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Holocene vegetation development in the catchment of Sägistalsee (1935 m asl), a small lake in the Swiss Alps

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Abstract

Pollen and plant macrofossils were analysed at Sägistalsee (1935 m asl), a small lake near timber-line in the Swiss Northern Alps. Open forests with *Pinus cembra* and *Abies alba* covered the catchment during the early Holocene (9000–6300 cal. BP), suggesting subcontinental climate conditions. After the expansion of *Picea abies* between 6300 and 6000 cal. BP the subalpine forest became denser and the tree-line reached its maximum elevation at around 2260 m asl. Charcoal fragments in the macrofossil record indicate the beginning of Late-Neolithic human impact at ca. 4400 cal. BP, followed by a extensive deforestation and lowering of the forest-limit in the catchment of Sägistalsee at 3700 cal. BP (Bronze Age). Continuous human activity, combined with a more oceanic climate during the later Holocene, led to the local extinction of *Pinus cembra* and *Abies alba* and favoured the mass expansion of *Picea* and *Alnus viridis* in the subalpine area of the Northern Alps. The periods before 6300 and after 3700 cal. BP are characterised by high erosion activity in the lake's catchment, whereas during the phase of dense *Picea-Pinus cembra-Abies* forests (6300–3700 cal. BP) soils were stable and sediment-accumulation rates in the lake were low. Due to decreasing land-use at higher altitudes during the Roman occupation and the Migration period, forests spread beween ca. 2000 and 1500 cal. BP, before human impact increased again in the early Middle Ages. Recent reforestation due to land-use changes in the 20th century is recorded in the top sediments. Pollen-inferred July temperature and annual precipitation suggest a trend to cooler and more oceanic climate starting at about 5500 cal. BP.

Introduction

The vegetation of the Alps is characterized by two major ecotones that are sensitive to climatic change: the transition from deciduous to coniferous forest and the forest-limit or tree-line, i.e. the transition from subalpine coniferous forest to alpine meadows. Traditional palaeobotanical studies on past tree-line fluctuations as indicators of climatic change have concentrated mainly on palynological results (e.g., Welten, 1982; Burga, 1988; Burga and Perret, 1998). Determining the location of the forest-limit and deciding on the local presence or absence of trees by pollen alone, however, is problematic (Birks and Birks, 2000). Long-distance pollen transport by wind plays a major role in high-altitude regions by diluting the signal of local, low pollen-producing vegetation.

Only a few palaeobotanical studies focusing on the forest-limit in the Alps have combined pollen analysis with the analysis of plant macrofossils to give evidence of the local occurrence of trees (Lang and Tobolski, 1985; Lang, 1993; Fedele and Wick, 1996; Wick and Tinner, 1997).

This is the second in a series of eight papers published in this special issue dedicated to the palaeolimnology of Sägistalsee. Drs. André F. Lotter and H. John B. Birks were the guest editors of this issue.

