

Rapid and widespread vegetation responses to past climate change in the North Atlantic region

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ABSTRACT

Ongoing anthropogenic perturbations to the atmosphere and biosphere increase the risk of future abrupt changes in the climate system and generate concern about the ability of natural ecosystems to respond to rapid climate change. Study of past climatic events and biotic responses can inform us about potential future change. Qualitatively fast local responses of plant taxa to abrupt late glacial climate oscillations have been reported from individual records and attributed to short migration distances in areas of high topographic relief. By using quantitative time-series analyses, we show that vegetation responses to late glacial climate change around the North Atlantic were rapid and widespread and occurred in areas of differing relief. Cross-correlation analysis of 11 high-resolution lacustrine records in eastern North America and Europe indicates vegetation-response times consistently of <200 yr and often <100 yr, despite regional differences in physiography and species composition. Vegetation lags of <200 yr confirm theoretical predictions, and the apparently tight coupling between vegetation and atmosphere suggests that recent climatic trends may already have begun to affect plant population abundances and distributions.

Keywords: Younger Dryas, vegetation, pollen, Quaternary, climate effects.

INTRODUCTION

Climate influences plant abundance, distribution, and community composition, and changes in climate should affect these aspects of the vegetation with a temporal lag determined by generation time, frequency of disturbances, and propagule dispersal distances (Clark et al., 1998; Webb, 1986). If current climate trends continue or accelerate, long lags (centuries to millennia) enhance the risk of future species extinctions, but short response times (years to centuries) imply that we must manage ecosystems already responding to recent climate changes. Most long-term ecological studies do not yet extend more than a few decades, too short a time to evaluate the full spectrum of vegetational response. However, rates of regional climatic change during some late Quaternary climatic oscillations were as fast or faster than projected temperature changes for the next century (Alley, 2000; Bond et al., 1993), enabling study of biotic responses to rapid climate change (Tinner and Lotter, 2001; Birks and Ammann, 2000; Peteet, 2000). High-resolution analyses of paired pollen and climate-proxy records from individual sites have demonstrated locally fast vegetation responses (Allen et al., 1999; Ammann et al., 2000; Birks and Ammann, 2000), but there has been no quantitative and systematic analysis of terrestrial vegetation response times. Here we provide evidence for broad and rapid vegetation responses to late glacial climate change.

DATA AND ANALYSES

We assembled 11 high-resolution lake records (Table 1) from North America and Europe with both a proxy for past vegetation com-

position (pollen) and for climate ($\delta^{18}\text{O}$ or chironomids) (Birks et al., 2000; Brooks and Birks, 2001; Levesque et al., 1993, 1997; Lotter et al., 1992; Schwander et al., 2000; Wick, 2000). Site-selection criteria included a pollen record and an independent climate proxy collected from the same core, sampling resolution sufficient to resolve centennial-scale or shorter lags, good dating control, and a clear signature of the Younger Dryas event in the climate proxy. For independent climate proxies, we accepted $\delta^{18}\text{O}$ data from lake marl and summer temperature estimates derived from fossil chironomid assemblages. We assumed that both types of temperature proxies responded to external environmental change with a time lag of <10 yr (Schwander et al., 2000; Walker, 1987). Close similarities between the lacustrine $\delta^{18}\text{O}$ records and oxygen isotope variations from Greenland ice cores (Grootes et al., 1993) indicate that the lake $\delta^{18}\text{O}$ records are sensitive to temperature and responded rapidly to broad climate shifts. Each pollen record contained the grain counts for 26–100 pollen types, too many variables for efficient time-series analysis; so, to summarize the primary patterns of variance in the pollen data, we performed principal components analysis (PCA) for each record (Davis, 1996) and retained the first three principal components for further analysis¹.

Cross-correlation analysis measures the correspondence and phase relationship between two time series across their entire temporal range of overlap, rather than evaluating vegetational response times to individual climatic events. We defined vegetation response times as the temporal lags corresponding to significant cross-correlations between the pollen and climate records. We separately prewhitened each principal component and climate-proxy time series (Wei, 1990) to ensure that each time series was stationary (invariant mean and variance for all time intervals) and without significant autocorrelations or partial autocorrelations. Prewhitening the data to meet these stringent criteria ensures that cross-correlation identification is strictly limited to the time scales of interest (decades to centuries) and not inflated by longer amplitude climatic controls.

