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

André F. Lotter
Geobotanisches Institut, Universität Bern, Altenbergrain 21, CH-3013 Bern, Switzerland, and Swiss Federal Institute for Environmental Science and Technology (EAWAG), CH-8600 Dübendorf, Switzerland

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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 – Macromains – 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 fluvioglacial 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, 111 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-mm 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.

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-

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.
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 14C 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 14C 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 14C-dated pollen diagrams from central Europe. The 14C 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 14C wiggle-matching (see Hajdas-Skowronke 1993; Hajdas et al. 1993, in press).

With the exception of the Late-glacial section, an absolute chronology (i.e. calibrated 14C years B.P.) was used in this study as it allows a more accurate estimation of rates than conventional 14C-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 14C date (14954±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 (Ia 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 14C 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.

![Fig. 2. Depth-age relationships in core SO89-23. A Uncalibrated AMS 14C ages measured on terrestrial plant macrofossils originating from cores SO89-23 and SO89-17. B Calibrated 14C ages, including ±2σ; all 14C ages refer to dates given in Hajdas et al. (in press).](image-url)
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 Bolling 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 ¹⁴C dates and also pollen studies shows that this transition lies in a zone of constant ¹⁴C 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 Bolling 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 Allerod 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
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 SO86-14, 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 concentrations 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.

Fig. 4. Percentage pollen diagram, core SO86-14, showing the Late-glacial period (main taxa only shown)
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 occu-
Fig. 5. Late-glacial pollen concentrations (pollen grains/cm³) for selected AP taxa and the sum of NAP in cores SO86-14 (above) and SO89-23 (below).

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/cm/year.

Figures (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...
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-7a, (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-7a, (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-7a, (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 Coraillo 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
Fig. 7. Holocene percentage pollen diagram, core SO89-23 (most important taxa only are shown). The $^1^3$C dates from cores SO89-17 (Hajdas et al. 1993, in press) and SO89-12 are indicated by one and two asterisks, respectively.
Fig. 8. Holocene percentage pollen diagram, core SO86-14 (most important taxa only are shown). The uppermost part of the sedimentary record is missing due to a coring artefact. A complete list of ¹⁴C dates for this core is given in Hajdas et al. (in press)
Fig. 9. Holocene pollen accumulation rates (PAR) for Soppensee core SO89-23
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 per-
centage 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 inten-
sified 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 Hu-
mulus/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 oc-
urs 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.) repre-
sents the vegetation of modern times. It is characterized
by high NAP values and especially Gramineae, and re-
fects 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 sedi-
ment studies combining pollen and stable isotope analy-
ses (e.g. Eicher and Siegenthaler 1976). All major Late-
glacial climatic shifts that are reflected in the Greenland
δ¹⁸O records can be correlated with events in the Swiss
terrestrial pollen record (Lotter et al. 1992a). The first
increase in δ¹⁸O 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
Bolling 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 Soppens-
see, however, it is not possible to test the hypothesis that
there was a lag in vegetation response to climate warm-
ing in the order of up to 300 years (cf. Wright 1984).

A late Bolling drop in δ¹⁸O values contemporaneous
with the decrease in birch in subzone CHb-3b, termed
Aegelsee oscillation, has been observed in many sedi-
ment records on the Swiss Plateau and has been corre-
lated with similar features in the Greenland oxygen-isoto-
pe records (Lotter et al. 1992a). A reliable estimation
of its duration is not possible on the basis of ¹⁴C dates
because of the short duration (Ammann and Lotter
1989). However, varve counts in the Soppensee sedi-
ments indicates a duration of ca. 100 years for the paly-
sideological oscillation, i.e. the Betula decline. Björck
et al. (1996) dated the Older Dryas in Sweden and neigh-
bouiring regions to 12 200 B.P. and suggests a duration
of 100-150 years. In the geochemistry data from Soppen-
see, the Aegelsee oscillation corresponds with a mini-
mum in organic carbon, which suggests decreased pro-
ductivity, at least within the aquatic system. On this ba-
sis, 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 pol-
len producers as suggested by Gaillard (1985) and
Wohlfarth et al. (1994) but was rather caused by a dis-
tinct, short-term climatic cooling. Whether it was ac-
panied by a dryer climate as postulated by Ammann
and Tobolski (1983) and Ammann (1989a) cannot be
determined on the basis of the available data. Investiga-
tions 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 tem-
poral 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 in-
vestigations 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 fre-
cently in sub-PAZ CHb-4a (Figs. 3 and 4). This feature
in the pollen curves is synchronous to the Gerzensee os-
cillation in the δ¹⁸O values (Lotter et al. 1992a). A syn-
chronous event has been observed as a sedimentological and
palynological feature in maritime Canada (Levesque
et al. 1993b) and has been termed the Killarney oscilla-
tion or the Amphi-Atlantic-Oscillation (Levesque et al.
1993a). At Soppensee, however, as at most European
sites, there is no sedimentological or geochemical evi-
dence for this 200-year-long isotopic fluctuation con-
temporaneous 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 ex-
ensively 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 cli-
matic 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
Fig. 10. High-resolution pollen percentage curves, the δ¹⁸O curve (%o 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).

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; Pälü, Beeler 1977), palaeobotanical investigations (Youngest Dryas, Behre 1978; Ganna, Schneider and Tobolski 1985; Rion-1 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 ¹⁴C age (e.g. Becker and Kromer 1986; Lotter 1991b). The δ¹⁸O 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...
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.
Based on the abundance of too small an amplitude to be recorded in lowland oscillation (ca. 7500-6500 B.P.) in the Alps. Moreover, pronounced oscillation that is also evident in the Greenland 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 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 Lobsegensee 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 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.](image-url)
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 below its pollen concentration 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-7a).

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-7a 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-7a, 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-7a). 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-7a 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 Bolling 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, glacio-logical, 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.

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