

Late-glacial and Holocene vegetation history and dynamics as shown by pollen and plant macrofossil analyses in annually laminated sediments from Soppensee, central Switzerland

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Received May 5, 1998 / Accepted October 9, 1998

Abstract. The palynostratigraphy of two sediment cores from Soppensee, Central Switzerland (596 m asl) was correlated with nine regional pollen assemblage zones defined for the Swiss Plateau. This biostratigraphy shows that the sedimentary record of Soppensee includes the last 15 000 years, i.e. the entire Late-glacial and Holocene environmental history. The vegetation history of the Soppensee catchment was inferred by pollen and plant-macrofossil analyses on three different cores taken in the deepest part of the lake basin (27 m). On the basis of a high-resolution varve and calibrated radiocarbon chronology it was possible to estimate pollen accumulation rates, which together with the pollen percentage data, formed the basis for the interpretation of the past vegetation dynamics. The basal sediment dates back to the last glacial. After reforestation with juniper and birch at ca. 12 700 B.P., the vegetation changed at around 12 000 B.P. to a pine-birch woodland and at the onset of the Holocene to a mixed deciduous forest. At ca. 7000 B.P., fir expanded and dominated the vegetation with beech becoming predominant at ca. 500 ¹⁴C-years later until sometime during the Iron Age. Large-scale deforestation, especially during the Middle Ages, altered the vegetation cover drastically. During the Late-glacial period two distinct regressive phases in vegetation development are demonstrated, namely, the Aegelsee oscillation (equivalent to the Older Dryas biozone) and the Younger Dryas biozone. No unambiguous evidence for Holocene climatic change was detected at Soppensee. Human presence is indicated by early cereal pollen and distinct pulses of forest clearance as a result of human activity can be observed from the Neolithic period onwards.

Key words: Vegetation dynamics – Palynology – Macroremains – Plant diversity – Laminated sediments – Climate change – Switzerland

Introduction

Pollen analyses have become increasingly refined since the early days of Swiss palynological research by Keller (1926, 1928) that revealed the major features of the

Late-glacial and Holocene vegetation development. Today dozens of pollen diagrams are available for lowland Switzerland (e.g. Lang 1985; Burga and Perret 1998). The Late-glacial environmental history is particularly well-studied in this region (e.g. Ammann et al. 1994). Pollen analytical studies of Swiss Late-glacial lake deposits in connection with stable-isotope investigations allowed a teleconnection with Greenland ice-cores and demonstrated the effect of large-scale palaeoclimatic events on the vegetation (e.g. Siegenthaler et al. 1984; Lotter et al. 1992a). With the advent of AMS ¹⁴C-dating, the Late-glacial radiocarbon chronology for the Swiss Plateau became well established (Ammann and Lotter 1989), whereas there are still only very few high-resolution, well dated Holocene pollen stratigraphies that allow estimates of past vegetation dynamics in this region. Several hypotheses for explaining the expansion of important tree taxa such as beech and fir have been put forward (e.g. Richoz et al. 1994; Ammann 1994; Haas 1996; Küster 1997) including factors such as natural or anthropogenically induced fires as well as human impact.

Palaeoecological studies of annually laminated sediments have a long tradition in Central Europe (e.g. Nipkow 1927; Welten 1944; Geyh et al. 1971; Lotter 1998). Palynological studies on such varved sediments can help to reliably estimate rates of tree expansion and of palynological change (e.g. Lotter et al. 1992b; Lotter and Kienast 1992; Peglar 1993; Ralska-Jasiewiczowa and van Geel 1992). In this context the laminated sediment record from Soppensee presents a unique opportunity to investigate the Holocene vegetation history on a sound and high-resolution chronological basis. Furthermore, palaeobotanical analyses can provide a reliable means of verifying the completeness of a sedimentary record. This is especially desirable as the Soppensee sediments form the basis for different multidisciplinary palaeoecological and palaeolimnological investigations (Fischer and McKenzie, in press; Hofmann, in press; Lotter, in press). Information about the vegetation type and the amount of vegetation cover, as well as knowledge of human impact in the catchment, are important prerequisites for the interpretation of such studies.

In this contribution, emphasis is laid on the specific features of the Late-glacial and Holocene vegetation history of this part of the Swiss Plateau in relation to the general trends described by Ammann et al. (1996). Furthermore, the available high-resolution Holocene chronology allows the investigation of past vegetation dynamics. Given such a high-resolution and well-dated Holocene chronology, the possible reaction of lowland vegetation to known climatic fluctuations will be discussed.

Site and methods

Soppensee is a small, eutrophic hard-water lake on the central Swiss Plateau (8°05'E, 47°05'30"N, Fig. 1). It lies at an elevation of 596 m asl in a region of intensive agriculture. The lake is of glacial origin, dating back to the end of the last glaciation. Typically, the sediments in the deepest part of Soppensee comprise about 6 m of organic sediments and several metres of clastic and fluvio-glacial deposits. Large parts of the Late-glacial and Holocene sediments of Soppensee are annually laminated (Lotter 1989, 1991a). The three cores analysed for this study (SO86-14, SO89-23, SO89-17; Fig. 1) were taken in the central, deep part (27 m) of the basin with a Kullenberg piston corer in 1986 and 1989 (details in Lotter et al. 1997).

Palaeobotanical analyses

For pollen analysis, 1 cm³ of fresh sediment was cut out of the core and spiked with *Lycopodium* tablets for estimating absolute pollen values. In core SO86-14 72, con-

and 98 taxa were identified. Core SO89-23 includes 265 samples with a total of 109 taxa. For percentage calculations the sum of arboreal (AP) and non-arboreal pollen (NAP) was taken to be 100%, with spores and pollen of aquatics being excluded.

The lower part of core SO89-17 (505-690 cm) was cut into 1-cm-thick slices, i.e. 8 cm³, treated with 10% HCl, 10% KOH, and then sieved through a 250-µm mesh for plant macrofossil analyses. Forty one different macrofossil types were identified in 302 samples. After identification and enumeration, the terrestrial plant remains were used for AMS ¹⁴C-dating (see Hajdas et al. 1993, in press).

Numerical analyses

Rarefaction analyses using the program RAREPOLL (Birks and Line 1992) were carried out using the raw counts of AP and NAP to estimate the palynological diversity. The lowest pollen counts (273 grains in core SO89-23, and 531 grains in core SO86-14) were used as reference sum.

Rates-of-palynological-change analyses using the program RATEPOL (J.M. Line and H.J.B. Birks, unpublished program) were carried out on percentage AP and NAP data. Taxa that had occurrences of less than three and abundances below 0.5% were excluded from the analyses. Chord distance between adjacent samples was used as a dissimilarity coefficient and no smoothing or interpolation of the data was done. In core SO86-14, the dissimilarities were standardized to 15 years (Fig. 11), whereas in core SO89-23 a time standardisation unit of 50 years was used (Fig. 12), which corresponds to the mean age difference between samples.

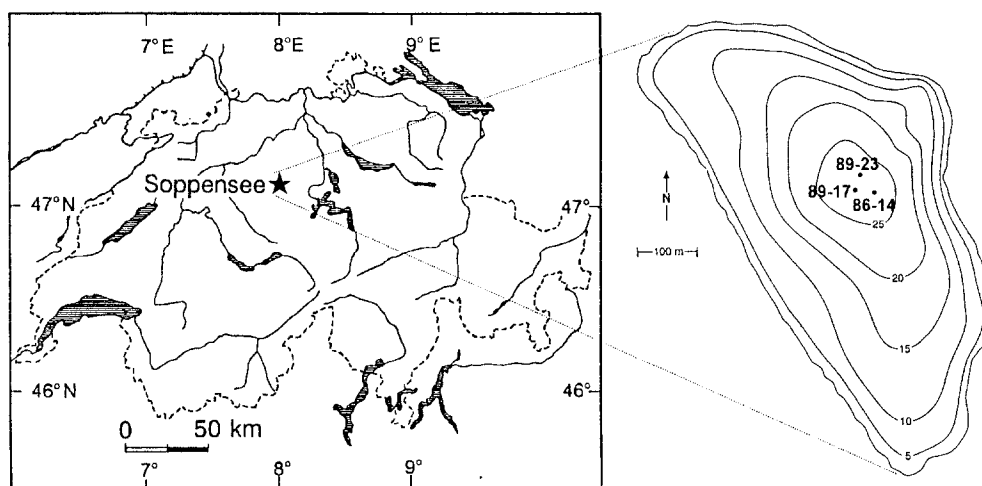


Fig. 1. Map of Switzerland showing the location of Soppensee (inset) and bathymetric map of Soppensee with location of cores used in this study (depths in metres). All cores were taken from the deepest part of the basin in water depths of 27 m

tinuous samples each containing 15 varves were sampled in the interval where *Abies* expanded using a specially designed sediment cutter (Segerström and Renberg 1986). The standard chemical procedure included treatment with 10% HCl, 10% KOH, 40% HF, acetolysis, mounting in glycerol, and staining with Fuchsin. With the exception of the lowermost Late-glacial samples, a total pollen sum of at least 500 grains was counted for each slide. In core SO86-14, 175 samples were analysed

Pollen zonation

Cores SO86-14 and SO89-23 were studied in detail palynologically, whereas only the transitions between pollen zones were analysed in core SO89-17. Following Ammann et al. (1996), the pollen and macrofossil diagrams are subdivided into nine regional pollen assemblage zones (PAZs). A detailed description of these regional PAZs as well as their relationship to the com-

monly used central European pollen zones according to Firbas (1949, 1954) and the chronozones according to Mangerud et al. (1974) is given by Ammann et al. (1996). The abbreviation CHb stands for the region of the Swiss Plateau, i.e. lowland Switzerland between the Alps in the south and the Jura mountains in the north, and between Lake Geneva in the west and Lake Constance in the east. The ^{14}C and absolute ages used for the zone boundaries were obtained from different Soppensee cores (Hajdas et al. 1993, in press) and may in some cases differ slightly from the ages attributed to these boundaries by Ammann et al. (1996).

Chronology

A radiocarbon chronology (Fig. 2a) consisting of over 100 AMS ^{14}C dates on terrestrial plant macrofossils (see Hajdas et al. 1993, in press) from cores SO89-23 (nine dates), SO86-14 (21 dates), and SO89-17 (71 dates) was used. This radiocarbon chronology allowed comparison with other conventionally ^{14}C -dated pollen diagrams from central Europe. The ^{14}C dates were calibrated according to Stuiver and Reimer (1993). A depth-age relationship was subsequently fitted to these dates using a cubic spline function (Fig. 2). Between 419.5 and 505.5 cm varve counts were used as a time-scale. This floating varve chronology was combined with the dendrochronologically calibrated radiocarbon chronology by ^{14}C wiggle-matching (see Hajdas-Skowronek 1993; Hajdas et al. 1993, in press).