Cross-correlation analysis also requires that time-series observations be evenly spaced, or nearly so, a condition violated by most geologic records. Altering the original data to even the spacing either results in artificially high correlations, if samples are added by interpolation, or unnecessary loss of data and resolution, if samples are dropped from more densely sampled sections. We instead calculated a geostatistical approximation of the cross-correlation function (Kirchner and Weil, 2000). The significance level ($\alpha = 0.05$) for each cross-correlation was estimated by bootstrapping (Efron and Tibshirami, 1993).

VEGETATION RESPONSES TO ABRUPT CLIMATE CHANGE

Our results indicate rapid responses of vegetation to climate across sites and continents (Fig. 1). Initial response times, indicated by the

¹GSA Data Repository item 2002115, Description of the principal component and cross-correlation analyses used, is available on request from Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301-9140, USA, editing@geosociety.org, or at www.geosociety.org/pubs/ft2002.htm.

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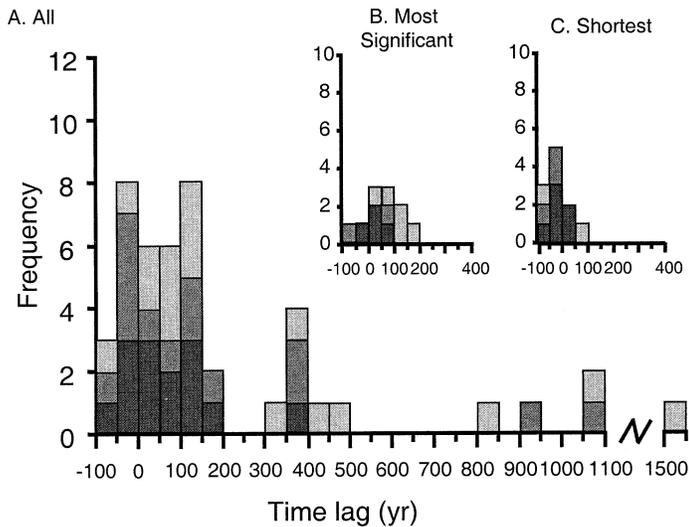


Figure 1. A: Frequency distribution of time lags associated with all significant ($P < 0.05$) cross-correlations between first three pollen principal components and climate proxies. Principal components are indicated as dark gray (PC1), medium gray (PC2), and light gray (PC3). Time lags shown are averages of temporal ranges shown in Figure 2. B: Subset of distribution in A, showing cross-correlation at each site with smallest P -value (across all principal components). C: Same as B, except showing cross-correlations with shortest time lag at each site.

shortest time lag at each site (Fig. 1C), are all < 100 yr. The most significant cross-correlation from each site indicates a median vegetation response time of 60 yr; the maximum response time is < 200 yr (Fig. 1B). When pooling the significant cross-correlations for all principal components from all sites, the median response time is 90 yr, and 76% of the significant time lags are < 200 yr (Fig. 1A). A few significant cross-correlations may be spurious (owing to the large number of comparisons), but the clustering of time lags near 100 yr strongly suggests a nonrandom distribution of cross-correlations. Figure 2 shows the cross-correlation results for each principal component across all sites. One-way analysis of variance (ANOVA) tests indicate no significant difference among North American and European sites in the distribution of initial response times ($F_{1,9} = 0.019$, $P = 0.89$), strongest cross-correlations ($F_{1,9} = 0.050$, $P = 0.83$), or general distribution of cross-correlations ($F_{1,47} = 2.327$, $P = 0.13$). Because the age controls for the European sites are based upon correlations to the GRIP (Greenland Ice Core Project) $\delta^{18}\text{O}$ record (Table 1) and the North American sites are based upon accelerator mass spectrometry dates, this congruence suggests that our results are not significantly affected

