Untangling a Holocene pollen record with forest model simulations and independent climate data

Heike Lischke [a,*], André F. Lotter [b,1], Andreas Fischlin [a]

[a] *Department of Environmental Sciences, Systems Ecology, Institute of Terrestrial Ecology, Swiss Federal Institute of Technology, Zürich, Switzerland*
[b] *Geobotanical Institute, University of Bern, Bern, Switzerland*

Abstract

Adaptation potential of forests to rapid climatic changes can be assessed from vegetation dynamics during past climatic changes as preserved in fossil pollen data. However, pollen data reflect the integrated effects of climate and biotic processes, such as establishment, survival, competition, and migration. To disentangle these processes, we compared an annually laminated late Würm and Holocene pollen record from the Central Swiss Plateau with simulations of a dynamic forest patch model. All input data used in the simulations were largely independent from pollen data; i.e. the presented analysis is non-circular. Temperature and precipitation scenarios were based on reconstructions from pollen-independent sources. The earliest arrival times of the species at the study site after the last glacial were inferred from pollen maps. We ran a series of simulations under different combinations of climate and immigration scenarios. In addition, the sensitivity of the simulated presence/absence of four major species to changes in the climate scenario was examined. The pattern of the pollen record could partly be explained by the used climate scenario, mostly by temperature. However, some features, in particular the absence of most species during the late Würm could only be simulated if the winter temperature anomalies of the used scenario were decreased considerably. Consequently, we had to assume in the simulations, that most species immigrated during or after the Younger Dryas (12 000 years BP), *Abies* and *Fagus* even later. Given the timing of tree species immigration, the vegetation was in equilibrium with climate during long periods, but responded with lags at the time-scale of centuries to millennia caused by a secondary succession after rapid climatic changes such as at the end of Younger Dryas, or immigration of dominant taxa. Climate influenced the tree taxa both directly and indirectly by changing inter-specific competition. We concluded, that also during the present fast climatic change, species migration might be an important process, particularly if geographic barriers, such as the Alps are in the migrational path. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: Forest modeling; Holocene; Pollen data; Climate change; Vegetation adaptation; Tree species migration; Competition; Sensitivity analysis

* Corresponding author. Present address: Landscape Inventories, Swiss Federal Research Institute WSL, Zürcherstr. 111, CH-8903 Birmensdorf, Switzerland. Tel.: +41-1-739-2533; fax: +41-1-739-2215.

E-mail address: lischke@wsl.ch (H. Lischke).

[1] Present address: Laboratory of Palaeobotany and Palynology, Budapestlaan 4, 3584 CD, Utrecht, The Netherlands.

1. Introduction

In the context of present and anticipated future rapid climate changes, the question of whether ecosystems are able to adapt fast enough to shifts in the local site conditions is crucial (see e.g. Kirschbaum, 1996). Focusing on boreal and temperate forested areas, one approach to assess natural adaptation rates is to examine forest responses to fast past climatic changes, e.g. the rapid temperature increase after the Younger Dryas. Such forest responses are preserved in Holocene pollen records (Davis, 1986, 1989; Huntley et al., 1989; Roberts, 1989). However, a transfer of adaptation rates to the present climate change estimated from pollen records is difficult, since it is not clear whether forests will respond in the same manner and with the same speed as in the Holocene.

The present situation, even if we neglect the human influence, differs strongly from that during Younger Dryas, concerning both climate and species distribution.

Furthermore, pollen records and isopoll maps integrate numerous processes involved in forest responses to changing environmental conditions: immediate ecophysiological responses of individuals, slower competitive abilities governing structural changes, and even slower migrational responses of individual species (Kirschbaum, 1996). All of these processes are influenced by climate. At a specific location, climate has a direct effect on the species-specific ability of individual trees to establish, survive, reproduce, and grow, and, thus, on their competitiveness. The outcome of this intra- and interspecific competition, in turn, shapes the successional patterns (e.g. Shugart, 1984) and the resulting steady-state.

Also species' migration into new suitable habitats is influenced by both, climate and biotic factors. Migration and its speed, such as documented in the maps of Huntley and Birks (1983), Burga (1988), Lang (1994) or Gliemeroth (1995) not only depend on the species' ability to disperse, but also on the climate-dependent local dynamics along the migrational path. Dispersal rates depend on species intrinsic, climate independent properties, such as dispersal ability as influenced by seed size or type and genetically determined minimal generation time, and on climate dependent features such as actual generation time and seed production.

Thus, a major issue is to identify, understand, and quantify the principle mechanisms underlying past vegetation responses to a changing climate. To assess the potential of the vegetation to adapt to future climate changes, it is particularly important to distinguish those processes which can be assumed to operate in the same way in the future from those factors and processes which depend on the actual situation.

To analyze integrative data such as pollen records, the most promising tools are dynamic ecological models. They should depict the main climate dependencies, processes, and interactions between species and individuals with an appropriate resolution. By testing different scenarios, e.g. of species interactions, and comparing the obtained results with pollen records, such models can give insight into the processes involved in vegetation responses and may be improved for future climate change impact assessment (Huntley et al., 1995).

The various types of ecological, particularly forest models (see review in Lischke, 2001), usually fulfill only parts of the above mentioned requirements. Ecophysiological 'big-leaf-models' (e.g. Bossel, 1996; Foley, 1994; Grote, 1998; Lüdecke et al., 1994; Melillo et al., 1993; Potter et al., 1993; Running and Gower, 1991) describe in detail ecophysiological processes and partly also climatic influences. However, they disregard the interactions between individuals and populations, which for example result in specific spatial structures. Individual based, position dependent models (e.g. SORTIE, Pacala and Deutschman, 1995; Pacala et al., 1996), in contrast, focus on the interactions between the individuals, with less emphasis on ecophysiology and climate. Besides, they require long computing times because every single tree of a stand is simulated in a Monte-Carlo approach. A compromise between these approaches are forest gap (or patch) models (Botkin et al., 1972). They describe species-specific establishment, growth, and death of individual trees and interactions among them, resulting in

typical succession patterns. By including explicit climate dependencies, they can account for climatic, immigration, and competitional influences on an individualistic, species-specific level. Therefore, they are suitable to test hypotheses on the effects of climate, immigration, and competition. Although the process functions and climate dependence functions are empirical, they are at least based on ecological considerations. Since only the trees in small forest patches are simulated in a Monte-Carlo approach, gap-models are fast enough for simulations encompassing several millenia. Furthermore, usually they require only a limited number of input variables, which is crucial in paleoecological studies, where these input data have to be reconstructed from various sources.

Simulations with patch-models have already been compared with vegetation patterns illustrated in Holocene pollen records in several studies: Solomon et al. (1981) compared the vegetation composition simulated by the patch-model FORET with a North American pollen record. They tested several combinations of the input assumptions: constant versus changing temperature, immigration of species versus presence of all species. From their simulations they concluded that the vegetation dynamics in the pollen source area was mainly controlled by direct climatic influence. Solomon and Bartlein (1992) tested simulations with FORET against three North-American pollen records and Lotter and Kienast (1992) and Fischlin et al. (1995b) used an annually varved pollen record (Lotter, 1989) from Central Switzerland to verify the successional pattern produced by the models FORECE (Kienast, 1987) and FORCLIM, respectively, given a constant climate and a sequential appearance of the tree taxa in the catchment area. Lischke et al. (1998a) repeated the latter two studies with the model FORCLIM using a seasonal, transient climate scenario obtained from GCM-simulations. In the four latter studies the simulations largely reproduced the pollen record, at least for the dominant taxa.

The conclusions, which can be drawn from such studies depend strongly on the source of the input data for climate or immigration dates. In particular, the independence of input data is crucial. In the earlier studies, climate input data or dates of species appearance were inferred from the pollen record to which the simulation results were compared. Such a circularity (Huntley et al., 1995) between cause (climate or immigration dates reconstructed from pollen) and effects (vegetation responses assessed from pollen) limits the insights, which can be gained about the factors, which control vegetation response. A correspondence between observed pollen and simulated vegetation may merely indicate that the models behaved consistently with those models which have been used for reconstructing the climate or the dates of appearance in the studied area. Moreover, with such an approach it is not feasible to separate time-lags between climate and species abundance which are due to succession from those due to real late immigration (Delcourt and Delcourt, 1991).

In the present study we tried to untangle the ecological processes leading to the species pattern in a Holocene pollen record with the help of the forest patch FORCLIM (Bugmann, 1994, 1996; Fischlin et al., 1995a). One goal was to break through the above mentioned circularity: we used (as far as available) climatic input scenarios and immigration dates from independent data sources.

Our specific questions were ''Which species' absence during the Holocene may be due to adverse climatic conditions, either acting directly or by affecting competitors, or to succession? And, for which species do we have to assume a later arrival?''

A straightforward approach would be to compare the pollen data with one single simulation based on the most probable scenarios of climate anomalies and immigration. However, such an approach at best validates (or better, does not falsify) the model assumptions and the used scenarios. It still does not assess the importance of the involved processes. Thus, we successively combined the different scenarios of climate, competition, and immigration to sort out which scenarios and assumptions were necessary to reproduce the data. These factors probably represent the most important influences. In this way,

we were able to investigate which taxa could not establish saplings or survive due to adverse climatic conditions, which ones were potentially suppressed by stronger competitors, and which ones we have to assume immigrated.

2. Data, model, and methods

2.1. Study site

Soppensee is located on the central Swiss Plateau (8°05′ E, 47°05′30″ N, see Fig. 1) at an elevation of 594 m a.s.l. The surrounding region is low and hilly; its present temperate climate is suitable for a majority of the Central and North European tree species. It, therefore, represents a good case study for temperate, Central European situations. It is bordered by the Alps in the south. The pollen source area was estimated (Lotter and Kienast, 1992) to be a circle of about 300 km².