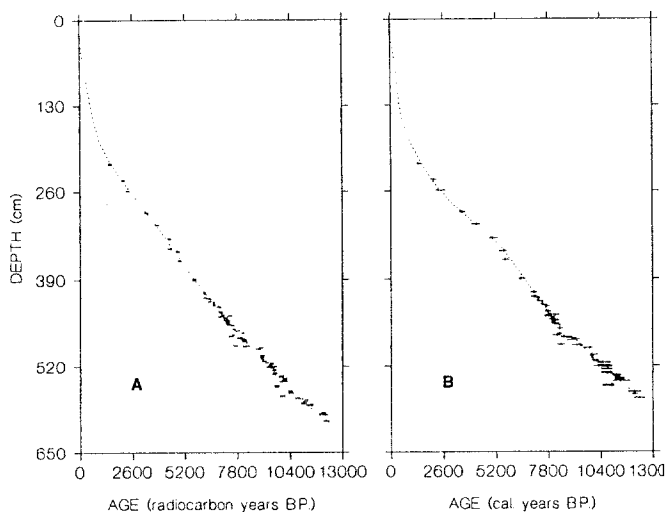


Fig. 2. Depth-age relationships in core SO89-23. **A** Uncalibrated AMS ^{14}C ages measured on terrestrial plant macrofossils originating from cores SO89-23 and SO89-17. **B** Calibrated ^{14}C ages, including $\pm 2\sigma$; all ^{14}C ages refer to dates given in Hajdas et al. (in press)

With the exception of the Late-glacial section, an absolute chronology (i.e. calibrated ^{14}C years B.P.) was used in this study as it allows a more accurate estimation of rates than conventional ^{14}C -ages and thus makes more ecological sense (cf. Lotter et al. 1992b). To avoid discrepancy problems due to chronological differences with other laminated sedimentary records (e.g. Zolitschka et al. 1992; Goslar et al. 1993; Björck et al. 1996; Hughen et al. 1998) the absolute chronology was only extended

back to that part of the Late-glacial period where these varve chronologies are consistent. Moreover, modelling of the youngest part of the chronology (Fig. 2) between the last ^{14}C date (1495 ± 55 B.P.) and the water/sediment interface (-40 B.P.) resulted in extremely low deposition times (years/cm). Pollen accumulation rates for the oldest and youngest part of the record were, therefore, not estimated.

Vegetation history

The vegetation history is inferred from the pollen records of Soppensee cores SO86-14 and SO89-23.

The Late-glacial period (>14 000 to 10 000 B.P.)

During the last decades the regional Late-glacial vegetation history of the Swiss Plateau has been intensively investigated on the basis of several detailed site studies (e.g. Welten 1982; Gaillard 1985; Ammann 1985; Rösch 1985; Lotter 1988).

The Late-glacial period on the Swiss Plateau can be subdivided into four regional PAZs (see Lotter et al. 1992a; Ammann et al. 1996) that are defined according to their dominant pollen taxa. The whole of CHb-1 (*Artemisia* PAZ, >14 000-12 700 B.P.) is correlated to the Oldest Dryas biozone (1a *sensu* Firbas 1949, 1954). It is characterized by the dominance of NAP (Figs. 3 and 4), with mainly heliophilous taxa such as *Artemisia* and Gramineae as well as Cyperaceae. The PAZ can be subdivided into three subzones. The subzone Chb-1a (*Pinus* sub-PAZ, >14 000 B.P.) is characterized by elevated values of *Pinus*, interpreted as due to long-distance transport, and reworked coniferous AP taxa (*Abies*, *Picea*; Fig. 3). The presence of these reworked pollen indicates persisting meltwater influence by the retreating Reuss glacier. For this period, a sparse herbaceous pioneer vegetation on open ground is inferred which includes *Dryas octopetala* (Fig. 6). Several ^{14}C dates from different localities on the Swiss Plateau indicate an age range of 14 000-14 600 B.P. (e.g. Lister 1988; Ammann and Lotter 1989).

With the onset of CHb-1b (*Helianthemum* sub-PAZ, >14 000 to ca. 13 500 B.P.) the occurrence of reworked taxa ends and heliophilous NAP dominate the pollen spectra. Pollen concentrations are low (Fig. 5). Vegetation consisting of grassland with alpine and steppe herbs is represented.

CHb-1c (*Betula nana* sub-PAZ, ca. 13 500-12 700 B.P.) is marked by the expansion of dwarf shrubs such as *B. nana*, *Salix* spp., and *Juniperus*. *Betula* and *Salix* pollen concentrations show a twofold increase at the onset of this zone (Fig. 5). *B. nana* pollen has been identified in several profiles from the Swiss Plateau (Gaillard 1983, 1984). Moreover, the plant-macrofossil records from Soppensee (Fig. 6), as well as those from many other sites on the Swiss Plateau (e.g. Ammann and Tobolski 1983; Gaillard 1984; Lotter 1988), clearly show that this first expansion phase in the *Betula* curve (see Figs. 3, 4) is attributable to increased input of *B. nana* pollen. During this zone the vegetation consisted of species-rich grasslands with dwarf-shrub heaths.

SOPPENSEE S089-23

Late-Glacial

Anal.: A.F. Lotter 1990

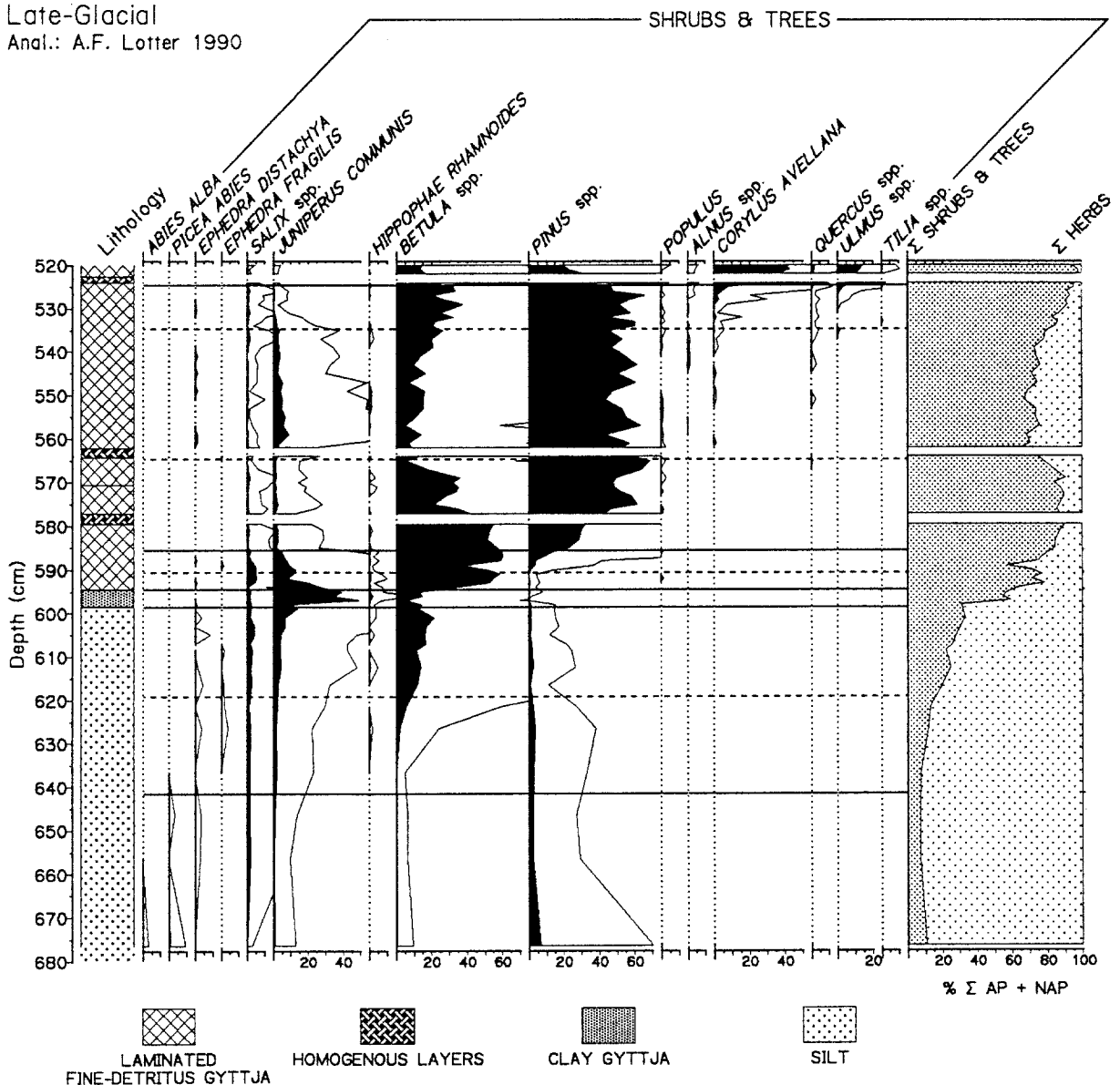
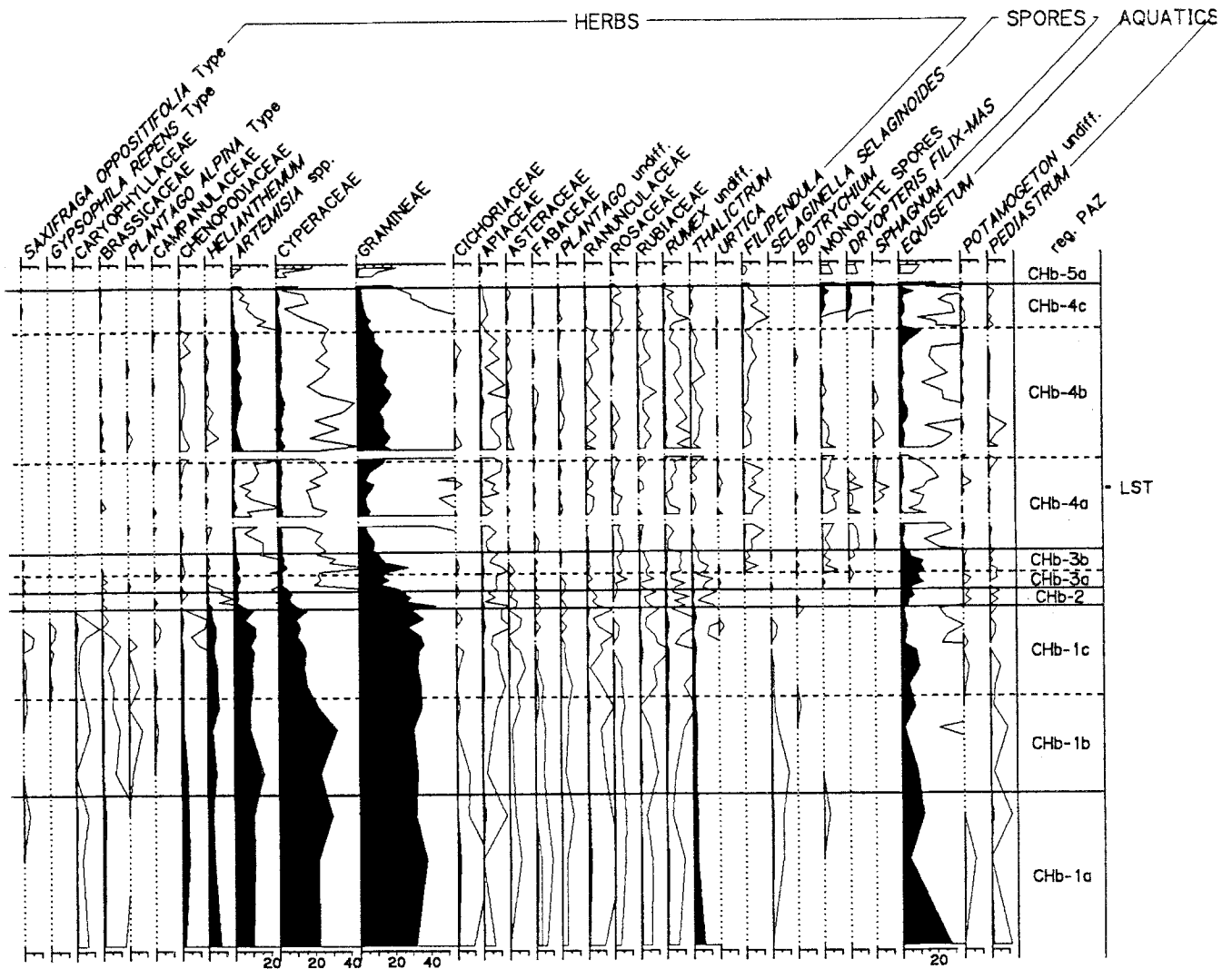


