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The anatomy of a climatic oscillation: vegetation change in eastern North America during the Younger Dryas chronozone

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Abstract

Century-scale climate changes reshaped circulation patterns over the North Atlantic and adjacent regions during the last glacial-to-interglacial transition. Here, we show that vegetation across eastern North America shifted dramatically at the beginning and end of the Younger Dryas chronozone (YDC: 12,900–11,600 cal yr B.P.), when changes in ocean circulation rapidly cooled and then warmed the North Atlantic sea-surface. On both the site-specific scale and the continental-scale, vegetation changed only gradually during the millennia before (15,000–13,000 cal yr B.P.) and after (11,000–9000 cal yr B.P.) the YDC, but climate changes ca 12,900 and 11,600 cal yr B.P. altered the vegetation on both spatial scales within centuries. Plant associations changed and some taxa rapidly migrated hundreds of kilometers (> 300 km within ~100 yr). In limited regions near the North Atlantic coast, abrupt cooling ca 12,900 cal yr B.P. resulted in a return to earlier vegetation types. Elsewhere, however, the vegetation patterns during the YDC were distinct from those of both earlier and later intervals. They indicate abrupt, ‘non-reversing’ seasonal temperature changes that were probably related to atmospheric circulation changes during the YDC, rather than to the direct influence of North Atlantic sea-surface temperatures. Atmospheric circulation patterns during the YDC were unique within the last 21,000 yr because of a unique combination of climate controls. Insolation, ice sheet extent, and atmospheric composition were significantly different from their full-glacial states, even when the North Atlantic returned to near full-glacial conditions. The YDC vegetation patterns demonstrate (1) rapid ecological responsiveness to abrupt climate change and (2) spatially varied patterns of YDC climate change.

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1. Introduction

Ocean circulation changes rapidly decreased and then increased North Atlantic sea-surface temperatures at the beginning and end of the Younger Dryas chronozone (YDC: ca 12,900–11,600 cal yr B.P.) (Ruddiman and McIntyre, 1981; Broecker et al., 1985; Stuiver et al., 1995; see also Appendix A). This ‘climatic reversal’ during deglaciation directly influenced regional climates and ecosystems in Europe, Greenland, and northeastern North America (Iversen, 1954; Dansgaard et al., 1984; Broecker et al., 1985; Mott et al., 1986). Contemporaneous abrupt changes influenced other parts of the world as well (Peteet, 1995; Rutter et al., 2000; Clark

et al., 2002), but no consensus has emerged regarding the extent to which a North Atlantic-type ‘climatic reversal’ (alternating warm–cool–warm conditions) was globally registered during the YDC (Peteet, 1995; Rutter et al., 2000; Ledru and Mourguiart, 2001). Other types of climate change were also widely recorded during the YDC because of atmospheric (Kneller and Peteet, 1999; Yu and Wright, 2001) and oceanic (Bluiner et al., 1998; Rühlemann et al., 1999; Clark et al., 2002) interactions. Furthermore ‘unidirectional’ progressions of dominant plant taxa continued in many regions without evidence of a ‘reversal’ (e.g. Shane, 1987; McGlone, 1995; Singer et al., 1998; Bennett et al., 2001).

The regional differences among vegetation changes during the YDC may help to identify processes that shape abrupt climate change and control ecological responses. We hypothesize that colder-than-previous North Atlantic sea-surface temperatures (Ruddiman and McIntyre, 1981) perturbed atmospheric circulation

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during the YDC, and as a result, widely modified (but did not uniformly reverse) climatic trends shaped by changes in insolation, ice sheet extent, and atmospheric composition (COHMAP, 1988; Webb et al., 1993; Bartlein et al., 1998; Kutzbach et al., 1998). Furthermore, because progressive changes in insolation continued during the 1300 yr of the YDC (Berger, 1978) and atmospheric carbon dioxide concentrations increased by ~30 ppmv across the interval (Monnin et al., 2001), conditions before the YDC probably differed substantially from those after the YDC.

