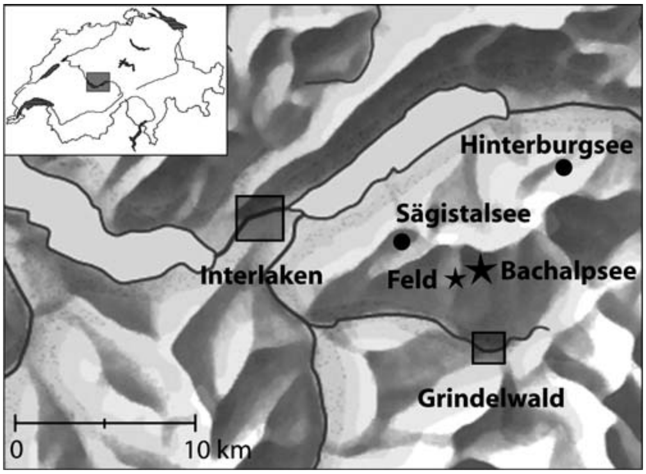


Fig. 1 Map of Switzerland (inset) with the location of the area investigated, showing Bachalpsee (2265 m a.s.l.), Feld (2130 m a.s.l.), Sägistalsee (1935 m a.s.l.) and Hinterburgsee (1515 m a.s.l.)

Lakes form a typical landscape element in the Alps. Besides being scenic spots that attract tourists, they are excellent archives storing the environmental history of atmospheric, terrestrial, and aquatic systems. The study of their sediments facilitates the assessment of diverse catchment influences (e.g. weathering or vegetation type and cover) on the aquatic ecosystem. By using different proxy-indicators, leads and lags in the reaction of different biota relative to climatic change can be studied and independent evidence for past climatic change can be obtained (Lotter 2003). Aquatic organisms, for instance, may respond faster to climatic change than terrestrial vegetation. In particular, trees are assumed to show a lagged response due to numerous factors, such as long generation times, migration and the effects of pedogenesis (Iversen 1964; Birks 1981; Kupfer and Cairns 1996). However, recent palaeobotanical studies suggest that the Holocene timber-line vegetation in the Alps was in dynamic equilibrium with climate (Tinner and Kaltenrieder 2005).

Finding suitable Alpine lakes is at times difficult because they are inaccessible or their sedimentary records are short or truncated due to prolonged glaciation of the catchment. Preliminary studies showed that the sediments of Bachalpsee in the Bernese Oberland (Fig. 1) reach back to the late-glacial period (B. Ammann, unpubl. data) and that the lake is thus suitable for a multi-proxy study of the Holocene environmental history.

The aims of this study were to look at the Holocene vegetation history of a lake above the modern tree-line and to use aquatic organisms as independent indicators of environmental change within its catchment. Specifically, we were investigating how the tree-line has evolved during the Holocene and whether it reached the catchment of Bachalpsee during the warmest phase of the Holocene. This investigation was part of a multi-proxy study involving different lacustrine archives along an altitudinal transect (Lotter et al. 1997a), so it was possible to compare the vegetation development and dynamics at Bachalpsee with records from lower elevations in the same region. In addition, the forest composition at the timber-line during the mid-Holocene is inferred from pollen and macrofossils studied in a sediment section from a mire close to Bachalpsee.

Sites

Bachalpsee (46°40′12″ N, 8°01′24″ E; Fig. 2) is an elliptically shaped lake of glacial origin in the Alpine vegetation belt of the calcareous northern Swiss Alps, close to the village of Grindelwald (Bernese Oberland; Fig. 1). The lake and its catchment are situated in the Jurassic sedimen-

Fig. 2 Aerial photograph of Bachalpsee (2265 m a.s.l.) and its catchment, looking towards the southeast, with the Wetterhorn (3701 m a.s.l.) in the background

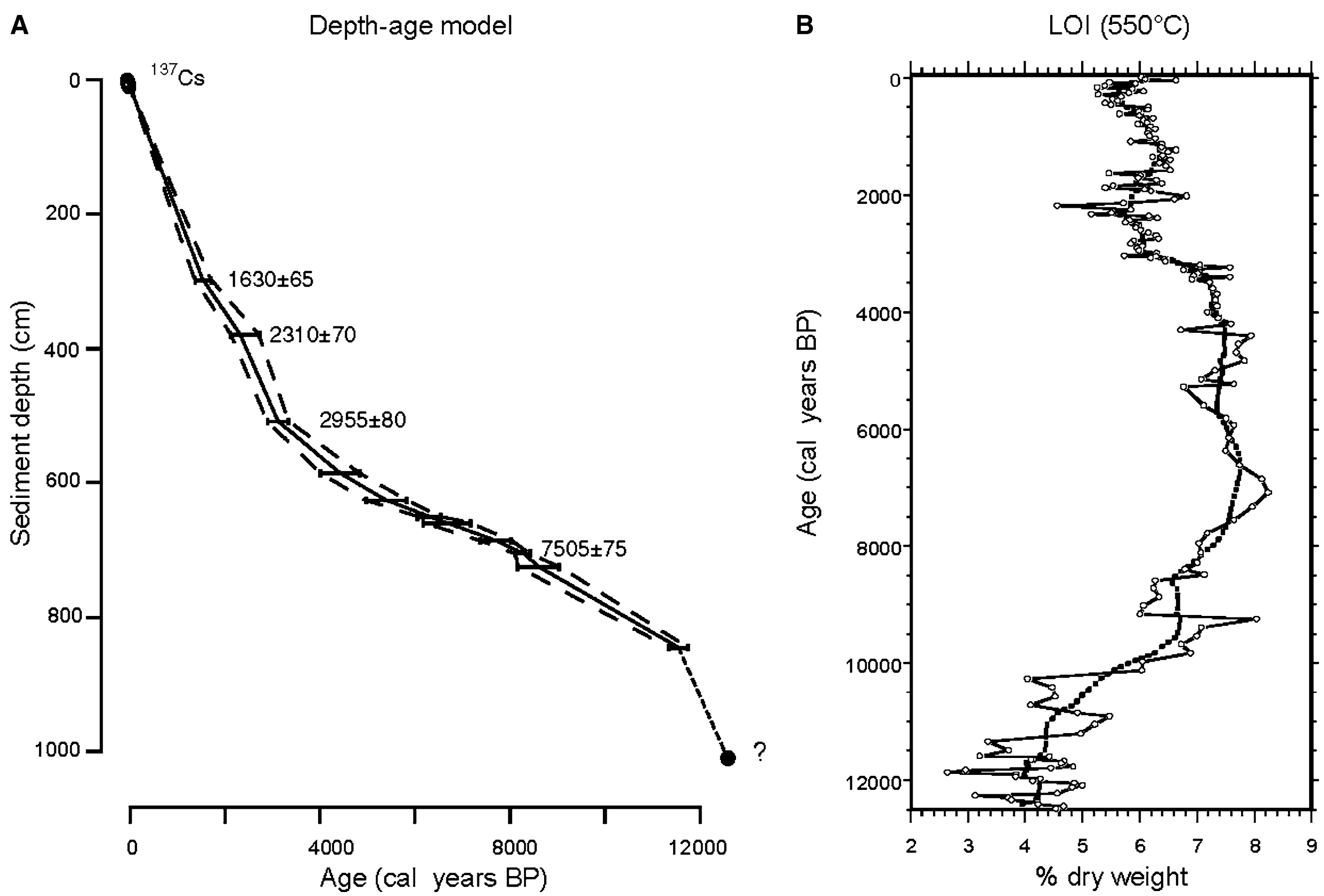


Fig. 3 **A** Depth-age relationship of the Bachalpsee core. The error bars indicate calibrated 2σ ranges for the ^{14}C dates (indicated with the uncalibrated age estimates) and the 95% age confidence intervals for the ages inferred from the pollen (see Table 1 and text for details). The filled circle indicates the "best-guess" estimate for the basal age of the record and the open circles indicates the ^{137}Cs age estimates and the core top. **B** Loss-on-ignition results after combustion of sediment at 550 °C. The dotted line represents a 9–sample running average