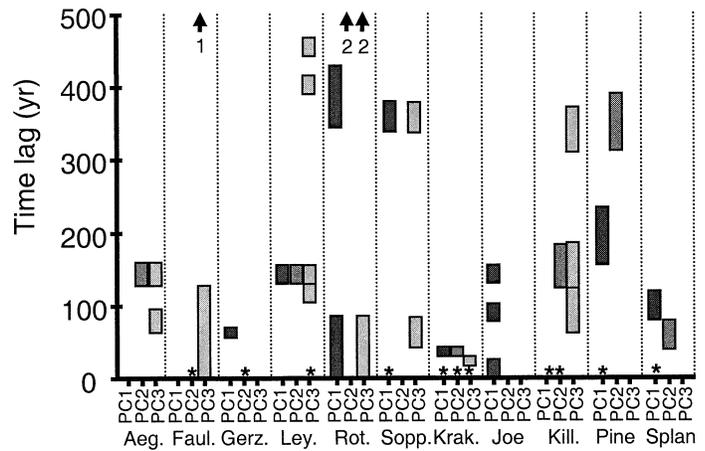


Figure 2. All significant cross-correlations associated with each principal component at each site (for full names, see Table 1). Length of each bar indicates minimum and maximum time lags, given median sampling resolution at each site. Asterisks indicate significant cross-correlations with small negative time lags, which we interpret to indicate rapid vegetation responses blurred slightly by sediment record. Arrows indicate significant correlations at time lags of > 500 yr.

by plateaus in the radiocarbon calibration curve. Lack of significant correlations between some principal components and the climate records (Fig. 2) suggests that some components of the vegetation are responding to biotic or abiotic variables not recorded in the climate proxies or are forced by climate at long frequencies removed by data filtering.

Details of the vegetation response vary among sites and regions, according to differences in initial environmental conditions, the local and regional species pool, and the climate events encompassed by each record. To provide insight into the underlying relationship between climate change and vegetational response, we show the data for two representative sites, Splan Pond (Levesque et al., 1997) and Rotsee (Lotter et al., 1992), and the resultant cross-correlations (Fig. 3). Both records include the Younger Dryas event (ca. 12.9–11.5 ka) and the Gerzensee-Killarney oscillation (ca. 13.2–12.8 ka). At Splan Pond, tree densities declined during the Younger Dryas (indicated by declines in *Picea*, *Populus*, and other arboreal pollen percentages and increases in *Cyperaceae* and *Poaceae*), and at least one taxon (*Alnus*) apparently migrated into the region (Fig. 3B). The first principal component separates boreal tree taxa (*Picea*, *Pinus*, *Populus*, and *Cupressaceae*) from shrubs (*Alnus*), and the second principal component discriminates herbaceous taxa (*Artemisia* and *Cyperaceae*) from trees and mosses (*Pinus*

TABLE 1. SITE AND CORE CHARACTERISTICS

Name	Lat	Long	Elevation (m)	Climate proxy	Age controls*	Time span (ka)	Resolution (yr)	Citation†
Aegelsee	46.65°N	7.54°E	995	$\delta^{18}\text{O}$	3GRIP, Top	11.00–12.63	33	Lotter et al. (1992)
Faulenseemoos	46.68°N	7.69°E	590	$\delta^{18}\text{O}$	4GRIP	10.62–14.73	87	Lotter et al. (1992)
Gerzensee	46.83°N	7.55°E	603	$\delta^{18}\text{O}$	112 GRIP	11.54–13.44	16	Schwander et al. (2000), Wick (2000)
Laysin	46.34°N	7.02°E	1230	$\delta^{18}\text{O}$	104 GRIP	10.54–13.51	22	Schwander et al. (2000), Wick (2000)
Rotsee	47.15°N	8.33°E	420	$\delta^{18}\text{O}$	6GRIP, Top	8.88–14.54	93	Lotter et al. (1992)
Soppensee	47.09°N	8.08°E	595	$\delta^{18}\text{O}$	2GRIP, Top	11.22–11.59	24	Lotter et al. (1992)
Kråknes Lake	62.03°N	5.00°E	38	chir.	80 AMS	9.99–13.63	73	Birks et al. (2000), Brooks and Birks (2001)
Joe Lake	46.76°N	66.67°W	335	chir.	2AMS, Top	11.45–13.01	64	Levesque et al. (1993, 1997)
Killarney Lake	46.01°N	66.63°W	75	chir.	2AMS, Top	12.31–13.09	31	Levesque et al. (1993, 1997)
Pine Ridge Pond	45.57°N	67.10°W	85	chir.	6AMS, Top	10.34–13.35	68	Levesque et al. (1993, 1994, 1997)
Splan Pond	45.26°N	67.33°W	106	chir.	3AMS, Top	11.16–13.58	41	Levesque et al. (1993, 1997)

Note: chir. is chironomid assemblages.

* Greenland Ice Core Project (GRIP): Ages determined by correlation between lake $\delta^{18}\text{O}$ record and GRIP $\delta^{18}\text{O}$ (Johnsen et al., 1997). The numbers indicate the number of tie points between the lake and GRIP $\delta^{18}\text{O}$ records. AMS: accelerator mass spectrometry ^{14}C date, calibrated to calendar years (Stuiver and Reimer, 1993). Top: Modern age assigned to coretop.

