

We dedicate this paper to Magdalena Ralska-Jasiewiczowa in appreciation of her many and innovative contributions to palaeoecology and vegetation history; in her paper 1964 she pioneered the idea of prehistoric human impact on vegetation dynamics as a factor for tree migration in Europe, and in a recent paper (Ralska-Jasiewiczowa et al. 2003) she linked a vast spatial coverage with a high degree of detail in several ecological processes.

The first rise and fall of *Fagus sylvatica* and interactions with *Abies alba* at Faulenseemoos (Swiss Plateau) 6900–6000 cal yr BP*

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ABSTRACT. Faulenseemoos is a former lake 150 × 600 m in size situated at the transition between the Swiss Plateau and the northern Alps. Analyses of pollen, charcoal, and varved-sediment chemistry at high temporal (176 levels at 6 year separation) and pollen-morphological resolution (186 pollen types in total) cover the period 6940–5750 cal yr BP. Ellenberg's ecological indicator values for plants adapted for Switzerland by Landolt are applied to the group of infrequent herb-pollen types, providing information on humidity, humus, light, and nutrients. *Fagus* probably arrived prior to 6940 cal yr BP. Climatic change destabilized the forests, allowing *Fagus* to build up its population. Later minor human impacts enabled *Fagus* to reach dominance in ca. 150 years. *Abies*, already present, increased slowly. The following ca. 305 years of *Fagus* dominance are characterized by intermittent minor disturbances. This period is subdivided into: ca. 80 years of non-disturbance, during which *Fagus* and *Abies* reached a maximum; ca. 115 years of inferred minor anthropogenic disturbance causing a temporary shallow minimum of *Fagus* and decline of *Abies*; ca. 40 years of non-disturbance; ca. 40 years following an inferred natural catastrophic event causing a temporary shallow minimum of *Fagus*; and ca. 30 years of inferred minor anthropogenic disturbance causing a temporary shallow minimum of *Fagus* and a decline of *Abies*. The *Fagus* dominance continued during the following ca. 280 years of non-disturbance, followed by ca. 60 years of minor forest instability probably due to change to a wetter climate. After this, most of the inferred old-growth *Fagus* forest suddenly collapsed, probably because of water-logging of soils in the wetter climate, as shown by the presence of pioneer-type moist-soil indicators and by the inferred absence of human impact. *Abies* was unaffected but then started to increase markedly ca. 200 years later, whereas *Fagus* did not recover in the absence of anthropogenic disturbance. We conclude that (1) climatic change triggered both the first rise and the first fall of *Fagus*, (2) intermittent minor human impact was essential for *Fagus* to reach and maintain its dominance, (3) prolonged absence of minor human impact was needed to create the conditions for its collapse, (4) *Abies* was hampered in its expansion by the expanding *Fagus* and (5) was suppressed by minor human impact, and (6) after the change to a wetter climate and the *Fagus* collapse *Abies* could expand in the absence of human disturbance.

KEYWORDS: *Fagus*, *Abies*, early human impact, Holocene climate, forest dynamics, montane forests, Switzerland

INTRODUCTION

The ecology and history of beech (*Fagus sylvatica* L.) in Europe has long held a fascination. Leuschner (1998), for example, states

on the basis of present-day observations that *Fagus* is the most successful plant species of central Europe (on the criterion of cover percentage), and that in Germany alone *Fagus* would have dominated 75% of the landscape if man had not interfered. From a palaeoecological viewpoint three questions are relevant for

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every area studied: When did *Fagus* arrive? When did the population expand? What factors – environmental (e.g. climatic change) or human impact – controlled these events? The temporal difference between the arrival of a taxon and its population expansion is often called establishment time (e.g. Bennett 1988, Willis 1994), a concept of relevance to all three questions. In the following we always use the term expansion in the sense of population expansion and never as spatial expansion (including migration and changes of range limits). The answers to the three questions obviously differ spatially and may include geographic gradients (e.g. east-west and south-north). On the basis of sites in south-eastern and east-central Europe (Slovenia, Hungary) Willis (1994) and Gardner and Willis (1999) deny any causal effect between human activity and the earliest *Fagus* expansion. For the Apennine peninsula the picture presented by Magri (1998) is differentiated for central and northern Italy. For the Pyrenees, in contrast, Reille and Lowe (1993) provide evidence for the spread of *Fagus* favoured by human impact. For southern Sweden Björkman (1996, 1997) described two examples where *Fagus* immigrated very late (ca. 900 and 400 ^{14}C yr BP) on abandoned farmland, i.e. after human impact. For intermediate areas such as Poland or Germany Ralska-Jasiewiczowa (1983) and Küster (1997) differentiate between southern mountain areas and northern lowlands; the effect of human impact is restricted to the latter. For the northern-alpine forelands Küster (1997) accepts for montane areas a model of *Fagus* expansion in which *Quercus*, *Tilia*, and *Ulmus* were replaced by forests rich in *Fagus* as a result of natural dynamics due to slope processes without human interference. For lowland situations of central Europe, however, he ascribes the expansion and dominance of *Fagus* to early shifting human colonization, in which settlements and their fields were established for decades rather than to shifting cultivation, in which fields were cultivated at different places every year. A secondary succession would start on the abandoned farmland with pioneer trees such as *Betula* and *Populus*, followed by *Fagus* that may have been already present in adjoining montane areas. An impressive west-east transect through Denmark, northern Germany, and Poland is presented by Ralska-Jasiewiczowa

et al. (2003), showing the correlation between *Fagus* expansion and human impact for a time distinctly younger, e.g. Bronze Age, than that considered here.

Faulenseemoos, studied in the present paper, lies at the transition from a lowland situation (Swiss Plateau) to the Alps, where both the lowland and the montane model seem possible. A summary for relevant sites on the Swiss Plateau is presented in Table 1. The most detailed studies for the period concerned are prepared at Wauwilermoos and Bibersee (Beckmann 2004).

Climatic changes contemporaneous with the arrival and population expansion of *Fagus* are controversial even in a limited area such as the Swiss Plateau. Richoz et al. (1994) present arguments for drier periods synchronous with the empirical limit of *Fagus* (ca. 7600 cal BP) and a first charcoal peak, and also for the rational limit (ca. 6800 cal BP) and a second charcoal peak. But they also present arguments for wetter conditions during the rise of *Fagus* (after ca. 6600 cal BP). Tinner and Lotter (2001) suggest a wetter climate coinciding with *Fagus* expansion already ca. 8200 cal BP.

Whether or not early human impact had an influence on the establishment and population expansion of *Fagus* is also discussed for areas as small as the Swiss Plateau. Richoz et al. (1994) and Richoz (1997) found at Lake Seedorf that the first establishment of *Fagus* (dated to ca. 6900 ^{14}C yr BP = ca. 7700 cal yr BP) directly followed forest fires (reconstructed from microscopic charcoal but not contiguous sampling), in which a human role is undecided. Erny-Rodmann et al. (1997) conclude for the area of Zürich (Wallisellen and Mozartstrasse) that forest fires enhanced the succession from mixed-oak forest to *Fagus*-dominated forest, and that *Fagus maxima* followed phases of human impact; but the record of microscopic charcoal was not established by contiguous sampling (a requirement for single events, according to Tinner et al. 1999), and natural and anthropogenic fires cannot be distinguished. The closest other site to Faulenseemoos is Sägistalsee in the northern-Alps (Wick et al. 2003), but situated at 1935 m a.s.l. and therefore above the forest belt of beech and more acting as “a distant mirror” (sensu Kalis 1985). The first arrival of *Fagus* is recorded there with single pollen grains ca.