tary rocks of the Helvetic Alpine nappe: the northern and southern parts of the region consist of sandy limestones and clayschists (Bajocien) with productive, base-rich soils, whereas very brittle micaceous clayschists (Oxfordien-Callovien) prone to erosion (Fig. 2) outcrop in the western and eastern parts (Günzler-Seiffert and Wyss 1938).

Four small streams enter the lake and deliver a high amount of suspended matter during snowmelt and after heavy precipitation. The natural lake used to have seasonal lake-level fluctuations of ca. 30 cm (Spengler 1974). However, the lake was dammed and the level raised by several meters in 1911/12 for hydroelectric power generation; thereafter the water level has been fluctuating up to 11 m in winter.

The present climate at Bachalpsee is characterised by 1780 mm annual precipitation, a mean annual temperature of 0 °C and mean summer and winter temperatures of 7 °C and − 6.7 °C, respectively. The lake is located ca. 100–200 m above the tree-line, at 2265 m a.s.l. and is today 16 m deep. The lake has a surface area of 8.03 ha and its hydrological catchment includes 1.87 km^2, ca. 27% of which consist of alpine pastures (for detailed vegetation characterisation see Hegg and Schneiter 1978) and ca. 52% of exposed bedrock and screes (Guthruf et al. 1999; Fig. 2).

A small mire, Feld (46°39′28″ N, 8°00′12″ E; 2130 m a.s.l.), close to Bachalpsee was studied for pollen and plant macrofossils. Feld, ca. 1 ha in size, is one of three small mires lying close together on the south-exposed slope 2 km SW of Bachalpsee. The surroundings are alpine pastures, with a few scattered *Picea abies* trees 2.5 m in height and *Pinus mugo* shrubs growing on the rocky and grassy ridges flanking the mire.

Methods

In May 1996 several overlapping sediment cores were recovered from the frozen Bachalpsee with a modified Livingstone piston corer with a diameter of 8 cm. A complete composite core of 1035 cm was sampled in contiguous 1 cm increments for the following analyses: Loss-on-ignition (LOI) was measured for 344 sediment samples according to Heiri et al. (2001). Pollen analysis of 152 samples was carried out by J.F.N. van Leeuwen and plant macrofossils from 225 samples were analysed by L. Wick following the methods described by Wick et al. (2003). W. Hofmann analysed 63 samples for Cladocera (for methods see Hofmann 2003) and I. R. Walker analysed 54 samples for chironomids (for methods see Walker 2001; Heiri and Lotter 2003).

The Bachalpsee pollen data were zoned numerically using optimal sum-of-squares partitioning (Birks and Gordon 1985). The application of a broken stick model (Bennett 1996) showed five statistically significant pollen assemblage zones (Fig. 4).

The mire of Feld was cored in October 1997 with a modified Livingston piston corer; the total sediment depth was 305 cm. The sediment studied was from a single core drive and consists of coarse-detritus gyttja above 232.5 cm and clayey gyttja with fine detritus below this level, with an abrupt transition between the two. Macrofossil analysis was carried out by W.O. van der Knaap and pollen analysis by J.F.N. van Leeuwen.

Results

Stratigraphy and chronology

The entire sediment sequence of more than 10 m is characterised by clastic deposits, mainly laminated grey to brown-grey clayey and sandy silts with intercalated