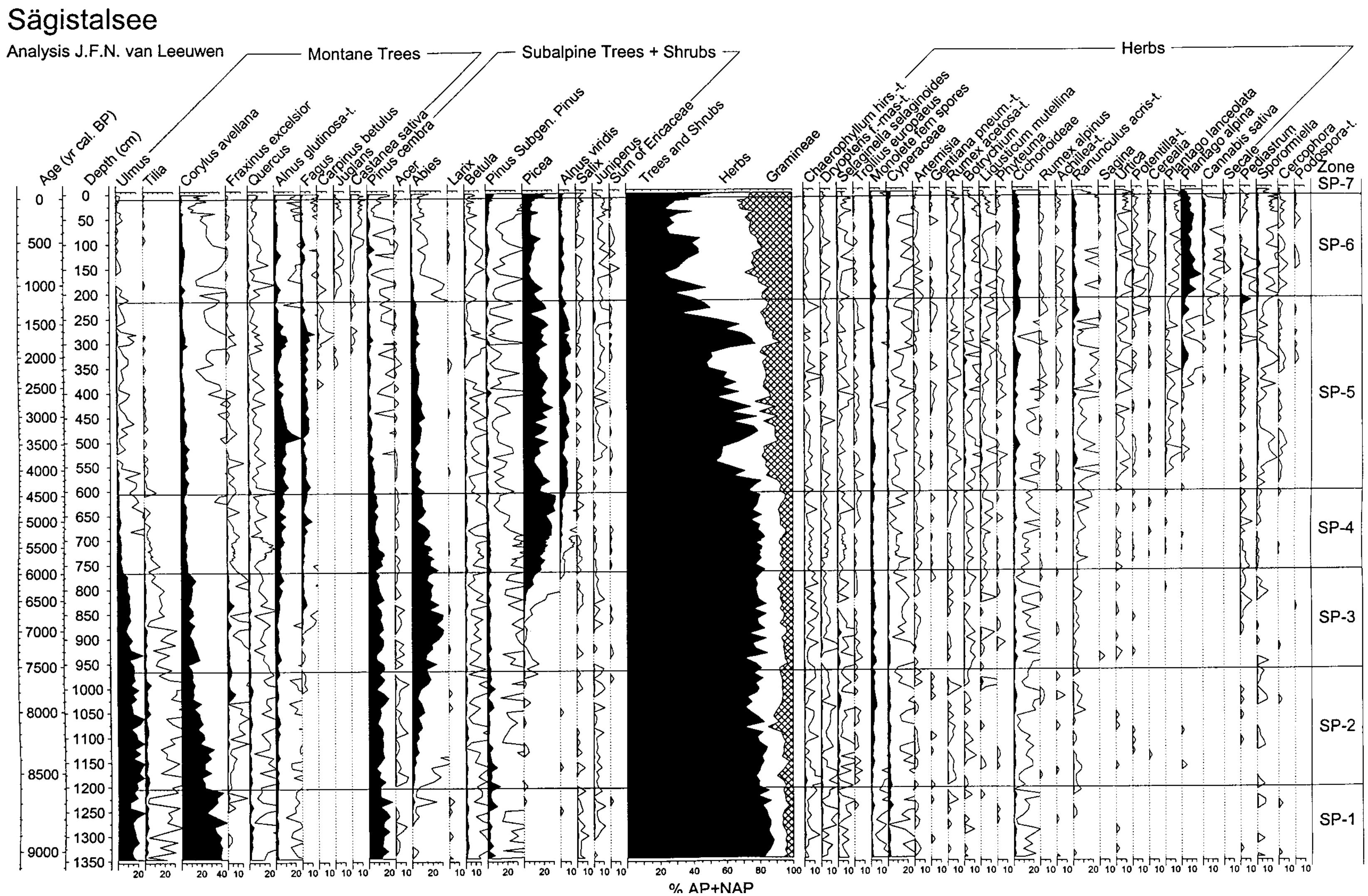

Fig. 1. Pollen percentage diagram of Sägistalsee (1935 m asl), showing selected pollen and spore types. Pollen types of aquatic plants are excluded from the pollen sum. The unshaded curves show 10× exaggeration of the percentage values.

Recently, several studies have shown the importance of analyzing different organisms and proxies for independent estimates of climatic fluctuations and tree-line oscillations (MacDonald et al., 1993; Birks and Ammann, 2000). The catchment vegetation, especially the presence or absence of forest in the catchment of a lake, influences the local climate (e.g., through hydrology and albedo), pedogenesis, and the chemical composition of the lake's water, which in turn influence the abundance and composition of aquatic biota.

The present investigation is part of a multidisciplinary study of a set of small mountain lakes where we have studied the influence of climate changes and catchment vegetation on different aquatic biota (see Lotter et al., 1997). The aim of this study was to determine and describe Holocene catchment vegetation of Sägistalsee in the Swiss Alps and to assess the human impact on it.

Study site

Sägistalsee (46°40′53″N; 7°58′39″E) is a small, 9.7 m deep lake of about 7.2 ha surface located at 1935 m asl close to modern tree-line. Ohlendorf et al. (2003) give an overview of the geology of the lake's catchment. The catchment of Sägistalsee is heavily grazed by cattle today. Due to human impact and grazing, the modern forest-limit in this part of the northwestern Swiss calcareous Alps is situated below Sägistalsee, but scattered single trees of *Picea abies*, the dominant tree of the subalpine forest, occur up to an altitude of ca. 2200 m asl.

In 1996 a 13.5 m long sediment core was taken with a modified Livingstone piston corer from the deepest part of the basin (see Lotter and Birks, 2003) and sampled for different analyses. The core dates back to 9060 cal. years BP and its chronology is based on 17 AMS radiocarbon dates on terrestrial plant remains as well as on ^{137}Cs dating (for details see Lotter and Birks, 2003).

Methods

For pollen analysis 1 cm³ of wet sediment was treated according to standard methods (see van der Knaap et al., 2000). *Lycopodium* tablets were added to estimate pollen concentrations (Stockmarr, 1971). The pollen percentage sum includes all pollen types of upland trees, shrubs, and herbs, whereas spores and pollen of aquatic taxa are excluded (Fig. 1).

For macrofossil analysis, sediment slices of 2 cm thickness and an average volume of about 40 ml were used. Wet sieving was done at a mesh width of 0.2 mm. The macrofossil diagram (Fig. 2) shows different macrofossil concentrations; periderm (bark) and wood are given as mm² and mm³. The sampling resolution ranges between a sample every 10 years (macrofossil zones SM-2 to 4) and a sample about every 70 years (upper part of zone SM-6).

Zonation of the pollen diagram was carried out using optimal sum-of-squares partitioning (Birks and Gordon, 1985) and the number of statiscally significant zones was assessed by a broken-stick model (Bennett, 1996). Zonation of the macrofossil diagram was done by visual inspection of the different curves.

A weighted averaging partial least squares transfer function (WA-PLS, see ter Braak et al., 1993) based on 129 sediment surface samples from lakes in different altitudes of the Alps (Lotter et al., 2000) was used to derive pollen-inferred July temperatures as well as pollen-inferred mean annual precipitation for all down-core pollen samples. The transfer function and the climate reconstructions were carried out using the software WAPLS (ter Braak and Juggins, 1993). A five-sample running mean and a LOWESS smoother (span = 0.2) were used to smooth the reconstructions (see Fig. 4).

Results

Pollen

Seven pollen-assemblage zones (SP-1 to SP-7) characterise the vegetation development in the catchment of Sägistalsee since 9060 cal. BP (Fig. 1).

SP-1: *Corylus – Ulmus – Pinus cembra* zone (9060 – 8610 cal. BP).
Upper boundary: expansion of *Abies alba*, decline of *Corylus*. Pollen resulting from long-distance transport dominates this zone, suggesting well-developed deciduous forests in the lower areas. *Corylus* and *Ulmus* most probably did not grow locally. There are no macrofossil findings to indicate that these taxa ever occurred above their present altitudinal limit (about 1400 m asl) in the Alps. 15–20% *Pinus cembra* pollen suggest local stands of Swiss stone pine in the catchment of Sägistalsee.

SP-2: *Ulmus – Corylus – Pinus cembra* zone (8610–7750 cal. BP).

Upper boundary: rational limit of *Abies*. This period is characterized by the immigration and gradual expansion of silver fir in the lake's catchment and a continuous decrease in *Corylus*. According to the relationship of (local) arboreal/non- arboreal pollen, the woodland near Sägistalsee remained rather open.