Table 1. Palynological events of the early pollen record of *Fagus* on the Swiss Plateau in years cal BP (many cells of the table are left empty because of insufficient dating)

	Wauwil and Bibersee Beckmann 2004	Faulensee This paper	Sägstalsee Wick et al. 2003	Seedorfsee Richoz et al. 1994	Lobsigensee Ammann 1989	Soppensee Lotter 1999	Wallisellen Haas 1996	Mozartstrasse Erny-Rodmann 1996
Distance to Faulensee	Wauwil 80 km to NE Bibersee 60 km to NE		32 km to E	50 km to WNW	50 km to NW	52 km to NNE	108 km to NE	100 km to NE
PAZ/age →	PAZ	PAZ	Age	Age	Age	Age	Age	Age
Event ↓								
F↓ = 1 st , slope of decline	In WB-14	FAF-11						
F↓ = 1 st , onset of decline	WB-13/14	FAF-10/11	ca. 6300	ca. 6300	ca. 6300	ca. 6000		
Peak F ₁	mid WB-13	FAF-4	ca. 6400	ca. 6400	ca. 6350	6350–6400	7900 (single sample 8290)	
Long-term increase	Onset WB-13							
Second rational limit	All WB-12	FAF-3						
First rational limit	Onset WB-12		6600					
Empirical limit	mid WB-11c	FAF-2	7000	ca. 7300	ca. 7300	ca. 7500	ca. 8030	7660–7800
Absolute limit	mid WB-11b	FAF-1		ca. 7450	ca. 7590	ca. 8000	8350, macro 8150	ca. 8000–8200
	WB-11a/11b	Lotter et al. 1996: Before the laminations Fig 2	7800	ca. 7700	ca. 7700	ca. 8200	ca. 8390	ca. 8200

7800 cal yr BP, and the first expansion is ca. 6600 cal yr BP. The first pollen indicators of human impact (*Plantago lanceolata* type) appear shortly after the *Fagus* expansion (ca. 6300 cal yr BP), but no connection could be inferred.

The history of *Fagus* after its establishment is complex as well. Many pollen diagrams from the Swiss Plateau as well as from southern Germany show as many as six prominent *Fagus* peaks and subsequent declines during the Holocene (see e.g. Ammann 1989, 1994, Clark et al. 1989, Richoz et al. 1994, Richoz 1997). Three are recorded in Faulenseemoos (Figs 1, 2). The two younger of these regional declines of *Fagus* are associated with human impact, whereas the oldest decline is considered in some cases to pre-date all traces of Neolithisation (Müller 1962, Ammann 1988). Full Neolithisation on the Swiss Plateau started ca. 6250 cal yr BP (ca. 5450 ¹⁴C yr BP) with the Egolzwiler culture (Stöckli 1995,

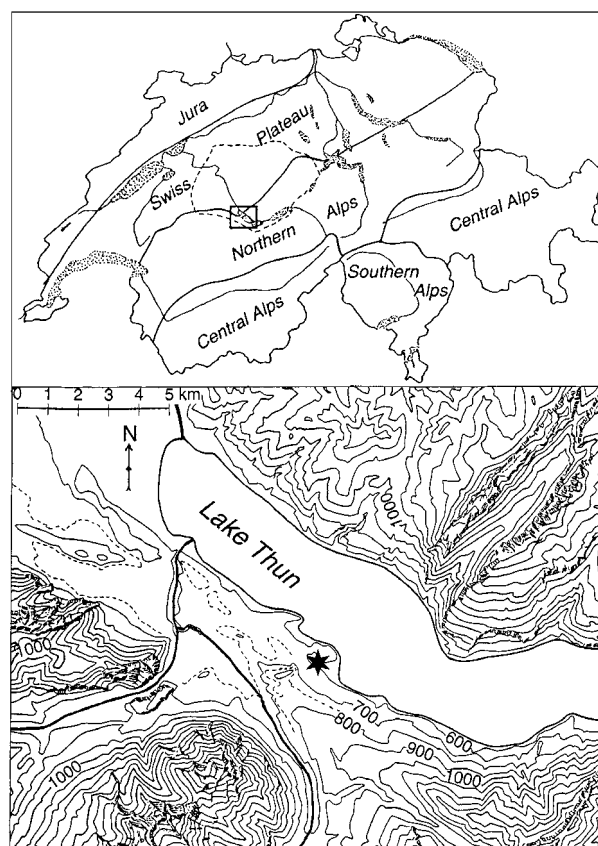


Fig. 1. Location of the study site of Faulenseemoos. Top: Switzerland; dashed line outlines area of floristic data used for interpretation of infrequent herb pollen types (explanation see text); rectangle outlines detailed map below. Bottom: Faulenseemoos is indicated with an asterisk; contour lines are drawn every 100 m (50 m for occasional dashed lines); rocky areas are coarsely hatched

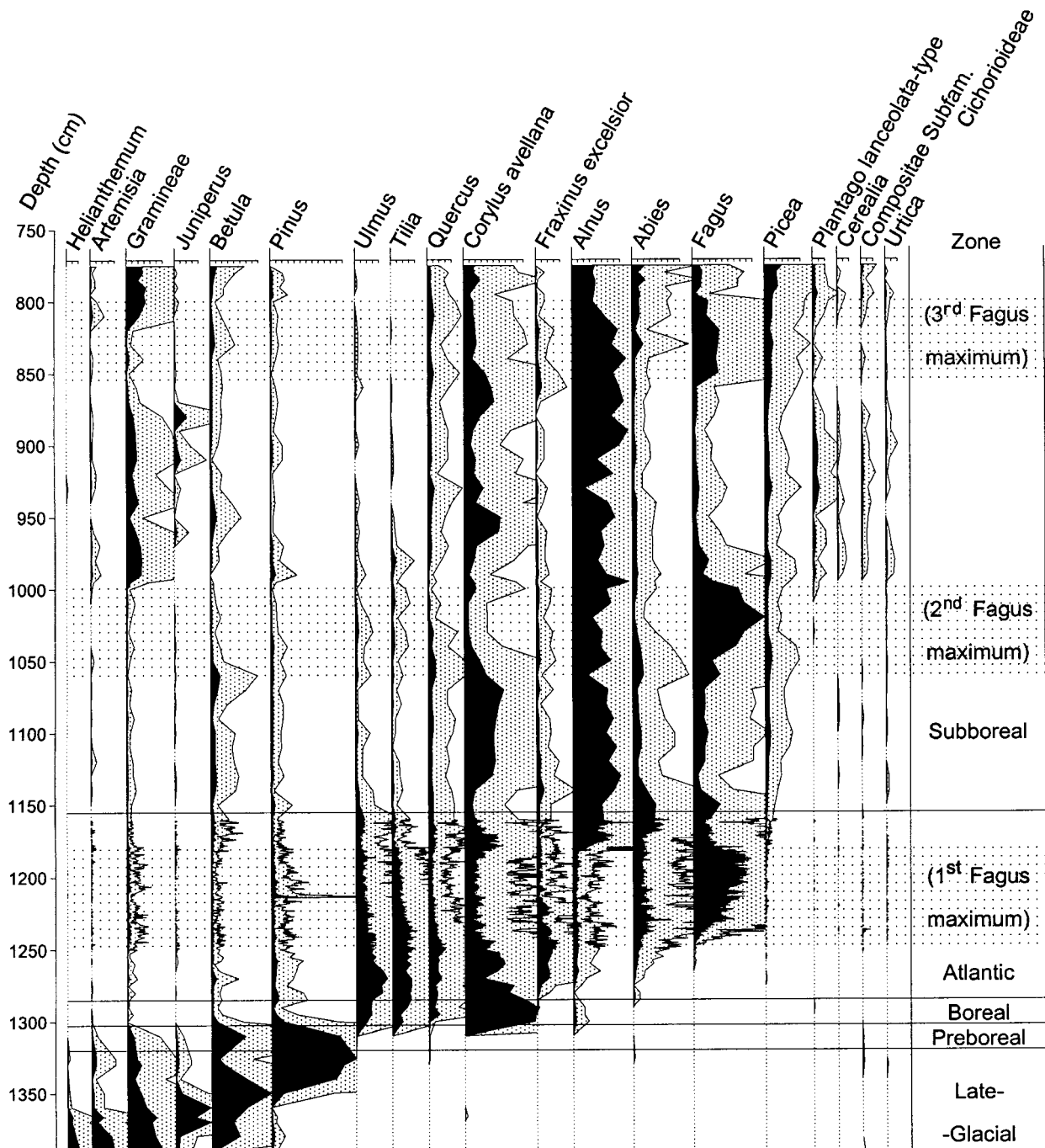


Fig. 2. Overview of selected pollen percentage diagram from of Faulenseemoos (redrawn from Lotter et al. 1996). Curves of individual pollen types are drawn in black according to percentage scale, with five-times exaggerated scale in grey. Preliminary chronostratigraphic subdivision follows Lotter et al. (1996). First, second, and third *Fagus* maxima are indicated

Erny-Rodmann et al. 1997, archaeological records of this culture are, however, absent near Faulenseemoos). Three hypotheses exist to explain this oldest beech decline (Ammann 1994, Lotter et al. 1996):

1. early human impact unknown to regional archaeologists;

2. inherent forest dynamics possibly illustrating the "mosaic-cycle" theory of Müller-Dombois (1987), Remmert (1987, 1991), Wis-

sel (1991), Ammann (1994), and Küttel (1994); especially the decline of an old-growth even-aged forest may be synchronous over a relatively large area;

3. natural abiotic causes such as changes in climate or groundwater levels.