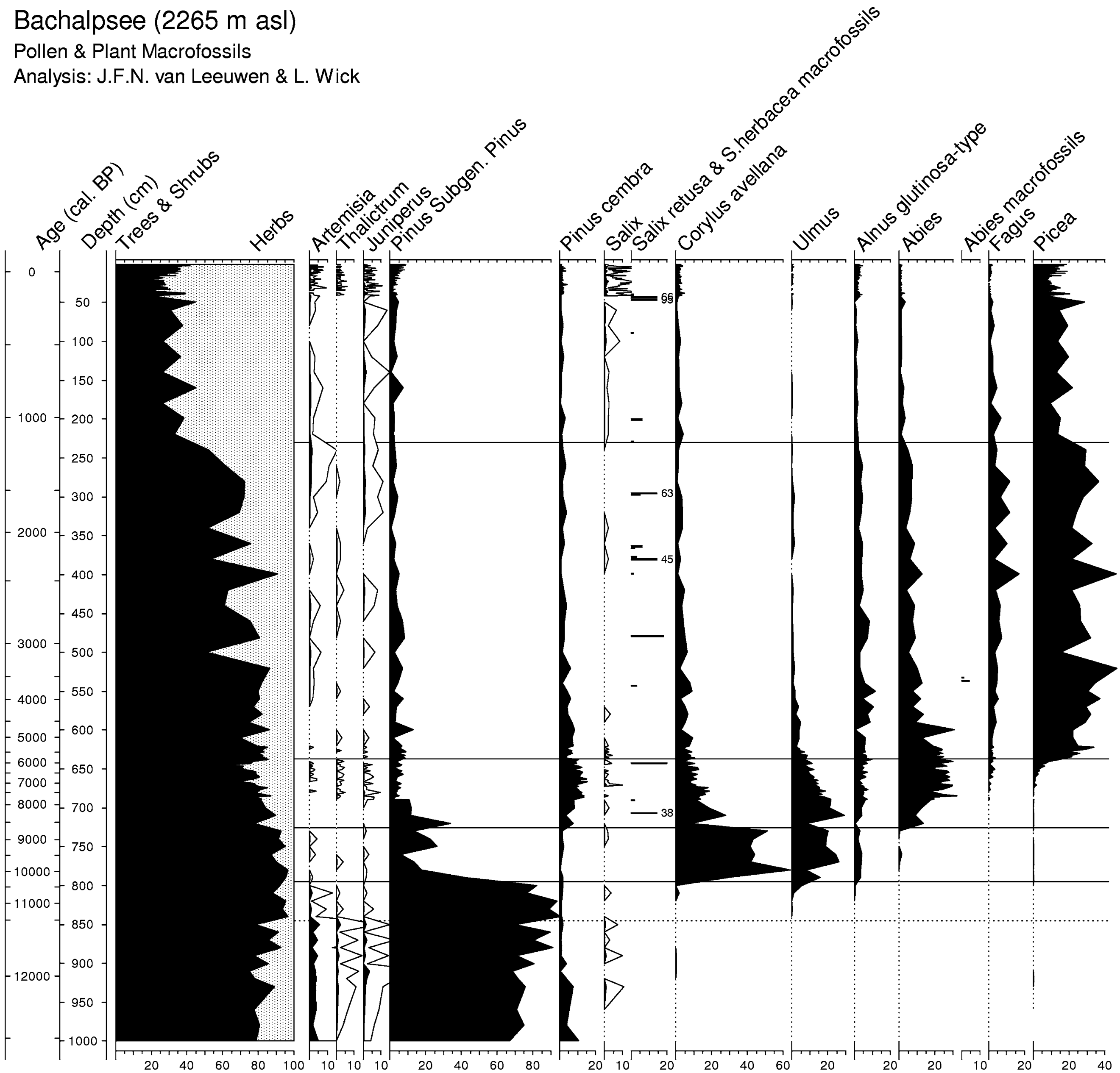


Fig. 4 Pollen and plant macrofossil diagram for Bachalpsee. Pollen percentages are shown as curves, whereas the counts of selected plant macrofossil occurrences are shown as histograms. Only a selection of taxa is shown (the complete records are available from the authors). Zones refer to pollen assemblage zones (PAZ), whereas the dotted line represents the late-glacial (Younger Dryas)—Holocene transition

turbidites of 0.5 to 5 cm thickness. Fig. 3B gives an overview over the amount of organic matter as estimated by LOI analysis.

The chronological framework of the Bachalpsee sediment record is based on several independent dating methods. The core top (A.D. 1996) and ^{137}Cs measurements (radioactive fallout peaks of A.D. 1963 and 1986) were used to date the topmost sediment layers. Four AMS radiocarbon dates were provided by identified remains of terrestrial plants (Fig. 3A; Table 1) and five additional dating points were provided by pollen-analytical correlation with the nearby well-dated Sägistalsee profile (Lotter and Birks 2003b; Table 1). The conventional radiocarbon ages were calibrated using CALIB 4.42 and the INTCAL98 calibration curve (Stuiver et al. 1998). Ages are expressed as calibrated years before present (cal B.P.). The depth-age relationship shown in Fig. 3A was established by linear interpolation between the dating points.

In the absence of datable organic matter and conspicuous features in the pollen curves our "best guess" for the basal age of the core is ca. 12,500 cal years B.P., although this age is poorly constrained and could be younger.

In the Feld sediment sequence, two AMS radiocarbon dates were obtained from *Carex rostrata* fruits (Table 1). The transition between the two sediment types at 232.5 cm

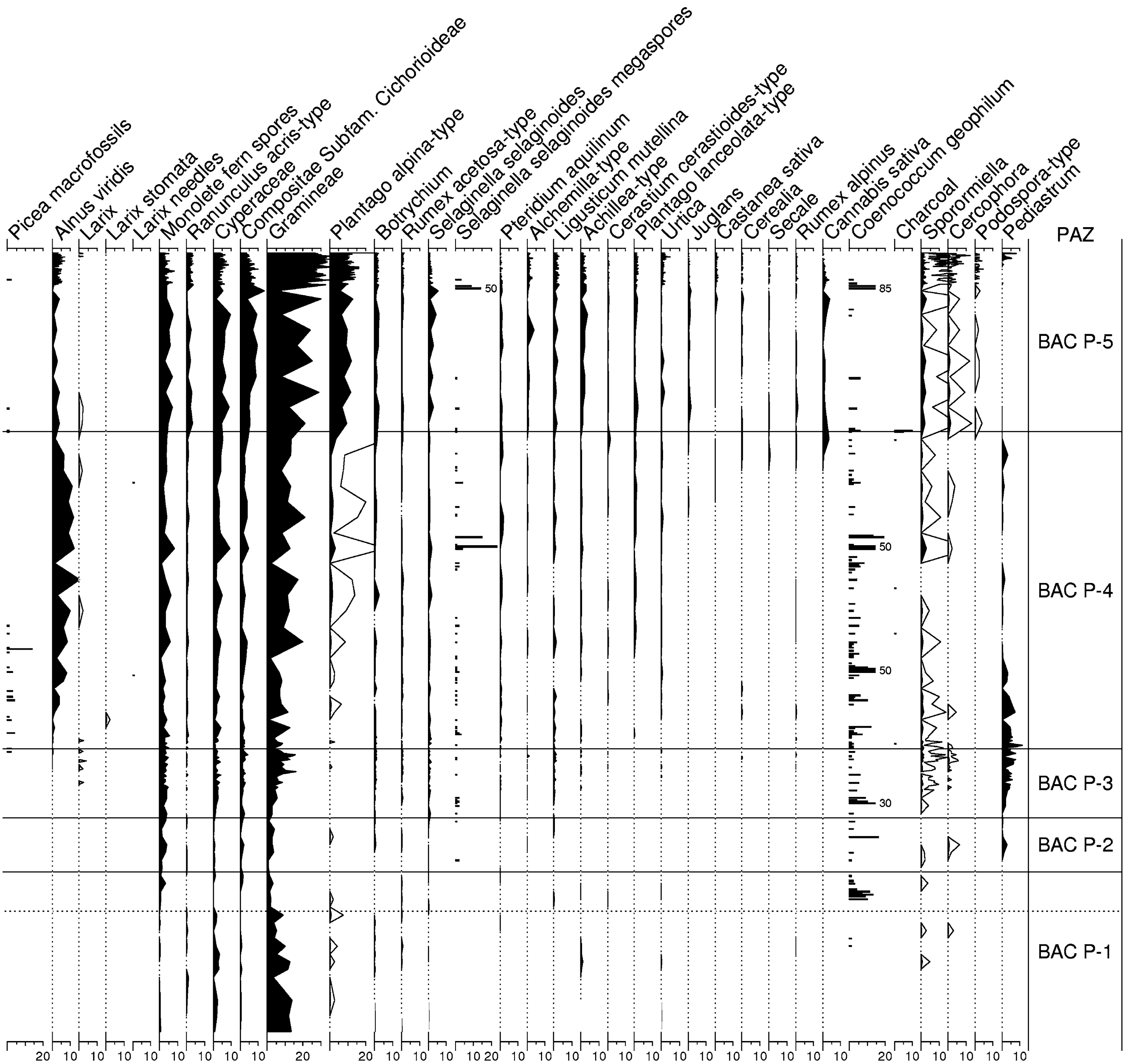


Fig. 4 Continued.