†Median temporal resolution of the pollen or climate record, for the more poorly sampled of the two.

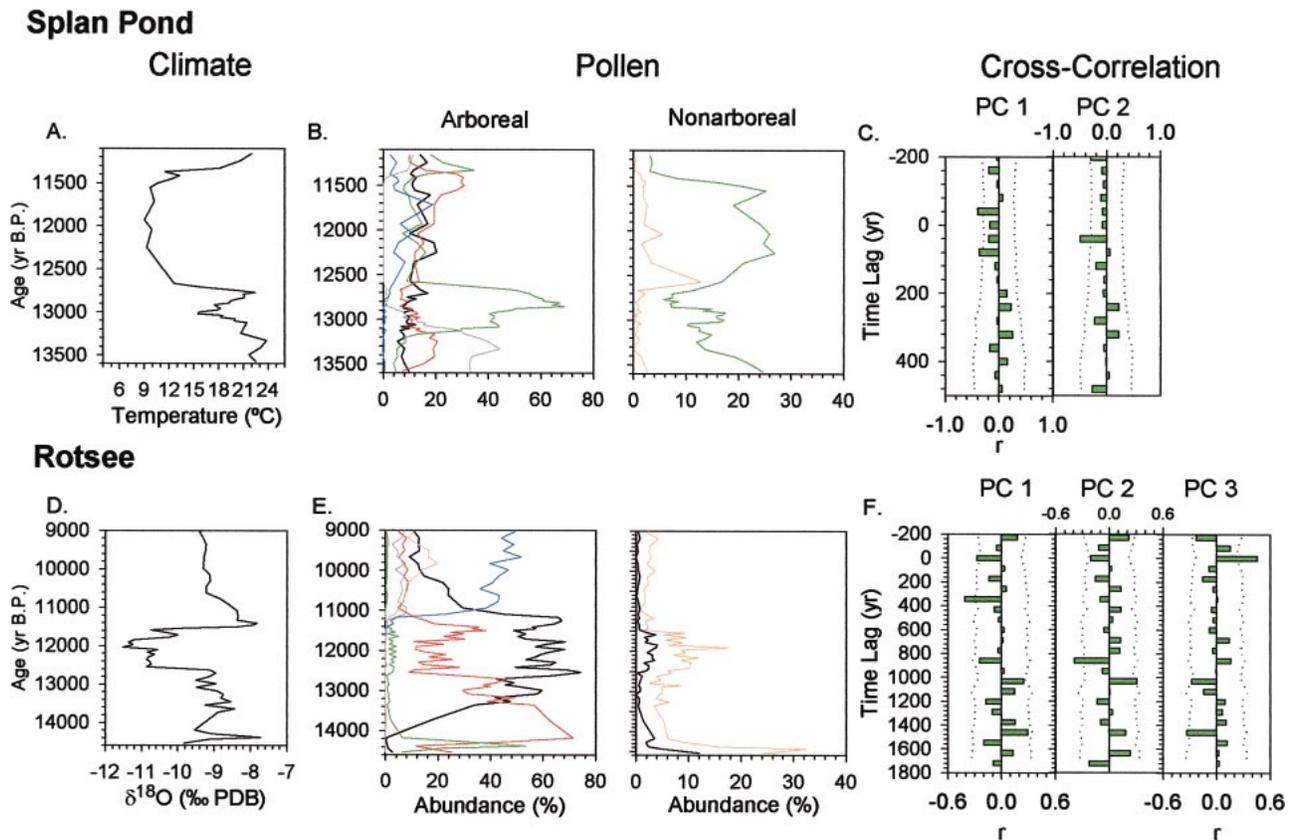


Figure 3. Time series plots for two sites—Splan Pond (Levesque et al., 1994) and Rotsee (Lotter et al., 1992), showing (A, D) climate proxy, (B, E) pollen percentages for selected types, and (C, F) cross-correlation between climate proxy and pollen principal components. For Splan Pond, arboreal pollen types shown are *Picea* (green), *Betula* (red), *Pinus* (black), *Alnus* (purple), and *Populus* (gray); nonarboreal pollen types are Cyperaceae (green) and Poaceae (orange). For Rotsee, arboreal pollen types shown are *Pinus* (black), *Betula* (red), *Corylus* (blue), *Quercus* (orange), and *Juniperus* (green); nonarboreal types are Poaceae (orange) and *Artemisia* (black). Each correlation plot shows correlation between climate proxy and pollen principal component for different temporal offsets; x-axis corresponds to strength of correlation, and y-axis corresponds to length of temporal offset. Positive offsets indicate vegetation lagging climate. Dashed lines in cross-correlation plots indicate upper and lower 95% confidence intervals. Positive vs. negative correlations are irrelevant, because sign of principal component scores is arbitrary. PDB—Peedee belemnite.

strobilus and *Lycopodium*); both principal components have response times of <100 yr (Fig. 3C).