Fig. 3. Percentage pollen diagram, core S089-23, showing the Late-glacial period (main taxa only shown)

The onset of the short CHb-2 (*Juniperus-Hippophaë* PAZ, ca. 12 700 to ca. 12 500 B.P.) corresponds to the onset of the Bølling biozone (Ib). It is marked by a steep increase in juniper pollen. Both juniper and sea buckthorn reach their highest values during this zone (Figs. 3, 4). The NAP concentrations remain high (Fig. 5), so that the vegetation during this zone was characterized by open shrub consisting of *Juniperus* and *Hippophaë rhamnoides* together with grassland plants. The increasing *Betula* pollen concentrations (Fig. 5) and the macrofossil finds of *B. pendula* (Fig. 6) show that the expansion of tree birch to form woodland took place during this zone, a phenomenon also described from other sites on the Swiss Plateau (cf. Ammann et al. 1996). The evidence from closely spaced AMS ^{14}C dates and also pollen studies shows that this transition lies in a zone of constant ^{14}C age at ca. 12 800-12 600 B.P. (Ammann and Lotter 1989; Lotter and Zbinden 1989).

CHb-3 (*Betula* PAZ, ca. 12 500-12 000 B.P.) can be subdivided into two sub-PAZs. Chb-3a (*Salix* sub-PAZ, ca. 12 500 to ca. 12 200 B.P.) forms the second part of the Bølling biozone (Ib) and is characterized by increasing birch percentages as well as a first birch pollen peak (Figs. 3, 4). *Betula* and *Salix* pollen concentrations also increase while NAP concentrations are still high (Fig. 5), which suggests an open birch woodland with willows. Concentration values for *Juniperus* and *Hippophaë* constantly decrease which may reflect the effect of increased competition for light with tree birches.

During Chb-3b (Poaceae-*Artemisia* sub-PAZ, ca. 12 200-12 000 B.P.), a first short regressive phase in vegetation development is shown by a decrease in *Betula* percentages mainly associated with an increase in grasses (Figs. 3, 4). *Pinus* pollen percentages start to increase during this subzone. This short-term palynological fluctuation has also been observed at central and



north-west European sites (Lowe et al. 1994) and is attributed to the classical Older Dryas biozone (Ic; Lotter et al. 1992a). *Betula* concentration values decrease, while NAP (including grasses) either decrease slightly or remain at the same high level as before and after the oscillation (Fig. 5). The increase in *Pinus* concentration during subzone Chb-3b suggests that this tree was migrating into the catchment. The inferred vegetation is open birch woodland in which the contribution of juniper and willow steadily declines.

Three subzones are recognised in Chb-4 (*Pinus* PAZ, 12 000-9500 B.P.). CHb-4a (*Betula* sub-PAZ, 12 000-10 800 B.P.) is correlated with the Allerød biozone (II). It is characterized by the rational limit of *Pinus*, and with *Betula* sub-dominating. *Pinus* concentration values increase constantly, whereas birch concentrations remain high (Fig. 5) and NAP concentrations gradually decrease. Macrofossil data clearly demonstrate that *Pinus sylvestris*

had its first local occurrence at Soppensee at the onset of CHb-4a (Fig. 6), a feature that is common at many sites on the Swiss Plateau (e.g. Tobolski 1985; Lotter 1988). *Betula pendula* macrofossils are more abundant than *B. pubescens*. These data indicate that the vegetation consisted of a pine-birch woodland. Presumably, *P. sylvestris* grew on drier soils of the slopes, whereas *B. pendula* occurred on dry humic soils in the level parts and *B. pubescens* on wetter soils of the catchment (cf. Atkinson 1992). The occasional occurrences of *B. nana* macrofossils indicate that some open grassland still persisted.

Towards the end of this zone, the Laacher See tephra (LST), a conspicuous volcanic ash layer originating from the Eifel mountains, western Germany, is found in the sediments. This layer has been dated at several sites to ca. 11 000 B.P. (Van den Bogaard and Schmincke 1985). Recent AMS dates, however, point to a ^{14}C age of

SOPPENSEE S086-14

Late-Glacial

Anal.: A.F. Lotter 1987-90

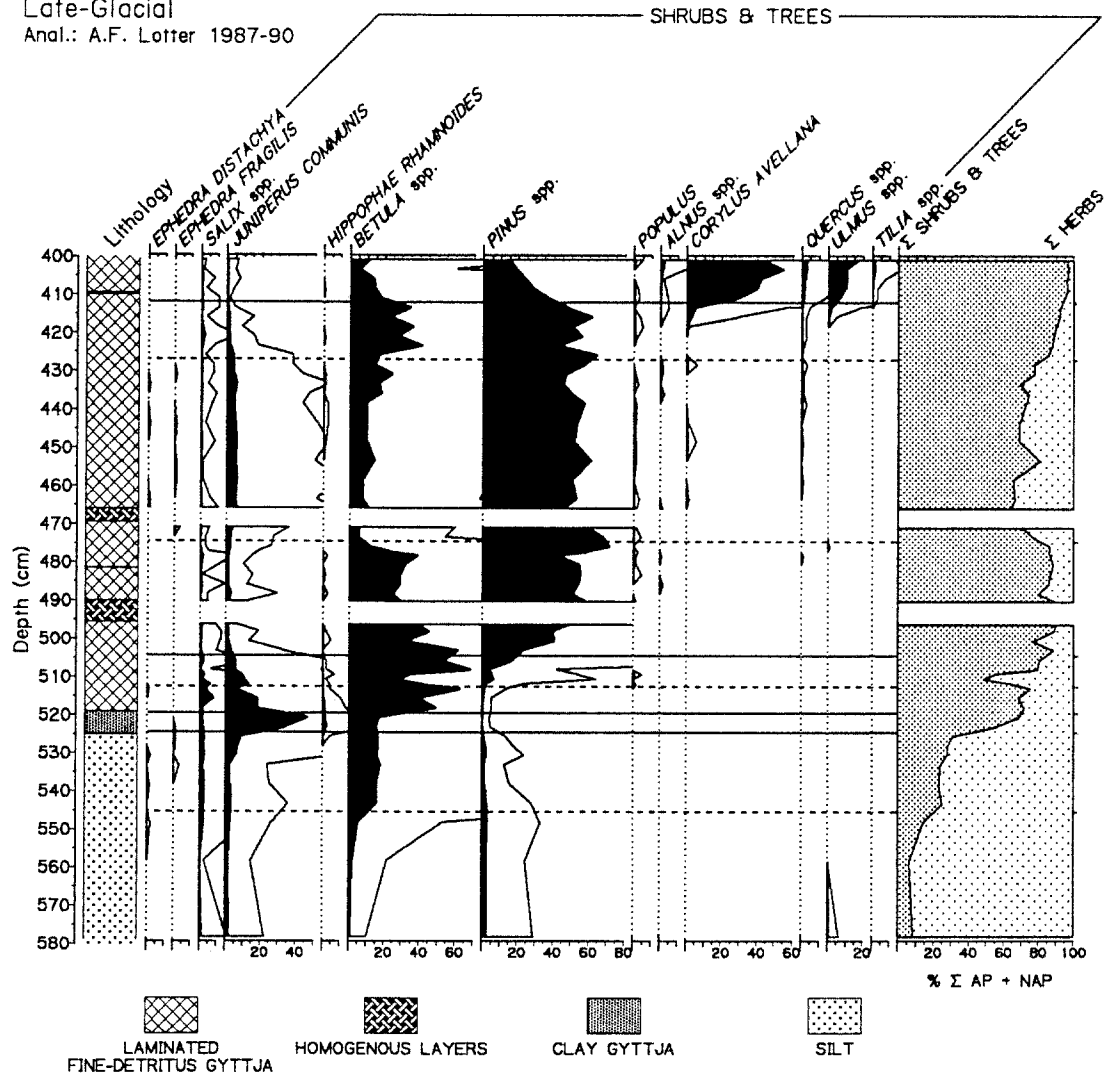


Fig. 4. Percentage pollen diagram, core S086-14, showing the Late-glacial period (main taxa only shown)