Table 1 Ages used to derive the depth-age relationships for Bachalpsee (BAC) and Feld (FEL)

Site	Depth (cm)	Dating method	Lab. code	δ^{13}C (‰ PDB)	^{14}C age ($\pm 1\sigma$)	Calibr. ^{14}C age	2σ range (cal B.P.)	Remarks/^{14}C dated material
BAC	0	Core top	–	–	–	– 46	–	–
BAC	3	^{137}Cs	–	–	–	– 36	–	Tschernobyl peak
BAC	8	^{137}Cs	–	–	–	– 13	–	1963 bomb peak
BAC	295–297	^{14}C	Ua-12933	– 27.56	1630 ± 65	1524[a]	1353–1694[b]	*Salix* cf. *retusa*
BAC	378–380	^{14}C	Ua-12386	– 25.99	2310 ± 70	2320[a]	2123–2707[b]	*Salix*, *Selaginella*, wood undiff
BAC	506–510	^{14}C	Ua-12932	– 27.63	2955 ± 80	3117[a]	2887–3340[b]	*Dryas*, *Salix*
BAC	585	P-I	–	–	–	4416	4009–4823	Correlation with SÄG 600 cm
BAC	625	P-I	–	–	–	5377	4937–5816	Correlation with SÄG 700 cm
BAC	650	P-I	–	–	–	6300	6065–6535	Correlation with SÄG 840 cm
BAC	659	P-I	–	–	–	6655	6172–7139	Correlation with SÄG 990 cm
BAC	705–706	^{14}C	Ua-12387	– 26.55	7505 ± 75	8295[a]	8114–8415[b]	wood undiff
BAC	725	P-I	–	–	–	8614	8174–9053	Correlation with SÄG 1205 cm
BAC	845	P-I	–	–	–	11,550	11,350–11,750	YD/Holocene transition
BAC	1020	Estimate	–	–	–	12,650	–	Estimated maximum basal age
FEL	195	^{14}C	Erl-4240	– 23.02	4420 ± 69	5034[a]	4858–5287[b]	*Carex rostrata* fruits
FEL	230	^{14}C	Erl-4241	– 23.41	5126 ± 71	5860[a]	5661–6095[b]	*Carex rostrata* fruits

P-I indicates ages inferred from pollen based on the correlation of the Bachalpsee pollen record with the pollen stratigraphy in nearby Sägistalsee (SÄG). Ages inferred from pollen are presented with the 95% age confidence interval for the correlation depth in the Sägistalsee record as presented in Lotter and Birks (2003a). For the Younger Dryas/Holocene transition the age of 11,550 cal B.P., has been used with a dating uncertainty of ± 200 years. See text for further details

[a]the median probability was used for the ^{14}C ages

[b]the 2σ interval was used for the ^{14}C ages

depth is abrupt and may represent a hiatus of unknown duration. We therefore consider the sediment below this level as undated.

Local vegetation history

Pollen spectra from sites at or above the tree-line such as Bachalpsee are strongly influenced by long-distance transport of wind-dispersed pollen from plants living at lower altitudes. In contrast, local herbaceous vegetation often consists of low pollen producers. Therefore, pollen analytical results from such sites need to be interpreted in combination with results of plant macrofossil analyses (Lang 1993; Birks and Birks 2000; Tinner and Theurillat 2003).

Plant macrofossil concentrations in the clastic sediments from Bachalpsee were very low. Therefore the results of pollen and plant macrofossil analyses are presented in the same diagram (Fig. 4). Not surprisingly the pollen diagram (Fig. 4) is dominated by long-distance transported pollen, thus largely reflecting the vegetation development of lowland Switzerland.

The lowermost pollen assemblage zone (BAC P-1; Fig. 4) is dominated by pine. The scarcity of plant macrofossils and also the very low LOI values (Fig. 3B) suggest that the vegetation in the lake's catchment was very open if not entirely absent. Based on the pollen assemblages this zone is attributed to the Younger Dryas and Preboreal biozones (Ammann et al. 1996). Based on the decreasing percentages of *Artemisia, Thalictrum* and Gramineae pollen, the onset of the Holocene (i.e. 11,550 cal B.P.) has been placed at a sediment depth of 845 cm (Fig. 4). Pollen and stomata analyses of several sites in the Bernese Alps suggest a forest limit below 1350 m a.s.l. during the Younger Dryas (Wick 2000).

Zone BAC P-2 (ca. 10,300–8600 cal B.P.) is characterised by high percentages of *Corylus* and *Ulmus* with decreasing amounts of *Pinus* pollen. *Ulmus* pollen percentages are relatively high (20%) suggesting that this tree was fairly abundant on the mountain slopes at lower altitudes. The absence of coniferous macrofossils may be taken as an indication that the forest limit was situated well below Bachalpsee. At nearby Sägistalsee (1935 m a.s.l.) *Pinus cembra* remains (Fig. 7) indicate that the treeline was above 2000 m a.s.l. at that time (Wick et al. 2003). However, macrofossils of herbaceous plants such as grasses, *Saxifraga*, *Dryas,* Caryophyllaceae and *Selaginella selaginoides* (Fig. 4) indicate open meadows in the catchment of Bachalpsee. Sediment organic matter content increased by about 3–4% (Fig. 3B), pointing to increasingly denser vegetation stabilising the catchment soils; furthermore the magnetic properties of the Bachalpsee sediments show a decrease in input from erosion (Lanci et al. 1999).

In zone BAC P-3 (ca. 8600–5800 cal B.P.) pollen values of *Abies* and *Pinus cembra* increased and single grains of *Larix* pollen were found. At Sägistalsee both *Abies* and *P. cembra* were growing locally (Fig. 7), but at Bachalpsee no macrofossil evidence for the local presence of these trees was found (Fig. 4). The regular occurrence of *Coenococcum geophilum*, a mycorrhiza species growing on woody plants, and the remains of periderm and wood of *Salix* (macrofossil evidence of *S. herbacea, S. retusa*) and

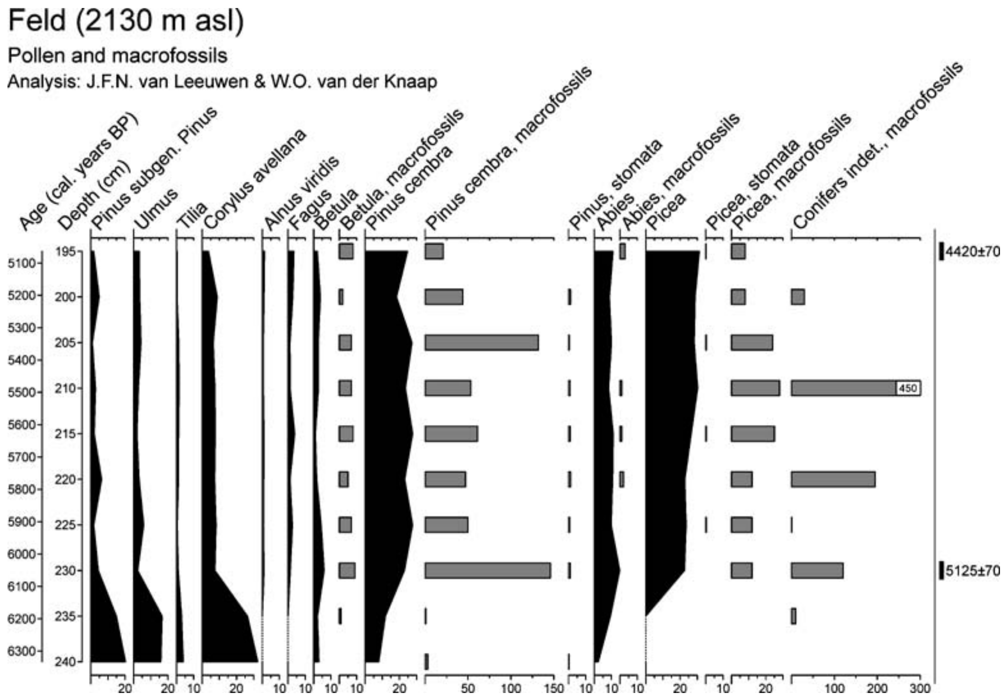


Fig. 5 Pollen and plant macrofossil diagram from the mire Feld. Pollen percentages are shown as curves, whereas the occurrences of *Pinus cembra* and *Picea* stomata and macrofossil counts are shown as histograms. Only a selection of taxa is shown (the complete records are available from the authors). The radiocarbon dates are given in conventional ^{14}C years B.P.