Faulenseemoos provides a good opportunity to study the alternative possibilities of the first increase and decline of *Fagus*, because the sediment core of this period is annually laminated

and therefore provides an excellent although floating chronology, with the possibility of a high temporal resolution (6 years on average in the present study). Welten (1944) carried out his classical studies on geochronology and vegetation history using the laminated sediments at this site. More recent research has concentrated mainly on the Late Glacial development of vegetation and the analyses of stable isotopes (Eicher & Siegenthaler 1976, Welten 1982, Lotter et al. 1992). A summary pollen diagram of the complete sequence is given by Lotter et al. (1996).

For the study of Holocene forest dynamics based on pollen diagrams, charcoal counts are an important aid (cf. Clark et al. 1989, Odgaard 1992, Tinner 1998, Tinner et al. 1999, 2000). In the period studied (ca. 6940–5750 cal yr BP), when the landscape around Faulenseemoos was still nearly fully forested, charcoal reflects forest fires, which might be anthropogenic or natural or an interaction between the two. Interaction in this period may consist of early human impact on the forest, leading to a change in fire susceptibility and thereby fire frequency.

High-resolution pollen analysis, both temporal (in this study 6 years on average; 176 levels analysed at 0.5-cm intervals) and in pollen identification (186 types), is one of the keys to detailed palaeoecological interpretation.

DESCRIPTION OF THE SITE AND ITS SEDIMENT

Faulenseemoos (46°40'48" N, 7°41'41" E; Swiss coordinates 169.800/619.520) lies close to Lake Thun in the Bernese Oberland (Fig. 1). The site lies on the Swiss Plateau in the submontane Fagion belt at an elevation of 590 m a.s.l., 4 km from the transition to the northern Swiss Alps. The site is a former lake, now overgrown, ca. 600 m long and 150 m wide. It is bordered on the long sides by hills ca. 100 m higher than the former lake and at the ends by former marshy areas now drained. The hill on the north side is steep and consists of limestone. It borders directly on the former lake with rocky outcrops ca. 75 m distant from the coring site. This side of the hill and most of the rest of it are covered today by *Fagus*-dominated forest, in which *Hedera* grows abundantly on the forest floor, the cliffs, and trees.

Several intervals of the sediment are annually laminated (varved). The section studied here lies in the longest laminated interval. Laminations were studied in microscopic thin-sections. At places their annual character has been evidenced by Welten (1944). The varves consist typically of couplets of a light calcite layer deposited in late spring and summer and a dark organic layer deposited in autumn to early spring. The calcite layer has typically fine material at the base and coarse crystals at the top, resulting in three micro-laminations. In the studied section, however, varves are not all completely developed. Two-layered sequences occur frequently, in which any two of the three layers are repeated several times. Individual layers range from well-developed to extremely thin and optically interrupted in the thin-sections. An extremely thin layer may interrupt a two-layered varve as a result of extreme weather conditions, or the organic layer may be interrupted by out-of-season calcite precipitation. Such sequences contain annual laminations, but visual separation of the years may be very difficult. Such problematical varves are not distributed evenly, but are clustered. The error in the varve chronology may therefore be unevenly distributed.

METHODS

FIELD METHODS

The material analysed is derived from cores FSM91-14 and -15; see Lotter et al. (1996) for coring methods and further details.

ANALYSIS

Annual laminations in the studied section were counted in microscopic thin-sections by André F. Lotter. One level was radiocarbon-dated by AMS. After calibration to calendar years BP (= before AD 1950) it was used to anchor the floating varve chronology.

Samples analysed for pollen and charcoal are contiguous and have a vertical thickness of 0.5 cm. Major turbidites were not analysed, resulting in missing samples at 1164.5 cm, 1194.5 cm, 1209.5 cm, 1210.0 cm, 1210.5 cm, 1218.5 cm, and 1219.0 cm. Sample volume is 0.5 ml; 3 or 5 tablets containing a known number of *Lycopodium* spores were added for the calculation of pollen concentration (Stockmarr 1971). Laboratory preparation was made by Brigitte Brogli in Bern. Pollen analysis was carried out by the second author.

Literature helpful for a high pollen-morphological resolution includes the Northwest European Pollen Flora I–VII (Punt 1976, Punt & Clarke 1980, 1981, 1984, Punt et al. 1988, 1995, Punt & Blackmore 1991),

Moore et al. (1991), and Reille (1992, 1995). Charcoal was counted by Madlena Beckmann and Florencia Oberli on the slides analysed for pollen and, in addition, at 2.5 cm intervals between 1250 and 1300 cm sediment depth in 1 cm thick samples. Charcoal particles counted have a minimum length of 10 μm .

Chemical analysis was carried out on a separate series of sediment samples. See Lotter et al. (1996) for laboratory methods.

The zonation of the pollen diagram was made subjectively to guide the interpretation. Zones are delimited to mark phases in the *Fagus* curve and in the other pollen types discussed.

DATING AND TIME SCALE

The time scale is based on varve counts anchored by the only radiocarbon date available, an AMS date of a piece of wood at 1231 cm depth: Lab. No. ETH-12 340; 5805 ± 70 ^{14}C yr BP, $-32.2 \pm 1.2\%$ $\delta^{13}\text{C}$.

Calibration according to Stuiver & Reimer (1993) using the INTCAL93 calibration set results in an age of 6696 ± 18 cal yr BP (i.e., calendar years before AD 1950 – method, B – probability distribution; 1σ – standard deviation). The period studied covers ca. 6940–5750 cal yr BP. Temporal resolution of the pollen diagram is 6 years on average. We are aware that the anchoring of our chronology depends on a single radiocarbon date, but this affects only the ages of the events not the duration of the processes.

MODERN ECOLOGICAL INDICATOR VALUES OF PLANTS APPLIED TO POLLEN

An early application of Landolt's (1977) indicator values to pollen stratigraphies was presented by Gaillard (1984) with an emphasis on the Late Glacial. For both the Late Glacial and the Holocene Beckmann (2004) discussed this approach in order to assess changes in ecological variables (e.g. humidity, nutrients etc). Here we applied ecological indicator values not to all taxa but to the ones summarized as infrequent herb-pollen types, with the aim of making accessible the considerable ecological information that otherwise would remain hidden or inaccessible. The rationale to do so and the methods are explained here.

