

Central European vegetation response to abrupt climate change at 8.2 ka

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ABSTRACT

Oxygen isotope records show a major climatic reversal at 8.2 ka in Greenland and Europe. Annually laminated sediments from two lakes in Switzerland and Germany were sampled contiguously to assess the response of European vegetation to climate change ca. 8.2 ka with time resolution and precision comparable to those of the Greenland ice cores. The pollen assemblages show pronounced and immediate responses (0–20 yr) of terrestrial vegetation to the climatic change at 8.2 ka. A sudden collapse of *Corylus avellana* (hazel) was accompanied by the rapid expansion of *Pinus* (pine), *Betula* (birch), and *Tilia* (linden), and by the invasion of *Fagus silvatica* (beech) and *Abies alba* (fir). Vegetational changes suggest that climatic cooling reduced drought stress, allowing more drought-sensitive and taller growing species to out-compete *Corylus avellana* by forming denser forest canopies. Climate cooling at 8.2 ka and the immediate reorganization of terrestrial ecosystems has gone unrecognized by previous pollen studies. On the basis of our data we conclude that the early Holocene high abundance of *C. avellana* in Europe was climatically caused, and we question the conventional opinion that postglacial expansions of *F. silvatica* and *A. alba* were controlled by low migration rates rather than by climate. The close connection between climatic change and vegetational response at a subcontinental scale implies that forecasted global warming may trigger rapid collapses, expansions, and invasions of tree species.

Keywords: varves, paleoclimate, pollen analysis, paleoecology, Holocene.

INTRODUCTION

On a global scale vegetational distribution and character mainly depend on climate. If the climate changes, plants are likely to respond rapidly according to their specific physiological potentials and limits. This applies if the amplitude of the climatic change exceeds the tolerance of the species, causing high mortality by frost, drought, or other fatal damages. In cases where the climatic impact does not surpass the physiological limits, however, the response of the vegetation to climate also depends on interspecific competition and interference. Moreover, some species better adapted to the new situation may be absent because of physical barriers or insufficient rates of spread. The result is a high complexity of the climate-driven vegetational dynamics. The difficulty in understanding this complexity is the main reason for contrasting opinions (Davis, 1984; Prentice et al., 1991; Peteet, 2000) and a growing controversy (Kullman, 1998) about how fast vegetation responded to climatic changes during the Holocene. Estimates range from decades to millennia, depending on the explaining model. The controversy centers on whether vegetation is in disequilibrium

(different rates of spread and physical barriers causing migrational lags; soil, competition, and microclimate effects delaying establishment and expansion) or in dynamic equilibrium with climate (Prentice et al., 1991). In this study we compare paleovegetational and independent paleoclimatic data, in order to test which model applies for the climatic reversal at 8.2 ka. Our analysis is based on two sites in central Europe that, in contrast to previous paleoecological studies, have time resolution and precision comparable to those of the Greenland paleoclimatic records (Dansgaard et al., 1993; Grootes et al., 1993; O'Brien et al., 1995). We address the rapidity and the nature of vegetation response to climatic change, showing the predominant role of life histories and physiological characteristics of species in driving interspecific competition dynamics on a subcontinental scale.

SEDIMENT AND CHRONOLOGY

The sediment cores analyzed for pollen in this study were taken from Soppensee (8°05'E, 47°05'N, 596 m above sea level [a.s.l.]) and Schleinsee (9°39'E, 47°37'N, 474 m a.s.l., 140 km apart), two small lakes in central Switzerland and southern Germany, respectively (Fig. 1). The analyses of pollen percentages and pollen accumulation rates at Soppensee gave

comparable results for all taxa, showing that percentage values are not affected by proportional problems (Lotter, 1999). Large sections of the sediments of both lakes are annually laminated (Clark et al., 1989; Lotter, 1989, 1999). The chronology of both lake records was established through varve counts on petrographic thin sections of epoxy-impregnated sediment (Lotter and Lemcke, 1999). Both floating varve chronologies were anchored at the Vasset-Killian Tephra layer, which was accelerator mass spectrometry radiocarbon dated to 8230 ± 140 ^{14}C yr B.P. According to the Soppensee varve chronology, this corresponds to 9407 ± 44 yr ago (Hajdas et al., 1993).