SP-3: *Abies – Ulmus – Corylus – Pinus cembra* zone (7750–6000 cal. BP).
Upper boundary: rational limit of *Picea*, immigration of *Alnus viridis*, decline of *Ulmus* and *Corylus*. *Abies* reached its maximum extent just before *Picea abies* spread into the catchment of Sägistalsee after 6500 cal. BP. At the same time, *Fagus sylvatica* expanded in the montane forests.

SP-4: *Picea – Abies – Pinus cembra* zone (6000–4470 cal. BP).
Upper limit: first decline of *Picea*, rational limit of *Alnus viridis*. *Picea* becomes the dominant tree species in the subalpine forest, whereas *Abies* and *Pinus cembra* continuously decline. Pollen grains of cereals (wind transport from lower regions), *Plantago lanceolata*, and *P. alpina* (both considered to be grazing indicators) point to Neolithic human activity in the lowland as well as near timber-line. The immigration of *Alnus viridis* coincided with early human impact in the Sägistalsee area.

SP-5: *Picea* – Gramineae – *Alnus viridis* zone (4470–1220 cal. BP).
Upper boundary: increase of *Plantago alpina*, decrease of *Picea* and *Alnus viridis*. This pollen zone is characterized by increasing human impact during the Bronze Age and the Iron Age: decreases of *Picea*, *Abies*, and *Pinus cembra* as well as the expansion of *Alnus viridis* point to forest clearance in the catchment of Sägistalsee. The use of the subalpine/alpine meadows near the lake as grazing areas is indicated by increasing pollen percentages of Gramineae, *Plantago alpina*, *P. lanceolata*, *Urtica*, *Ligusticum mutellina*, Compositae, Ranunculaceae, *Rumex*, and *Juniperus*. Reduced grazing pressure during the Migration period (ca. AD 350–500 or 1600–1450 cal. BP) allowed the woodlands to recover.

SP-6: Gramineae – *Picea – Plantago alpina* zone (1220–20 cal. BP).
Upper boundary: decline of *Plantago alpina*, increase of *Picea*. A decrease of *Picea*, *Abies*, and *Alnus viridis* and up to 80% non-arboreal pollen suggest extensive deforestation during the Middle Ages. Cattle breading was an important aspect of the economy during this period, as shown by the strong dominance of indicators of pasture (e.g. *Plantago alpina*, Compositae, *Potentilla*-type).

SP-7: *Picea* – Gramineae – *Pinus* zone (20 to –46 cal BP).
Declining grazing indicators and re-expansion of *Picea* and *Pinus* (this pollen type includes *P. sylvestris* and the tree-line species *P. mugo*) suggest decreasing human impact in the catchment of Sägistalsee since the 1930's.

Plant macrofossils

The tree-macrofossil concentrations in zone SM-1 (Fig. 2) are very low, suggesting that rather open woodlands formed by *Pinus cembra* and *Betula pubescens* covered the catchment of Sägistalsee between 9060 and 8500 cal. BP. The understory was rich in dwarf shrubs such as *Rhododendron* and *Vaccinium*. In open areas *Salix retusa* and *S. herbacea* occurred.

Around 8500 cal. BP *Abies alba* started to expand (zone SM-2). The first *Abies* macrofossils appear when pollen reach only about 3% (Fig. 3), indicating that in the subalpine environment the silver fir expanded at the same time as in lower areas. *Selaginella selaginoides*, dwarf shrubs (*Salix*, Ericaceae, *Dryas octopetala*), and a large number of herbaceous taxa indicate fairly open forests until about 6150 cal. BP (zones SM-2 to 4). The herb vegetation is dominated by alpine and pioneer plants, whereas tall herbs play a minor role, suggesting dry subcontinental conditions and/or poorly developed soils. The absence of *Abies* and a slight decrease in *Pinus cembra* macrofossil concentration in zone SM-3 suggest a temporary forest opening between 8350 and 8000 cal. BP that may be related to a climatic oscillation. There is no significant change in tree pollen percentages during this period.

Zone SM-5 (6150–3700 cal. BP), characterised by the expansion of *Picea abies*, represents the most favourable period for forest growth around Sägistalsee: high tree-macrofossil concentrations, decreases in pioneer herbs, and maximum *Picea* pollen percentages suggest well-developed and stable forests composed of *Picea abies*, *Pinus cembra*, and *Abies alba*. The first *Picea* macrofossils occur at very low *Picea* pollen percentages (2.5–3%). In the upper part of zone SM-5 macroscopic charcoal fragments indicate the beginning of late-Neolithic human activity in the catchment of Sägistalsee at about 4300 cal. BP. This coincides with the first indicators of pasture in the pollen record and with the expansion of *Alnus viridis*. The increase in charcoal is considered to be caused by human-made fires, because natural forest fires in the northern Alps are very rare. A change to a cooler and wetter climate as recorded for the middle Holocene would rather lead to a decrease in natural fire events.

High charcoal concentrations at two levels at the beginning of zone SM-6 (3700 cal. BP) point to stronger human impact, leading to deforestation and intensive pasturing during the Bronze Age. *Abies alba* and *Pinus cembra* macrofossils decrease dramatically and become very rare, whereas *Picea* shows only a temporary minimum. Human activity is shown by continuous records of charcoal fragments, plant macrofossils indicating open vegetation (e.g., *Rumex*, *Ranunculus*, *Saxifraga*, *Selaginella selaginoides*, *Dryas octopetala*, and *Loiseleuria procumbens*) and *Sagina saginoides* seeds. The latter species could point to soil disturbance near the lake by grazing animals.