2.2. The Soppensee pollen record

Pollen data from the annually laminated sediments of Soppensee (Lotter, 1989, 1999) was used for the comparison with the model simulations. To allow a comparison between the subfossil pollen record and the model outputs, sidereal (calendar) years rather than radiocarbon years have been used as the time unit. All dates derived from the paleo-record have, therefore, been calibrated (Stuiver and Reimer, 1993) and eventually expressed as calendar years before present (cal. BP). The annual laminations of the Soppensee sediment allowed for a relatively precise chronological assessment (Lotter, 1989).

In this study, we use the following terminology for the periods: late Würm: before 12 000 cal. BP, Younger Dryas: 12 000 cal. BP to 11 000 cal. BP, Holocene: after 11 000 cal. BP.

The pollen record from Soppensee (Fig. 3a) is typical for the central part of the Swiss Plateau. It
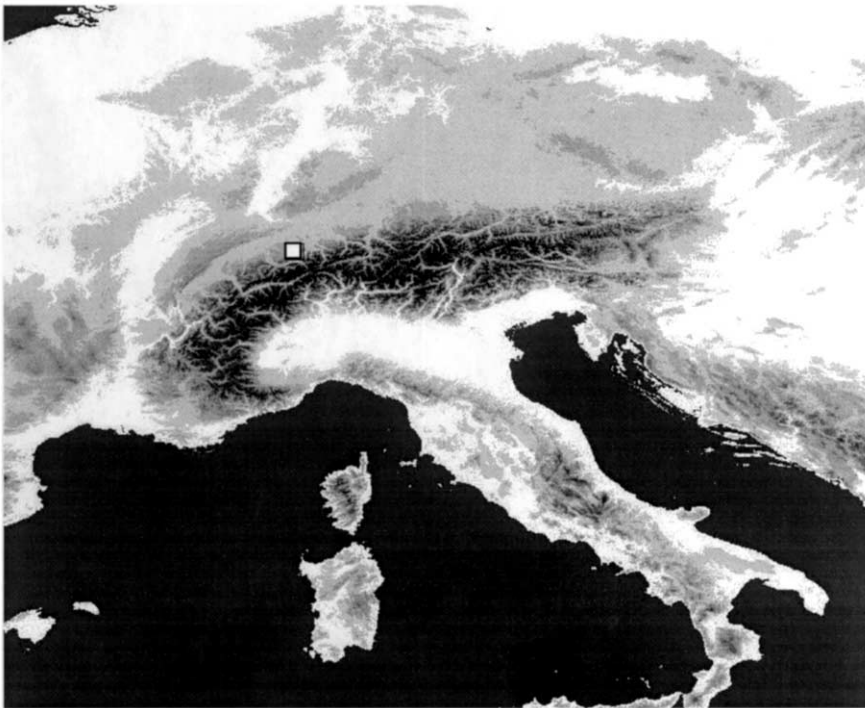

Fig. 1. Situation of study site (rectangle) at the north slope of the European Alps.

Table 1
Species included in simulations

Species	I	R
Abies alba	8220	1
Larix decidua	8220	0.25
Picea abies	6530	1
Pinus cembra	12 600	4
Pinus montana	*	4
Pinus silvestris	*	4
Taxus baccata	6830	1
Acer campestre	9980	0.25
Acer platanoides	9980	0.25
Acer pseudoplatanus	9980	0.25
Alnus glutinosa	9170	4
Alnus incana	9170	4
Alnus viridis	9170	4
Betula pendula	*	4
Carpinus betulus	3190	3
Castanea sativa	2710	0.25
Fagus silvatica	7100	1
Fraxinus excelsior	9930	1
Populus nigra	10 500	0.25
Populus tremula	10 500	0.25
Quercus petraea	10 880	1
Quercus pubescens	10 880	1
Quercus robur	10 880	1
Salix alba	12 460	4
Sorbus aria	4920	0.25
Sorbus aucuparia	4920	0.25
Tilia cordata	10 010	0.25
Tilia platyphyllos	10 010	0.25
Ulmus scabra	10 880	2

I: immigration dates (years cal. BP) of tree taxa assumed in simulations; from Ammann et al. (1996). R: representation factors to convert biomass into pollen percents (Andersen, 1970; Faegri and Iversen, 1975). Corylus was excluded from the evaluation. *: taxon was present at the beginning of the simulation.

goes back to the end of the last glaciation and covers the whole Holocene period to the present day without hiatus (Lotter, 1999). The major tree species pattern, as evidenced by the pollen record, shows that the reforestation lead to a birch woodland that was then followed by a pine forest around 12 800 cal. BP (Lotter, 1991). During the climatic cooling of the Younger Dryas, this pine–birch woodland opened up for a duration of approximately 1150 years (Hajdas et al., 1993). With the subsequent climatic warming the pine–birch woodland became denser again, and decidu-

ous trees such as *Ulmus*, *Quercus*, *Acer*, *Tilia*, and *Alnus* started to appear on the Swiss Plateau (Ammann et al., 1996). Shade-tolerant trees such as *Abies* and *Fagus* appeared only around 7100 and 6700 cal. BP, respectively.

2.3. Immigration scenarios

For the Swiss Plateau there are many pollen diagrams from other sites available that cover the last 15 000 years (see, e.g. Ammann et al., 1996; Burga and Perret, 1998; Lang, 1985). These studies yield a temporal sequence of maps of the abundance of different tree taxa for the entire region which fit consistently into pollen maps of Switzerland (Burga and Perret, 1998) and Europe (Huntley and Birks, 1983). They allow the estimation of the earliest arrival dates of the tree species in the region close to Soppensee. Estimations such as these have been done by Ammann et al. (1996), and it is from their analysis that we derived the earliest arrival dates used in our simulations (Table 1). As usually done, the time of arrival is defined as the rational limit, i.e. the time of the first steep increase in the pollen numbers (Birks, 1986; Lang, 1994).

2.4. Biomass to pollen conversion

Quantitative conversion of fossil pollen records into past plant abundances has been a major issue for palaeobotanists for a long time (see, e.g. Sugita, 1994). To allow a comparison between model output (biomass) and pollen data (pollen percent) we converted the simulated biomasses into relative pollen percentages. We applied the conversion factors R_i of Iversen (Faegri and Iversen, 1975) as used in Lotter and Kienast (Lotter and Kienast, 1992) and those of Andersen (1970). For eight species without listed conversion factors we used the medium value 1. The factors R_i (cf. Table 1) are an estimate for the ratio between the representation p_i/P of a taxon i in the pollen record P and its representation v_i/V in the vegetation V:

$$R_i = \frac{p_i/P}{v_i/V} \Rightarrow \frac{p_i}{P} = R_i \cdot \frac{v_i}{V}, \quad V = \sum_j v_j, \quad P = \sum_j p_j$$

(1)

We assumed that 'vegetation representation' (Faegri and Iversen, 1975) refers to the total basal area ba_i of a taxon (such as in Davis, 1963). To get an estimate for ba_i, we multiplied the simulated mean biomass b_i of each species with the fraction of maximum biomass $b_{max,i}$ relative to the maximum basal area $ba_{max,i}$ as given by FORCLIM.

$$vi := ba_i \cong b_i \cdot \frac{ba_{max,i}}{b_{max,i}} \qquad (2)$$

Pollen percents ($100 \times p_i/P$) were then calculated according to Eqs. (1) and (2).

2.5. Comparison of pollen data and simulation results

Simulation results and pollen data were initially compared visually, to judge the qualitative resemblance. For quantitative comparison, all model output and pollen data were first smoothed by filtering with a Gaussian Low-Pass-Filter (critical period 500 years), since most short term fluctuations are mainly due to the remaining intrinsic variability of the simulated stochastic process (Bugmann et al., 1996) or to sampling uncertainties in the data. Then, a similarity index (similarity) (Cormack, 1971; Wolda, 1981) was computed for each simulation according to Eq. (3):

$$similarity = 1 - \frac{\sum_{i=1}^{n_{specs}} \sum_{j=1}^{n_{times}} |data_{i,j} - simulation_{i,j}|}{\sum_{i=1}^{n_{specs}} \sum_{j=1}^{n_{times}} data_{i,j} + simulation_{i,j}} \qquad (3)$$

2.6. Scenarios of climate anomalies

The climate data used for the scenario simulations were derived from different sources. All were calculated from past anomalies relative to the present climate.

Present climate was estimated with data from the station Huttwil (17.5 km north-west of Soppensee, 639 m a.s.l.), which was assumed to be representative for the Soppensee pollen source area. Huttwil has an annual mean temperature of 8.12 °C, a mean yearly precipitation sum of 129

cm (SMA, 1901–1990) and a mean field capacity of $\sim$ 35 cm.

The temperature anomaly scenario is based on different reconstructions: (a) a combined reconstruction of summer temperatures from aquatic vegetation, insects and oxygen isotopes from various lakes in the Swiss Central Plateau (Ammann et al., 1994) for the late Würm, and from oxygen isotopes from the sediment of lake Zuerich, about 50 km north-east of Soppensee (Lister, 1989) for the Holocene and (b) cladocera-inferred summer temperatures (Lotter et al., 2000) for the whole period. Temperature anomalies were then calculated by comparing these data with the modern mean July temperatures. Fig. 2 shows the resulting temperature scenario for the entire period of investigation. In most simulations, we assumed that the temperature anomalies are uniformly distributed over the annual cycle. However, temperature anomalies in the past were presumably not distributed uniformly over the year; for example, simulations with the global circulation model 'CCM' (Kutzbach and Guetter, 1988) in Huntley and Prentice (1993) yielded higher July temperatures than today and lower or similar January temperatures than those of the present. To assess the influence of such changes in the seasonality with the same mean values, we increased the yearly mean temperature anomalies by 1 °C for the summer months (April–September) and decreased them by 1 °C during winter.

The precipitation scenario (Fig. 2) is based on a combined pollen- and lake-level reconstruction by Guiot et al. (1993) for gridpoint 8° E 47° N for the time after 9000 radiocarbon years BP (i.e. after ca. 10 000 cal. BP). We assumed average values of the precipitation anomaly classes and interpolated linearly between 10 000 (-45 cm/year) and 5750 cal. BP (-20 cm/year). For the time before 10 000 cal. BP no precipitation reconstructions were available in the required resolution. Since global climate-model simulations (COHMAP Members, 1988) indicate that also before 9000 cal. BP the Central European climate was dryer than at present, we assumed the precipitation anomaly to remain constant between 13 000 and 10 000 cal. BP.