Ericaceae (macrofossil evidence of *Vaccinium, Rhododendron*) point to dwarf-shrub formation in the catchment. The LOI values reached their highest levels between 6.5% and 8% (Fig. 3B) in the period of ca. 8000–3000 cal B.P. indicating somewhat less input from erosion. This is also supported by the relatively low sediment-accumulation rates in the same period (Fig. 3A).

During zone BAC P-4 (ca. 5800–1200 cal B.P.) *Picea* pollen increased greatly (Fig. 4). According to the macrofossil analyses scattered *Picea* trees (needles, anthers, seeds and seed wings, bud scales, periderm) and possibly also *Abies* (budscales, periderm) grew close to the lake, indicating that the timber-line had reached the elevation of Bachalpsee.

The dated part of the Feld sediment sequence (2130 m a.s.l., 2 km SW of Bachalpsee) is synchronous with the first millennium of zone BAC P-4 of Bachalpsee. Among the macrofossils of conifers in these sediments (Fig. 5), *Pinus cembra* needles were very abundant (20–120 per level analysed), *Picea* needles were abundant (4–19 per level), whereas *Abies* needles were scarce (1 per level). Seeds and female cone scales from *Pinus cembra* and *Picea* were frequent while only one from *Abies* was found. No *Larix* macrofossils were found, however single pollen grains were encountered in the lower, undated part of the sequence. This suggests a dominance of *Pinus cembra* trees near the pool, abundant *Picea* trees and scattered *Abies*, whereas *Larix* was not growing locally. The *Betula* seeds (2–8 per level analysed) and catkin scales (0–2 per level) are likely to have been transported by wind from lower elevations. The abundance of *Pinus cembra* near Feld compared to the absence of its macrofossils in Bachalpsee may be explained by the exposed situation of the partially rocky mountain ridges near Feld. These form a particularly suitable habitat for this tree as compared to the sheltered cirque around Bachalpsee, a situation unfavourable for *Pinus cembra*. Although it requires more light and is better drought-adapted, *Larix* has habitat preferences similar to *Pinus cembra* (Ellenberg et al. 1992) and today in the Central Alps the two trees grow together at the tree-line ecotone (2000–2400 m a.s.l.). The situation near Feld would seem favourable for *Larix* while that near Bachalpsee is unfavourable. The absence of *Larix* macrofossils in Feld is therefore significant and suggests extreme scarcity of this tree in the area. The scarce findings of *Larix* macrofossils and pollen at Bachalpsee as well as at Sägistalsee (Wick et al. 2003) and Hinterburgsee (Heiri et al. 2003b) suggest that there were no permanent larch populations but rather single, isolated individuals growing in favourable habitats in the study area.

At Bachalpsee a decrease in *Picea* recorded in plant macrofossils (but not in pollen, Fig. 4) around 3000 cal B.P. is concurrent with a decrease in organic matter content (Fig. 3B). Macroscopic charcoal as well as pasture indicators in the pollen diagram (e.g. *Plantago alpina,* Compositae Subfam. Cichorioideae) point to human deforestation of the lower parts of the Bachalpsee catchment. The higher percentages of the coprophilous fungal spores *Sporormiella, Cercophora* and *Podospora* (Fig. 4) suggest increased grazing by cattle (van der Knaap and van Leeuwen 2003). *Sagina saginoides* seeds (not shown), a plant that grows on nutrient-rich habitats trampled by animals, also indicate that the Bachalpsee catchment has been used for grazing since the Bronze Age. Similar evidence was found at Sägistalsee where the onset of anthropogenic deforestation was dated to ca. 3600 cal B.P. (Wick et al. 2003).

Zone BAC P-5 (ca. 1200 cal B.P. to today) is characterised by a strong increase in herb pollen, especially grasses and *Plantago alpina,* suggesting an increase in human impact. High numbers of macroscopic charcoal fragments, among them parts of charred *Picea* needles, point to deforestation by fire during the Middle Ages (Fig. 4). The pollen and the plant-macrofossil record suggest continuous human influence and the absence of trees near the lake up to the present.

Palaeolimnology of Bachalpsee

Chironomids have shown to be excellent indicators of past climatic change (Walker et al. 1991; Lotter et al. 1999; Walker 2001; Heiri et al. 2003a). Several chironomid records have indicated late-glacial and Holocene climatic oscillations in Central Europe and the Alps (e.g. Hofmann 1983; Heiri et al. 2004; Heiri and Millet 2005). In contrast to chironomids, there are no cold stenothermal Cladocera but rather cold-tolerant species (Meijering 1983). The complexity and diversity of littoral habitats determines largely the faunal assemblages of chydorids in lakes (Whiteside and Harmsworth 1967). However, chydorid assemblages in surficial lake sediments show distinct changes along altitudinal (Lotter et al. 1997b) and latitudinal gradients (DeCosta 1964; Korhola 1999). Most cladoceran studies in the Alps have focused on nutrient enrichment (e.g. Boucherle and Züllig 1983), whereas only a few studies have so far used their potential as climatic indicators (Hofmann 2000; Lotter et al. 2000).

Concentrations of chironomid head-capsules were low in the highly inorganic sediments of Bachalpsee (Fig. 6) as compared with lowland lake sediments, and extremely low in the basal, late-glacial part. This reflects low productivity coupled with a high sediment-accumulation rate throughout the history of the lake. Moreover, only a few benthic chydorid species were found, while planktonic Cladocera (e.g. *Bosmina, Daphnia*) were completely absent. The subfossil chironomid assemblages represent a mixture of rheophilous (running-water) chironomids (*Diamesa, Cricotopus/Orthocladius,*