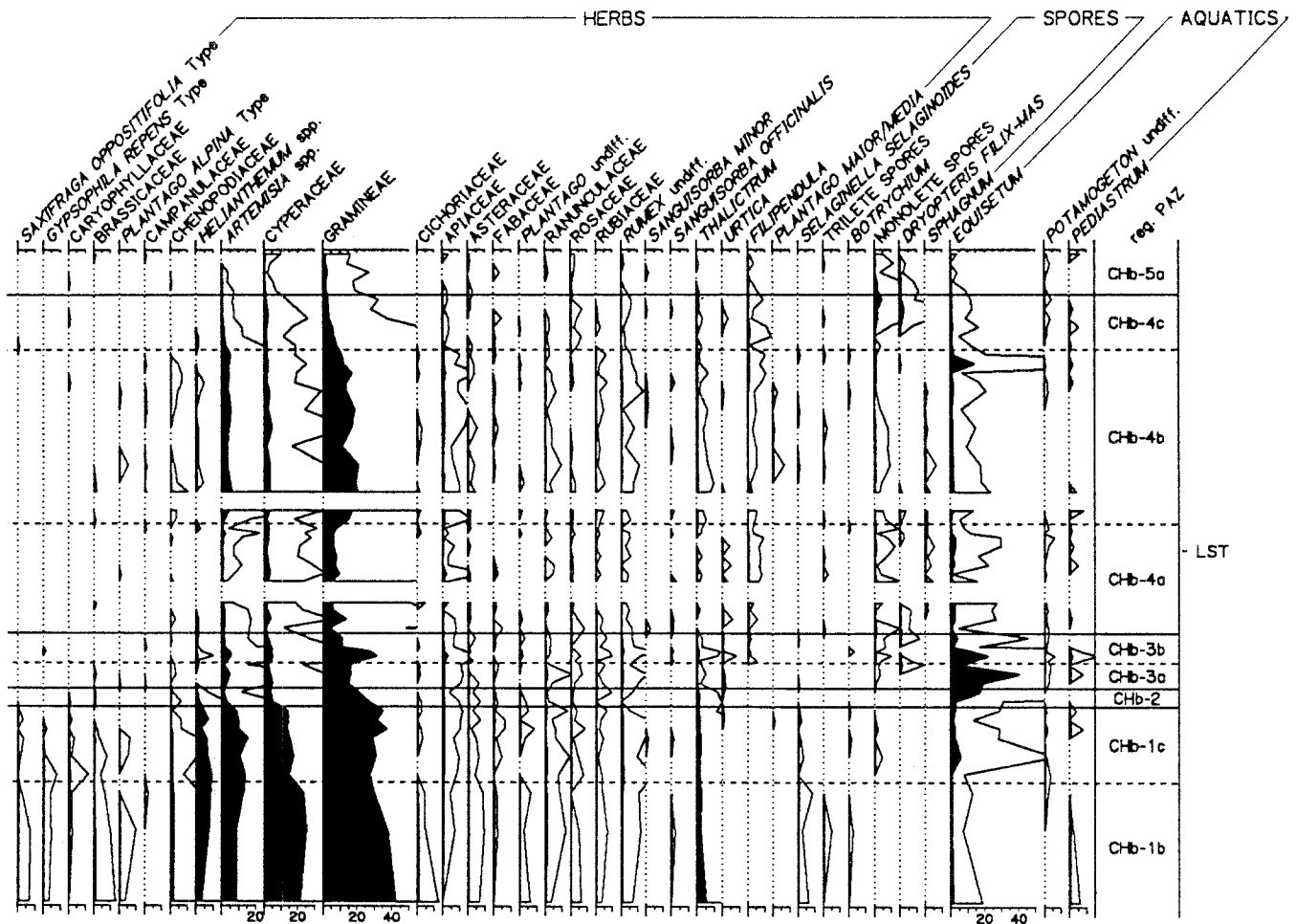
11 230±40 B.P. (Hajdas et al. 1995). The samples containing the LST show higher percentages of Gramineae pollen, a phenomenon that has been observed at different sites (Lotter and Birks 1993; Birks and Lotter 1994).

Towards the middle of PAZ CHb-4a the marker layer #1, which consists of littoral carbonate-rich sediment, interrupts the stratigraphy (Lotter et al. 1997). Comparison of the Soppensee curves with those from other sites on the Swiss Plateau, such as Rotsee (Lotter 1988) located 15 km to the south-east, shows no evidence for substantial erosion. On the basis of the pollen evidence from core S086-14, this homogenous layer is dominated by *Betula* pollen and must, therefore, have originally been deposited in the littoral during PAZ CHb-3.

Chb-4b (Poaceae-NAP sub-PAZ, 10 800-10 000 B.P.) is equivalent to the Younger Dryas biozone (III). In the percentage diagrams, this zone is characterized by declining *Betula* values and increasing NAP values, especially Gramineae and heliophilous taxa (e.g. *Juniperus*, *Artemisia*; Figs. 3, 4). Towards the end of this zone, *Betula* percentages increase slightly. The concentrations values for *Betula* and *Salix* are low, whereas *Pinus* con-

centrations remain on a constantly high level (Fig. 5) and the NAP concentrations remain constant or increase somewhat. The macrofossil diagram shows a decrease in both *Betula* and *Pinus* concentrations, with somewhat more *B. pubescens* remains towards the end of the zone (Fig. 6). There are still scattered macrofossil records for *B. nana* in the second part of this subzone. On the basis of these features, the vegetation during this period may be inferred to be a pine woodland with some openings and also some stands of juniper and birch, the latter most probably on wetter soils. This is in contrast to results presented by Gaillard and Lemdahl (1994) for a site on a comparable altitude on the south-western Swiss Plateau, where they found no signs of major openings in the pine woodland for the same period.

Marker layer #2 interrupts the stratigraphy shortly after the onset of this zone. It contains pollen assemblages that indicate a substantially older age than the sediment below and above it. Comparison with other palynological investigations give no indication for a hiatus in the pollen stratigraphy.



The Holocene (10 000 B.P. to the present)

Subzone Chb-4c (*Betula-Corylus* sub-PAZ, 10 000-9500 B.P.; Figs. 3, 4, 7, 8) represents the start of the Holocene and corresponds to the Preboreal biozone (IV). It is characterized by high *Pinus* values, decreasing NAP percentages, and a secondary peak in *Betula*. Moreover, mesophilous trees such as *Corylus*, *Quercus*, and *Ulmus* attain their empirical limit during this subzone. Pollen accumulation rates (PAR) reveal an overall increase in *Betula*, *Pinus*, and *Salix*, whereas total NAP remains more or less constantly high (Figs. 5, 9). The concentration of pine and birch macrofossils, especially *B. pendula*, increases as well (Fig. 6). The vegetation during this zone consisted of a pine-birch woodland which, according to the PAR, might have been more dense than during PAZ CHb-4a.

The change to regional PAZ CHb-5 (*Corylus-Quercetum Mixtum* PAZ, 9500-8200 B.P., 10 500-9250 cal. B.P.) is marked by the rational limit for *Corylus* (Figs. 7, 8). This PAZ corresponds to the Boreal biozone.

It can be subdivided into two parts: subzone CHb-5a (*Ulmus-Quercus* sub-PAZ, 9500-9100 B.P., 10 500-10 100 cal. B.P.) is characterized by decreasing percentages for *Pinus* and *Betula* and also NAP, and increasing values for mesophilous deciduous taxa such as *Corylus*, *Ulmus*, *Quercus*, *Tilia* and *Alnus*. The same pattern holds true for the PAR (Fig. 9) which show the highest overall values for the whole core in subzone CHb-5a. The macrofossil record shows decreasing *Pinus* and *Betula* values, while the first macroremains of *Populus* and *Tilia* are recorded (Fig. 6).

During the second part, namely CHb-5b (*Fraxinus-Hedera* sub-PAZ, 9100-8200 B.P., 10 100-9250 cal. B.P.) *Corylus* reaches its highest values, while pine and birch percentages are low (Figs. 7 and 8). *Alnus* and thermophilous taxa such as *Hedera* and *Viscum* spread, whereas *Fraxinus* reaches its empirical limit towards the end of this zone. Total PAR are still very high (Fig. 9) due to the presence of high pollen producers such as hazel, elm, oak, and alder. On the basis of the *Alnus* PAR (Fig. 9) and supported by the alder macrofossil occur-