After the Roman invasion in the 1st century AD and during the Migration period (AD 350–500), human impact decreased and reforestation started in the catchment of Sägistalsee, as shown by increasing occurrences of *Pinus cembra* and *Abies* macrofossils and by an increase in tree pollen percentages. The radiocarbon age 1730 ± 70 ^{14}C years BP (see Lotter and Birks, 2003) of these tree macrofossils excludes reworking of shallow water sediments. Low values of grass and *Plantago alpina* pollen suggest that the subalpine grazing areas were temporarily abandoned. The overall decrease of *Picea* macrofossils at around 1300 cal. BP indicates early Medieval forest clearance and lowering of the forest-limit to its modern elevation.

Pollen-inferred July temperature and mean annual precipitation

Pollen-inferred July temperature reconstruction for Sägistalsee shows a warm early and middle Holocene with a general trend of 2–3 °C cooling during the whole Holocene, as evidenced by the LOWESS smoother in Fig. 4. Heiri and Lotter (2003) found a comparable trend in chironomid-inferred July temperatures in the same sediment core. The warmest July temperatures are inferred for the early Holocene. A first cooling step occurred between about 8500 and 7500 and a second one between about 6000 and 5000 cal. BP. Several short oscillations in pollen-inferred July temperature become evident in the smoothed, 5-sample-averaged curve, the largest of which occurred between about 7500 and 7000 cal BP (Fig. 4).

The reconstruction of the mean annual precipitation shows a trend of slightly increasing pollen-inferred precipitation that is in the order of about 100 mm between the mid and late Holocene (Fig. 4). After a substantial increase in the early Holocene the pollen-inferred mean annual precipitation levels off between 1600 and 1700 mm yr^{-1}. A less humid phase is inferred for the period between about 5800 and 5200 cal BP.

Discussion

Reconstructing local vegetation development based only on pollen percentages is problematic because of long-distance transport of pollen (Birks and Birks, 2000). Especially at sites near tree-line, where local pollen production is low, pollen records are dominated by regional pollen input, and it is hardly possible to decide about local presence or absence of trees and the location of the forest-limit (Lang, 1993; Wick and Tinner, 1997). The relationship between arboreal and non-arboreal pollen percentages, often used as a rough (and in many cases insufficient) measure of the degree of landscape openness (see e.g., Sugita et al., 1999), is not suitable in mountainous areas. In order to overcome the problem of long-distance transport and to get reliable information about tree-line fluctuations and local vegetation history in a lake's catchment, plant macrofossil analysis is needed (Lang and Tobolski, 1985; Lang, 1993; Fedele and Wick, 1996; Wick and Tinner, 1997). Plant macrofossils allow the estimation of the time of immigration and expansion of a species much better than is possible with pollen. Conifer stomata in pollen slides have often been used as indicators of local occurrence of trees (Welten, 1982; Ammann and Wick, 1993). However, at Sägistalsee only pine stomata are recorded regularly, whereas *Picea* and *Abies* stomata are extremely rare (Fig. 3). Tree species, the degree of needle decomposition, and preparation methods (e.g., sieving) may determine the frequency of stomata in the pollen slides (Wick, 1994).

The macrofossil and pollen records of Sägistalsee and Hinterburgsee (1514 m asl; Heiri et al., 2003) and the pollen records of Aegelsee (995 m asl) and Schwarzmoos (1770 m asl) located west of our study area (Wegmüller and Lotter, 1990) suggest that *Abies* was present at Sägistalsee earlier than at the sites in the lower subalpine and in the montane areas. The first