To explore the patterns of climate and vegetation change during the YDC, we use the dense network of fossil pollen records in eastern North America (Webb et al., 1993; Grimm et al., 2001) to link regions with unambiguous North Atlantic-type ‘oscillations’ or ‘reversals’ (Mott et al., 1986; Shane, 1987; Peteet et al., 1990; Mayle and Cwynar, 1995) to regions that changed in other ways. By using maps and time-series of pollen data to illustrate gradients between regions, we assess the broad-scale patterns of vegetation response that are depicted by assembling evidence for site-specific changes. Although reduced sensitivity of the vegetation to climate in some regions has been cited as a reason that a ‘climatic reversal’ was not universally recorded (Shane, 1987; Wright, 1989; Yu and Eicher, 1998; Peteet, 2000), we propose instead that (1) vegetation responses were coherent across sub-continental regions where climate changed and (2) regional climate differences were more important than biotic factors for shaping the particular vegetation responses at individual sites. The ecological response to climatic change was likely rapid (Ammann et al., 2000; Tinner and Lotter, 2001), but spatially varied because plant taxa responded individually in a non-linear fashion with respect to climate (Bartlein et al., 1986; Webb et al., 1993; Huntley, 1996; Thompson et al., 1999) and because the climate changes themselves varied spatially (Fig. 1).

2. Conceptual framework

Like the climatic events and variations of the 19th- and 20th-centuries that have been expressed in different regions in different ways (e.g. ENSO events, Diaz and Markgraf, 1992; the 1815 Tambora eruption, Schweingruber et al., 1991; and ‘global warming,’ Jones, 1994; Mann et al., 1999; Houghton et al., 2001), oceanic and atmospheric circulation changes during the YDC likely also produced spatially varied climate responses. Several paleoclimate simulations have addressed the nature of climates during the YDC (Rind et al., 1986; Manabe and Stouffer, 1997; Schiller et al., 1997). Potential differences among regional climate changes, and attendant vegetation changes, during the YDC can be illustrated using the paleoclimate simulations and the

modern relationship between pollen abundance and climate for eastern North America (Fig. 1).

The Rind et al. (1986) simulations, although obsolete by today’s standards, are available through the NOAA World Data Center for Paleoclimatology and can serve as an illustrative example. They show that close to the North Atlantic, the colder-than-previous sea-surface temperatures likely had a direct cooling effect on both summer and winter temperatures (see locations 1 and 2 in Fig. 1C), but that the specific combination of seasonal changes probably differed in other regions. Elsewhere, climatic responses depended on the mechanism of transmission and regional controls, such as insolation or synoptic circulation patterns (see also Shuman et al., 2002). Colder-than-earlier conditions in winter likely extended well inland during the YDC, but were more moderate there than near the coast (Fig. 1C; location 4) (see also Manabe and Stouffer, 1997; Schiller et al., 1997). However, greater-than-modern summer insolation combined with atmospheric circulation changes during the YDC also produce higher-than-modern summer temperatures in the mid-continent (Rind et al., 1986) (Fig. 1B; location 4). Some intermediate areas (e.g. Fig. 1C; location 3) may have experienced little temperature change. Consequently, the absence of change in some paleoclimatic records likely indicates neither insensitivity to climate change nor the absence of synoptic-scale climate change. The difference among climates before, during, and after the YDC probably varied both seasonally and spatially. Moreover, the combination of cold winters and warm summers in the mid-continent may have had no modern equivalent (Fig. 1C, location 4).

Modern climate–pollen relationships (Bartlein et al., 1986; Webb et al., 1993; Huntley, 1996; Thompson et al., 1999) illustrate the manner in which vegetation could have responded to spatially varied changes in the combination of seasonal conditions. For example, spruce (*Picea*) and the northeastern species of pine (*Pinus*) tolerate a similar range of winter temperatures (Fig. 1C), but the northeastern species of pines grow under higher summer temperatures than spruce (Fig. 1C and D) (Webb et al., 1993; Thompson et al., 1999). As a result, a decrease in both winter and summer temperatures could have led to a transition from pine to spruce populations (Fig. 1C, location 2), but cooler-than-earlier winters in combination with warmer-than-earlier summers (i.e. a change in direction simulated for location 4, Fig. 1C) could have resulted instead in a transition from spruce to pine or a taxon tolerant of even warmer conditions, such as elm (*Ulmus*).