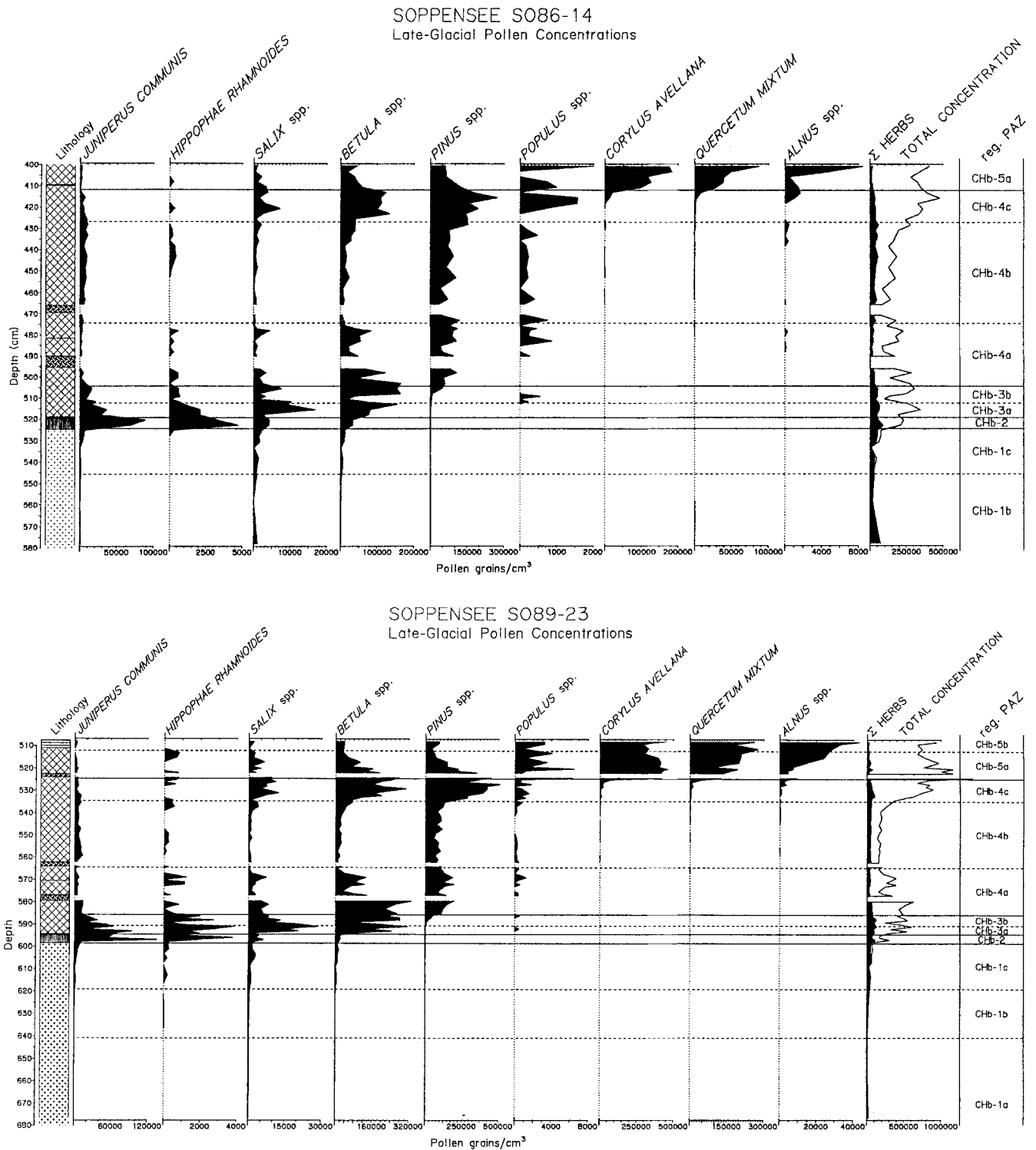


Fig. 5. Late-glacial pollen concentrations (pollen grains/cm³) for selected AP taxa and the sum of NAP in cores S086-14 (above) and S089-23 (below)

rences (Fig. 6), alder was already abundant in the catchment. Its percentage representation appears to be suppressed by the high *Corylus* values.

PAZ CHb-6 (Quercetum Mixtum-Corylus PAZ, 8200-7000 B.P., 9250-7800 cal. B.P.) corresponds to the Older Atlantic biozone (VI). In subzone CHb-6a (*Corylus* sub-PAZ, 8200-7700 B.P., 9250-8500 cal. B.P.) the percentages and PAR of *Corylus* decrease steadily as *Fraxinus* increases (Figs. 7, 8). The other

Quercetum Mixtum taxa (*Ulmus*, *Quercus*, *Tilia*, and *Acer*) remain at a constant level. PAR (Fig. 9) and macrofossil abundance (Fig. 6) decrease simultaneously with the increase of *Fraxinus* but this is not true for *Alnus* (Figs. 7, 8). This might be an indication of habitat competition between the two taxa. With the decrease of hazel, the total PAR values also decrease to 8000-12 000 grains/cm³/year.

During subzone CHb-6b (*Fagus-Abies* sub-PAZ, 7700-7000 B.P., 8500-7800 cal. B.P.), the *Corylus* decline continues, whereas *Alnus* percentages and PAR increase substantially. The increase in *Alnus* is paralleled by a renewed higher concentration of *Alnus* macrofossils (Fig. 6). *Abies* and *Fagus* reach their empirical limit during this subzone (Figs. 7, 8). The first *Abies* seeds are found towards the end of this subzone (Fig. 6) which points to local presence of this tree in the catchment. Early immigration of *Abies* (before 7000 B.P.; ca. 7800 cal. B.P.), is also known from other sites in the central Swiss Plateau (e.g. Lotter 1988).

The vegetation during CHb-6 is considered to be a mixed deciduous forest with *Ulmus*, *Fraxinus*, and *Alnus* likely on wet soils, *Quercus*, *Acer*, and *Tilia* on drier soils, and *Corylus* as an understorey shrub. The high abundance of *Tilia* macrofossils found at Soppensee and also at Rotsee (Lotter 1988) suggests that this tree played an important role on the slopes around these lakes.

PAZ CHb-7 (*Fagus-Abies-Alnus* PAZ, 7000-1300 B.P., 7800-1250 cal. B.P.) encompasses a long period of rather low vegetation dynamics, characterized by the dominance of beech, fir and alder. In subzone CHb-7a

(*Quercetum Mixtum-apophyte* sub-PAZ, 7000-2250 B.P., 7800-2200 cal. B.P.), three subdivisions are recognised as follows: CHb-7a₁ (*Pinus-Corylus* part, 7000-5500 B.P., 7800-6300 cal. B.P.), which is attributed to the Younger Atlantic biozone (VII), includes the expansion of fir and beech and the subsequent decline in *Ulmus* and *Tilia*. In CHb-7a₂ (*Abies* part, 5500-4150 B.P., 6300-4700 cal. B.P.), the empirical limit of the Cerealia curve is achieved. This and the records for anthropogenic indicator taxa, such as *Plantago lanceolata* (Behre 1981), indicate the presence of Neolithic agriculture (Figs. 7, 8). In CHb-7a₃ (*Fagus* part, 4150-2250 B.P., 4700-2200 cal. B.P.), there is a further increase in anthropogenic impact on the vegetation (cf. higher NAP values). The palynostratigraphical separation of the Younger Atlantic and the Subboreal biozones (VII/VIII *sensu* Firbas 1949) that takes place during this sub-PAZ is often not straightforward for sites on the Swiss Plateau. It is usually carried out on the basis of archaeological evidence of settlements of the Cortaillod culture in the pollen diagrams (Ammann 1989a; Hadorn 1992; Richoz et al. 1994).

Shortly after the onset of sub-PAZ CHb-7b (*Carpinus-Juglans-Secale* sub-PAZ, 2250-1300 B.P., 2200-1250 cal. B.P.), which corresponds to the Older

Soppensee SO89-17

Macrofossils
Anal.: A.F. Lotter 1991

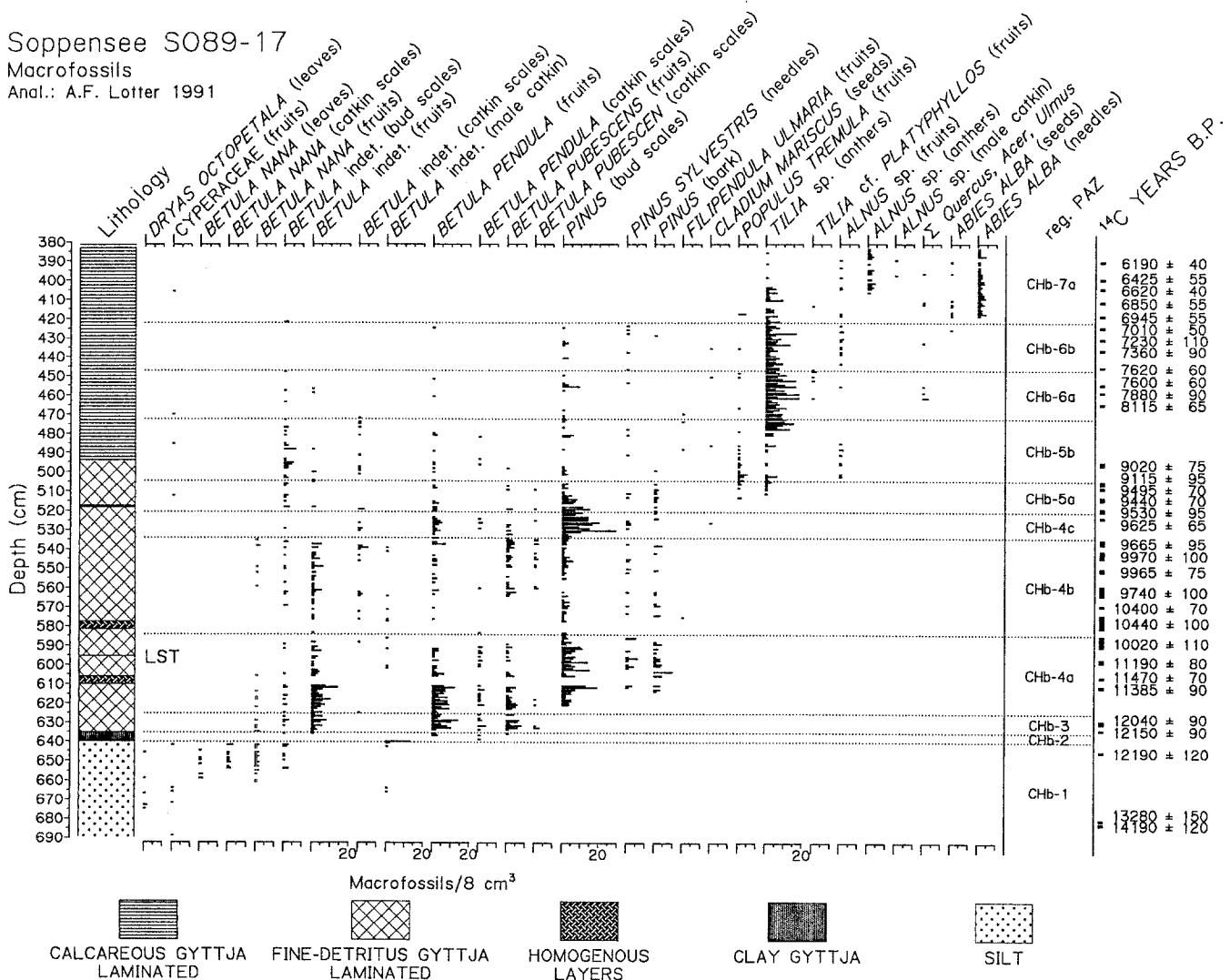


Fig. 6. Macrofossil concentrations in core SO89-17 (most abundant taxa only). A complete list of ¹⁴C ages is given in Hajdas-Skowronek (1993) and Hajdas et al. (in press)

Subatlantic biozone (IX), the Roman colonization of the Swiss Plateau, dated to ca. 2000 B.P., takes place. In many other pollen stratigraphies this event is correlated with a distinct *Quercus* peak located between two *Fagus* peaks (Lotter 1988; Ammann 1989a; Richoz et al. 1994; Richoz 1998). Specific indicator pollen for this event, such as *Juglans*, *Castanea* and *Secale*, however, occur only during the second part of this sub-PAZ (Fig. 7). This suggests that Roman land-use at Soppensee may not yet have been as intensive as at other locations on the Swiss Plateau. The short recovery phase, indicated by increasing AP percentages and PAR (e.g. *Fagus*, *Abies*, *Fraxinus*) is attributed to the Migration Period (Richoz et al. 1994; Richoz 1998).