2.7. Forest model

All simulations were made with the dynamic forest model FORCLIM (version 2.4.0.2) (Bugmann, 1994, 1996; Fischlin et al., 1995a), a stochastic patch-model, which has been verified along climatic gradients in the European Alps (Bugmann, 1994) and North America (Bugmann and Solomon, 1995), with empirical distributions of European tree species in temperature–precipitation space (Bugmann, 1996) and with data from European pristine forests (Badeck et al., 2001).

The model simulates the fate of individual trees, which are aggregated to cohorts, on 1/12 ha patches; the dynamics of the entire forest are obtained by averaging over 200 patches (Bugmann et al., 1996). The trees compete for light by shading all smaller trees. Growth rates and establishment and survival probabilities are species-specific and depend on the bioclimatic variables yearly degree day sum, mean temperature of the coldest month ('minimum winter temperature'), drought stress, and flooding stress. The dependence functions are defined as a maximum rate multiplied with a modifier function which ranges from 0 to 1. Thus, the range where the functions are zero defines where a species can not exist at all. Additionally, the continuous non zero values define the relative strength of a species, and thus its competitiveness. To calculate the drought stress a bucket model for soil water is used (Bugmann, 1996).

To describe the response to wet soils in the study area, a sensitivity of trees to high soil water contents and the associated poor soil aeration was introduced to the model. From the percent soil water content calculated by the bucket model, the percent soil air was derived, assuming an average pore volume of 55%. The percent oxygen content Ox is then estimated by 20% of the percent soil air. The growth then depends with

$$\varphi(Ox) = \frac{\text{Max}(Ox - Ox_{\text{crit,s}}, 0)}{(\text{Max}(Ox - Ox_{\text{crit,s}}, 0) + 0.005)}$$

on the oxygen content, with $Ox_{\text{crit,s}}$ a species specific critical oxygen content. The $Ox_{\text{crit,s}}$ values were compiled from indicator values of species flooding tolerance (Ellenberg, 1986; Landolt, 1977; Lyr et al., 1992), which were transformed to the range between 0% O_2 (e.g. for *Alnus incana*) and 3% O_2 (e.g. for *Tilia platyphyllos*).

The bioclimatic variables are determined from monthly mean temperatures and precipitation sums, which are stochastically generated based on long-term site specific means, standard deviations (S.D.), and cross correlations. For the climate change simulations, the means were changed. Since the effects of CO_2 on mature trees are not yet fully understood, they are not included in the
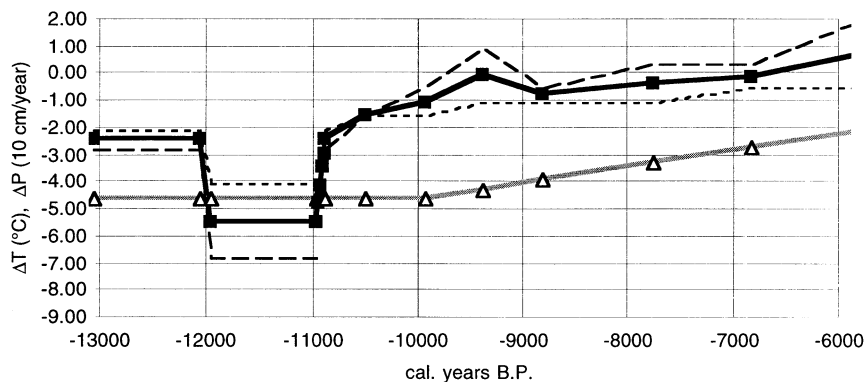

Fig. 2. Climate anomaly scenarios used in simulations. Black squares, solid black line: yearly mean temperature anomaly as used in simulations. Hatched line: temperature anomaly derived from aquatic vegetation and oxygen isotope data (Ammann et al., 1994; Lister, 1989). Dotted line: temperature anomaly derived from cladoceran and chironomids (Lotter et al., 2000). White triangles, grey line: anomaly of annual precipitation derived from (Guiot et al., 1993).

model. The model assumes that all species produce the same, constant number of seeds per year. Individuals compete for light; shading decreases the probability of the establishment of a cohort and affects growth rate as well as mortality. The 30 most important Central European tree species listed in Table 1 were included in the simulations and assigned to the taxa of the pollen record, i.e. the genera. In the following, we usually use the names of the genera, except when we have to distinguish between the species of a genus.

Simulations were run on a SUN Sparc 5 workstation with the batch version RASS (Thöny et al., 1994) of the simulation software RAMSES (Fischlin, 1991). Simulations were started at 13 060 cal. BP and run for 7000 years on an annual time step, assuming that the pollen data stem from the same period.

2.8. Simulation experiments

To study the different potential causes for the species pattern (Table 2, column 1) simulations were run with various combinations of input scenarios.

The simulations were started approximately 13 000 cal. BP, i.e. when the Swiss Plateau became reforested, mainly by birch (Ammann et al., 1996). Consequently, we assumed in all simulations that the study site was not forested at that time, but that pedogenesis was in a stage which would not impede tree growth and that a seed bank consisting at least of the pioneer taxa *Betula* and *Pinus* was present or that these seeds could be transported easily to the site from already forested, adjacent regions.

Table 2 gives an overview over the different scenarios used in the simulations and their combinations: climate anomalies either changed in time according to Fig. 2 (transient climate, 'tra'), to study the impact of climate change, or were kept constant over the entire period ('co', 'coS') to study the influence of succession. Constant anomalies were either average values (-1.5 °C and -39 cm/year), or selected (ΔT–ΔP) combinations ('coS'). These combinations are shown in Fig. 2 as triangles and squares. The transient scenarios were combined with each other or with

the constant average value of the other climate variable ($\Delta T = -1.5$ °C, $\Delta P = -39$ cm/year). In one simulation an increased seasonality was assumed.

To investigate the influence of immigration, seeds were assumed to be present at different times: either from the beginning of the simulations (13 060 cal. BP), the beginning of Younger Dryas (ca. 12 000 cal. BP) or from the taxon's earliest appearance date derived from independent pollen records (Table 1).

A soil field capacity of 35 cm was assumed in most simulations. Yet, geomorphologic maps indicate that the pollen source area around Soppensee is heterogeneous, particularly with respect to the field capacity. Since field capacity influences drought stress and thereby tree growth, we assumed in one simulation the pollen source area to consist of soils with field capacities varying between 35, 50 and 55 cm. Their relative proportions were estimated to be 40:40:20%.

To study how much climate or immigration affects the species pattern indirectly through interspecific competition, in one simulation experiment, interspecific competition was excluded. This was achieved by a simple model modification which ignores the effect of shade on a tree caused by trees belonging to other species.

To assess whether the species pattern reflects transient changes of the system or could also be explained by equilibrium results, a series of 15 simulations with constant climate input and species set was run into equilibrium, each corresponding to one discrete time point (squares in Fig. 2). For each simulation, the climate anomaly at this specific time and the species set at this time as given in Table 2, row 3g was used. For example, one simulation was run corresponding to the conditions at 9900 BP, i.e. with $\Delta T = -1$ °C, $\Delta P = -46$ cm/year and all species except *Abies* and *Fagus*. Equilibrium values were determined by averaging the simulation results over the last 300 years. The resulting equilibrium values were then linearly interpolated.

2.9. Sensitivity to climate scenario

The baseline climate anomaly scenario we used

Table 2
Scenarios used in simulation experiments and similarity of results to pollen data

Experiment: Effects of...	Fig.	Climate scenario		Seasonal	Intersp. competition	Immigration of taxa (years cal. BP)			Heterogeneity	Sim. Index
		ΔT (°C)	ΔP (cm/year)			Before 13 060	12 000	Acc. to tab. 1		
Succession	3b	co −1.5	co −39	−	+	All			−	0.3
Succession	−	coS	coS	−	+	All			−	0.35
Climatic change	3c	co −1.5	tra	−	+	All			−	
Climatic change	3d	tra	co −39	−	+	All			−	0.45
Climatic change	3e	tra	tra	−	+	All			−	0.48
Seasonality	−	tra	tra	+	+	All			−	0.5
Immigration	3f	tra	tra	−	+	PiBePoSa	AO, AbFa		−	0.55
Immigration	3g	tra	tra	−	+	PiBePoSa	AO	AbFa	−	0.59
Immigration	−	tra	tra	−	+	PiBePoSa		All	−	0.64
Heterogeneity	3h	tra	tra	−	+	PiBePoSa	AO	AbFa	+	0.61
Interspecific competition	3i	Tra	tra	−	−	PiBePoSa	AO	AbFa	−	
Dynamics vs. equilibrium	3j	coS	coS	−	+	PiBePoSa	AO	AbFa	−	

co: climate parameter constant over simulation period; coS: series of constant climate parameters, triangles and squares from Fig. 2; tra: transient, i.e. climate parameters change acc. to Fig. 2; All: All taxa (see Table 1); PiBePoSa: *Pinus, Betula, Populus, Salix*; AbFa: *Abies, Fagus*; AO: All other taxa, i.e. all except *Pinus, Betula, Populus, Salix, Abies* and *Fagus*.

has to be considered as a 'best estimate'; the real climate might have departed from this scenario. Therefore, we tested which changes in the climate scenarios are required to explain the presence/absence pattern of the four major species *Abies*, *Picea*, *Quercus*, and *Fagus* by the climate dependences of the model.