The vegetation responses to the YDC climate changes, probably also differed spatially, due to the non-linearity of the climatic response surfaces (Bartlein et al., 1986; Webb et al., 1993; Huntley, 1996) (Fig. 1D). Because most plant taxa have

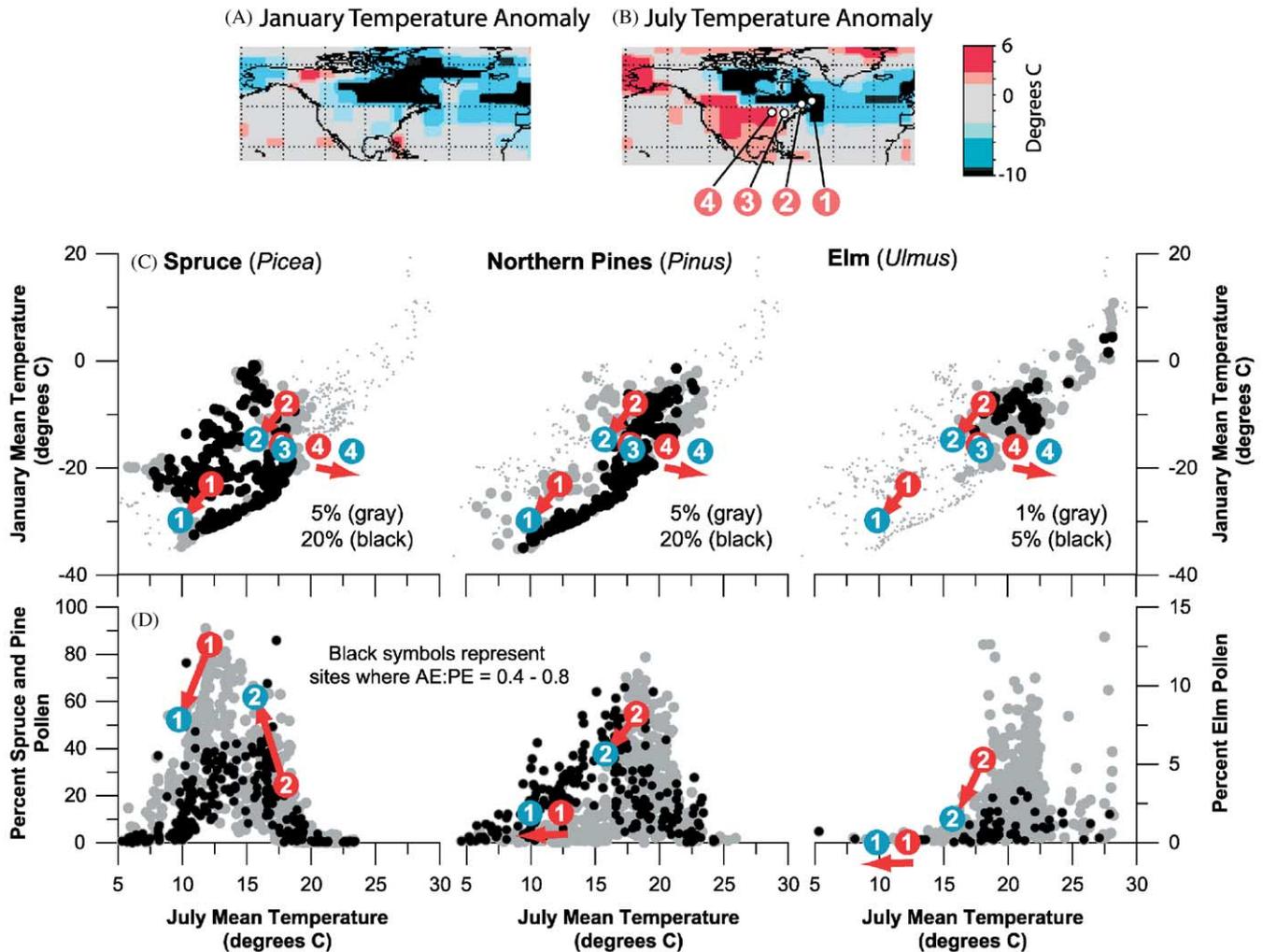


Fig. 1. Spatial patterns of climate change and vegetation response during the YDC. Maps show the difference between YDC and modern surface temperatures during January (A) and July (B), as simulated by the GISS GCM (Rind et al., 1986; Rind, 1994). Colder-than-modern temperatures over the North Atlantic are shown in shades of blue, and warmer-than-modern temperatures over the mid-continent are shown in red. Changes in mean January and July temperatures (C), simulated by the GISS model (Rind, 1994), are used to represent the possible differences between four locations along an east–west transect (B). Red symbols (C) represent simulated conditions before the YDC and blue symbols represent simulated conditions during the YDC. Red arrows illustrate the simulated magnitude and direction of temperature change. The modern percentages of spruce (*Picea*), northeastern pine (*Pinus*), and elm (*Ulmus*) pollen (C) are also plotted as large grey and black symbols, which represent two levels of abundance for each taxon. Small grey symbols represent the climatic position of all modern pollen surface samples from eastern North America. The modern percentages of each taxon is also shown with respect to a single climate variable, mean July temperatures (D), with responses to simulated conditions at locations 1 and 2 before (red) and during the YDC (blue) also shown (D). Smaller black symbols (D) highlight a selection of modern pollen samples within a specific range of moisture conditions, in order to show that moisture explains much of the variance at a given temperature. To avoid the ranges of southern and western pine species, which have different climatic tolerances (Thompson et al., 1999), the pine data shown are from the region north of 39° N latitude and east of 110° W longitude.

Gaussian-like relationships between their abundance and climate conditions, spatially uniform cooling can produce different responses among locations along a climate gradient (Huntley, 1996) (Fig. 1D). Because the highest abundance of most taxa occurs only at a narrow range of conditions, the center of a taxon's range should be as sensitive to climate change as the edge of the range (contrast locations 1 and 2 for spruce in Fig. 1D). Any climate change at the center of a taxon's range could trigger a deviation from the small set of 'optimal' conditions and cause a decline from the high abun-

dances there (Fig. 1D, location 1). In contrast, a wide range of conditions can produce low to intermediate abundances (e.g. location 1 for pine and elm in Fig. 1D). The optimal conditions that control the highest abundances include a combination of temperature and moisture-dependent factors (Prentice et al., 1991, 1992; Webb et al., 1993; Thompson et al., 1999) such that abundance can be low at the optimal growing season temperature if moisture availability (Fig. 1D) or the combination of winter and summer temperatures is sub-optimal. Thus, we anticipate that the extent and manner