POLLEN STRATIGRAPHY AND VEGETATION HISTORY

Pollen records at Soppensee and Schleinsee show abrupt changes ca. 8.2 ka. The most prominent among them is the marked decrease of *Corylus* within <150 yr, from ~30% to 13% and 40% to 16% at Soppensee and Schleinsee, respectively (Fig. 2). Although the *Corylus* percentages show minor fluctuations before and after 8.2 ka (Clark et al., 1989; Lotter, 1999), the magnitude and the rapidity of the decline at 8.2 ka have no equivalents during the entire Holocene. Thereafter the *Corylus* values increased again, but did not reach the high level characteristic for the period before 8.2 ka. This collapse in *Corylus* was not restricted to Switzerland and southern

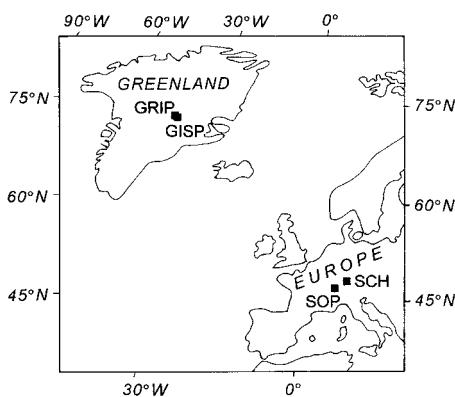
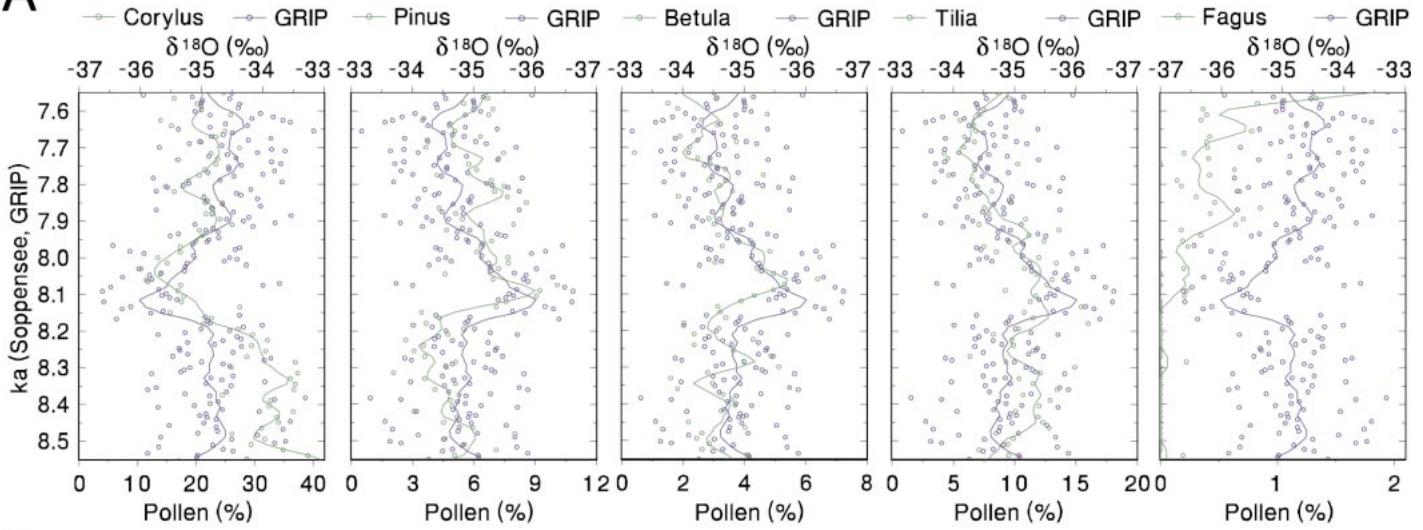


Figure 1. Location of Soppensee (SOP), Schleinsee (SCH), and Greenland ice cores. GRIP, European Greenland ice-core project; GISP, U.S. Greenland Ice Sheet Project 2.