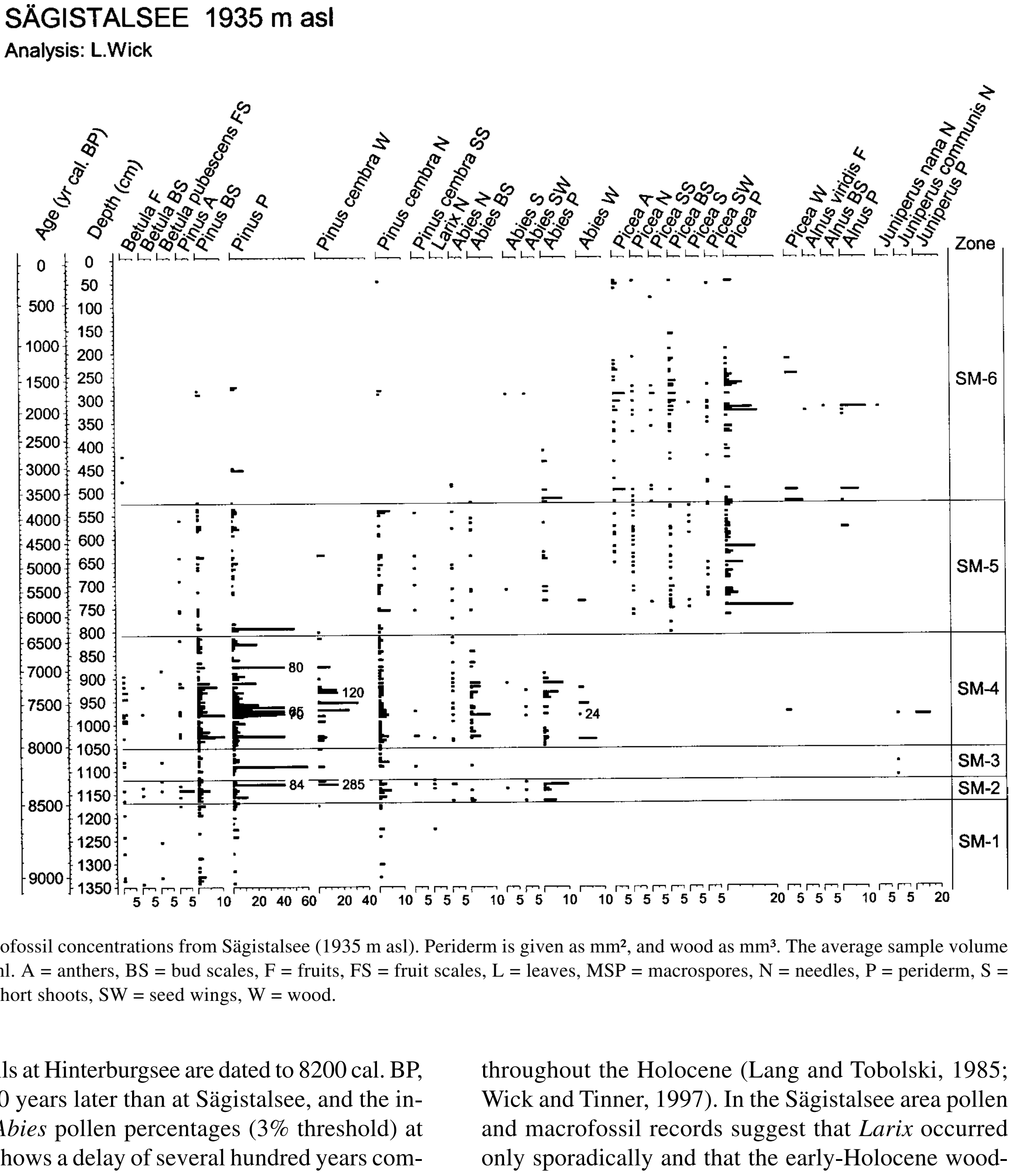

Fig. 2. Macrofossil concentrations from Sägistalsee (1935 m asl). Periderm is given as mm², and wood as mm³. The average sample volume is about 40 ml. A = anthers, BS = bud scales, F = fruits, FS = fruit scales, L = leaves, MSP = macrospores, N = needles, P = periderm, S = seeds, SS = short shoots, SW = seed wings, W = wood.

macrofossils at Hinterburgsee are dated to 8200 cal. BP, i.e., ca. 300 years later than at Sägistalsee, and the increase in *Abies* pollen percentages (3% threshold) at Aegelsee shows a delay of several hundred years compared to Sägistalsee. The *Abies* expansion at Schwarzmoos (poorly dated) and Hinterburgsee was more or less synchronous. At the lowland sites on the Swiss plateau the expansion of *Abies* is dated to around 7800 cal. BP (Ammann et al., 1996; Lotter, 1999).

The macrofossil record from Sägistalsee reveals Holocene vegetation patterns considerably different from those in the Central and Southern Alps. In the latter regions *Larix decidua* played a major role in the early-Holocene *Pinus cembra* forests and continued to be an important constituent of the subalpine forests throughout the Holocene (Lang and Tobolski, 1985; Wick and Tinner, 1997). In the Sägistalsee area pollen and macrofossil records suggest that *Larix* occurred only sporadically and that the early-Holocene woodlands were much more open than in the Central Alps (see also Wegmüller and Lotter, 1990). The early-Holocene *Pinus cembra*-*Abies alba* forests at Sägistalsee are of great interest with respect to both plant ecology and past climatic conditions. Today, *Pinus cembra* forests are restricted to the Central Alps, characterised by a subcontinental climate. The rare stands of Swiss stone pine growing in the Northern Alps might therefore be relics.

The modern distribution of silver fir below about 1700 m asl suggests that *Abies alba* is a typical montane