of climate change during the YDC can be mapped by tracking systematic variations in the response of vegetation, and that the vegetation responses will not be limited to ecotones.

3. Methods

To investigate the patterns of YDC vegetation change, we examine the changing gradients in the network of fossil pollen records from eastern North America (Webb et al., 1993; Grimm et al., 2001). To confirm that the vegetation changes coincided with abrupt climate changes at the beginning and end of the YDC, we review selected pollen stratigraphies along an east–west transect across eastern North America (Figs. 2–4). Then, like Jacobson et al. (1987), we map pollen data from the North American Pollen Database (<http://www.ngdc.noaa.gov/paleo/pollen.html>) to show changes in the composition of ecological communities (Fig. 5A and B), and use the squared chord-distance dissimilarity measure (Overpeck et al., 1985) to quantify the amount of vegetation change over time (Fig. 5C and D). The four time series of maps (Fig. 5) show the major patterns of change from 14,000 to 10,000 cal yr B.P. The maps for 12,000 cal yr B.P. represent conditions during the YDC (12,900 to 11,600 cal yr B.P.; see Appendix A), and maps for 13,000 and 11,000 cal yr B.P. depict conditions just before and after it. In addition, we summarize lake-level data from the northern United States, in order to document moisture-balance changes that may help explain some of the patterns in the pollen data.

3.1. Age control

Pollen sample ages were estimated by linear interpolation between radiocarbon dates, after calibrating the existing radiocarbon dates into calendar years (Stuiver et al., 1998). To ensure that the calibrated chronologies were robust, we followed the approach of previous mapping efforts (Webb et al., 1983; Gaudreau and Webb, 1985; Webb et al., 1993) and critically evaluated the pollen stratigraphies to check for regional consistency in the vegetation histories. To demonstrate the consistency, we point to the patterns in the selected pollen stratigraphies, beginning at the onset of the European Bölling/Allerød chronozone, ca 14,600 cal yr B.P. (Fig. 2). The age models used for the pollen diagrams (Fig. 2) include between three and seven radiocarbon dates within the interval of interest (16,000–10,000 cal yr B.P.), except Smoot Lake Bog, Ohio, which only has one (Shane and Anderson, 1993).

To account for previously recognized old-carbon contamination, dates from two sites in the east–west transect were adjusted before calibrating the ages into

calendar years. Dates from Pretty Lake, Indiana, were adjusted by 920¹⁴C yr (see Williams, 1974) and the adjusted chronology matches well with near-by sites (Shane and Anderson, 1993) (Fig. 2). Dates from Chatsworth Bog, Illinois (King, 1981), have been adjusted by ~500–1000 ¹⁴C yr, in accordance with new AMS radiocarbon dated chronologies from Illinois (E. Grimm, pers. comm.). Chronologies for some of the mapped data (Fig. 5) have been similarly adjusted (Webb et al., 1993; Shuman, 2001).