To assess this sensitivity to deviations in the climate scenario, we determined for various combinations of winter and summer temperature anomalies, whether climate prevented the species to exist. Winter (December–February) temperature anomalies (dTw) were varied systematically from -10 to 3.5 °C, summer (June–August) temperature anomalies (dTs) from -8 to 16 °C in steps of 0.5 °C. For spring and fall temperature anomalies, the average between summer and winter temperature anomaly was taken. Each pair of dTw and dTs was combined with the present climate (monthly means and S.D. of temperature means and precipitation sums) at Huttwil. For the precipitation anomaly the values -25, -30, -40, -45 and -65 cm/year were used. These correspond to the precipitation anomalies of the baseline scenario (Fig. 2) at 6500, 7500, 9000 and 12 500 BP. The value -65 cm/year was obtained by extrapolating the precipitation anomaly between 9000 and 13 000 BP.

With each of these climata, 200 stochastic weather realizations and the resulting bioclimatic variables drought stress, day degree sum and minimum winter temperature (= temperature mean of the coldest month) were calculated with the submodel FORCLIM-E. For each realization, we determined whether the bioclimatic variables were within the range of the model's species specific climate dependences for establishment and growth (which determines mortality) (see Eq. (4)).

where s: species, i: realization; β: establishment (1: possible, 0: not possible), γ: growth (1: possible, 0: not possible), μ: mortality, dd: day degree sum, dd_{min}, dd_{max}: minimum and maximum dd for growth and establishment, wiT: mean temperature of the coldest month, wiT_{min}: minimum wiT for establishment, drstr: drought stress index, $drstr_{max}$: maximum drstr for growth.

The mere consideration of these bioclimatic limits, however, does not take into account that occasional death of all individuals affects population dynamics much more drastically than occasional lack of offspring. Therefore, we used the simple model in Eq. (5) for the presence or absence of a species in realization i. A species was considered to be generally present if it was present in more than 80% of the realizations. Such a high threshold was chosen because lower ones, corresponding to shorter periods of existence, do not allow the trees to reach maturity, i.e. to produce pollen.

$$\text{presence}_{s,i} = \min(1,(1 - \mu_{s,i})(\text{presence}_{s,i-1} + \beta_{s,i}))$$

$$\text{presence}_s = \begin{cases} \text{yes} & \text{for } \dfrac{1}{200}\sum_{i=1}^{200} \text{presence}_{s,i} > 0.8 \\ \text{no} & \text{else} \end{cases}$$

(5)

In the resulting species distribution areas in the dTw/dTs-space, the dT-values of the baseline scenario at specific times (12 500, 9000, 7500, and 6500 BP) were marked. From these points the shortest distances were determined which leave the distribution areas of the species not present in the pollen data set, but remain in the distribution area of species present in the pollen.
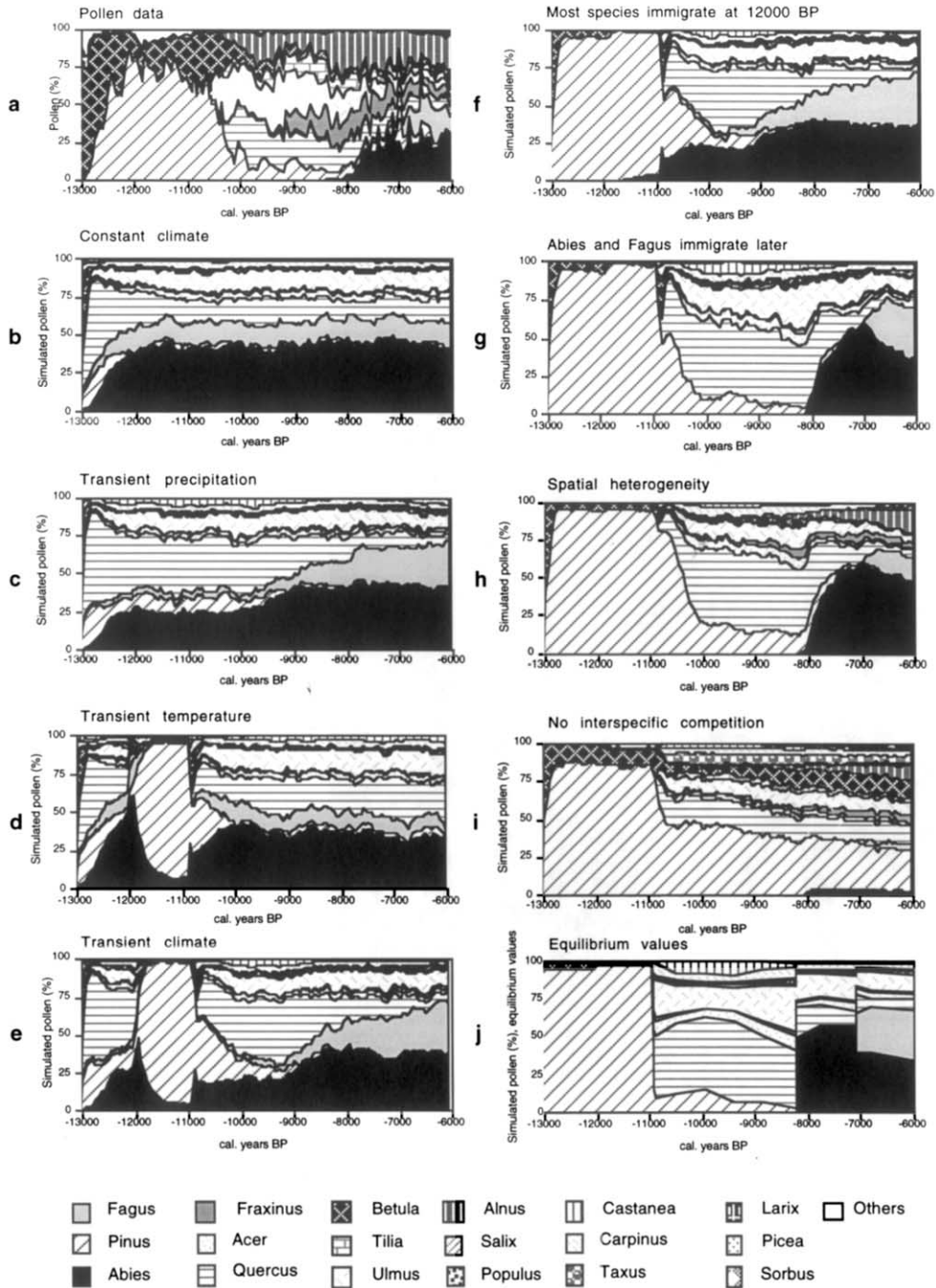
$$\beta_{s,i} = \begin{cases} 1 & \text{for } dd_i > dd_{min,s} \wedge dd_i < dd_{max,s} \wedge wiT_i > wiT_{min,s} \\ 0 & \text{else} \end{cases}$$

$$\gamma_{s,i} = \begin{cases} 1 & \text{for } dd_i > dd_{min,s} \wedge dd_i < dd_{max,s} \wedge drstr_i > drstr_{max,s} \\ 0 & \text{else} \end{cases}$$

$$\mu_{s,i} = \begin{cases} 1 & \text{for } \gamma_{s,i} + \gamma_{s,i-1} = 0 \\ 0 & \text{else} \end{cases}$$

(4)

Fig. 3.

3. Results

The various combinations of scenarios for climate, immigration, and spatial heterogeneity (Table 2) gave us the ability to test whether climatic change, successional dynamics, or immigration controlled the appearance of taxa in the pollen record. And, they permitted to investigate the importance of interspecific competition and transient forest responses. The results are shown in Fig. 3b–j and in Table 2, the pollen data in Fig. 3a.

3.1. Effects of succession

Fig. 3b shows the typical result of a simulation where seeds of all species were present and temperature and precipitation anomalies were kept constant at their means during the entire simulation period. After a transient phase, *Abies*, *Fagus*, *Quercus*, and *Ulmus* dominated the forest. Other simulations (not shown) were run under several combinations of constant precipitation and temperature anomalies occurring along the climate scenario. None of these simulations resembled the pollen record (Fig. 3a). Moreover, in all these simulations, successional changes in the species composition ceased after about 1000 years (cf. Fig. 3b). This contrasts sharply with the lively dynamics in the pollen record during the entire observation period of 7000 years. This difference is also reflected by the low similarity index between the simulation with average climate and the pollen data (Table 2). Succession alone does not appear to be able to explain the species changes found in the pollen record.

3.2. Effects of climatic change

To assess the effect of a changing climate, in the following simulations (Fig. 3c–e) we drove the forest dynamics with transient climate scenarios (Fig. 2). Again, seeds of all species were assumed to be present already in the beginning of the simulations.

Fig. 3c shows the results from applying a transient precipitation and a constant temperature scenario. A few characteristics of the pollen record could be reproduced, namely the increasing fraction of *Fagus* and *Abies* accompanied by a decrease in *Pinus* and *Quercus*. In turn, the simulation with transient temperature and constant precipitation (Fig. 3d) was able to mimick one major characteristic of the pollen record: the abrupt change at the end of the Younger Dryas (ca. 11 000 cal. BP) from a pine dominated forest to a mixed deciduous forest. This change was reflected by an increase of the similarity index from 0.35 to 0.45 (Table 2).