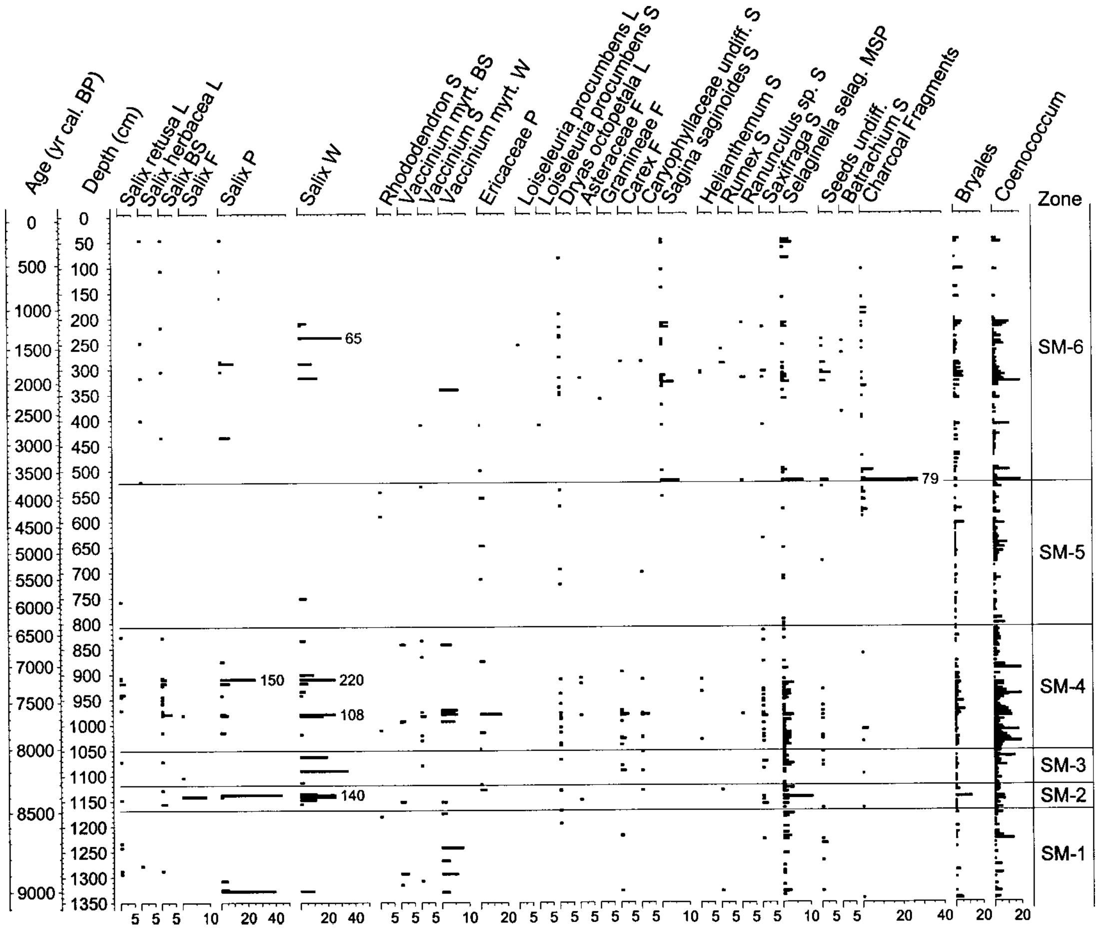

Fig. 2. Continued.

species sensitive to cold temperatures (frost) and reduced humidity. However, *Abies* has also been recorded in a few subalpine *Pinus cembra-Larix* stands in the Central Alps of Valais, where silver fir trees occur as high as 1900 m asl, and the limit of stunted individuals is 2100 m asl (Lingg, 1986a). Several authors consider these few stands as remnants of widespread *Pinus cembra-Abies* (*-Larix*) forests (Kuoch, 1954; Kral and Mayer, 1993; Lingg, 1986a). According to dendroecological studies in the Valais the limiting factors for silver-fir growth at high altitudes are late-summer (August and September) temperatures and, to a lesser extent, April and May temperatures, whereas winter minimum temperatures are less important (Lingg, 1986b). For Sägistalsee this implies a subcontinental climate with long growing seasons until about 6500 cal. BP, when increasing oceanicity, accompanied by a longer snow cover in spring and decreasing solar radiation (clouds, fog), may have reduced the growth potential of *Pinus cembra* and *Abies* and favoured the mass expansion of *Picea abies* and *Alnus viridis*. The continental character of the early-Holocene climate is supported by pollen-inferred July temperature and mean annual precipitation (Fig. 4). However, the sporadic occurrence of *Abies alba* in the recent forests and the isolated stands of *Pinus cembra* suggest that climate may not have been the only cause for changes in subalpine forest composition. Considering the continuous human activity since the late Neolithic and the great sensitivity of *Pinus cembra* and *Abies* to fire and grazing, the recent dominance of *Picea* can, at least partly, be attributed to human impact. The pollen deposition at Sägistalsee is, for a large part, dominated by pollen originating from lowland vegetation, especially before the immigration of *Abies alba* and the subalpine taxa *Picea abies* and *Alnus viridis*. This has, of course, an influence on the reconstruction of past climate. However, the modern empirical pollen-cli-