Vegetation history at Rotsee is more complex. Peaks in *Juniperus*, Poaceae, and *Artemisia* pollen abundances match the Younger Dryas signature in the $\delta^{18}\text{O}$ record, but *Pinus* and *Betula* pollen abundances show no clear correspondence to the Younger Dryas oscillation. Pollen abundances for temperate tree taxa such as *Corylus*, *Quercus*, and *Ulmus* quickly increased after the Younger Dryas termination, suggesting that these taxa migrated rapidly into the region or expanded from local populations too small to be detected (Bennett, 1988). These qualitative observations are reinforced by the cross-correlation analysis. The first principal component discriminates temperate tree from herb pollen types (e.g., *Corylus*, *Ulmus*, *Quercus*, *Alnus* versus Poaceae, *Artemisia*, Cyperaceae, *Thalictrum*) and includes significant cross-correlations at 0–86 yr and 344–430 yr that may represent different response times for the herbaceous and immigrant tree taxa. The second principal component has high loadings for *Pinus* and *Betula* and significant cross-correlations at 860–946 and 1032–1118 yr. Thus, initial responses at Rotsee appear to be as rapid as at other sites, but some vegetation components may be responding more slowly or responding to other environmental variables not captured in the $\delta^{18}\text{O}$ record.

Consistently rapid vegetation responses to climate across sites and continents suggest that this is a general pattern not limited to certain species combinations or accidents of topography. In both the Swiss Alps and Maritime Canada, the vegetational response included both

the replacement of the dominant taxa by new arrivals (migration) and changes in the frequency of the existing taxa (Webb, 1986), and both types of response appear to have occurred within one to two centuries. Because the two regions differ greatly in physiography, fast response times cannot be attributed solely to high topographic relief shortening the distance between vegetational zones (Ammann et al., 2000). Mapped syntheses of pollen records support rapid migration at continental scales (Ritchie and MacDonald, 1986), likely promoted by the establishment of distant satellite populations by rare long-distance seed dispersal (Clark et al., 1998).

MECHANISMS AND IMPLICATIONS

The observed response times are consistent with gap-scale models of forest succession in closed temperate forests, which predict that compositional changes should lag a stepped climate event by 100–200 yr (Davis and Botkin, 1985). Initial response times <100 yr at many sites (Figs. 1 and 2) may be due to several factors. First, abrupt climate change may increase the mortality rates for mature trees via increased susceptibility to fire, wind, and disease. The interplay between climatic stress and decimating disturbances is documented in the historic record (Secretst et al., 1941) and is a likely cause of the middle Holocene *Tsuga* decline in eastern North America (Yu et al., 1997). Second, low tree densities near treeline may have reduced light limitation upon seedling establishment, enabling faster sapling growth and succession, as well as enabling establishment of immigrant tree species. Third, the

late glacial plant communities included a significant herbaceous component, which may be able to respond more rapidly to climate change, owing to shorter generation times. Kråkenes, the northernmost site and the site with the highest herbaceous component, has the shortest response times (Fig. 2). However, fast responses cannot be attributed solely to the inclusion of herbaceous taxa in our analyses, because (1) the pollen diagrams suggest equally fast responses for arboreal taxa, and (2) 12 of 16 principal components with high loadings for arboreal types (and low loadings for herbaceous taxa) had lags of <200 yr.

The evidence for a rapid and widespread vegetation response to late glacial climate oscillations indicates a tight coupling between the vegetation and atmosphere. To test the generality of our findings, the quantitative comparisons of pollen and independent climate proxies should be extended to other vegetation regions and times, to see whether closed-canopy temperate and tropical forests responded as rapidly to past climate change. Future plant migrations may be limited by anthropogenic fragmentation of the landscape or enhanced by accidental or intentional anthropogenic dispersal of propagules. Given these caveats, we infer from our synthesis of data from the last deglaciation that widespread and nearly synchronized alterations in vegetation composition and plant distributions will quickly follow any future climate change and that such responses will persist for several centuries after the initial perturbation.

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