During the regional PAZ CHb-8 (*Quercus*-NAP PAZ, 1300-150 B.P., 1250-200 cal. B.P.), a major change in the landscape is indicated by increasing NAP (both percentage values and PAR, especially Gramineae; Figs. 7, 9) and declining AP values. Considerable clearance of the *Fagus-Abies* forest took place in the context of intensified arable and pastoral farming. Subzone CHb-8a (*Humulus/Cannabis* sub-PAZ, 1300-800 B.P., 1250-700 cal B.P.) is mainly characterized by an increase in *Humulus/Cannabis* pollen-type that is attributed to hemp retting. High representation of *Humulus/Cannabis* are often observed at sites on the Swiss Plateau (Lotter 1988; Ammann 1989a; Richoz et al. 1994). This feature is often related to the foundation of monasteries in the twelfth and thirteenth centuries A.D. If, however, the extrapolated chronology is correct, this phenomenon occurs substantially earlier than at other sites.

The uppermost regional PAZ (CHb-9, NAP-*Pinus-Picea* PAZ, 150 to -40 B.P., 200 to -40 cal. B.P.) represents the vegetation of modern times. It is characterized by high NAP values and especially Gramineae, and reflects intensive land-use which includes both arable and pastoral farming.

Climate history

Most of the recent Late-glacial climatic reconstructions are based, not only on palaeobotanical results, but also on a combination of different biological proxy-data such as coleoptera (e.g. Elias and Wilkinson 1985; Gaillard and Lemdahl 1994), molluscs (e.g. Chaix 1985), or chironomids (e.g. Walker et al. 1991; Brooks et al. 1997). There is a long tradition in Switzerland of sediment studies combining pollen and stable isotope analyses (e.g. Eicher and Siegenthaler 1976). All major Late-glacial climatic shifts that are reflected in the Greenland $\delta^{18}\text{O}$ records can be correlated with events in the Swiss terrestrial pollen record (Lotter et al. 1992a). The first increase in $\delta^{18}\text{O}$ values recorded in many calcareous sediments from the Alps (e.g. Eicher 1987, 1994) and which reflect major warming, is synchronous with the transition from CHb-1c to CHb-2 (i.e. Oldest Dryas to Bølling biozone, ca. 12 700 B.P.). However, on the basis of changes in fossil insect assemblages from a site on the south-western Swiss Plateau, Gaillard and Lemdahl (1994) suggest a first climatic warming starting as early as ca. 13 000 B.P., i.e. during the dwarf birch phase of subzone CHb-1c. With the available data from Soppensee, however, it is not possible to test the hypothesis that there was a lag in vegetation response to climate warming in the order of up to 300 years (cf. Wright 1984).

A late Bølling drop in $\delta^{18}\text{O}$ values contemporaneous with the decrease in birch in subzone CHb-3b, termed Aegelsee oscillation, has been observed in many sediment records on the Swiss Plateau and has been correlated with similar features in the Greenland oxygen-isotope records (Lotter et al. 1992a). A reliable estimation of its duration is not possible on the basis of ^{14}C dates because of the short duration (Ammann and Lotter 1989). However, varve counts in the Soppensee sediments indicates a duration of ca. 100 years for the palynological oscillation, i.e. the *Betula* decline. Björck et al. (1996) dated the Older Dryas in Sweden and neighbouring regions to 12 200 B.P. and suggests a duration of 100-150 years. In the geochemistry data from Soppensee, the Aegelsee oscillation corresponds with a minimum in organic carbon, which suggests decreased productivity, at least within the aquatic system. On this basis, it is assumed that this regressive phase in vegetation development was not the result of natural succession stages and/or changes in the representation of high pollen producers as suggested by Gaillard (1985) and Wohlfarth et al. (1994) but was rather caused by a distinct, short-term climatic cooling. Whether it was accompanied by a dryer climate as postulated by Ammann and Tobolski (1983) and Ammann (1989a) cannot be determined on the basis of the available data. Investigations of fossil insect remains do not show any changes in insect-inferred temperature on the Swiss Plateau for this time (Elias and Wilkinson 1985; Gaillard and Lemdahl 1994) which might well be related to the coarser temporal resolution of these studies.

Varve counts indicate that subzone Chb-4a, i.e. the Allerød biozone, has a duration of ca. 600 years which corresponds well with the results from comparable investigations in northern Germany (Merkt 1994). Also, the duration between the deposition of LST and the onset of the Younger Dryas biozone, i.e. the reaction of the vegetation to the climatic cooling, which is about 200 years at Soppensee, agrees well with the results from other laminated lake sediments (e.g. Kaiser 1993; Merkt 1994, Lotter et al. 1995). Just before the deposition of LST, an increase in *Betula* percentage values occurs frequently in sub-PAZ CHb-4a (Figs. 3 and 4). This feature in the pollen curves is synchronous to the Gerzensee oscillation in the $\delta^{18}\text{O}$ values (Lotter et al. 1992a). A synchronous event has been observed as a sedimentological and palynological feature in maritime Canada (Levesque et al. 1993b) and has been termed the Killarney oscillation or the Amphi-Atlantic-Oscillation (Levesque et al. 1993a). At Soppensee, however, as at most European sites, there is no sedimentological or geochemical evidence for this 200-year-long isotopic fluctuation contemporaneous with the increase in birch pollen (Lotter et al. 1992a).

The effect of the climatic cooling of the Younger Dryas on the vegetation (subzone Chb-4b) has been extensively discussed in the literature. Depending on the altitude or latitude of the investigated site there may be a complete or partial deforestation such as is the case at Soppensee. Whether or not vegetation is reacting to climatic change without time-lag has often been debated (e.g. Wright 1984; Ammann 1989b; Lotter et al. 1995). On the time-scales available in palaeoecological studies there has generally been no observation of a noticeable

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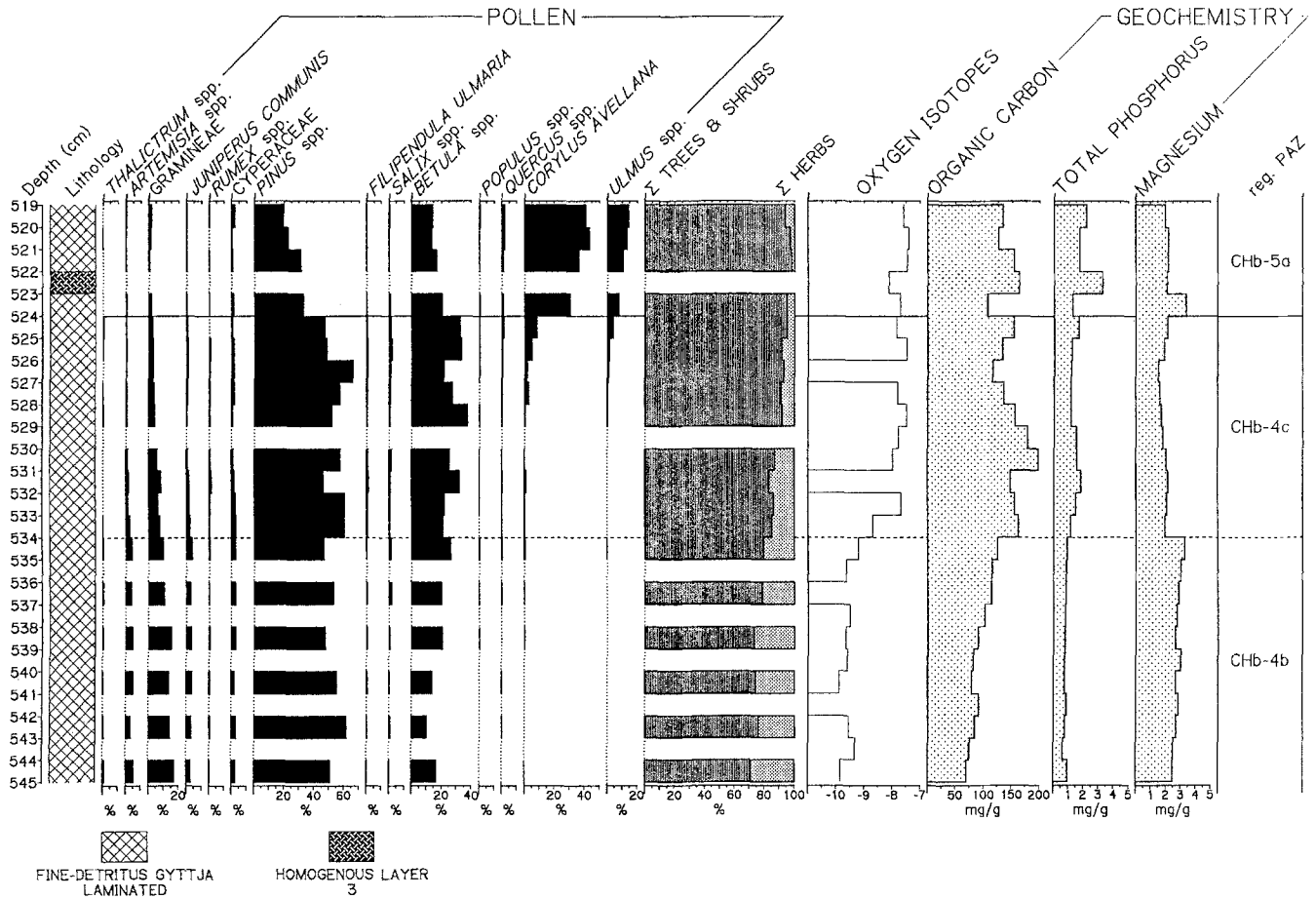
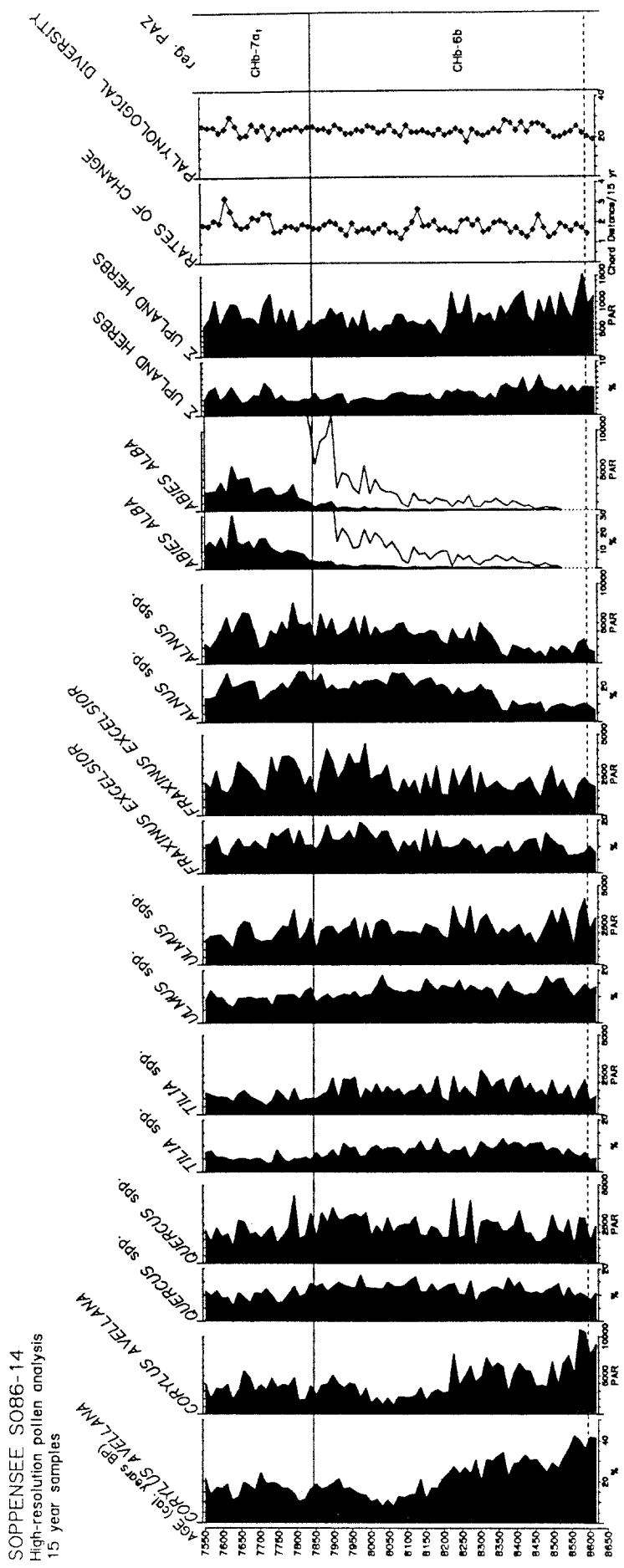