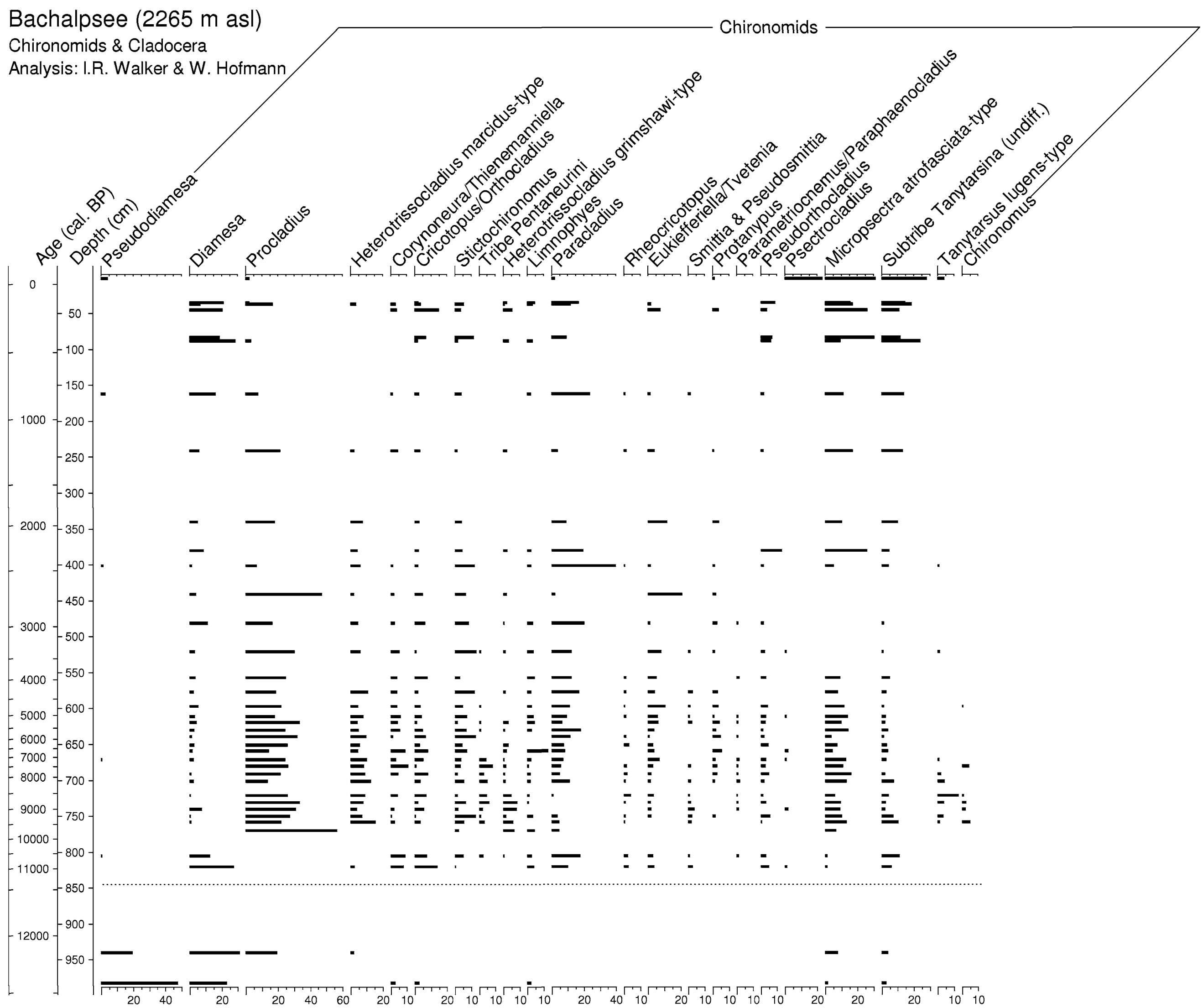
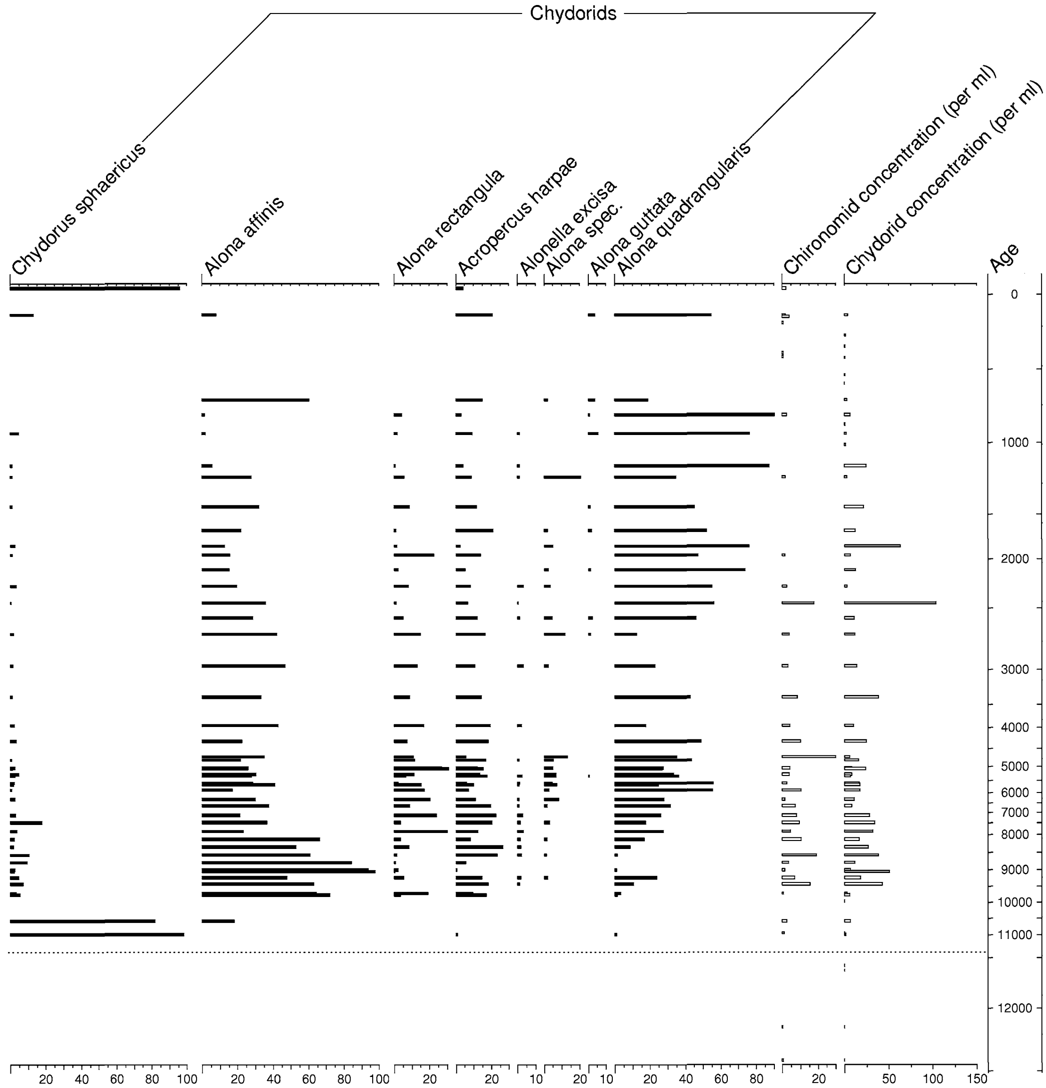


Fig. 6 Chironomid and benthic cladoceran percentage diagram for Bachalpsee. Only selected taxa are shown (the complete records are available from the authors). The dotted line represents the transition from the late-glacial period (Younger Dryas) to the Holocene

Rheocricotopus, Eukiefferiella/Tvetenia, Smittia and *Parametriocnemus/Paraphaenocladius*) and lake taxa, indicating that these composite faunas were derived from inflowing streams as well as from the lake itself.