3.2. Mapping technique and dissimilarity measure

The pollen percentage data were mapped by interpolating pollen percentage data to a network of grid points spaced at 50-km intervals by locally weighted averaging using a tri-cubic function (Cleveland and Devlin, 1988; Huntley et al., 1989). Fossil-pollen sites within ~300-km of each grid point were weighted according to distance from the grid point (lateral and elevational distance to account for topography) as well as by pollen-sample density and age control (Williams et al., 2001; Shuman et al., 2002). Pollen abundances were calculated as percentages of the sum of all tree, shrub, and herb pollen. Squared chord-distances (SCDs) were used to measure the dissimilarity between fossil and modern pollen assemblages (Overpeck et al., 1985; Williams et al., 2001), by comparing each fossil pollen sample with all modern samples from North America. Samples with minimum SCD values greater than 0.15 were considered to have no modern equivalent (Fig. 5C). SCDs are also used to show the amount of change between 1000-yr intervals (Fig. 5D), by comparing data for each mapped interval with those from the next interval (Jacobson et al., 1987; Williams et al., 2001).

4. Results

4.1. Time-series data

The transect of pollen diagrams (Fig. 2) reveals that (1) the largest changes in pollen percentages at each site correspond to the boundaries of the Bölling/Allerød and Younger Dryas chronozones, ca 14,600, 12,900, and 11,600 cal yr B.P., (2) smaller, progressive changes occurred during the chronozones, and (3) the expression of the changes differed between sites, but in a systematic fashion. Adjacent sites show similar histories, with each site recording percentages and trends that are intermediate between those at neighboring sites. Given that the vegetation history is consistent between adjacent sites (Fig. 2) and that the timing of the YDC has been accurately captured by bulk sediment radiocarbon dates in several studies from eastern North America (e.g.