The low proportion of herb pollen (8.6% of the pollen sum on average) reflects the mostly forested landscape around Faulenseemoos in the period studied. Herb pollen includes a large number of types (106) resulting from the high pollen-morphological resolution of the analysis. In earlier studies we have shown that a high pollen-morphological resolution can contribute considerably to the interpretation of a pollen diagram in terms of past ecology and past vegetation (van der Knaap & van Leeuwen 1995, van der Knaap et al. 2000). In these studies many pollen types of herbs contributed to the final result, including mostly those that occurred often enough to form continuous curves in at least part of the sequence. In the pollen diagram of Faulenseemoos presented here, however, only five pollen types of herbs reach levels high enough to allow interpretation of changing abundance of plants (Cyperaceae, Gramineae,

Hedera, *Humulus lupulus*, monoletic fern spores). The remaining 101 types are infrequent (in total, 2.8% of the pollen sum on average) and display interrupted pollen curves or scattered occurrences only. Close visual inspection of these infrequent herb pollen types may suggest shifts in the vegetation along the lake shore more or less synchronous with major shifts in tree pollen, but this is so weakly pronounced that it defies straightforward interpretation. The ecological information hidden in the infrequent herb pollen types needs therefore to be somehow summarized to make it available for interpretation. A summary of pollen based on plant taxonomy or on pollen morphology, for example addition of the pollen types to family level (shown in Fig. 3a, right), results in at least a few additional pollen curves with interpretable levels, but with the loss of the ecological information contained in pollen types identified to genus or species level. In this paper we summarize the ecological information hidden in the infrequent herb pollen by allocating known ecological indicator values of plant species to the pollen types, and adding them for the whole group (Fig. 3b). This results in curves of the kinds of ecological indication used (humidity, humus, light, and nutrients; temperature is not used). This summarizes hidden ecological information (Fig. 4). Ellenberg's ecological indicator values of plant species (Ellenberg 1974, 1979, Ellenberg et al. 1992) adapted for Switzerland by Landolt (1977) are used.

Ecological indicator values of the total of infrequent herb pollen (Fig. 4) were calculated by (1) identifying which plant species are related to each of the 101 infrequent herb pollen types, (2) allocating the ecological indicator values of plant species to pollen types under consideration based of the geographical distribution of plant species in relation to the study site, and (3) averaging each ecological indication in each pollen sample, as follows.

(1) The connection between plant species and pollen types was made by consulting pollen-morphological literature and reference slides. This was necessary because most pollen types can be derived from more than one plant species, which may differ in their ecological indications.

(2) Plant species are weighted according to their occurrence near the site today, but ignoring their present-day abundance. Plant species occurring today in a wide region of the Swiss Plateau and a smaller part of the northern pre-Alps close to the study site (outlined in Fig. 1, top) receive the weight 1, other plant species of the Swiss flora are down-weighted to 0.1 (Welten & Ruben Sutter 1982; data derived from Swiss Web Flora, September 2000). An ecological indicator value of a pollen type (e.g., humidity value of Gramineae) is calculated by addition of the values of the constituent plant species multiplied by its weight, followed by normalizing to 1 the total indicative impact of the pollen type for the ecological indication. The result is usually complex for pollen types representing several plant species, as shown by examples in Figure 5.

(3) Ecological indicator values are summarized within each pollen sample for the total of infrequent herbs by adding the ecological indicator values of the constituent pollen types multiplied by the counts of the

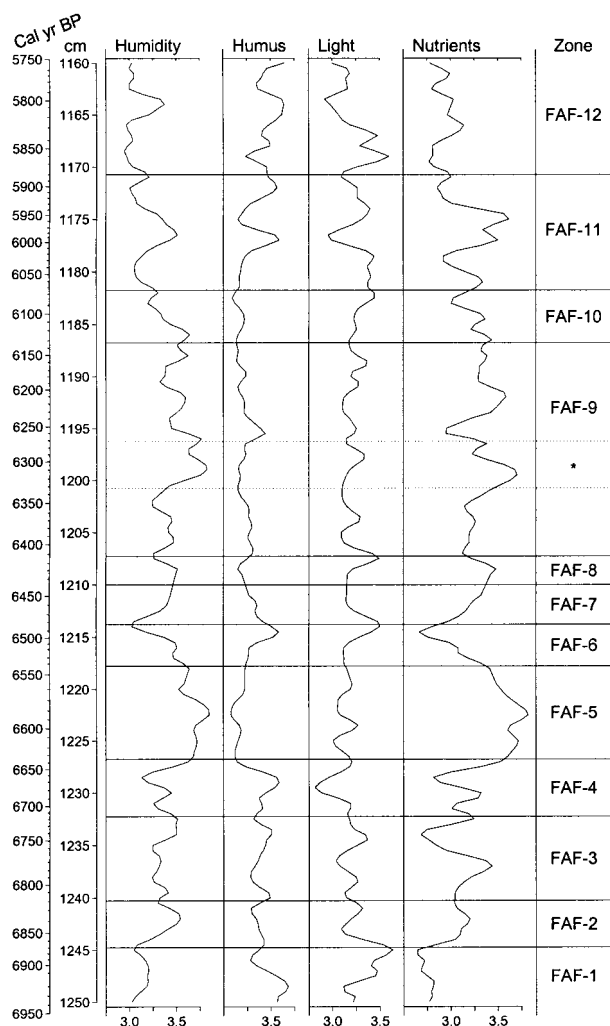


Fig. 4. Ecological indicator values summarized for the group of infrequent herb pollen in Faulenseemoos 1250–1160 cm sediment depth (See Fig. 3b). Values smoothed with 4th-order filter [value N of sample n replaced by $(N_{n-2}+4N_{n-1}+6N_n+4N_{n+1}+N_{n+2})/16$]. See text for definition and calculation of ecological indicator values

pollen types, followed by calculating the average ecological indicator value in each sample for each selected ecological indication. Statistical errors resulting from counting of pollen, calculation of ecological indicator values for pollen types, and summarizing ecological indicator values for the total of infrequent herb pollen are not given because the calculation of these errors is beyond our capacity. The results are presented as a diagram with curves of ecological indicator values of infrequent herb pollen (Fig. 4).

The following ecological indications are used (Landsolt 1977):

Humidity value

- 1 – on very dry soil
- 2 – on dry soil
- 3 – on medium dry to damp soil
- 4 – on damp to very damp soil
- 5 – on wet, water-saturated soil

Humus value

- 1 – on raw soil (without humus top layer)
- 2 – on soil with little humus cover
- 3 – on soil with average humus content (usually as mull)
- 4 – on humus-rich soil (mull or mould) over mineral soil
- 5 – rooting almost solely in humus-rich soil

Light value

- 1 – in very shady situations
- 2 – in shady situations
- 3 – in half-shade
- 4 – chiefly in full light, sometimes in light shade
- 5 – always in full light

Nutrient value

- 1 – on very poor soil
- 2 – on poor soil
- 3 – on medium poor soil
- 4 – on rich soil
- 5 – on soil with an excess of nutrients (usually N)

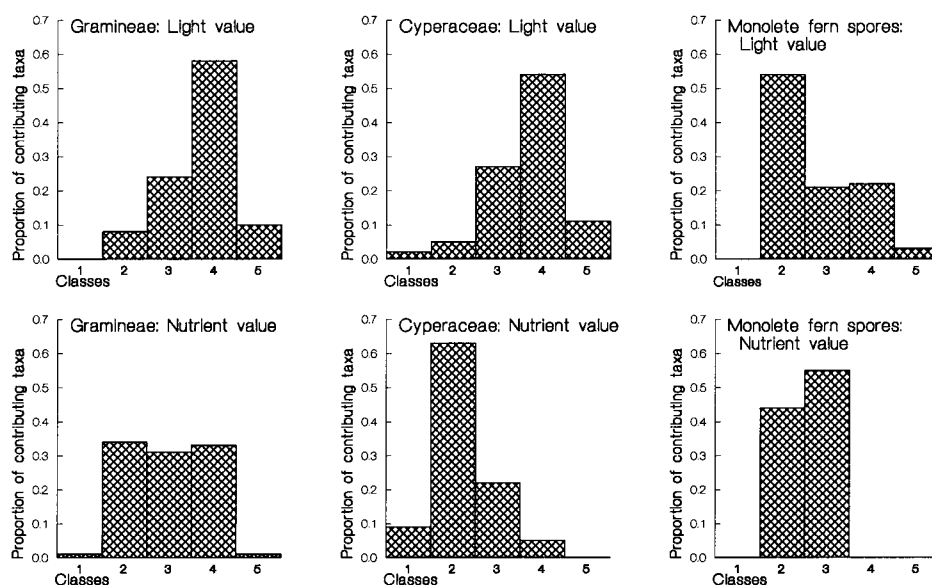


Fig. 5. Examples of ecological indicator values of pollen types; see text for explanation

RESULTS

Pollen percentages, pollen influx and charcoal concentrations, ecological indicator values of infrequent herbs, sediment chemistry, and a summary of data relevant for the interpretation are shown in Figures 3a, b, 4, 6–8.