Optimal-sum-of-squares zonation of the chironomid record reveals two statistically significant assemblage zones. A late-glacial assemblage zone characterised by the two cold-water taxa *Pseudodiamesa* and *Diamesa* (Fig. 6) is clearly separated from the Holocene assemblages. In lakes, *Pseudodiamesa* is restricted to high-arctic and alpine habitats, whereas *Diamesa* typically dominates the fauna of glacial meltwater streams (Walker and Mathewes 1989; Walker 1991; Lotter et al. 1997b). Zonation of the chydorid record also revealed a significant change in assemblages at the transition from the Younger Dryas to the Preboreal (Fig. 6).

During the early and mid-Holocene, concentrations of chironomid head capsules and chydorid remains as well as their taxonomic diversity increase. The latter can be attributed to the appearance of more temperate taxa. Amongst the chironomids, *Procladius, Micropsectra radialis*-type and *Paracladius* dominate the assemblages during the early and mid-Holocene. The onset of the early Holocene is characterised by a short phase with *Chydorus sphaericus* dominance in the cladoceran assemblages. Increased sediment organic matter, as evidenced by a 3–4% rise in LOI (Fig. 3B) starting at ca. 10,300 cal B.P., is interpreted as reduced soil erosion because of denser vegetation in the catchment rather than higher productivity in the water column. Magnetic analyses of the Bachalpsee sediment clearly show a decreased background signal from the catchment bedrock (Lanci et al. 1999). The first occurrence and the subsequent increase in *Pediastrum* microfossils (Fig. 4) is probably the effect of a combination of less turbid water and a longer open water season (i.e. warmer summers) that allowed these green algae to bloom in Bachalpsee. Concurrently with this first increase in organic matter around 10,000 cal B.P. (Fig. 3), *Alona affinis* and *A. quadrangularis*



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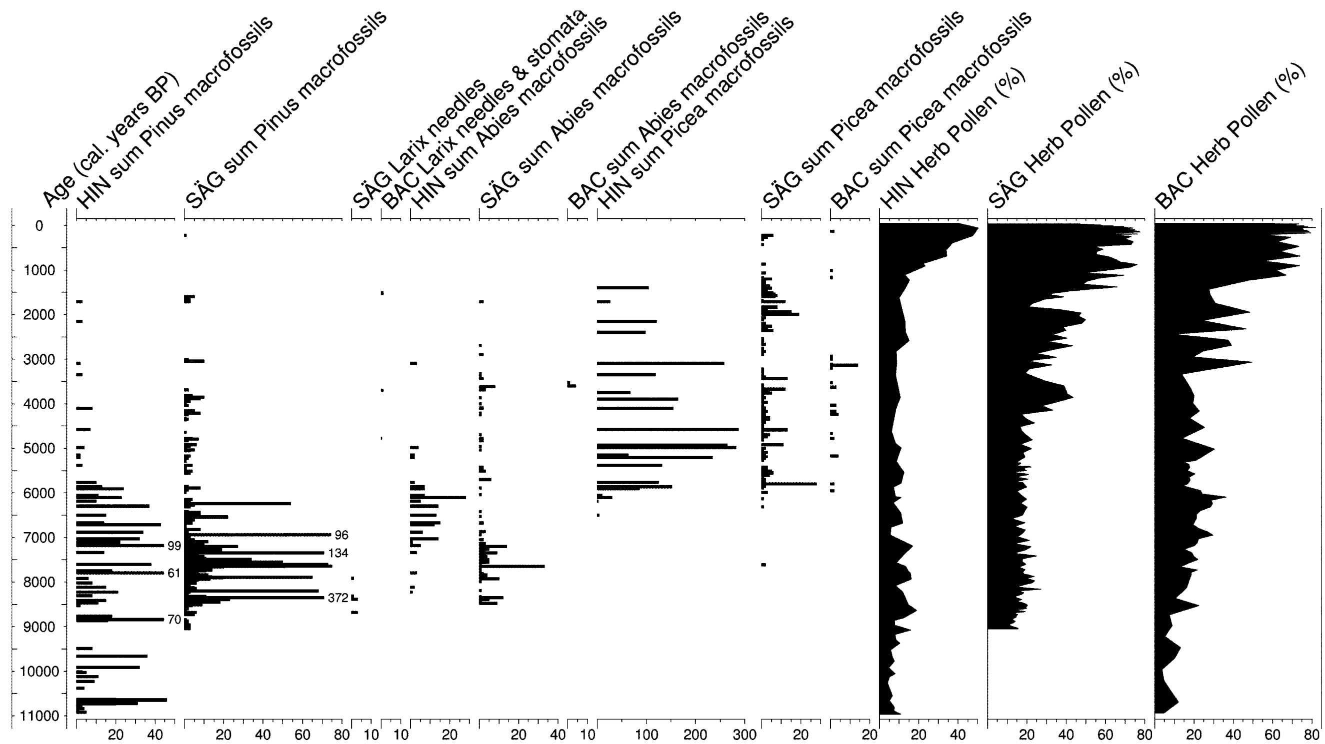

Fig. 7 Comparison of macrofossils of tree-line trees and herb pollen from Hinterburgsee (HIN: 1515 m a.s.l.; after Heiri et al. 2003b), Sägistalsee (SÄG: 1935 m a.s.l.; after Wick et al. 2003), and Bachalpsee (BAC: 2265 m a.s.l.; this study). Counts of all identifiable macrofossils of each taxon are presented for each site. Note that the Sägistalsee record begins at ca. 9000 cal B.P., whereas the other two records extend back to the late-glacial period. Moreover, the macrofossils have not been analysed for the sediments covering the past 1200 years.

became the dominant chydorids for the rest of the Holocene (Fig. 5). This may have been the consequence of decreased water turbidity and subsequent deeper light penetration that may have promoted periphytic algal growth and increased the area of suitable littoral habitats for benthic Cladocera.

According to their modern distribution in the Alps *C. sphaericus* and *A. quadrangularis* are cold-tolerant species (Lotter et al. 1997b). The Holocene chironomids and chydorid assemblages are typical of a lake in the subalpine-alpine zone at or above the tree-line. However, midges such *Chironomus* or Pentaneurini and also *Procladius*, together with chydorids such as *Alonella excisa* and *Alona rectangula*, have their centre of distribution in the subalpine zone (Lotter et al. 1997b; Hofmann 2003; Heiri and Millet 2005). Their occurrence in the early to mid-Holocene suggests that this phase was the warmest interval in the Bachalpsee record.