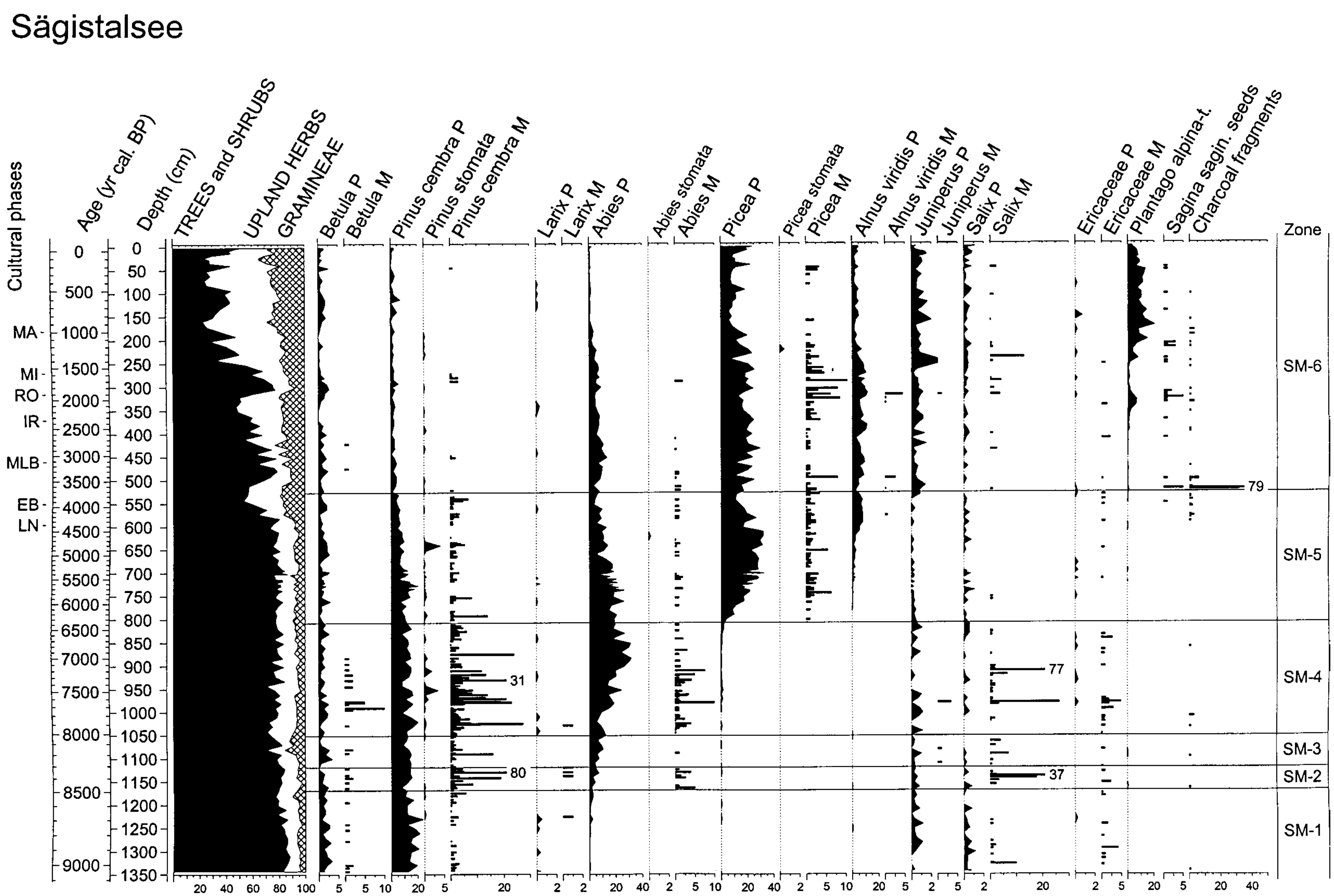

Fig. 3. Pollen percentages (P), stomata, and plant macrofossil concentrations (M) of selected taxa. Plant macrofossils are summarized, whereby values for periderm and wood are divided by 5. Cultural phases: LN = Late Neolithic, EB = Early Bronze Age, MLB = Middle and Late Bronze Age, I = Iron Age, R = Roman occupation, MI = Migration period, MA = Middle Ages.

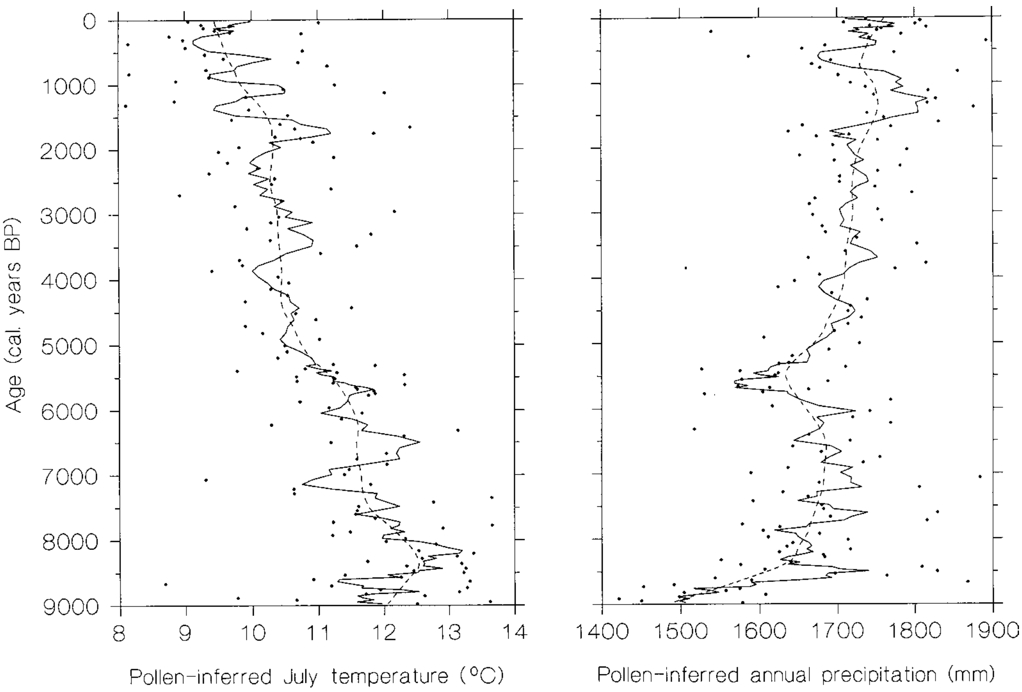

Fig. 4. Pollen-inferred July temperatures and mean annual precipitation. The reconstructions are based on a weighted averaging partial least squares transfer function for the Alps. The dots represent the inferred values, whereas the solid line is a 5-sample running mean and the dashed line a LOWESS smoother (span = 0.2). The sample specific errors of reconstruction range between 1.4 and 2.2 °C for July temperature and between 196 and 284 mm for precipitation.

mate relationships as modelled with the WA-PLS transfer functions take account of the optima of each pollen taxon and it is assumed that these have not changed during the Holocene (Birks, 1995). Due to the lack of quantitative Holocene climate reconstructions from the Alps as well as taking into consideration the sample-specific errors of reconstruction for both inferred climate parameters, it is difficult to evaluate these pollen-inferred reconstructions (Fig. 4). However, the general trend of a warmer early to mid Holocene and a more temperate late Holocene agrees well with estimates of the amount of solar radiation during summer for this period (e.g., Kutzbach and Street-Perrott, 1985). Some of the early-Holocene short-term fluctuations in the temperature reconstruction, such as the temperature minima between 9000 and 8500 cal. BP, at around 7200 cal. BP, and at 6000 cal. BP may correspond to climate oscillations recorded in the Alps (Zoller, 1960, 1977; Patzelt, 1977; Wick and Tinner, 1997). In the late Holocene, however, the effects of deforestation by humans (e.g., between 4200 and 3700 cal. BP, and after 1500 cal. BP) interfere with the pollen-climatic signal.