The pollen influx diagram (Fig. 6) shows extreme high-frequency fluctuations synchronous among pollen types. It seems unlikely that this is caused by synchronism in pollen production. In zone FAF-3 and -4 the influx of most pollen types is lower than in the preceding and following zones, and it seems unlikely that this reflects trends in pollen production. These phenomena may have resulted from errors in the time scale (maxima/minima caused by under-/over-counting of varves), pollen-sedimentary processes (maxima caused by sediment focussing), and/or the statistical errors in laboratory procedures (sampling volume, amount of *Lycopodium* spores added and counted, selective loss of *Lycopodium* spores during preparation). No realistic error estimation, however, can be made. The pollen influx data are therefore used with great caution. Charcoal data are given as concentrations, in order to avoid some errors.

The interpretation of inferred humidity (Fig. 4) needs some comment. A shift to drier conditions shifts the humidity to higher values (e.g. zone FAF-2) and vice-versa (e.g., FAF-11), for the following reasons. Pollen of infrequent herbs, on which the indicator values are based, derives in part from the belt of treeless vegetation on the humid lake shore between the riparian forest and the lake, in part from treeless vegetation at larger distances that for the greater part may grow on dry soils. Whenever the lake level dropped the belt of treeless vegetation became temporarily broader and thus contributed more pollen, shifting the inferred humidity to higher values.

DESCRIPTION OF POLLEN ZONES

Zone FAF-1 (ca. 6937–6866 cal yr BP; duration ca. 71 years)

Important trees in the landscape close to Faulenseemoos were *Corylus avellana*, *Tilia cordata*, *Ulmus*, *Quercus*, and *Fraxinus excelsior*. *Abies alba* was present in moderate quantities, though rare close to the lake (no *Abies stomata* recorded). *Fagus sylvatica*

was present in very small quantities if at all, and it crossed the 1% threshold of pollen at 1247.0 cm (ca. 6910 cal yr BP). The low percentage of total herb pollen indicates that the landscape was totally forested and lake-shore vegetation was present but of small cover. The pollen assemblage of this zone does not give any indication of human impact on vegetation. Charcoal analysis was extended 50 cm downwards from the base of this zone at 2.5-cm intervals (data not shown). The charcoal concentrations in this section are similar to those in this zone or slightly lower, suggesting absence of forest fires at the analysed levels.

Zone FAF-2 (ca. 6866–6817 cal yr BP; duration ca. 49 years)

Expansion of herb vegetation along the lake shore is suggested by increasing Gramineae, Cyperaceae, and monolet fern spores. *Hedera* and *Humulus* increased and *Salix* and *Corylus* decreased in the edge of the forest along the shore. Ecological indicator values of infrequent herb pollen suggest declining humus and light and increasing humidity and nutrients, likely reflecting changes in the herbaceous shore vegetation. These vegetation changes cannot be explained in terms of human impact, since pollen indicating human impact is absent. Charcoal peaks suggest forest fires within tens of km of the site, but there are no pollen indications of opening of the forest. These inferences may be explained by a drier climate, causing lower lake levels followed by expansion of herb vegetation on the fresh shores, and also drier soils increasing the forest-fire susceptibility. The decline of *Fraxinus* may also be explained by drier soils. This interpretation is supported by the coincidence with the beginning of a warm phase with glacier retreat and increasing forest limits in the Alps (6000 ¹⁴C yr BP = ca. 6850 cal yr BP; the end of the European Cool phase CE-4 of Haas et al. 1998; the later part of the period with glaciers smaller than today of Hormes et al. 2001, Tinner & Ammann 2001). This likely implies drier conditions. Also Richoz (1997, see also Haas et al. 1998) infers a change to drier climate around 6000 ¹⁴C yr BP on the basis of an important change in vegetation composition and a significant lake-level lowering at Lake Seedorf, 50 km north-northwest of Faulenseemoos.

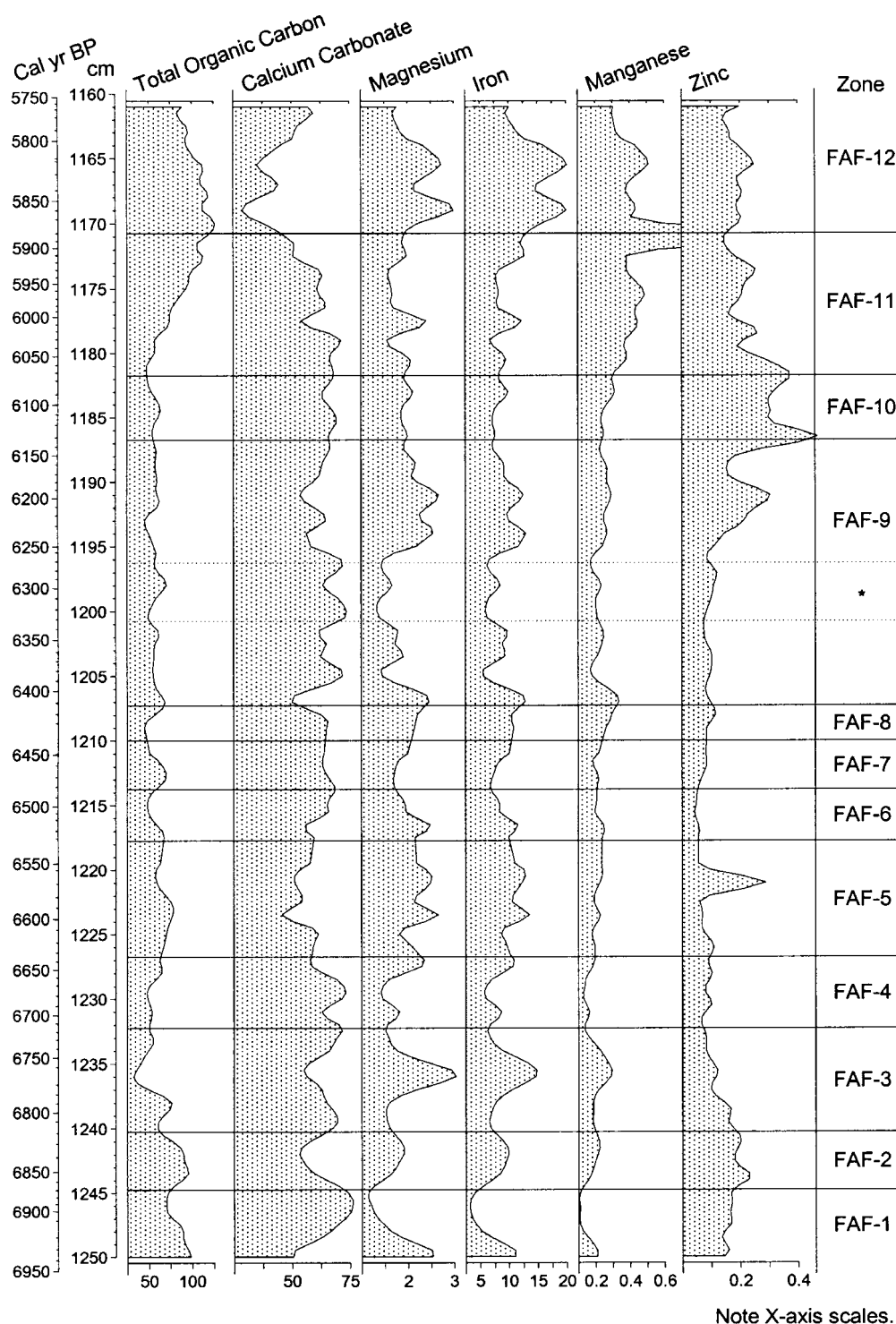


Fig. 7. Chemical composition of the studied lake sediments of Faulenseemoos 1250–1160 cm sediment depth. Values smoothed with 4th-order filter [value N of sample n replaced by $(N_{n-2}+4N_{n-1}+6N_n+4N_{n+1}+N_{n+2})/16$]; data for turbidite layers omitted prior to smoothing

In this zone *Fagus* expanded for the first time and *Abies* increased, taking advantage of the temporary imbalance in the upland forests and replacing *Corylus*, *Fraxinus*, and *Quercus*. This may be considered as natural succession, triggered by the imbalance of forest ecosystems caused by climatic change.