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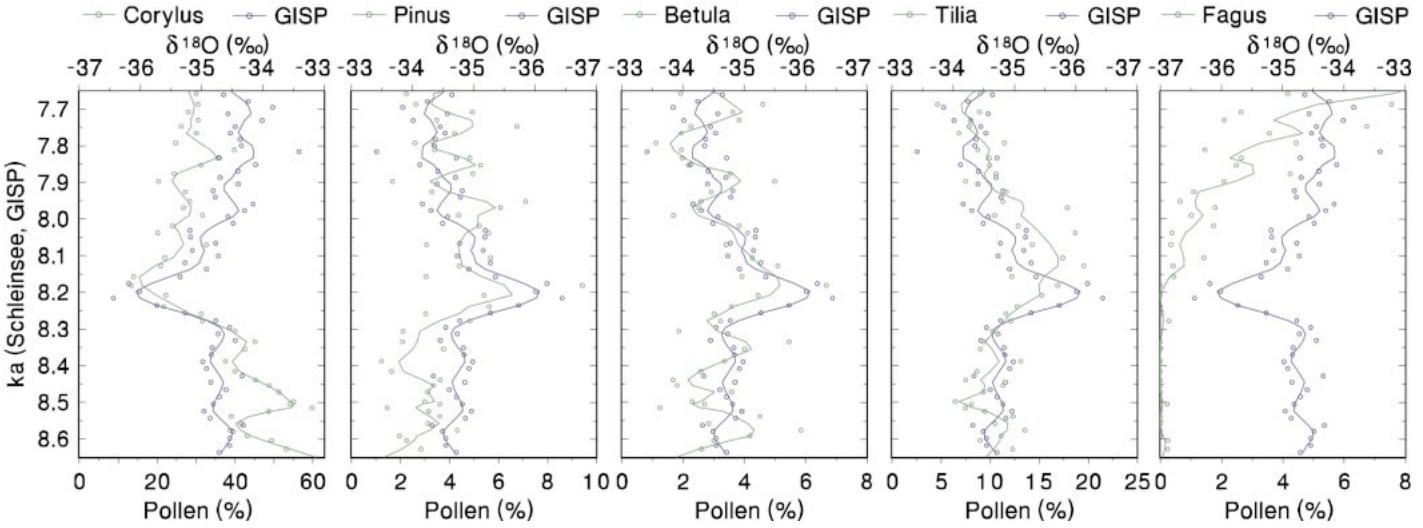


Figure 2. Selected pollen types from (A) Soppensee (Switzerland) and (B) Schleinsee (Germany), and oxygen isotopes from Greenland. Pollen percentages are compared with records of $\delta^{18}\text{O}$ from Greenland ice. GRIP, European Greenland ice-core project; GISP, U.S. Greenland Ice Sheet Project 2. Mean temporal sample resolution is 15.0 yr for Soppensee, 22.4 yr for Schleinsee, 5.3 yr for GRIP, and 18.3 yr for GISP data. For better comparison of common trends, pollen and oxygen isotope data were lowess smoothed (tension 10%). Oxygen isotope curves were inverted for matching with *Pinus*, *Betula*, and *Tilia*. Chronologies for pollen records were assessed by varve counts and correlated with Greenland oxygen isotope records according to their absolute ages.

Germany. A comparable, still unexplained *Corylus* decline at 8.2 ka is also documented in the pollen diagrams of Lake Gosciaz (Ralska-Jasiewiczowa et al., 1998), another locality with varved sediments and hence highly reliable chronology in central Poland, ~1000 km north east of Soppensee. At Soppensee and Schleinsee (Fig. 2), the *Corylus* decline was accompanied by sudden increases of *Pinus* and *Betula*. Other increasing pollen types were *Tilia* (Fig. 2), as well as—but less pronounced—*Fraxinus excelsior* (ash), *Quercus* (oak), *Ulmus* (elm) and *Alnus* (alder) (Clark et al., 1989; Lotter, 1999). The time ca. 8.2 ka was not only characterized by strong pollen oscillations, but also by the appearance of pre-

viously absent or very rare taxa (i.e., *Fagus* and *Abies*).

The pollen data suggest the presence of open, light-demanding continental woodlands with *Corylus* as a small canopy tree or an understory shrub prior to 8.2 ka. These communities were replaced by closed and more oceanic woodlands after 8.2 ka. *Tilia* was the dominant tree during the period from 8.6 to 7.6 ka. It was probably growing on the slopes around the lakes together with *Ulmus*, *Quercus*, and *Acer*. On the moister soils of the valley bottoms *Fraxinus*, *Ulmus*, and *Alnus* likely replaced *Tilia* and *Quercus* (Lotter, 1999). While the increases of *Pinus*, *Betula*, and *Tilia* were only temporary (Fig. 2), the collapse of

Corylus and the expansion of *Fagus* marked the onset of the development of modern central European vegetation, leading over millennia to the present characteristically beech-dominated forests.