However, for the late Würm (before 12 000 cal. BP) a mixed deciduous forest with *Quercus* and *Abies* was simulated, in contrast to the pine dominated forest in the pollen data. In the Holocene *Fagus* and *Abies* appear much too early, and *Fraxinus* and *Alnus* are underrepresented. Thus, neither the transient temperature nor the transient precipitation scenario alone can explain the pollen record. A simulation with transient precipitation and temperature scenarios (Fig. 3e) resulted in an increase of the similarity index up to 0.48 (Table 2) which is mostly due to a slower increasing portion of *Fagus* in the Holocene. However, in the late Würm still *Quercus*, *Abies* and *Ulmus* are

Fig. 3. Comparison of pollen record with forest model simulations under various input scenarios (Table 2, Fig. 2). (a) Holocene annually laminated pollen record from Soppensee. (b–j) Simulations with dynamic forest patch model FORCLIM. Simulated pollen percentages are determined from basal area of species, corrected by *R*-values. (Table 1). (b) All modern species present, constant climate, average temperature and precipitation. (c) All modern species present, transient precipitation, constant temperature. (d) All modern species present, constant precipitation, transient temperature anomaly. (e) All modern species present, transient precipitation and temperature. (f) Immigration of all species except *Betula*, *Pinus*, *Salix* and *Populus* at 12 000 cal. BP, transient temperature and precipitation. (g) Immigration of *Abies*, and *Fagus* at years given in Table 1, of all other species except *Betula*, *Pinus*, *Salix* and *Populus* at 12 000 cal. BP, transient temperature and precipitation. (h) Same as in g, simulated area heterogeneous with respect to field capacity: 40% 35 cm, 40% 50 cm, 20% 55 cm. (i) Same as in g, no interspecific competition. (j) Equilibrium values of simulations for constant climates and species sets according to g, at 10 discrete time points (triangles and squares in Fig. 2). The equilibrium values were interpolated.
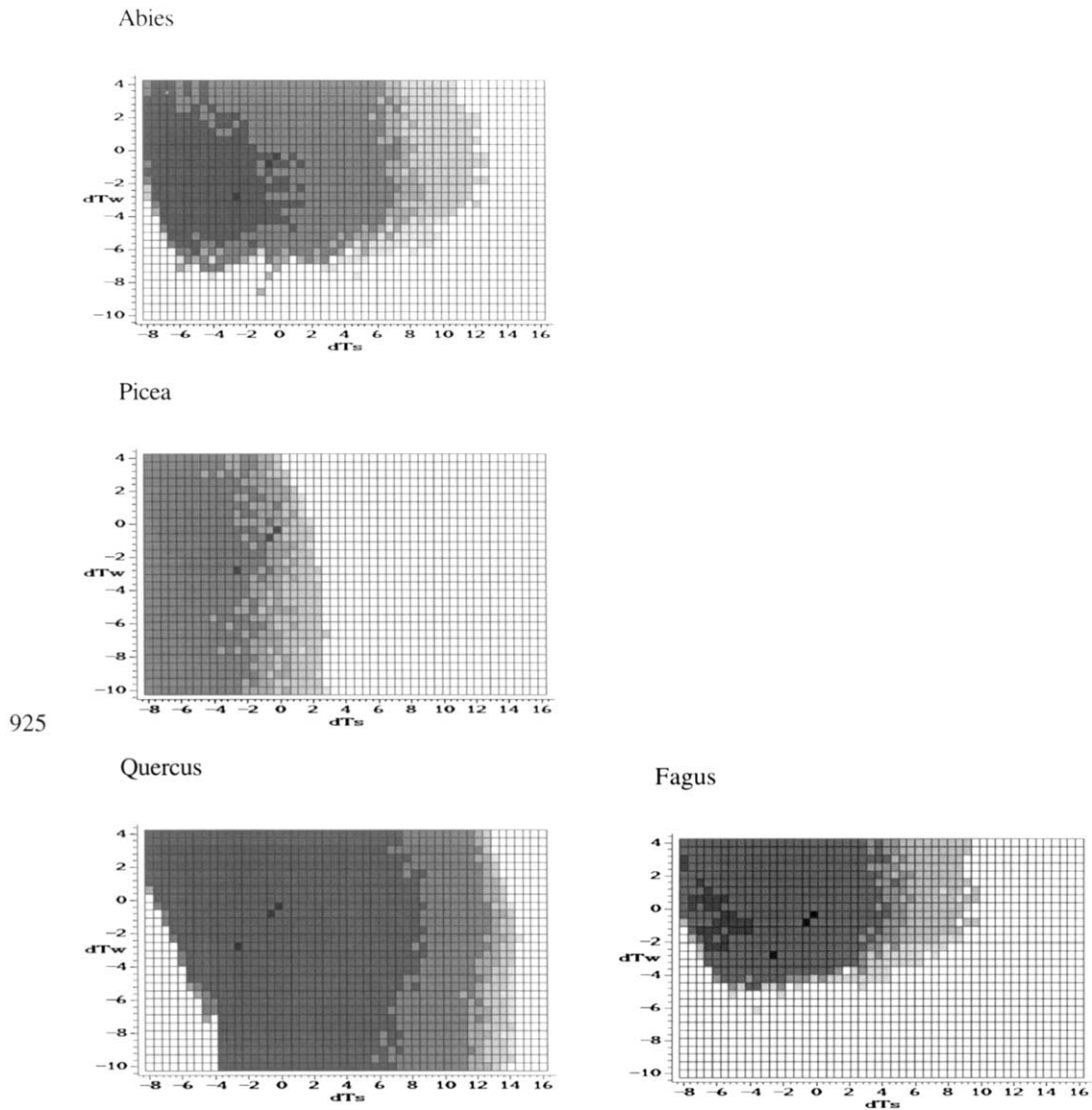
Fig. 4. Sensitivity of species' climate dependencies to climate anomaly scenario. The shaded areas show the combinations of summer and winter temperature anomalies (dTs, dTw) in °C where the taxa can exist according to their climate dependencies in the model FORCLIM. The different shadings indicate the taxa's presence at different precipitation anomalies according to the climate scenario (see Fig. 2) at selected times. White: taxon not present, light grey: taxon present at $\Delta P = 30$ cm/year (7500 BP), medium grey: taxon present at $\Delta P = 40$ cm/year (9000 BP), dark grey: taxon present at $\Delta P = 45$ cm/year 12 500 BP), very dark grey: taxon present at $\Delta P = 65$ cm/year (12 500 BP, precipitation anomaly extrapolated). The three black points indicate the temperature anomalies at 12 500, 9000, and 7500 BP, from bottom to top.

present, in the Holocene *Abies* and *Fagus* appear too early, and *Alnus* and *Fraxinus* are still under-represented. Hence, it appears that climate changes had a considerable influence on the vegetation pattern, but this effect was not strong enough to explain all major changes observed in the pollen record, particularly not the absence of mixed deciduous species during the late Würm.

Simulations with seasonal variations (± 1 °C) in the transient scenarios (not shown) differed

only slightly from those of the yearly mean anomaly (Table 2). Hence, seasonal anomalies in this order of magnitude seem to have only a minor effect. They were, therefore, left out in all subsequent simulation experiments.

The sensitivity tests (Fig. 4) show that the presence/absence of *Abies*, *Quercus*, *Fagus* and also *Picea* could only be explained by climate alone, if the winter temperature anomaly (dTw) was decreased by − 5, − 7, and − 4.7 °C at 12 500, 9000 and 7500 BP, respectively, combined with small decreases in the summer temperature anomaly (Table 3). At 12 500 BP also dTs had to be decreased by 1.5 °C. This means that a mere increase in seasonality does not suffice. The tests further revealed that the species' distribution areas in the dTs/dTw-space are shaped differently, because the species react differently to winter and summer temperatures and to precipitation. *Abies* and *Fagus* are limited mainly by low winter temperatures, *Picea* by high summer temperatures and low precipitation affecting drought, and *Quercus* by low summer temperatures affecting day degree sum. Furthermore, the species' distance to their distribution border differs. For example, *Fagus* is close to it at all times, which means that it can be excluded only by a small temperature decrease.

3.3. Effects of immigration

Fig. 3f shows the simulations where all species except those present in the late Würm (*Pinus*, *Betula*, *Populus*, *Salix*) were excluded until the beginning of the Younger Dryas, which is much earlier than their appearance in the pollen record.

The major difference between the simulation and the pollen record remains in the still too early appearances of *Abies* and *Fagus*.

In the following simulation (Fig. 3g) the dominating species *Abies* and *Fagus* were assumed to immigrate at the times indicated in Table 1. Now, for the first time the simulation depicts the major characteristics of the pollen data, except for the too low abundances of *Fraxinus* and *Alnus*. When we assumed that *all* species immigrated according to Table 1 (simulation not shown) the qualitative pattern changed only to a minor extent, although the similarity index increased further (Table 2). Mainly, the small shares of *Castanea* and *Carpinus* were replaced by *Tilia*. Compared with the pollen record, *Fraxinus* and *Alnus* were still underrepresented during the Holocene.

3.4. Effects of a spatially varying field capacity

Under the assumptions of a spatially heterogeneous field capacity (Fig. 3h) the flood tolerant taxa *Fraxinus* and *Alnus* reached higher simulated abundances during the Holocene, similar to *Betula* during the earliest part of the simulation period. Qualitatively, this simulation agrees best with the data.

The last two simulations were not compared with the pollen data, but to other simulations to analyze the model behavior. The spatial heterogeneity depicted by the average of three simulations would have only complicated these evaluations. Therefore, for simplicity we used in the following analyses the simulation without heterogeneity (Fig. 3g) as a reference.

Table 3
Minimum change in temperature anomalies required to explain species presence/absence in the pollen data

Years (BP)	Taxa present in pollen				Summer temperature		Winter temperature	
	Quercus	*Abies*	*Picea*	*Fagus*	dTs	ΔdTs	dTw	ΔdTw
12 500	−	−	−	−	−4	−1.5	−7.5	−5
9000	+	−	−	−	−0.5	0	−7.5	−7
7500	+	+	+	−	−0.3	0	−5	−4.7
6500	+	+	+	+	0	0	0	0

dT: temperature anomaly (°C), ΔdT: difference to temperature anomaly scenario (there ΔTs = −ΔTw) in Fig. 2 (°C).

3.5. Effects of interspecific competition

To distinguish between the direct effect of a changing climate on the tree taxa and the indirect effect of climate influenced competition (i.e. the effect of climate on the fundamental vs. the realized niche), we ran a simulation where the boundary conditions were the same as in Fig. 3g, but interspecific competition was excluded (Fig. 3i). The comparison to the simulations with interspecific competition (Fig. 3g) suggests that competition had only a small influence during late Würm and Younger Dryas. Later, the species composition is strongly affected by competition: *Fagus* and *Abies* reach much higher fractions under competition than in the non-competitive situation. Obviously, these taxa, which are themselves directly climate controlled, are capable of outcompeting or at least dominating species from other taxa.