Zone FAF-3 (ca. 6817–6712 cal yr BP; duration ca. 105 years)

Abies expanded slowly. Four isolated occurrences of *Cerealia* and two of *Plantago major* pollen indicate the creation of small forest clearances. Zoller and Erny-Rodmann (1994)

found in eastern Switzerland 0.1% *Cerealia* pollen at 1 km distance of prehistoric arable fields of Neolithic and later age. This pollen value is comparable to our record, but the cultural landscape may not be comparable as the first phase of full Neolithisation on the Swiss Plateau is dated as later (ca. 6250 cal yr BP; Egolzwiler culture). Nevertheless, the cereal fields may have lain no more than 1 km from Faulenseemoos. The decline of *Ulmus* ca. 6790 cal yr BP followed by two charcoal maxima ca. 6775 and 6766 cal yr BP may be explained by large-scale outbreak of Dutch elm disease, accumulation of dead wood, and forest fires. It is not improbable that human impact played a role. The events may have kept the forest in a state of imbalance, enabling *Fagus* to expand rapidly. The relative contributions of human impact and climatic change to the rapid *Fagus* expansion are difficult to assess. They depend on the relative importance of causes of forest imbalance, including the drier climate inferred for zone FAF-2, natural or anthropogenic forest fires, large-scale Dutch elm disease possibly favoured or triggered by human action, and other human impacts in the form of leaf-fodder collection, forest grazing, and creation and abandonment of arable fields (e.g. Peglar 1993, Ralska-Jasiewiczowa et al. 2003).

Zone FAF-4 (ca. 6712–6632 cal yr BP; duration ca. 81 years)

Fagus and *Abies* expanded to a maximum, whereas *Alnus glutinosa* type, *Corylus*, *Fraxinus*, and *Quercus* declined. Indications of human impact on vegetation are absent. A maximum of *Hedera* is unexplained (but see also zone FAF-7); the high values show that the plant grew close to the lake.

Zone FAF-5 (ca. 6632–6540 cal yr BP; duration ca. 92 years)

High charcoal influx combined with two occurrences of *Cerealia* and a *Fraxinus* maximum suggest slash-and-burn cultivation and tree-fodder collection (in accordance with Kalis 1988). Also the shallow *Fagus* minimum and *Abies* beginning to decline may be the result of human impact on forest. Presence of cattle along the lake shore is suggested by the increased nutrient and humidity values of infrequent herb pollen pointing to expansion of treeless marsh vegetation, and by maxima of *Humulus* and *Salix*, which may have expanded due to withdrawal of the near-shore forest edge.

Zone FAF-6 (ca. 6540–6480 cal yr BP; duration ca. 60 years)

Fagus increased again, likely at the cost of slight decreases in *Tilia cordata* and *Ulmus*. The decline of *Fraxinus* may indicate the end of tree-fodder collection and the abandonment of the forest by farmers. The general minimum of herb pollen and decreased nutrient and humidity values of infrequent herb pollen suggest a decline of treeless vegetation on the shore, indicating that the shore was undisturbed by cattle.

Zone FAF-7 (ca. 6480–6438 cal yr BP; duration ca. 42 years)

At the base of this zone, ca. 75 years after the ending of inferred human impact on the forest, *Fagus* percentages drop to a sudden minimum and sudden, extreme maximum values are reached by *Pinus* subgen. *Pinus* (20.3%; average for entire section is $1.7 \pm 1.8\%$) and *Hedera* (18.8%; average is $1.5 \pm 2.3\%$). Such a high *Hedera* value is quite exceptional and its coincidence with *Pinus* subgen. *Pinus* is highly unusual. A possible explanation is that a catastrophic event such as a storm or landslide damaged or removed some of the *Fagus* forest on the steep rocky hill bordering the lake close to the coring location. As a result, full light could reach *Hedera* and *Pinus sylvestris* growing on the now exposed rocks, which stimulated abundant flowering, and pollen transport to the lake was not hampered by a filter of trees. *Corylus* declined; the lack of increase of this pioneer tree suggests that any catastrophic event was of small spatial extension, taking place in a habitat unsuited for *Corylus*. The absence of slumps in the sediment and the uniform sediment chemistry (Fig. 7) indicate that any catastrophic event did not affect the water body and must therefore have been minor. If a minor event produced such a strong pollen signal, it must have taken place in close proximity to the coring location. The unexplained *Hedera* maximum of zone FAF-4 may also be related to vegetation dynamics on this hillside.

Zone FAF-8 (ca. 6438–6410 cal yr BP; duration ca. 28 years)

The pollen signature is similar to that of zone FAF-5, indicating human impact on vegetation (*Fraxinus* maximum; infrequent herbs indicating maximum humidity and nutrients

and minimum humus; *Salix* maximum; shallow but clear *Fagus* minimum; *Abies* declining further). The main differences with zone FAF-5 are that Cerealia and a charcoal maximum are absent. This zone is interpreted as a phase of human impact similar to that of zone FAF-5 but of shorter duration.

Zone FAF-9 (ca. 6410–6130 cal yr BP; duration ca. 280 years)

Fagus was a dominant tree and *Abies* remained at a constant minimum, indicating that the forests were generally in a stable condition during the entire zone. Nevertheless, the 60-yr long middle period ca. 6332–6272 cal yr BP (1196.25–1200.75 cm, marked on the diagrams with a star) has some pollen characteristics in common with zone FAF-3: a *Pediastrum* maximum indicative of a high nutrient status of the lake water; and with zones FAF-5 and FAF-8: a modest *Fraxinus* maximum possibly related to leaf-fodder collection; and maximum humidity and nutrient values and minimum humus values of infrequent herbs possibly indicating cattle grazing on the lake shore. This interpretation, however, is tentative, for it is not supported by other pollen trends. One Cerealia occurrence dated to ca. 6270 cal yr BP and two occurrences of *Plantago major* ca. 6255 cal yr BP are synchronous with the Egolzwiler culture, which is the first full Neolithisation on the Swiss Plateau (Stöckli 1995). This pollen, however, may have been transported to the site from long distances, because other indications for human impact based on pollen or charcoal are lacking.

Zone FAF-10 (ca. 6130–6070 cal yr BP; duration ca. 60 years)

The lower zone limit around 6130 cal yr BP coincides with several indicators for a cooler climate, e.g. a distinct drop in the Alpine timberline well dated at Lago Basso in the Italian Alps (Wick & Tinner 1997) and in the Valais/Central Alps (Tinner et al. 1996, Tinner & Theurillat 2003) as well as with lower July temperatures inferred from chironomids (Heiri et al. 2003). It is also the beginning of the Central European cool phase CE-5 according to Haas et al. (1998) and the approximate beginning of the cool phases Rotmoos I (Patzelt 1977) or Piora I (Zoller 1960).

Two isolated occurrences of Cerealia suggest field cultivation, whereas indications for tree-fodder collection, forest grazing, and cat-

tle along the lake shore are absent. The cereal cultivation may have been neither on a large scale nor close to the site. The increase of *Corylus* suggests that more light penetrated the forest whereas other trees hardly changed, suggesting some forest instability. The cause may be climatic, because hints for anthropogenic impact near the site are nearly lacking and the cool phase around 6130 cal yr BP seems to be widespread.

Zone FAF-11 (ca. 6070–5877 cal yr BP; duration ca. 193 years)

Several long-lived, shade-tolerant trees of dry soils declined dramatically (*Fagus*, *Tilia cordata*, *Tilia platyphyllos*, *Ulmus*), while shorter-lived, light-demanding (“pioneer”) trees and shrubs increased (*Corylus* plus several others of wet soils: *Alnus glutinosa* type, *Betula*, *Salix*, *Sambucus nigra*, and somewhat later *Populus*). A general decline of herbaceous shore vegetation is indicated by total herb pollen (declining especially in the upper half of the pollen zone) and is in agreement with the decline of the humidity value, suggesting that the lake shore became overgrown with shrubs (*Salix*) and trees (*Alnus glutinosa*) rather than herbs.