Previous studies near tree-line in the Central and Southern Alps revealed strong fluctuations in plant-macrofossil concentrations which were considered as forest openings or timber-line oscillations caused by short-term climatic changes (Wick and Tinner, 1997). Because of the site location about 200–250 m below the natural forest-limit, these climatic oscillations are not mirrored in the macrofossil record of Sägistalsee, except for a period lacking *Abies* macrofossils between about 8300 and 8000 cal. BP (Figs. 2 and 3, zone SM-3). Considering dating errors, this event may fit well with the 8200 cal. BP event recorded in stable-isotope curves of Greenland ice cores (Dansgaard et al., 1993; Grootes et al., 1993) and lake sediments (von Grafenstein et al., 1999). Wick and Tinner (1997), Haas et al. (1998), and Tinner and Lotter (2001) showed that this temporary climatic deterioration had a major impact on both subalpine/alpine and lowland ecosystems. The Misox oscillation described from the Southern Alps that is contemporaneous with the 8200 year event strongly affected silver fir stands at higher altitudes (Zoller, 1960). Except for a slight increase in Gramineae pollen this event is not reflected in the pollen data of

Sägistalsee and therefore does not show up in the curve of pollen-inferred July temperature. Previous investigations near timber-line have shown that at sites with a high proportion of regional pollen transport, fine-scale vegetation changes often are not recorded in pollen-percentage diagrams (e.g., Wick and Tinner, 1997). The chironomid assemblages of Sägistalsee, however, point to a cooler climate around 8200 cal. BP (Heiri and Lotter, 2003).

Comparisons of the palaeobotanical record with sedimentological and geochemical data from Sägistalsee (Hirt et al., 2003; Koinig et al., 2003; Ohlendorf et al., 2003) show a strong relationship between the vegetation cover in the catchment of Sägistalsee and the water chemistry and erosional processes. During the early Holocene (ca. 9000–6300 cal. BP), when open *Pinus cembra* and *Pinus cembra-Abies* woodlands covered the catchment, erosional input of clastic carbonates was high. Soil erosion is indicated by high *Coenococcum* concentrations in the macrofossil record (zones SM-2 to early SM-4). Considering the rather low pollen percentages, the high macrofossil concentrations of *Salix* and Ericaceae during this period may partly be due to erosional activity. The effects of the expansion of *Picea* in the lake's catchment at about 6300 cal. BP are shown as distinct changes in all the geochemical and sedimentological records. Additionally, this change in the vegetation cover had a major impact on the lake's chironomid fauna (Heiri and Lotter, 2003). Relatively dense *Picea-Pinus cembra-Abies* forests led to a stabilisation of the soils and a reduction of erosion in the lake's catchment between 6300 and 3700 cal. BP. The period of maximum forest density at Sägistalsee (Zone SM-5) probably coincided with the maximum elevation of the timber-line. According to plant-macrofossil studies at nearby Bachalpsee individual trees were able to grow at or above 2265 m asl during this time (Lotter et al., unpublished data).

During the late Holocene the vegetation near the Alpine timber-line has increasingly been influenced by humans. Whereas Neolithic impact was moderate, deforestation and grazing pressure since the Bronze Age led to decreases of the forest-limit of at least 200–300 m below its natural level and to a mass expansion of *Alnus viridis* (Wick and Tinner, 1997). As in the Southern Alps, *Pinus cembra* was not able to form new populations in the Northern Alps and became very rare. Also, *Abies alba*, due to its high sensitivity to fire and grazing, could not adjust to the changing environmental conditions. Thus the predominance of *Picea abies* and *Alnus viridis* (the latter is represented in the pollen rather than in the macrofossil record) in the subalpine area of the Northern Alps may at least partly be a consequence of human activity. Bronze Age forest clearance, indicated by high concentrations of macroscopic charcoal, and pasturing in the catchment of Sägistalsee destabilized the soils and facilitated erosional processes, as shown by changes in the mineral magnetic record (Hirt et al., 2003) and by an increase in detrital calcite concentrations in the sediment (Koinig et al., 2003; Ohlendorf et al., 2003). Increased soil erosion in the catchment since the Bronze Age is also shown by higher sediment accumulation rates (Lotter and Birks, 2003).

A close relationship exists between the vegetation in the catchment of Sägistalsee and aquatic faunas during the last 4000 years (Heiri and Lotter, 2003). Periods with increased human activity and deforestation at 4000–3500 cal. BP (Bronze Age), 2400–2000 cal. BP (Iron Age), and after 1500 cal. BP (early Middle Ages) correspond to strong decreases in accumulation rates of chironomid head-capsules. Heiri and Lotter suggest that the fluctuations in the chironomid assemblages were caused by changes in the oxygen regime of the lake due to increased nutrient inwash. Fungal spores related to animal faeces (e.g., *Sporormiella*, *Cercophora*) and high percentages of grazing indicators in the pollen record support this hypothesis. Apart from a few *Batrachium* seeds between 2700 and 1500 cal. BP aquatic plant macrofossils that might indicate changes in the aquatic ecosystem are absent. Decreasing pasturing resulted in forest recolonisation in the catchment of Sägistalsee as also recorded in other parts of the Alps since the early 20th century (van der Knaap et al., 2000).

Conclusions

The pollen and plant-macrofossil studies at Sägistalsee provide new information about Holocene environmental changes in the catchment close to tree-line in the Swiss Northern Alps. The following points deserve special mention:

1. The early-Holocene forests consisting of open *Pinus cembra* and *Abies alba* stands suggest a sub-continental climate until about 6500 cal. BP.
2. The tree-line reached its maximum elevation (about 2250 m asl) between ca. 6000 and 3500 cal. BP, i.e., considerably later than in the Central and Southern Alps.

3. A lack of *Abies* macrofossils between ca. 8300 and 8000 cal. BP mirrors a decline of the forest-limit caused by a major climatic oscillation that corresponds to the 8200 cal. BP event recorded in the Greenland ice cores.
4. Deforestation and pasturing during the Bronze Age and Iron Age and since the Middle Ages led to a temporary lowering of the timber-line to or below the elevation of Sägistalsee.
5. Pollen-inferred July temperature and mean annual precipitation suggest a trend towards cooler and wetter climate after about 5500 cal. BP.
6. The (near-)extinction of *Pinus cembra* and *Abies alba* and the modern predominance of *Picea abies* in the subalpine area of the Northern Alps are likely to reflect both a climatic change from subcontinental to more oceanic conditions and increasing human impact since the Bronze Age.

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