3.6. Effects of equilibrium responses

Fig. 3j shows the sequence of equilibrium values according to the scenario of Fig. 3g, ordered along the time axis. This sequence is similar to the transient simulation in Fig. 3g during long periods. Differences appear in the beginning and particularly after the steep temperature increase around 11 000 cal. BP and after the immigration of *Abies* and *Fagus*. At these times, the transient simulation required several centuries to reach the equilibrium values.

4. Discussion

Using a plausible combination of input scenarios, which were based on proxy data independent of pollen, it was possible to simulate a long term forest development which resembled to a large extent that found in the annually laminated pollen record from Soppensee.

The results have to be considered in the light of the numerous uncertainties inherent in such studies of past vegetation dynamics (Lischke et al., 1998a). These include the climatic forcing (Prentice et al., 1991), the interpretation of the comparison data, the not clearly defined boundary conditions, such as the earliest arrival dates, and uncertainties of the model itself.

Climatic input had to be generated by combining reconstructions from several proxy data sources. This involves many uncertainties (Bradley, 1991). The used reconstructions had to be taken from other locations than Soppensee. Temperature reconstructions were from other lakes in the Swiss Central Plateau, and precipitation reconstructions were from a grid-point of a continental scale map. However, since the climate of the Swiss Central Plateau can be regarded as rather homogenous (Livingstone and Lotter, 1998), we assume that they are representative for the Soppensee area. Furthermore, the sensitivity tests reveal, that the presence/absence of the species as defined by the forest models' climate dependences is robust to small deviations in the climate scenarios. Rather strong changes, in particular strong decreases in winter temperature are necessary to explain the species pattern by temperature alone. The difference of the used scenario to the two underlying ones (± 1 °C) is not sufficient. Temperature reconstructions based on beetle remains (Atkinson et al., 1987) yielded such low temperatures in the late Würm. However, it is not clear, whether these findings can be transferred to Central Europe. In addition, beetles are to a certain degree able to choose suitable habitats and therefore reflect rather the local microclimate than a regional climate as implicitly assumed in these reconstructions.

Another drawback is that it is difficult to reconstruct climate extremes, such as late frost, wildfires, and wind, that may be of importance for trees and their competitive abilities.

In addition, relating tree biomass simulations to data from pollen records is not problem-free. Each simulation represents the forest dynamics at one single location, whereas the pollen in the Soppensee sediment stems from the entire catchment of the lake and neighboring areas with potentially heterogeneous site conditions, and thus forest compositions. Yet, the pollen source area of Soppensee is small, about 300 km^2 (Lotter and Kienast, 1992), and has a maximum altitudinal range of about ± 100 m, so that it can be

regarded as nearly homogenous with respect to altitude. The heterogeneity of soil properties was taken into account by averaging several simulations with differing field capacity values, which yielded a considerable improvement of the simulation results. Also the dating of the pollen record can introduce a bias. This bias could be kept small, since the used sediment is annually laminated. In previous studies (Fischlin et al., 1995b; Lischke et al., 1998a; Solomon and Bartlein, 1992; Solomon et al., 1981), ^{14}C-dated pollen records were used. However, the ^{14}C time scale is not 1:1 linear with the sidereal time scale (calendar years), thus it can not be directly compared with the simulations which are based on calendar years. Here, all data are based on a sidereal time scale, which was only possible because we used an annually laminated pollen record.

Pollen data are typically represented as fractions which makes them very sensitive even to small biases in the observations or in the conversion factors. Furthermore, the conversion factors relate pollen fractions to the 'representation in the vegetation' (Faegri and Iversen, 1975), which is not a clear measure of species abundance, such as e.g. tree numbers or biomass. The drawbacks of these representation factors have often been discussed (Birks and Gordon, 1985). However, in this study they were the only way to obtain at least a rough estimate for the relation between pollen and some variable characterizing species abundance. Today only few forests remain in the Soppensee area, so that not sufficient surface pollen data are available to calibrate sophisticated pollen dispersal models, e.g. those of Sugita (1994) or Prentice (1988), which probably would yield more reliable abundance estimates.

Finally, also the forest model itself, i.e. its process functions and parameter values contain uncertainties. Due to the empirical derivation, the species' parameters in gap models rather reflect a mixture of the realized and the fundamental niche and not the fundamental niche alone, as implicitly assumed in the model structure. Maybe as a consequence of this, gap models tend to perform well in regions where their parameter values have been derived, but less well in other regions (Badeck et al., 2001). However, as long as no models are

available, which at the same time describe detailed ecophysiology and tree interactions, still requiring a manageable amount of input and computing time, we consider the gap model approach as the most suitable one for this study.

In our study we could break through the circularity between the causes and effects of vegetation dynamics (Huntley et al., 1995), since we had available input data which was sampled largely independently from the comparison data. The precipitation scenario was partly derived from other pollen records, but corrected with physical data (Guiot et al., 1993). The temperature scenario, reconstructed from aquatics, cladocera and oxygen isotopes in lake sediments is completely independent from pollen data. Compared, e.g. with GCM derived Holocene climate scenarios, the used scenarios offered the advantage of a higher spatial and, in the case of temperature, also higher temporal resolution. In contrast to other studies (Fischlin et al., 1995b; Lischke et al., 1998a; Lotter and Kienast, 1992; Solomon et al., 1981), the immigration dates were not inferred from the comparison pollen record itself, but from a sequence of pollen maps. Of course, such maps only indicate that a species appears at a specific area at a certain time.

Our approach to add successively different input scenarios for the simulations not only allowed us to discover a combination of plausible input scenarios that reproduced the data rather well, but also to disentangle the processes leading to the pattern of the pollen record, which would not have been possible with either paleo data or simulations alone.

Even with the uncertainties inherent in the input scenarios and the model, we can assess how vegetation at Soppensee might have developed, namely by a combination of climate effects, local biotic processes, and immigration.

During the late Würm many of the absent taxa were not impeded by climate as defined by the baseline scenario. The sensitivity tests indicated that winter temperatures would have had to be considerably lower to exclude in particular *Quercus* and *Abies*. These species' absence can be due to late immigration as indicated by pollen maps or to a not completed pedogenesis (Pennington,

1995). *Pinus* and *Betula*, the taxa found in that period in the pollen record, are pioneering species with respect to soil quality (Mayer, 1984).

During Younger Dryas and Holocene, a major part of the vegetation pattern at the study site appeared to be determined by climate. Note, that some taxa, e.g. *Picea* were excluded by drought during the entire period. Temperature was particularly important: the biggest increase in agreement between pollen data and simulation (Table 2) occurred when the temperature scenario was introduced. This agrees well with the results of Solomon et al. (1981) and Prentice et al. (1991) for Eastern North America. In a similar simulation study at the Lago di Annone in Northern Italy (Keller et al., 2002), climate had a only a minor direct influence. Although only about 200 km away, this site has mean yearly temperatures, which are about 4 °C higher, and thus would have allowed also during the cooler periods for the existence of many species.

The relationship between climate and the occurrence of a species depends on the biotic environment, since climate affects a species not only directly through climate dependent processes, such as establishment, growth, and death, but also indirectly through changing competition. The simulations with and without competition suggest that the development of the Holocene vegetation was, to a large extent, determined by the outcome of interspecific competition as corroborated by Bennett and Lamb (1988) and only to a smaller extent by the direct effects of climatic changes.

Vegetation was in equilibrium with climate during most of the studied period (Fig. 3g and j). However, rapid changes of climate (such as at the end of Younger Dryas) or of the set of dominant species (such as at the arrival of *Abies* and *Fagus*) triggered a secondary succession, which required several centuries before equilibrium was reached again (Prentice, 1986).

Migration played a dominant role, as also found for North America (Davis, 1981; Davis et al., 1986) and in the study at the Lago di Annone (Keller et al., 2002). In particular, *Abies* and *Fagus* arrived later at the study site than the climatic conditions would have allowed. Similar to climatic change, immigration had a strong influence on competition (Bennett and Lamb, 1988); after the appearance of *Abies* and *Fagus* in the pollen data as well as in the simulation results (Fig. 3a and g), the relative abundances of less dominant taxa, such as *Pinus*, *Ulmus*, and *Quercus* declined strongly.

Although the obtained results can explain the vegetation dynamics only at the study site, the simulations allow some conjectures about what happened also along the migrational paths and thereby about what controls migration.

It is unlikely that migration of the delayed taxa *Abies*, *Fagus*, and *Quercus* was slowed down by unfavorable climate conditions, if the landscape between refugia and study area was homogenous and flat. In this case, temperature would have increased between the study area and the glacial refuge. This implies, that if temperature was high enough for a species at the study area (such as for *Abies* from 11 000 cal. BP on), it was also high enough on the way between the glacial refuge and the study area. This was probably the case for subpopulations migrating around the Alps. Their speed was limited by the species' intrinsic maximum migration rate. Competition probably played a minor role, at least for the dominant taxa *Abies* and *Fagus*.

In a complex topography such as Southern and Central Europe, however, temperature gradients were not monotonous; mountain ranges such as the Alps were not only topographic barriers for the transport of seeds, but represented also an additional steep temperature gradient which forced the tree species either to wait until the temperatures were favorable enough to pass the mountains, or to migrate along the longer way around them.

This is demonstrated by a comparison with the study at the Lago di Annone (Keller et al., 2002) which is situated in Northern Italy, at the southern slope of the Alps. It shows that *Abies alba* and *Fagus silvatica* had appeared there about 1800 (400) years earlier than at Soppensee. The glacial refuges of both species were in the mountains of Southern Italy and the Southern Balkan. The pollen maps of (Lang, 1994) suggest, that the Soppensee population of *Abies* came from its refuge in Southern Italy, passed by Northern Italy

and from there either traversed the Alps or dodged them west, which explains the rather long time difference. The Soppensee population of *Fagus* probably stemmed from the Balkan refuge, whereas the Lago di Annone population either stemmed from Southern Italy or from a side branch of the Balkan population. This parallel migration explains why the two lakes were reached rather short after another.

5. Conclusions

Our non-circular simulation analysis of the late Würm/Holocene Soppensee pollen data supported findings of other studies of past vegetation adaptation.