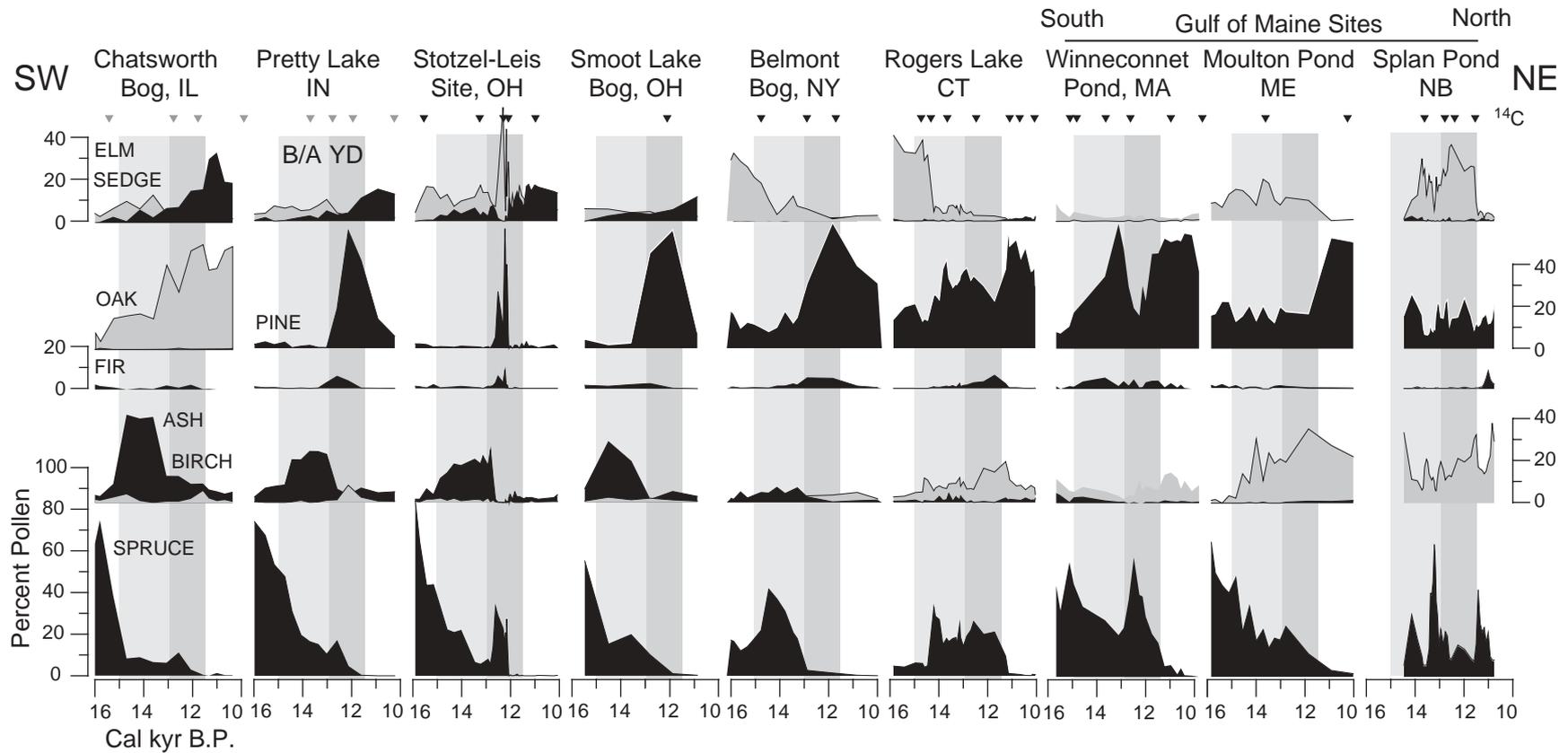


Fig. 2. Late glacial pollen stratigraphies from nine sites in eastern North America (from left to right: King, 1981; Williams, 1974; Shane, 1987; Shane and Anderson, 1993; Spear and Miller, 1976; Davis, 1969; Suter, 1987; Davis et al., 1975; Mayle and Cwynar, 1995). Light grey bars mark the European Bölling/Alleröd chronozone (B/A), from ca 15,000 to 12,900 cal yr B.P. Dark grey bars indicate the Younger Dryas chronozone (YDC), from ca 12,900 to 11,600 cal yr B.P. (see Appendix A with regard to these ages). Sedge (*Cyperaceae*) and birch (*Betula*) pollen percentages are shown in grey. Oak (*Quercus*) pollen percentages are also shown in grey, but are shown only for Chatsworth Bog, Illinois, where no significant pine (*Pinus*) pollen (black) was recorded (King, 1981). Triangles indicate the position of calibrated radiocarbon dates. Grey triangles denote dates that have been adjusted for old carbon.

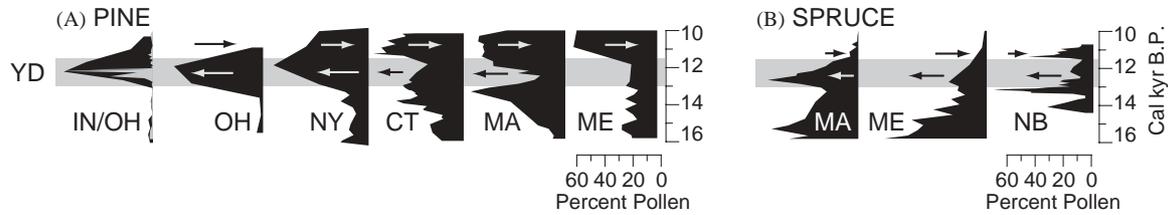


Fig. 3. Pine and spruce pollen percentages track abrupt range shifts. Records of pine (*Pinus*) (A) and spruce (*Picea*) (B) pollen percentages are plotted with time on a vertical axis to show changes in their geographic distributions. Arrows indicate the east–west range shifts of pine (A) and the north–south range shifts of spruce (B). Each site is labeled by state as in Fig. 2. The Stotzel-Leis site in Ohio (Shane, 1987) is shown in grey in inset A, and superimposed upon the stratigraphy from Pretty Lake in Indiana (Williams, 1974).