Fig. 10. High-resolution pollen percentage curves, the $\delta^{18}\text{O}$ curve (‰ PDB, after Fischer 1996) and geochemistry data (mg/g dry sediment weight; M. Sturm, unpublished data) at the transition from the Younger Dryas (Chb-4b) to the Preboreal biozone (Chb-4c)

lag in the reaction of terrestrial vegetation to the climatic change of the Younger Dryas (e.g. Lotter et al. 1992a, 1995). At Soppensee, the end of subzone CHb-4b is synchronous with the last major shift in the $\delta^{18}\text{O}$ record (Fischer and McKenzie, in press; Fig. 10). Both events are commonly dated to 10 000 B.P., an age that lies within a plateau of constant ^{14}C age (Ammann and Lotter 1989; Lotter and Zbinden 1989). On the basis of varve counts, the $\delta^{18}\text{O}$ shift that represents the transition from the Younger Dryas to Preboreal biozone took place within ca. 60 years (Fischer 1996). This time-span corresponds well with Greenland ice-core studies. At the temporal resolution of ca. 30 years/cm which is achieved at Soppensee, it is noteworthy that, not only is the vegetation change synchronous with the oxygen isotope shift, but also the erosional input, as represented by the magnesium concentration, and the lake productivity, as represented by organic carbon values, reacted immediately (Fig. 10). These changes in erosional input and in lake productivity indicate clearly that, on the one hand, the climatic warming at the end of the Younger Dryas biozone was very rapid. It is clear from the decrease in magnesium values, that, we are seeing not only higher pollen production but also denser vegetation cover that was probably largely responsible for the reduced level of soil erosion.

The occurrence of *Cladium mariscus* macrofossils in the Soppensee sediments as well as at other Swiss Plateau sites (e.g. Tobolski 1985) during the Preboreal biozone (i.e. CHb-4c) suggests a warmer climate. However, there is evidence for a Preboreal climatic oscillation from continental records (Preboreal oscillation, Lotter et al. 1992a) and Greenland ice cores (Hammer et al. 1986) as well as from geomorphological and glaciological studies (Schlaten, Patzelt 1977; Palü, Beeler 1977), palaeobotanical investigations (Youngest Dryas, Behre 1978; Ganna, Schneider and Tobolski 1985; Rionl and Splügen-1, Wick and Tinner 1997; CE-1, Haas et al. 1998) and geochemical analyses (Hölzer and Hölzer 1994). According to Björck et al. (1996), this Preboreal oscillation took place about 300 years after the Younger Dryas/Preboreal transition and had a duration of ca. 150 years. Accurate dating by radiocarbon is, once again, hampered by the presence of a plateau of constant ^{14}C age (e.g. Becker and Kromer 1986; Lotter 1991b). The $\delta^{18}\text{O}$ record from Soppensee unfortunately gives no unambiguous evidence for this oscillation. Nevertheless, the organic carbon content in the Soppensee sediments (Fig. 10) as well as at some sites in the Black Forest (Hölzer and Hölzer 1994; Lotter and Hölzer 1994) show a marked decrease during the second half of subzone



SOPPENSEE S086-14
 High-resolution pollen analysis
 15 year samples

Fig. 11. Comparison of pollen percentages (%) and pollen accumulation rates (PAR) for selected taxa, based on high-resolution pollen analysis, at the transition from zones Chb-6 to Chb-7, i.e. from the Older to the Younger Atlantic biozone. Each of these 72 contiguous samples comprises 15 varves. The silhouette lines for the *Abies* percentage and PAR values represent a x10 exaggeration. The palynological diversity is based on a rarefaction analysis standardized on a pollen sum of 531 grains

Chb-4c. It can, however, only be speculated as to whether the decline in aquatic productivity and the corresponding decrease in *Betula* percentages, concentrations and PAR (Figs. 3-5, 9) at Soppensee reflect this Preboreal oscillation.

Towards the end of subzone Chb-5b (Boreal biozone), the Vasset/Killian tephra (VKT) originating from the French Massif Central (Juvigné 1992), was found in the laminated Soppensee sediment. Palynostratigraphically, this tephra layer is often found near a third Boreal peak in *Corylus*, before the hazel percentages eventually decline. Radiocarbon dates of plant material gave an age of 8230 ± 140 B.P., corresponding to an absolute age of 9407 ± 44 cal. B.P. (Hajdas-Skowronek 1993; Hajdas et al., in press). Other sites where this tephra has been found in biostratigraphies include Schleinsee in southern Germany (Geyh et al. 1971) and Lobsigensee on the Swiss Plateau (Ammann 1989a).

Recently, several authors have suggested independently that the Holocene climate was not as stable and uniform as commonly thought. Based on studies of North Atlantic ocean cores, Bond et al. (1997) proposed phases of abrupt climatic change on millennial scales with a cyclicity of 1470 ± 500 years. Recent studies on timberline fluctuations in the Alps by Wick and Tinner (1997) corroborate these results by well-dated timberline oscillations that are synchronous with the climatic oscillations found in the North Atlantic. The most pronounced oscillation that is also evident in the Greenland ice cores (e.g. Meese et al. 1994) occurred around 8200 cal. B.P. (ca. 7400 B.P.) and was related to the Misox oscillation (ca. 7500-6500 B.P.) in the Alps. Moreover, based on the abundance of *Najas* seeds in sediments of a Swiss lowland lake, Haas (1996) recently proposed a series of three wet and cool phases interrupted by two dry and warm phases between ca. 8500 and 7900 cal. B.P. He associated the oldest of these dry phases (D2, ca. 8270-8110 cal. B.P.) with the 8200 cal. B.P. Greenland event. In the Soppensee record, this event can be expected near the middle of subzone Chb-6b. Haas (1996) argues that *Corylus* was considerably reduced during the wet phases. Given a chronological uncertainty of the order of about 50 years, the features of the hazel curve might be largely comparable (Fig. 11). Nevertheless, the reaction of fir and beech to the reduction of hazel seems to be mainly local rather than driven by a regional climatic pattern. There is no unambiguous evidence for these or any other climatic oscillations (e.g. van Geel et al. 1996) during the middle and late Holocene, either in the pollen stratigraphy or in any other biostratigraphy from Soppensee (Hofmann, in press; Lotter, in press). The observed Holocene climatic oscillations may have been of too small an amplitude to be recorded in lowland Switzerland.

Holocene vegetation dynamics

The varved sediment of Soppensee represents a solid chronological basis that allows estimates of rates of vegetation change and assessment of vegetation dynamics on a high-resolution time-scale. Commonly, rates of past vegetational change are inferred by estimating rates of

palynological change (e.g. Jacobson and Grimm 1986; Lotter et al. 1992a; extensive discussion in Odgaard 1994). The estimates of Holocene palynological change for Soppensee (Fig. 12) suggest high rates at the onset of the Holocene (between ca. 11 000 and 10 500 cal. B.P.), during the mid-Holocene (between ca. 7500 and 5500 cal B.P.), and especially for the last ca. 2000 years. These features, especially the high rates of change in the early and late-Holocene, agree well with the general features presented by other authors (e.g. Jacobson et al. 1987; Huntley 1992; Odgaard 1994), and suggest that the major changes in terrestrial vegetation on a broader geographical scale were caused by climatic change and by human activity.