Vegetation, as represented by tree species, responded in an individualistic manner (Davis, 1981). The temporal pattern of vegetation development at this particular site was shaped not by one general cause such as the changing climate, but by several, including biotic causes. During late Würm, delayed immigration or incomplete soil formation were most important. Later, climate controlled the general pattern of vegetation by changing directly the living conditions and by moderating the competition among the species.

Hence, adaptation of the vegetation around Soppensee to climatic change consisted of a combination
- of successional changes at the time scale of several centuries after rapid changes in the boundary conditions, such as the climate change at the end of Younger Dryas, or the immigration of dominant species,
- of equilibrium shifts with slowly changing climate,
- and of tree species immigration.

Our results thus corroborate the conclusions of Huntley (1990), Huntley and Webb (1989) that climatic change is the major factor driving the compositional change of vegetation on the time-scale of millennia, whereas during faster changes such as the one at the end of the last glaciation, succession and migration can also play an important role.

An analogous situation could occur during the comparably fast present and expected future climatic change. Particularly migration might be important, if species which are better adapted to the new conditions are blocked behind geographical barriers or otherwise impeded by adverse conditions along the migrational path. In the Alps, e.g. it might be that some drought adapted species, which are already present in the insubrian zone (Kloetzli et al., 1996), could not cross the Central Alps in time. Unless assisted by man, this could lead to intermediary forest decline, especially due to drought stress at some presently already warm and dry sites. For example, in the valley of the river Rhône (Valais), as demonstrated by several simulation studies on the sensitivity of the forests to various climatic change scenarios (Brzeziecki et al., 1995; Fischlin and Gyalistras, 1997; Lischke et al., 1998a).

For a better understanding and projection, also migration as reflected by sequences of pollen maps, should be reduced to constant and time-dependent processes. To this aim, forest dynamics coupled with seed production and transport should be simulated in entire regions or along potential migrational paths and compared with several pollen records. First simple migration models have been developed (Chave, 1999; Collingham et al., 1996; Easterling et al., 2001). However, these models are either confined to a few species (Collingham et al., 1996; Jesse, 1999) or to relatively small regions (Chave, 1999; Easterling et al., 2001) or their description of the dispersal is rather rule-based than mechanistic (He et al., 1999). The presented local study shows the potential of patch models such as FORCLIM or its much faster distribution-based version DISC-FORM (Lischke et al., 1998b) for more realistic migration studies, given reliable independent climate input data.

T. Löffler for his valuable comments and suggestions and to B. Roy for her corrections not only of the English.

References

Ammann, B., Lotter, A.F., Eicher, U., Gaillard, M.J., Wohlfarth, B., Haeberli, W., Lister, G., Maisch, M., Niessen, G., Schlüchter, C., 1994. The Würmian Late-glacial in lowland Switzerland. J. Quaternary Sci. 9 (2), 119–125.

Ammann, B., Gaillard, M.-J., Lotter, A.F., 1996. Switzerland. In: Berglund, B.E., Birks, H.J.B., Ralska-Jasiewiczowaand, M., Wright, H.E. (Eds.), Palaeoecological Events during the last 15 000 years: Regional Syntheses of Palaeoecological Studies of Lakes and Mires in Europe. Wiley, Chichester, UK, pp. 647–666.

Andersen, S.T., 1970. The relative pollen productivity and pollen representativity of North European trees and correction factors for tree pollen spectra. Danm. Geol. Unders. Ser. II 96, 1–99.

Atkinson, T.C., Briffa, K.R., Coope, G.R., 1987. Seasonal temperatures in Britain during past 22 000 years, reconstructed using beetle remains. Nature (London) 325, 587–592.

Badeck, F.W., Lischke, H., Bugmann, H., Hickler, T., Hönninger, K., Lasch, P., Lexer, M.J., Mouillot, F., Schaber, S., Smith, B., 2001. Tree species composition in European pristine forests. Comparison of stand data to model predictions. Climatic Change 51 (3/4), 307–347.

Bennett, K.D., Lamb, H.F., 1988. Holocene pollen sequences as a record of competitive interactions among tree populations. Trends Ecol. Evol. 3 (6), 141–145.

Birks, H.J.B., 1986. Late-quaternary biotic changes in terrestrial and lacustrine environments, with particular reference to north-west Europe. In: Berglund, B.E. (Ed.), Handbook of Holocene Palaeoecology and Palaeohydrology. Wiley, Chichester, UK, pp. 3–65.

Birks, H.J.B., Gordon, A.D., 1985. Numerical Methods in Quaternary Pollen Analysis. Academic Press, London, UK.

Bossel, H., 1996. TREEDYN3 forest simulation model. Ecol. Model. 90 (3), 187–227.

Botkin, D.B., Janak, J.F., Wallis, J.R., 1972. Rationale, limitations and assumptions of a northeastern forest growth simulator. IBM J. Res. Dev. 16, 101–116.

Bradley, R., 1991. Global changes of the past. Office for interdisciplinary Earth Studies, University Corporation for Atmospheric Research, Boulder, Colorado, USA.

Brzeziecki, B., Kienast, F., Wildi, O., 1995. Modelling potential impacts of climate change on the spatial distribution of zonal forest communities in Switzerland. J. Veg. Sci. 6 (2), 257–268.

Bugmann, H., 1994. On the ecology of mountainous forests in a changing climate: a simulation study. Ph.D. Dissertation, No. 10638, Environmental Sciences, Swiss Federal Institute of Technology (ETHZ), Zürich, Switzerland.

Bugmann, H., 1996. A simplified forest model to study species composition along climate gradients. Ecology 77 (7), 2055–2074.

Bugmann, H., Solomon, A.M., 1995. The use of a European forest model in North America: a study of ecosystem response to climate gradients. J. Biogeogr. 22, 477–484.

Bugmann, H., Fischlin, A., Kienast, F., 1996. Model convergence and state variable update in forest gap models. Ecol. Model. 89, 197–208.

Burga, C.A., 1988. Swiss vegetation history during the last 18 000 years. New Phytol. 110, 581–602.

Burga, C.A., Perret, R., 1998. Vegetation und Klima der Schweiz seit dem jüngeren Eiszeitalter. Ott Verlag, Thun, Switzerland.

Chave, J., 1999. Study of structural, successional and spatial patterns in tropical rain forests using TROLL, a spatially explicit forest model. Ecol. Model. 124, 233–254.

COHMAP Members, 1988. Climatic changes of the last 18 000 years: observations and model simulations. Science 241, 1043–1052.

Collingham, Y.C., Hill, M.O., Huntley, B., 1996. The migration of sessile organisms: a simulation model with measurable parameters. J. Veg. Sci. 7 (6), 831–846.

Cormack, R.M., 1971. A review of classification. J. Royal Statistical Soc. 134 (3), 321–353.

Davis, M.B., 1963. On the theory of pollen analysis. Am. J. Sci. 261, 897–912.

Davis, M.B., 1981. Quaternary history and the stability of forest communities. In: West, D.C., Shugart, H.H., Botkin, D.B. (Eds.), Forest Succession: Concepts and Application. Springer, New York, Heidelberg, pp. 132–153.

Davis, M.B., 1986. Climatic instability, time lags and community disequilibrium. In: Diamond, J., Case, T. (Eds.), Community Ecology. Harper & Row Publishers Inc, Cambridge, UK, pp. 269–284.

Davis, M.B., 1989. Lags in vegetation response to greenhouse warming. Climatic Change 15, 75–82.

Davis, M.B., Woods, K.D., Webb, S.L., Futyma, R.P., 1986. Dispersal versus climate: expansion of Fagus and Tsuga into the Upper Great Lakes region. Vegetatio 67, 93–103.

Delcourt, H.R., Delcourt, P.A., 1991. Factors that structure communities: 5.1 issues. In: Quaternary Ecology—A Paleoecological Perspective. Chapman & Hall, London, UK, pp. 122–124.

Easterling, W.E., Brandle, J.R., Hays, C.J., Guo, Q., Guertin, D.S., 2001. Simulating the impact of human land use change on forest composition in the Great Plains agroecosystems with the Seedscape model. Ecol. Model. 140, 163–176.

Ellenberg, H., 1986. Vegetation Mitteleuropas mit den Alpen in ökologischer Sicht. Eugen Ulmer Verlag.

Faegri, K., Iversen, J., 1975. Textbook of Pollen Analysis. Munksgaard, Copenhagen, Denmark.

Fischlin, A., 1991. Interactive modeling and simulation of environmental systems on workstations. In: Möller, D.P.F., Richter, O. (Eds.), Analyse dynamischer Systeme in Medizin, Biologie und Ökologie, vol. 275. Springer, Berlin, Heidelberg.

Fischlin, A., Gyalistras, D., 1997. Assessing impacts of climatic change on forests in the Alps. Global Ecol. Biogeogr. Lett. 6, 19–37.

Fischlin, A., Bugmann, H., Gyalistras, D., 1995a. Sensitivity of a forest ecosystem model to climate parametrization schemes. Environ. Pollut. 87 (3), 267–282.

Fischlin, A., Lischke, H., Bugmann, H., 1995b. The fate of forests in a changing climate: model validation and simulation results from the Alps, Systems Ecology, Swiss Federal Institute of Technology, Zurich, no. 25, p. 18.

Foley, J.A., 1994. Net primary productivity in the terrestrial bioshpere: the application of a global model. J. Geophys. Res. 99 (D10), 20773–20783.

Gliemeroth, A.K., 1995. Paläoökologische Untersuchungen über die letzten 22 000 Jahre in Europa.

Grote, R., 1998. Integrating dynamic morphological properties into forest growth modelling: II. Allocation and mortality. For. Ecol. Manage. 111, 193–210.

Guiot, J., Harrison, S.P., Prentice, I.C., 1993. Reconstruction of Holocene precipitation patterns in Europe using pollen and lake-level data. Quarter. Res. 40, 139–149.