Three isolated occurrences of Cerealia suggest some cultivation of fields. The decline of herb pollen suggests that no forest clearing existed near the lake, so cereal cultivation likely did not occur close to the lake. Also, indications for tree-fodder collection or forest grazing are lacking. This suggests no human impact on the forest close to the lake. A likely explanation for the replacement of stable climax-type forest of dry soils by pioneer-type forest of moist to wet soils, without human impact and without any transitional phase of herb-rich vegetation, would be a major hydrological shift to wetter conditions not only on wet but also on dry soils, causing massive die-back of old-growth forest and replacement with shorter-lived trees. This can only be explained by a markedly wetter climate. The gradual increase of total organic carbon and decrease of calcium carbonate (Fig. 7) suggest changing hydrological conditions, likely rising lake levels. The modest charcoal peaks may have resulted from the increased availability of fuel caused by forest die-back, in spite of the wetter climate. Forest fires would suppress *Tilia* and *Ulmus* growing mixed with *Fagus*. *Abies*

seems to be unaffected. The gradual decrease of *Fagus* pollen after its sudden collapse may in part have been caused by a gradual development of an *Alnus glutinosa* band along the shore, filtering the *Fagus* pollen.

An additional explanation for the catastrophic collapse of *Fagus* lies in the ca. 340-year-long human abandonment of the forests in the preceding two pollen zones. This abandonment would enable *Fagus* to grow undisturbed to full age. Only a minor disturbance would suffice to cause collapse of the over-mature *Fagus*-dominated forest. The inferred shift to a wetter climate may have taken place earlier than the response of the vegetation, and it may have been gradual, after which no more than a small trigger would have been needed to overturn the old-growth and nearly even-aged *Fagus* forest.

Zone FAF-12 (ca. 5877–5753 cal yr BP; duration ca. 124 years)

The main events are a dramatic increase of *Abies* and *Ulmus* and a decline of *Corylus*, whereas indications for human impact continue to be minor (two occurrences of *Cerealia*, one of *Plantago major*). This is possibly natural succession independent of farmers. Two factors may have contributed to the advantage of *Abies* over *Fagus*: lack of anthropogenic disturbance and the shift to a wetter climate.

SUMMARY OF *FAGUS* AND *ABIES* DYNAMICS AND THEIR CAUSES

The dynamics of *Fagus sylvatica* and its interactions with *Abies alba* ca. 6940–5750 cal yr BP at Faulenseemoos are summarized here.

Zone FAF-1 (duration ca. 71 years). The pollen diagram starts with undisturbed deciduous forests with little or no *Fagus*. *Abies* is already present in moderate quantities.

Zone FAF-2 (duration ca. 49 years). *Fagus* started to expand, probably due to natural disturbance of the forests resulting from a change to drier climatic conditions. No human impact is apparent. *Abies* slightly expanded.

Zone FAF-3 (duration ca. 105 years). *Fagus* rapidly expanded, likely as a result of instability of existing forests caused both by drier climate and by minor human impact, the Dutch

elm disease, and the resulting increase of fire frequency. *Abies* expanded slowly.

Zone FAF-4 (duration ca. 81 years). *Fagus* and *Abies* reach a maximum expansion, forming a dense forest canopy.

Zone FAF-5 (duration ca. 92 years). Human impact (slash-and-burn cultivation, tree-fodder collection, grazing on the lake shore) is inferred to have caused a shallow *Fagus* minimum and a slight *Abies* decline.

Zone FAF-6 (duration ca. 60 years). Inferred human impact came to an end, allowing *Fagus* to expand further and the forest to become dense up to the lake shore. *Abies* did not recover, probably due to competition by *Fagus*.

Zone FAF-7 (duration ca. 42 years). A catastrophic event of small spatial extent is inferred to damage some of the *Fagus* forest on a nearby steep slope in favour of *Pinus sylvestris* and *Hedera*.

Zone FAF-8 (duration ca. 28 years). As in zone FAF-5 but less pronounced, human impact caused a temporary minimum of *Fagus* and a decline of *Abies*.

Zone FAF-9 (duration ca. 280 years). Inferred human impact was absent or minor and forests were stable. *Fagus* had recovered and was dominant. *Abies* remained at a minimum, apparently not able to compete with *Fagus*.

Zone FAF-10 (duration ca. 60 years). *Corylus* increased and forests became lighter, by absence of notable human impact suggesting climatic change. *Fagus* was little affected, declining only slightly, whereas *Abies* increased slightly.

Zone FAF-11 (duration ca. 193 years). The old-growth *Fagus* forest, undisturbed for about 340 years, collapsed, and pioneer trees, mostly of wet soils, took over without gap and without notable human impact. This was likely triggered by increased fire frequency in forests destabilised by water-logging of soils due to a wetter climate, which may already have begun in zone FAF-10.

Zone FAF-12 (duration ca. 124 years). Due to the absence of notable human impact, *Abies* was able to expand where *Fagus* had grown. Climate continued to be wetter than it was before the *Fagus* collapse, which may have favoured *Abies*.

DISCUSSION

SEPARATING HUMAN AND ENVIRONMENTAL
IMPACTS ON VEGETATION

The separation of different impacts on vegetation (human action, climate, hydrology, slope processes) depends on considerations of the ecology of plant species, vegetation types, and landscapes. Details and considerations are explained here on the basis of Figure 8.

Circa 15 pollen types listed by Erny-Rodmann et al. (1997) as potentially indicative of prehistoric settlements are also present in Faulenseemoos, but most do not show clear trends and are here not considered indicative. A few that are potentially indicative of anthropogenic grassland occur mainly in zone FAF-11, but in so low quantities that an interpretation is doubtful (*Achillea* type, *Plantago lanceolata* type, *Rumex acetosella*, *Trifolium repens* type, and *Hypericum perforatum* type not listed by Erny-Rodmann et al. (1997). Beckmann (2004) presents a careful discussion of early findings of synanthropic pollen types for the Swiss Plateau in a central European context.

The impact of early and full Neolithic cultures on vegetation was relatively small. The scarce direct evidence in our data includes scattered occurrences of pollen indicative of forest clearance (*Cerealia*, *Plantago major*, *Trifolium repens* type, and elevated values of *Artemisia*). The two main indicator pollen types, *Cerealia* and *Plantago major*, occur as isolated grains only and (with one exception) never in two consecutive samples; they may therefore not have originated from close by the site. They nevertheless support other suggestions of human impact in zones FAF-3 and -5.

Indirect pollen evidence of human impact on vegetation includes variations in the relative abundances of forest trees and lake-shore plants (Behre 1981, Beckmann 2004). However, it is difficult to separate indirect evidence of human impact from other causes of vegetation change. We therefore infer human impact on vegetation near the site only if several indications point in this direction. Herb pollen is little abundant (8.6% of the pollen sum on average) and is mostly derived from vegetation on the lake shore, whereas phases of deforestation (defined as forest replaced by treeless vegetation) are not apparent. Maxima of *Fraxinus excelsior* were found to be indica-

tive of tree-fodder collection by Aaby (1986) in Bundsø, Denmark, and by Kalis (1988) in Rurtal near Aachen, Germany; this interpretation is followed here (zones FAF-5, -8, and mid part of -9). Simultaneous cattle grazing along the lake shore is suggested by maxima of *Humulus lupulus* and *Salix*, interpreted as withdrawal of forest trees from the lake shore, and by ecological indicator values of infrequent herb pollen combining high humidity and nutrient values and low humus values, interpreted as trampling, nutrient-enrichment, and removal of plant material from the lake shore. High *Pediastrum* values indicate a high nutrient status of the lake water, associated with cattle on the shore. Minima of *Fagus* and declines of *Abies*, *Ulmus*, *Tilia cordata*, and *T. platyphyllos* may be human-induced. Charcoal maxima indicate forest fires, potentially human-induced.