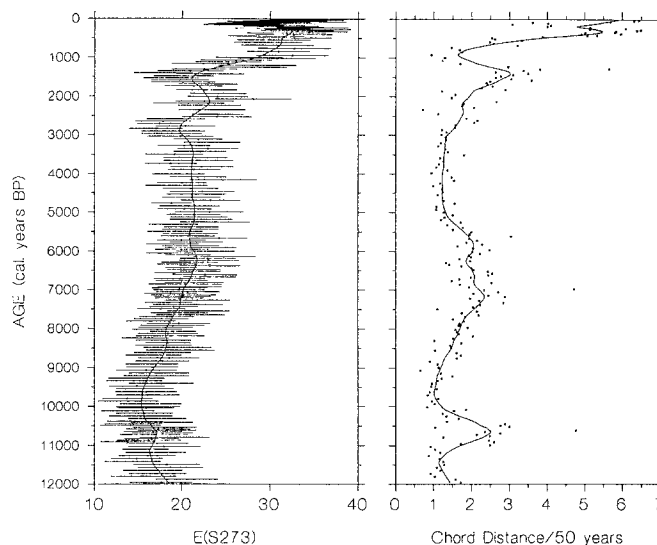


Fig. 12. Palynological diversity based on a rarefaction analysis standardized on a pollen sum of 273 grains and rates of palynological change per 50 years using chord distance as dissimilarity coefficient

At Soppensee, as well as at many other Central European sites, substantial changes in vegetation occur at the transition between subzones Chb-4c and Chb-5a, i.e. at the transition from the Preboreal to the Boreal biozone. PAZ CHb-5 is characterized by a progression from a pine-birch woodland to a mesophilous, deciduous forest consisting of thermophilous taxa such as *Corylus*, *Ulmus*, *Quercus*, *Tilia* and *Acer*, and with *Alnus* and *Populus tremula* on wetter soils. The varve-based chronology shows that the apparently rapid change in pollen assemblages is real and thus is not an artefact of the ^{14}C plateau at 9500 B.P. (Becker and Kromer 1986; Lotter 1991b). Several hypotheses have been put forward to account for the fast increase of hazel. According to Huntley (1993), a higher seasonality during this time with a more continental and drier climate, in combination with higher fire frequency, would have favoured the rapid expansion of *Corylus* (Ammann 1989b).

The change from a pine-birch woodland to a mixed coniferous forest took place within less than a century. As this rapid vegetational change was occurring over wide geographical areas throughout Central Europe such fast migration rates are difficult to explain. Taxa such as *Corylus*, *Ulmus*, *Quercus*, *Alnus* and *Tilia* must have

been present in very low population densities centuries before their expansion in the catchment took place. Very low pollen values for these taxa from as early as the Younger Dryas and Preboreal biozones (Figs. 3-5) favours this hypothesis. Bennett (1988), for instance, proposes that "intrinsic rate of population increase" should also be considered as a biological mechanism to explain vegetation succession in the Holocene.

The expansion and establishment of beech and fir, both shade-tolerant trees present during subzone Chb-7a led to an increase in the rates-of-change curve (Fig. 12). It has been suggested that the expansion of beech and fir may be related to light competition and increased disturbance regimes (e.g. dryer climate and fire; Richoz et al. 1994; Haas 1996; Richoz 1998). There are, unfortunately, no charcoal data available for the Soppensee record. Nevertheless, the high-resolution pollen diagram, consisting of 72 contiguous, 15-year-duration samples, may help to assess the vegetation dynamics during the phase of *Abies* pollen expansion (Fig. 11). *Abies* pollen percentages and PAR are very low for 450 years before they increase in a first step that lasts 165 years. In a second step, they increase again for 60 years before the empirical limit, i.e. the onset of CHb-7a, is reached. Analysis of the *Abies* PAR shows an exponential increase with time, i.e. it corresponds with the classical exponential population growth model. Similar studies suggest that a taxon may be present in a catchment despite low pollen concentrations and may, after having reached a certain population density, expand exponentially (Bennett 1983, 1988). This implies that the migration of a tree, at least at the margins of its range, does not consist of a "front" but represents rather single trees, or small outlying populations, that may expand exponentially after reaching a critical population density (e.g. Watts 1973; Godwin 1975). After the expansion of fir, the shade-intolerant *Quercetum Mixtum* taxa, *Ulmus* and *Tilia* and to a lesser extent *Quercus* and *Fraxinus*, decreased in abundance (cf. decreasing percentage and PAR values during Chb-7a₁).

The diversity of a vegetation depends on disturbance regimes (both natural and anthropogenic) and on the patchiness of vegetation types on a landscape-scale. Various methods have been proposed to assess modern biological diversity. In palaeoecology, the number of taxa encountered may be used as an indication of past diversity. Rarefaction analysis is commonly used to assess the palynological diversity (Birks and Line 1992; Odgaard 1994). Although palynological diversity and vegetation diversity are correlated, the palynological diversity still underestimates the floristic diversity due to taxonomical, productivity, and dispersal bias (many different plants may produce the same pollen type, some taxa are rarely encountered as pollen). Odgaard (1994) modelled the relationship between palynological and floristic richness by using a hyperbolic tangent function based on their modern relationship. As such modern studies are not available for central Europe, I have used the untreated rarefaction data (i.e. the number of pollen taxa that would be encountered if the pollen sum was to be kept constant) as a measure for the past palynological diversity (Fig. 12). This palynological diversity broadly

follows the rates-of-change curve (Fig. 12). It indicates a lower diversity during the early Holocene with an increasing trend until the middle Holocene. After ca. 7000 cal. B.P. (i.e. after the expansion of *Fagus*), the curve levels off and remains more or less constant for 4500 years. Then, after ca. 2500 cal. B.P., the palynological diversity shows its first increase between ca. 2500 and 1500 cal. B.P. and eventually a second, even bigger increase between ca. 1500 cal. B.P. and the present day. This overall Holocene trend in palynological diversity can be interpreted as the result of vegetation succession starting from a relatively low diversity at the beginning of the Holocene, to higher levels in the mid-Holocene. Judging from the palynological diversity and the rates-of-change data (Fig. 12) the vegetation must have been very stable and the vegetation dynamics very low after the establishment of the fir-beech forest at Soppensee in the mid-Holocene. The major changes that occurred during the late Holocene were caused by increased anthropogenic disturbances since the Iron Age.

Human impact

The Soppensee pollen record includes very early occurrences of *Cerealia* pollen. Similar results have been obtained elsewhere in central Europe (e.g. Küster 1989; Haas 1996). Apart from these single *Cerealia* pollen, there is some evidence, in the form of artefacts, for the presence of Mesolithic peoples in the catchment (E. Nielsen, personal communication).

Human impact became an increasingly important ecological factor after the Neolithic period (CHb-7a₂ onwards). Disturbances in the vegetation are indicated by higher percentages and PAR of pioneer shrubs and trees such as *Betula*, *Juniperus* and *Salix*. Within CHb-7a₃ increased NAP values indicate larger clearings of the beech-fir forest during the Bronze Age and Iron Age in the catchment of Soppensee.

On the Swiss Plateau, the Elm Decline is not as steep and abrupt as in north-western Europe (Peglar 1993). At Soppensee, the gradual decline in *Ulmus*, as well *Quercus* and *Tilia*, starts as early as subzone Chb-6a (Figs. 7-9) and occurs in several stages over a time-span of more than 3000 years. Around 5000 B.P. (ca. 6000 cal. B.P.), the *Ulmus* curve reached very low values (Chb-7a₂). The initial declines may have been mainly caused by the competition for light between *Abies/Fagus* and *Ulmus* (Heitz-Weniger 1976), whereas the last decline has often been attributed to anthropogenic effects (e.g. Rösch 1985; Ammann 1989a). The high-resolution pollen analytical data at the transition between Chb-6b and Chb-7a in the Soppensee profile, however, show no immediate major change concurrent with the *Abies* expansion (Fig. 11). Only slightly declining trends can be observed in the PAR curves for *Ulmus*, *Quercus*, and *Tilia* at the time of fir expansion. The last major decline in *Ulmus* percentages and PAR during Chb-7a₂ is associated with indicators of human impact (Figs. 7-9).

The major anthropogenic changes in vegetation took place in the Middle Ages as a result of extensive forest clearance which is reflected by the drastic changes in pollen percentage and PAR values at the transition from Chb-7b to Chb-8a.

Conclusions

The palaeobotanical analyses of the laminated Soppensee sediment enable detailed reconstruction of the vegetation history over the last 15 000 years. The main conclusions are as follows:

1. The classical Late-glacial climatic changes such as the transition from the Oldest Dryas to the Bølling biozone, as well as the Younger Dryas biozone, are clearly reflected in the pollen record. The detection of shorter climatic oscillations such as the Aegelsee oscillation (i.e. Older Dryas biozone) or the Preboreal oscillation depends largely on the degree of high-resolution sampling.
2. No unambiguous evidence for any of the Holocene climatic oscillations observed either in the Greenland stable-isotope record or in geomorphological, glaciological, and palynological studies from the Alps has been detected.
3. Holocene climatic oscillations have a smaller amplitude than those of the Late-glacial. Holocene climatic oscillations, however, are probably best studied at ecotonal boundaries such as the timberline, where even small changes in the physical environment may have a large effect on the vegetation. If lowland sites are chosen for Holocene climate studies, cores from the deepest part of a lake basin may be suitable for reconstruction of palaeolimnological features, whereas littoral cores may perhaps better reflect effects of climatic and hydrological changes (e.g. Haas 1996; Magny 1993).
4. The early and mid-Holocene migration of taxa such as hazel, elm, oak, fir and beech may be regarded as the result of simple exponential growth of initially small, isolated tree populations rather than the result of a tree migration as a closed front.
5. Vegetation dynamics were high during the early and mid-Holocene due to the expansion of tree taxa. After the establishment of a fir-beech forest, there is a long phase of vegetation stability. The highest rates of change, however, occurred as a result of the increasing human impact on vegetation in the Iron Age and especially during the Middle Ages.
6. Early traces of *Cerealia* pollen point to early farming activity that is supported by regional archaeological evidence for a human presence.

Acknowledgements. I should like to thank M. Sturm, A. Zwyssig and I. Hajdas for their help during field work, K. Bieri-Steck and O. Schläfli for the preparation of the pollen samples, and I. Hajdas for the preparation of the macrofossil samples. E. Nielsen provided information on regional archaeological evidence. B. Berglund, S. Bohncke, M.-J. Gaillard, T. Litt and H.E. Wright Jr. made valuable comments on earlier drafts. M. O'Connell and H. Juggins are thanked for linguistic improvements to the manuscript. This study was supported by the Swiss National Science Foundation (grants 21-26567.89 and 20-31155.91).

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