Hajdas, I., Ivy, S.D., Beer, J., Bonani, G., Imboden, D., Lotter, A.F., Sturm, M., Suter, M., 1993. AMS radiocarbon dating and varve chronology of lake Soppensee: 6000 to 12 000 14C years BP. Climate Dyn. 9, 107–116.

He, H.S., Mladenoff, D.J., Crow, T.R., 1999. Linking an ecosystem model and a landscape model to study forest species response to climate warming. Ecol. Model. 114, 213–233.

Huntley, B., 1990. European post-glacial forests: compositional changes in response to climatic change. J. Veget. Sci. 1, 507–518.

Huntley, B., Birks, H.J.B., 1983. An Atlas of Past and Present Pollen Maps for Europe: 0–13 000 Years Ago. Cambridge University Press, Cambridge, UK.

Huntley, B., Webb, T. III, 1989. Migration: species' response to climatic variations caused by changes in the earth's orbit. J. Biogeogr. 16, 5–19.

Huntley, B., Prentice, I.C., 1993. Holocene vegetation and climates of Europe. In: Wright, H.E.J., Kutzbach, J.E., Webb, T. III, Ruddiman, W.F., Street-Perrottand, F.A., Bartlein, P.J. (Eds.), Global Climates Since the Last Glacial Maximum. University of Minnesota Press, Minneapolis, USA, pp. 136–168.

Huntley, B., Bartlein, P.J., Prentice, I.C., 1989. Climatic control of the distribution and abundance of beech (Fagus) in Europe and North America. J. Biogeogr. 16, 551–560.

Huntley, B., Cramer, W., Morgan, A.V., Prentice, H.C., Alien, J.R.M., 1995. Predicting the response of terrestrial biota to future environmental changes. In: Huntley, B., Cramer, W., Morgan, A.V., Prentice, H.C., Alien, J.R.M. (Eds.), Past and Future Rapid Environmental Changes: The Spatial and Evolutionary Responses of Terrestrial Biota, vol. 16. Springer, Berlin, Germany, pp. 561–566.

Jesse, K.J., 1999. Modelling of a diffusive Lotka-Volterra-System: the climate-induced shifting of tundra and forest realms in North-America. Ecol. Model. 123, 53–64.

Keller, F., Lischke, H., Mathis, T., Moehl, A., Wick, L., Ammann, B., Kienast, F., 2002. Effects of climate, fire, and humans on forest dynamics: forest simulations compared to the palaeological record. Ecol. Model., in press.

Kienast, F., 1987. FORECE—A forest succession model for southern central Europe, No. ORNL/TM-10575, Oak Ridge National Laboratories, Oak Ridge, Tennessee, USA, p. 69.

Kirschbaum, M.A.F.A., 1996. Climate change impacts on forests. In: Watson, R. (Ed.), Climate change 1995—Impacts, Adaptations and Mitigation of Climate Change: Scientific-Technical Analyses: Contribution of Working Group II to the Second Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK, pp. 95–131.

Kloetzli, F., Walther, G.R., Carraro, G., Grundmann, A., 1996. Anlaufender Biomwandel in Insubrien. Verhandlungen der Gesellschaft für Ökologie (Bremen, Germany) 26, 537–550.

Kutzbach, J.E., Guetter, P.J., 1988. The influence of changing orbital parameters and surface boundary conditions on climate simulations for the past 18 000 years. J. Atmospheric Sci. 43 (16), 1726–1759.

Landolt, E., 1977. Ökologische Zeigerwerte zur Schweizer Flora. Veröff. Geobot. Inst. ETH Zürich 64, 5–208.

Lang, G., 1985. Swiss lake and mire environments during the last 15000 years. J. Cramer, Vaduz, Liechtenstein.

Lang, G., 1994. Quartare Vegetationsgeschichte Europas: Methoden und Ergebnisse. Gustav Fischer, Jena, Germany.

Lischke, H., 2001. New developments in forest modeling: convergence between applied and theoretical approaches. Nat. Resour. Model. 14 (1), 71–102.

Lischke, H., Guisan, A., Fischlin, A., Williams, J., Bugmann, H., 1998a. Vegetation responses to climate change in the Alps—modeling studies. In: Cebon, P., Dahinden, U., Davies, H., Imboden, D., Jaeger, C. (Eds.), A view from the Alps: Regional Perspectives on Climate Change. MIT Press, Boston, USA, pp. 309–350.

Lischke, H., Löffler, T.J., Fischlin, A., 1998b. Aggregation of individual trees and patches in forest succession models—capturing variability with height structured random dispersions. Theoretical Population Biol. 54, 213–226.

Lister, G.S., 1989. Reconstruction of palaeo air temperature changes from oxygen records in Lake Zürich: the significance of seasonality. Ecologiae Geologicae Helveticae 82 (1), 219–234.

Livingstone, D.M., Lotter, A.F., 1998. The relationship between air and water temperatures in lakes on the Swiss Plateau: a case study with palaeolimnological implications. J. Palaeolimnol. 19, 181–198.

Lotter, A.F., 1989. Evidence of annual layering in Holocene sediments of Soppensee, Switzerland. Aquatic Sci. 51, 1.

Lotter, A.F., 1991. Absolute dating of the late-glacial period in Switzerland using annually laminated sediments. Quaternary Res. 35, 321–330.

Lotter, A.F., 1999. Late-glacial and Holocene vegetation history and dynamics as evidenced by pollen and plant macrofossil analyses in annually laminated sediments from Soppensee (Central Switzerland). Veget. History Achaeobot. 8, 165–184.

Lotter, A.F., Kienast, F., 1992. Validation of a forest succession model by means of annually laminated sediments. Geol. Sur. Finland (Special Paper) 14, 25–31.

Lotter, A.F., Birks, H.J.B., Eicher, U., Hofmann, W.S.J., Wick, L., 2000. Younger Dryas and Allerod summer temperatures at Gerzensee (Switzerland) inferred from fossil pollen and cladoceran assemblages. Palaeogeogr. Palaeoclimatol. Palaeoecol. 159, 349–361.

Lüdecke, M.K.B., Badeck, F.-W., Otto, R.D., Häger, C., Dönges, S., Kindermann, J., Würth, G., Lang, T., Jäkel, U., Klaudius, A., Ramge, P., Habermehl, S., Kohlmaier, G.H., 1994. The Frankfurt Biosphere Model: a global process-oriented model of seasonal and long-term CO_2 exchange between terrestrial ecosystems and the atmosphere. I. Model description and illustrative results for cold deciduous and boreal forests. Clin. Res. 4, 143–166.

Lyr, H., Fiedler, H.-J., Tranquillini, W., 1992. Physiologic und Ökologie der Gehölze. Gustav Fischer Verlag, Jena, Stuttgart.

Mayer, H., 1984. Waldbau. Gustav Fischer, Stuttgart.

Melillo, J.M., McGuire, A.D., Kicklighter, D.W., Moore, B. III, Vorosmarty, C.J., Schloss, A.L., 1993. Global climate change and terrestrial net primary production. Nature 363, 234–240.

Pacala, S.W., Deutschman, D.H., 1995. Details that matter: the spatial distribution of individual trees maintains forest ecosystem function. OIKOS 74, 357–365.

Pacala, S.W., Canham, C.D., Saponara, J., Silander, J.A., Kobe, R.K., Ribbens, E., 1996. Forest models defined by field measurements: estimation, error analysis and dynamics. Ecol. Monogr. 66 (1), 1–43.

Pennington, W., 1995. Lags in adjustment of vegetation to climate caused by the pace of soil development: evidence from Britain. Vegetatio 67, 105–118.

Potter, C.S., Randerson, J.T., Field, C.B., Matson, P.A., Vitousek, P.M., Mooney, H.A., Klooster, S.A., 1993. Terrestrial ecosystem production: a process model based on global satellite and surface data. Global Biogeochem. Cycles 7 (4), 811–841.

Prentice, I.C., 1986. Vegetation responses to past climatic variation. Vegetatio 67, 131–141.

Prentice, I.C., 1988. Records of vegetation in time and space: the principles of pollen analysis. In: Huntley, B., Webb, T. III (Eds.), Vegetation History. Kluwer, The Hague.

Prentice, I.C., Bartlein, P.J., Webb, T., 1991. Vegetation and climate change in eastern North America since the last glacial maximum. Ecology 72 (6), 2038–2056.

Roberts, L., 1989. How fast can trees migrate? Science 243, 735–737.

Running, S.W., Gower, S.T., 1991. FOREST-BGC, A general model of forest ecosystem processes for regional applications. II. Dynamic carbon allocation and nitrogen budgets. Tree Physiol. 9, 147–160.

Shugart, H.H., 1984. A Theory of Forest Dynamics. The Ecological Implications of Forest Succession Models. Springer, New York, USA.

SMA, 1901–1990. Schweizerische Meteorologische Anstalt (SMA), Zurich, Switzerland.

Solomon, A., Bartlein, P.J., 1992. Past and future climate change: response by mixed deciduous–coniferous forest ecosystems in northern Michigan. Can. J. Forest Res. 22, 1727–1738.

Solomon, A.M., West, D.C., Solomon, J.A., 1981. Simulating the role of climate change and species immigration in forest succession. In: West, D.C., Shugart, H.H., Botkin, D.B. (Eds.), Forest Succession: Concepts and Application. Springer, New York, USA, pp. 154–177.

Stuiver, M., Reimer, P.J., 1993. Extended 14C data base and revised CALIB 3.0 14C age calibration program. Radiocarbon 35, 215–230.

Sugita, S., 1994. Pollen representation of vegetation in quaternary sediments: theory and method in patchy vegetation. J. Ecol. 82 (4), 881–897.

Thöny, J., Fischlin, A., Gyalistras, D., 1994. RASS: towards bridging the gap between interactive and off-line simulation. In: Halin, J., Karplusand, W., Rimane, R. (Eds.), The Society for Computer Simulation International, P.O. Box 17900, San Diego, CA 92177, USA, pp. 99–103.

Wolda, H., 1981. Similarity indices, sample size and diversity. Oecologia 50, 296–302.