Two phases of climatic change are inferred. The first phase starts ca. 6866 cal yr BP (zone FAF-2). The decline of *Fraxinus* is interpreted as a result of soils becoming drier, and the decline of *Corylus* as closing of the forest canopy because of drier conditions. This may have destabilized the forests, making them more sensitive to forest fires, which would explain the charcoal maxima. Fluctuations in ecological indicator values of infrequent herb pollen and in some herb and shrub pollen types indicate expanding shore vegetation, which in the absence of human-indicator pollen is interpreted as lower lake levels, supporting the inference of drier conditions. This may imply less precipitation or higher temperatures or both. Our interpretation is corroborated by indications of a warm phase, such as minimum glacier extent, minimum lake levels, and maximum altitudes of forest limits in the Alps around ca. 6850 cal yr BP (Patzelt 1977, Richoz 1997, Wick & Tinner 1997, Haas et al. 1998, Maisch 2000, Tinner & Theurillat 2003). The second climatic phase starts ca. 6130 cal yr BP (zone FAF-10), when an increase of *Corylus* suggests forest destabilisation. Subsequent succession from forests of dry soils to forests of wet soils after ca. 6070 cal yr BP (zone FAF-11), and expansion of *Abies* after ca. 5877 cal yr BP (zone FAF-12) point to moister climatic conditions. Changes in sediment chemistry after ca. 6000 cal yr BP point to lake-level change. Our interpretation of moister conditions is corroborated by

numerous data sets that infer the beginning of the cool and moist period for central Europe recorded by several authors.

Localized slope instability close to the coring site is inferred at ca. 6480 cal yr BP (zone FAF-7), when *Pinus* subgen. *Pinus* and *Hedera* pollen reach a sudden maximum. The pollen diagram does not support any interpretation in terms of human impact or climate at this point.

ABIES ALBA

Abies has usually a place in the montane forest similar to that of *Fagus*, and they often coexist. Nevertheless, *Abies* seems to have responded to anthropogenic disturbance in a manner opposite to that of *Fagus*. Minor anthropogenic disturbance favouring *Fagus* seems to suppress *Abies*, possibly because it lent *Fagus* competitiveness over *Abies*. On the other hand, *Fagus* failed to recover after its collapse following climatic change to wetter conditions, likely outcompeted by *Abies*, which was able to expand thanks to the wetter climate and the absence of anthropogenic disturbance.

FAGUS SYLVATICA

The interpretation given suggests that triggers for both the first rise and the first fall of *Fagus* at Faulenseemoos were forest destabilisation due to climatic change, but also that climatic change alone was insufficient. Minor anthropogenic disturbance was a prerequisite for *Fagus* to expand to dominance. It is also likely that subsequent repeated minor human impact was needed for *Fagus* to maintain its dominance. This is suggested by the inference that *Fagus* rapidly recovered after temporary human impact in two periods of tree-fodder collection and forest grazing, whereas the tree collapsed after being left to grow undisturbed for a period of about 340 years, when it had likely formed old-growth forest. The collapse is inferred to have been caused by increased fire frequency in forests destabilised by water-logging of soils due to a change to wetter climate about 60 years earlier. Earlier there had been a period of about 75 years of non-disturbance preceding a catastrophic event that was inferred to damage part of the forest, but *Fagus* recovered within decades.

The first *Fagus* maximum took place during

a relatively warm and/or dry period with dry soils, preceded and followed by a cooler and/or wetter periods with wetter soils. Nevertheless, *Fagus* has a wide tolerance for temperature, precipitation, and soil conditions, as shown by its wide geographical, altitudinal, and ecological distribution in Europe. *Fagus* forests grow in landscapes with average temperatures between 4 and 12°C (Ellenberg 1978), although it is sensitive to late frost in spring. *Fagus* at Faulenseemoos is therefore not limited in its growth by temperature. Our results indicate that the triggers for population expansion and collapse of *Fagus* are changes in the environment and the resulting destabilisation of forests. The destabilisation during *Fagus* expansion was in our case caused by climatic change followed by minor human impact. The destabilisation during *Fagus* decline depended on the long period of undisturbed conditions causing *Fagus* to form old-growth forest sensitive to changing soil moisture. Summarizing, the interpretation is that *Fagus* at Faulenseemoos (1) needed minor disturbance in order to expand to dominance, (2) required low levels of disturbance to maintain its dominance, and (3) was very sensitive to changes in soil moisture when it had formed old-growth forest after several centuries of non-disturbance. The combination of climatic and human disturbance was essential for *Fagus* expansion and maintenance of dominance; one separate factor might not have done it.

Of the three possible causes of the *Fagus* decline outlined in the introduction, the last, natural abiotic causes such as changes in climate or groundwater levels, is confirmed. Early human impact unknown to regional archaeologists of hypothesis 1 is confirmed as such, but it favoured expansion and dominance rather than decline. Inherent forest dynamics of hypothesis 2 likely played a role when the forest was undisturbed for several centuries, making it sensitive to disturbance.

According to Green (1990), a common phenomenon in biological systems is that a rare population is triggered to explosive growth by a cataclysm (such as a fire, a storm, a cometary impact), whereby the time lag between the first appearance of a population and the population explosion can be long, for trees up to several thousand years. Computer simulations by Green (op. cit.) indicate that dispersal across the landscape is important

in the process: abrupt transitions and explosive growth occur only if dispersal distances are short. The population expansion of *Fagus* recorded at Faulenseemoos fits this picture to some degree, with the combination of climatic change and minor human impact functioning as triggers. The data of Faulenseemoos (Fig. 2) are not conclusive about the moment of first *Fagus* establishment because of lack of time control in the relevant earlier period. This is a problem inherent in pollen analysis (see the discussion by Bennett 1988). However, we can reasonably assume that *Fagus* was locally present in small quantities for at least several centuries prior to its population expansion, because of the position of Faulenseemoos between two sites where *Fagus* pollen was first recorded many centuries prior to the expansion (Seedorfsee and Sägistalsee; see Tab. 1).

This study contributes some new data to the on-going discussion about the causes of the spread of *Fagus* in central Europe. Küster (1997) proposes two different mechanisms of *Fagus* expansion in central Europe, namely natural processes on steep slopes in montane areas, and shifting colonization in lowland situations. Our results for Faulenseemoos add climatic change, resulting in a more complex picture, namely that *Fagus* started to expand as a natural process enhanced by a change to drier conditions, was then stimulated to expand more strongly and maintain its dominance for several centuries by a low level of anthropogenic pressure including grazing, and finally, after several centuries of non-disturbance resulting in old-growth forest, collapsed due to a change to wetter conditions. The same mechanisms have most likely played a role in the *Fagus* expansion at Seedorfsee 50 km west-northwest of Faulenseemoos (Richoz 1997), which took place at the same time. Haas et al. (1998) concluded for this site that a period of drought was probably a decisive factor for the *Fagus* expansion, and Richoz (1997) had reconstructed forest fires on the basis of charcoal, but was indecisive about human impact. Gardner and Willis (1999), on the other hand, argue that the spread of *Fagus* in central Europe at the time of Neolithisation (Bandkeramik) was entirely coincidental rather than causal, and that the tree was later suppressed as a result of anthropogenic activities, mainly grazing. They support their opinion with four low-resolution pollen diagrams

(sampling intervals > 150 years during the first *Fagus* maximum; few pollen types distinguished) from Slovenia and Hungary. Apart from the position of the sites outside our geographical area of interest (Küster 1999), this is insufficient support, as such data fail to show minor human activity, whereas deforestation due to stronger human activity is undisputed. A suggestion by Küster (1997) that the early expansion of *Fagus* in southern parts of central Europe was favoured by the proximity of the seed source in the mountains is not supported by the data for northern Switzerland. The expansion of *Fagus* at Faulenseemoos lying at the foot of the Alps took place 1400 years later than in Zürich (Erny-Rodmann et al. 1997) or Soppensee (Lotter 1999, Tinner & Lotter 2001, see Tab. 1), lying on the Swiss Plateau away from the Alps, and 400 years later than at Le Loclat (Hadorn 1992), lying 65 km NW of Faulenseemoos at the foot of the Jura Mountains. However, more data points are needed to detail the patterns of *Fagus* expansion in this part of the Northern Pre-Alpine Foreland.

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