CLIMATE CHANGE AND VEGETATION RESPONSE

Climatic cooling at 8.2 ka, as recorded by Greenland ice cores (Dansgaard et al., 1993; Grootes et al., 1993; O'Brien et al., 1995) and European lake sediments (Von Grafenstein et al., 1998), occurred on a northern hemispherical or even global scale. However, despite the wealth of paleobotanical and geomorphological data for Holocene timberline and glacier

oscillations (Wick and Tinner, 1997), no unambiguous evidence of vegetation response to the 8.2 ka event has as yet been reported from central European lowland pollen records. The isotope data suggest a climate cooling of ~ 2.8 °C in Greenland and 1.7 °C in mean annual air temperature in central Europe (Von Grafenstein et al., 1998). Given the chronological reliability and sampling time resolution in the lacustrine varved sequences from central Europe, it is possible to compare the pollen data from Soppensee and Schleinsee with the Greenland oxygen-isotope records. If the oxygen data from GRIP and GISP2 are compared according to their stratigraphic variations, a chronological ambiguity of ~ 100 yr is found between the two sites (Fig. 2). Soppensee and Schleinsee show a similar chronological shift (Fig. 2). Taking into account the dating uncertainties such as varve counting errors and especially radiometric dating errors for the Vasset-Killian Tephra, the chronologies of the two lacustrine records are comparable within a discrepancy range of ~ 50 yr. In Figure 2 the central European pollen and the Greenland isotope records were matched on the basis of their respective chronologies. With regard to the variations of pollen and oxygen isotopes, it is striking that Soppensee fits chronologically with the GRIP (European Greenland Ice-core Project) and Schleinsee with the GISP (U.S. Greenland Ice Sheet Project) oxygen isotope record (Fig. 2). This can only be due to similar coincidental errors in the Greenland and in the varve chronologies. However, Figure 2 shows that the average age of the 8.2 ka event is the same for both the Greenland and the central European records (8175 ± 45 yr ago).

It is striking that the adjustment of vegetation to both the rapid climatic cooling and the subsequent warming occurred without any substantial time lag or with a delay of only a few decades. *Corylus* responded to the climatic cooling at 8.2 ka within the sample resolution of 0–20 yr at Schleinsee, whereas the response was more complex and to a certain degree delayed at Soppensee. *Pinus* and *Betula* show a lagged response of 0–20 and 20–40 yr, respectively (Fig. 2). Similar delays shorter than 20 yr in vegetational response to climatic change have also been noticed for the Younger Dryas—Preboreal transition (Lotter et al., 1992; Ammann et al., 2000). The response of *Tilia* to both climatic cooling and rewarming was delayed at Schleinsee, but not at Soppensee (Fig. 2). At both sites the expansion of *Fagus* followed the climatic change so rapidly (within <20 yr) that a few *Fagus* individuals (single pollen grains found, Fig. 2) must have already been present in isolated favorable microhabitats with moist soil

and air conditions. This implies that the relatively late expansion of *Fagus* in central Europe was not primarily a consequence of a migrational lag, as conventionally suggested (see Lang, 1994). It is more likely that it was due to unsuitable climatic conditions (see also Huntley et al., 1989).

A minimum of winter solar radiation and a maximum of summer solar radiation in the Northern Hemisphere ca. 9 ka (Kutzbach and Webb, 1993) resulted in a greater seasonal contrast than today, with a prevalence of hot summers and cold winters. In the northern mid-latitudes evaporation was at a maximum and therefore moisture availability (precipitation minus evaporation) was at a minimum (Kutzbach and Webb, 1993). Furthermore, a strong negative precipitation anomaly occurred in our study area (<-400 mm annual precipitation in comparison to today; Guiot et al., 1993), so that plant species were most likely exposed to severe and prolonged drought stress. Considering the hotter and drier summers, climatic conditions were comparable to continental sites (annual average temperature 10 °C, precipitation <500 – 700 mm), where central European tree species are at their physiological drought limits (Lischke et al., 1998). It is likely that this inhibited the expansion of *Abies alba* and *Fagus silvatica*, because both species have high air and soil-moisture requirements and are extremely sensitive to late frost in spring. *Corylus avellana*, however, would have been favored, because it is considered to be more tolerant of seasonal drought than other arboreal species of central Europe (Huntley, 1993).

The high early Holocene abundance of *Corylus* is one of the most striking enigmas of northwestern and central European vegetational history. In today's succession the short-statured *Corylus avellana* is normally overtopped and hence replaced by higher growing trees within 100 yr (Huntley, 1993). During the early Holocene, however, *Corylus* was able to maintain considerable population densities for several millennia, as suggested by its high pollen values. Evidently, the higher growing canopy trees were not able to out-compete *Corylus*. The existing hypotheses have recently been reassessed and grouped into six categories (Huntley, 1993). The correlation over hundreds of years between *Corylus* pollen values and oxygen isotopes (Fig. 2) provides direct evidence that the early Holocene abundance of *Corylus* was caused by climatic conditions rather than other factors, such as human assistance and fire, which may have played a secondary or marginal role. After the *Corylus* collapse, even minor fluctuations in the oxygen isotope curves from Greenland are generally faithfully accompanied by *Corylus*

(Fig. 2). Moreover, our charcoal data are convincingly correlated with neither the oxygen isotope nor the pollen data. The simplest explanation for a correlation between *Corylus* pollen and oxygen isotopes would be that cold temperatures affected *Corylus*. This, however, is unlikely, because the range of the climatic change did not exceed the climatic tolerance of *Corylus avellana*, which is of less, or comparable, sensitivity to colder winters and cooler summers than the other thermophilous tree species (Huntley, 1993; Fassl, 1996).