Aquatic biota from lakes in the same region of the Alps have been used to reconstruct late-glacial and Holocene climatic change (Lotter et al. 2000; Heiri and Lotter 2003, 2005; Heiri et al. 2004). Recent studies have shown that there are several critical elevations where significant changes in the composition of assemblages of aquatic organisms such as diatoms, Cladocera or chironomids occur. These may be considered as "aquatic ecotones" which are relevant for the reconstruction of past climate change (Heegaard et al. 2006). Bachalpsee, however, is situated well beyond the highest aquatic ecotonal boundary located at ca. 2000–2100 m a.s.l.. Moreover, Livingstone et al. (2005) realised that lakes above 2000 m a.s.l., unlike lowland lakes, have a thermal regime in which their lake water temperature is only indirectly linked to altitude and is decoupled from ambient air temperatures. Currently available organism-based climate inference models for the Alps (Lotter et al. 1997b; Heiri et al. 2003a) do not, however, allow for these effects as yet and may therefore produce unrealistic results for such high-elevation sites. For these reasons we did not use the chydorid and chironomid data to quantitatively reconstruct past climatic conditions at Bachalpsee.

Regional tree-line history

At present, *Picea abies* is the dominant tree in the subalpine forests of the region. Together with *Pinus cembra* and *P. mugo* it forms the modern tree-line that is located between 1900 and 2000 m a.s.l. in this region of the Alps. However, the potential, climatically determined forest limit would be located at elevations of between 2000 and 2200 m a.s.l. (Landolt 1992). The results from Bachalpsee must be interpreted in a regional context and can directly be compared with two other lakes that have been studied by the same analysts and using the same methodology. Hinterburgsee (1515 m a.s.l.) is situated in the subalpine spruce forest belt, whereas Sägistalsee (1935 m a.s.l.) is a lake at the present-day tree-line formed by *Picea abies* and *Pinus mugo*. The sediment records from both lakes have been analysed for pollen and plant macrofossils, with the

Hinterburgsee record reaching into the late-glacial period (Heiri et al. 2003b) and the Sägistalsee core to ca. 9000 cal B.P. (Lotter and Birks 2003a).

The Hinterburgsee record shows reforestation up to at least 1600 m a.s.l. by *Pinus cembra* and *Betula pubescens* around 11,000 cal B.P. (Fig. 7). *Pinus cembra* macrofossils were also present in the oldest part of the Sägistalsee core, suggesting that this tree had already formed the tree-line before 9000 cal B.P. at elevations around 2000 m a.s.l. or higher. In contrast, the scattered early Holocene pine and birch macrofossils found at Bachalpsee are interpreted as being wind-transported from lower elevations. *Larix* needles found in the early Holocene Sägistalsee sediments show that scattered individuals of this pioneer tree were also a growing at this elevation in the Bernese Oberland (see also Wegmüller and Lotter 1990), probably on the more minerogenic soils (Wick et al. 2003).

Around 8500 cal B.P. *Abies alba* became established in the catchments of both Hinterburgsee and Sägistalsee and occurred together with *Pinus cembra* as a timberline tree. With regard to the more temperate aquatic fauna found at Bachalpsee during this time (Fig. 4) it is conceivable that warmer and/or longer summers could have favoured the expansion of *Abies* in the Northern Alps. In view of the large amount of clastic sediment (Ohlendorf et al. 2003; Heiri et al. 2003b) the *Pinus cembra–Abies alba* stands must have been fairly open, thus favouring soil erosion.

The local *Picea* expansion brought a change in the subalpine forest composition. Light-requiring trees such as *Larix*, but also *Pinus cembra* and *Abies alba*, were likely to be out-competed by *Picea abies* at lower elevations (Hinterburgsee, Fig. 7), whereas at the tree-line ecotone (Sägistalsee, Fig. 7) *Picea* dominated the forest although *Pinus cembra* and *Abies alba* could coexist with it. The establishment of spruce took place ca. 6500 cal B.P. at Hinterburgsee, ca. 6300 cal B.P. at Sägistalsee and ca. 6000 cal B.P. at Bachalpsee (Fig. 7). This range lies within the chronological uncertainties of the age-depth models of the three sediment records. It is therefore not possible to decide whether this offset in timing represents a real lag along the altitudinal gradient and might reflect local upslope edaphic limitations (Kupfer and Cairns 1996), or whether it is due to uncertainties inherent in the dating and age-depth models of the different records. Nevertheless, the local presence of *Picea abies* macrofossils at Bachalpsee (Fig. 4) and Feld (Fig. 5) gives evidence that the tree-line reached its maximal Holocene elevation above 2250 m a.s.l. in the Northern Alps between ca. 6000 and 3000 cal B.P. These results are consistent with other findings from the Bernese Oberland (Wegmüller and Lotter 1990; Wick et al. 2003).

These mid-Holocene highest tree-lines contrast strongly with those in the Central and Southern Alps, where the maximum elevation of the forest limit (formed by *P. cembra* and *Larix*) had already been reached during the early Holocene, i.e. some 4000–5000 years earlier (Wick and Tinner 1997; Burga and Perret 1998; Tinner and Theurillat 2003; Tinner and Ammann 2005). Migrational lags cannot account for these huge differences as both species were present in the Northern Alps. Moreover, Holocene temperatures seem to have been comparable between the Northern and the Central Alps and are reflected by Central Alpine tree-line fluctuations and vegetation modelling results (Heiri et al. 2004, 2006). These apparent differences may imply that the tree-line in the Northern Alps during the early and mid-Holocene was not primarily controlled by temperature but rather by other factors (see for example Tinner and Kaltenrieder 2005). The formation of a suprasubalpine belt (consisting of *P. cembra* and *Larix*, Landolt 1992) above the subalpine *Picea* forest is thought to be the result of dry conditions in combination with high solar irradiance. Such conditions will have an effect on the composition of tree-line species in that *Picea* as a less drought-resistant tree is not able to colonise this elevational belt, whereas both *P. cembra* and especially *Larix* are able to cope with such conditions. The absence of *Larix* in such a suprasubalpine belt during the early and mid-Holocene but also during the present-day situation in the Bernese Oberland (Wegmüller and Lotter 1990; Heiri et al. 2003b; Wick et al. 2003) strongly indicates a more continental climate with dryer conditions in the Central Alps as compared to the Northern Alps. It is likely that in the Northern Alps climatic conditions near the tree-line were not as continental and as dry as in the Central Alps, thus preventing *Pinus cembra* and *Larix* from colonising higher elevations, but allowing *Abies* to expand into these during the early to mid-Holocene (see for example Tinner and Kaltenrieder 2005).

Anthropogenic depression of the forest limit occurred as early as the Bronze Age, as shown by elevated numbers of macroscopic charcoal particles in combination with pasture-indicating pollen types, coprophilous fungal spores and decreased tree macrofossil concentrations at Sägistalsee and Bachalpsee. During the past 3000 years the forest limit has been lower than 2200 m a.s.l. (i.e. below Bachalpsee) and during the Middle Ages it was even lower than 1900 m a.s.l. (i.e. below Sägistalsee, Fig. 7).

At Hinterburgsee and Sägistalsee there is evidence of several centennial-scale early to mid-Holocene climatic fluctuations in the chironomid records (Heiri and Lotter 2003) and this can be related to local and regional fluctuations in tree-line elevation (Wick et al. 2003) or even correlated with ice-rafted debris events in the North Atlantic (Heiri et al. 2004). At Bachalpsee, however, such fluctuations could not be detected, because the temporal resolution of the chironomid and cladoceran data sets is too coarse and also because the lake and its catchment were too far away from any ecotone.

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