If *Corylus* did not decline due to climatic change directly, its decrease might be related to a shift in interspecific competition. Dry weather conditions with enduring drought stress are characterized by increased mortality (Asthäler, 1984; Peterken and Mountford, 1996), a (continual) reduction of radial and height growth, as well as by foliage loss (Piggott and Pigott, 1993), and hence crown thinness of the affected tree species. We hypothesize that before 8.2 ka, when seasonal drought was frequent, *Corylus*, which is often abundant in early stages of primary and secondary successions, filled the canopy gaps created by the succumbed trees. Moreover, the light-demanding and short-grown *Corylus* was favored by the crown thinning and the growth reduction of the concurrent tree species. Mediterranean sites with severe and prolonged droughts may be used as a seasonal-drought analogue for the early Holocene situation. Vegetational transects show that *Corylus avellana* is still able to grow normally under severe drought stress, whereas *Tilia cordata*, one of the most drought-resistant trees of non-Mediterranean Europe (Asthäler, 1984), was not observed to grow higher than 0.4–0.5 m, although the individuals were 20 yr and older (Piggott and Pigott, 1993).

At 8.2 ka, when temperatures decreased by ~ 1.5 – 2 °C over Europe for decades, drought stress decreased. This favored all taller growing and longer lived tree species and allowed the formation of dense and more shaded stands, in which *Corylus* was rapidly outcompeted. The temporary expansion of the low-temperature adapted *Betula* and *Pinus* (Fig. 2) might be directly related to climatic cooling, but their contribution to the displacement of *Corylus* was not significant. Although both species can grow higher than *Corylus*, their capacity to form dense and shaded stands is very small, so that *Corylus* could have survived as an understory shrub. It is more likely that the replacement of the shade-intolerant *Corylus* was driven by the temporary expansion of *Tilia* and other thermophilous trees (*Quercus*, *Ulmus*, *Fraxinus excelsior*) (Clark et al., 1989; Lotter, 1999), as well as by the invasions of *Fagus silvatica* and *Abies alba*

(Fig. 2). *Tilia* is a taxon with high shade tolerance and capacity. Moreover, *Fagus silvatica* and *Abies alba* are the tree species with the highest shade capacity and tolerance in Europe (Ellenberg, 1986). After 8.1 ka (Fig. 2), the same successional mechanism caused a long-lasting decrease of *Tilia* and other thermophilous taxa (*Quercus*, *Ulmus*, *Fraxinus excelsior*), which were partly outcompeted by the higher growing and more shade-tolerant *Fagus silvatica* and *Abies alba*. However, the successful expansion of the latter two species suggests that after 8.2 ka climatic conditions did not return to the early Holocene mode with its frequent (summer) droughts and (spring) frosts.

Considering that an abrupt climatic change was the main determinant for the reorganization of central European vegetation ca. 8.2 ka, we suggest that global climatic change as forecasted for the next decades could force a similar development. Vegetation modeling based on general-circulation models shows drastic vegetational responses to the forecasted global climatic change within <100 yr (Lischke et al., 1998). In some simulations the dominant species collapsed within ~50 yr after temperatures increased. The most extreme responses are predicted for sites with continental dry climate in eastern Germany and Switzerland (Lindner et al., 1997; Lischke et al., 1998), where, due to an increase in drought stress, none of the central-European tree species could survive. This agrees with our finding that important drought-sensitive tree species (e.g., *Abies alba*, *Fagus silvatica*) could collapse within a few years or decades, leading to a vegetational structure comparable to the one before 8.2 ka. However, better adapted exotic trees may expand rapidly, altering forest ecosystems and hence economies, depending on their primary production. We therefore emphasize that existing models forecasting vegetational responses to climatic change should integrate dormant exotic species imported for economic or ornamental reasons and (as yet) tamed in gardens and plantations.

SUMMARY

Our data provide strong support for the dynamic equilibrium hypothesis at a subcontinental scale. The inertia of tree species to climatic change ca. 8.2 ka was remarkably small or absent. Vegetational dynamics were closely connected with climate change and can be explained by different life-history strategies and physiological tolerances of the species involved. The resulting interspecific competition patterns are of such complexity that their fully climatically driven response eluded recognition for a long time.

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