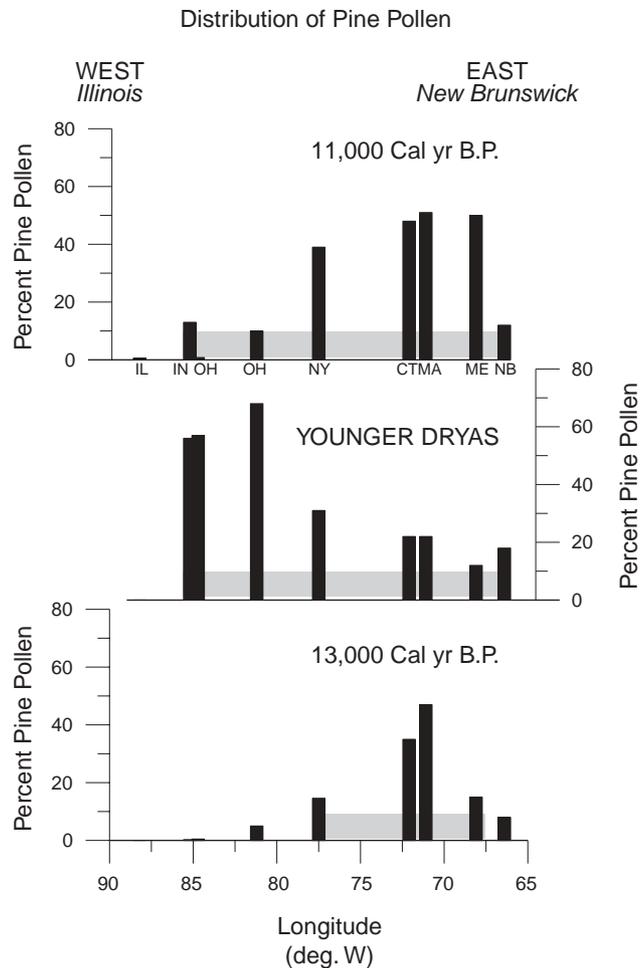


Fig. 4. The abundance of pine pollen across eastern North America before, during, and after the YDC. Histograms represent the percent pine (*Pinus*) pollen at each of nine sites (Fig. 2) at 13,000, 12,000 (YDC), and 11,000 cal yr B.P. The percentages are plotted with respect to longitude to show changes in abundance across the range of pine. Each site is labeled by state, as in Fig. 2. Horizontal grey bars mark the range of sites where the presence of pine populations is indicated by pollen percentages of >10%. For comparison to modern, see Fig. 1D.

Alpine Swamp, New Jersey, Peteet et al., 1990; sites in Ohio in Shane, 1987; Shane and Anderson, 1993; sites in Maritime Canada in Mott et al., 1986), the age control

provided by calibrated radiocarbon dates at the sites reviewed here appears to be adequate.

The vegetation changes coincided with the timing of major changes in North Atlantic sea-surface temperatures (Ruddiman and McIntyre, 1981; Stuiver et al., 1995), and punctuated the more gradual, long-term trends in the pollen data. The vegetation that existed prior to the YDC became established at the onset of the Bölling/Alleröd chronozone, ca 14,600 cal yr B.P. (Fig. 2), when relatively cold-tolerant assemblages were replaced by relatively thermophyllous communities. At sites from central Illinois to eastern Ohio, the initial spruce-dominated assemblages rapidly changed to those containing abundant ash (*Fraxinus*) populations. To the east, in Connecticut and New York, spruce populations increased in abundance and replaced tundra-like assemblages containing abundant sedge (Cyperaceae). Increased pine and birch (*Betula*) populations reduced the dominance of spruce along the southern Gulf of Maine. The assemblages that became established at each site then shifted only gradually until rapid changes, ca 12,900 cal yr B.P., marked the onset of the YDC (Fig. 2).

At the beginning of the YDC, as sedge-dominated plant communities replaced spruce woodlands in Maritime Canada (Mayle and Cwynar, 1995), the peak abundance of spruce populations (which had shifted north into Canada by 13,000 cal yr B.P.) abruptly shifted south into Massachusetts (Figs. 2 and 3). A simultaneous decline in ash populations can be traced from Illinois to Connecticut, as sites from New York to Indiana record an expansion of pine populations (Fig. 2). Small increases in fir (*Abies*) and birch populations are also diagnostic of the YDC at many sites, but in Illinois, warm-tolerant elm and oak (*Quercus*) populations also became significantly more abundant during the YDC than before (Fig. 2) (King, 1981).

Most pollen diagrams, consequently, have distinctive pollen zones that date to the YDC (Fig. 2). Most YDC-age pollen assemblages differ from those that existed earlier and later. For example, although spruce populations expanded again at the Stotzel-Leis site during YDC, pine and fir populations were abundant there only during the YDC (Shane, 1987) (Fig. 2). (Sedge

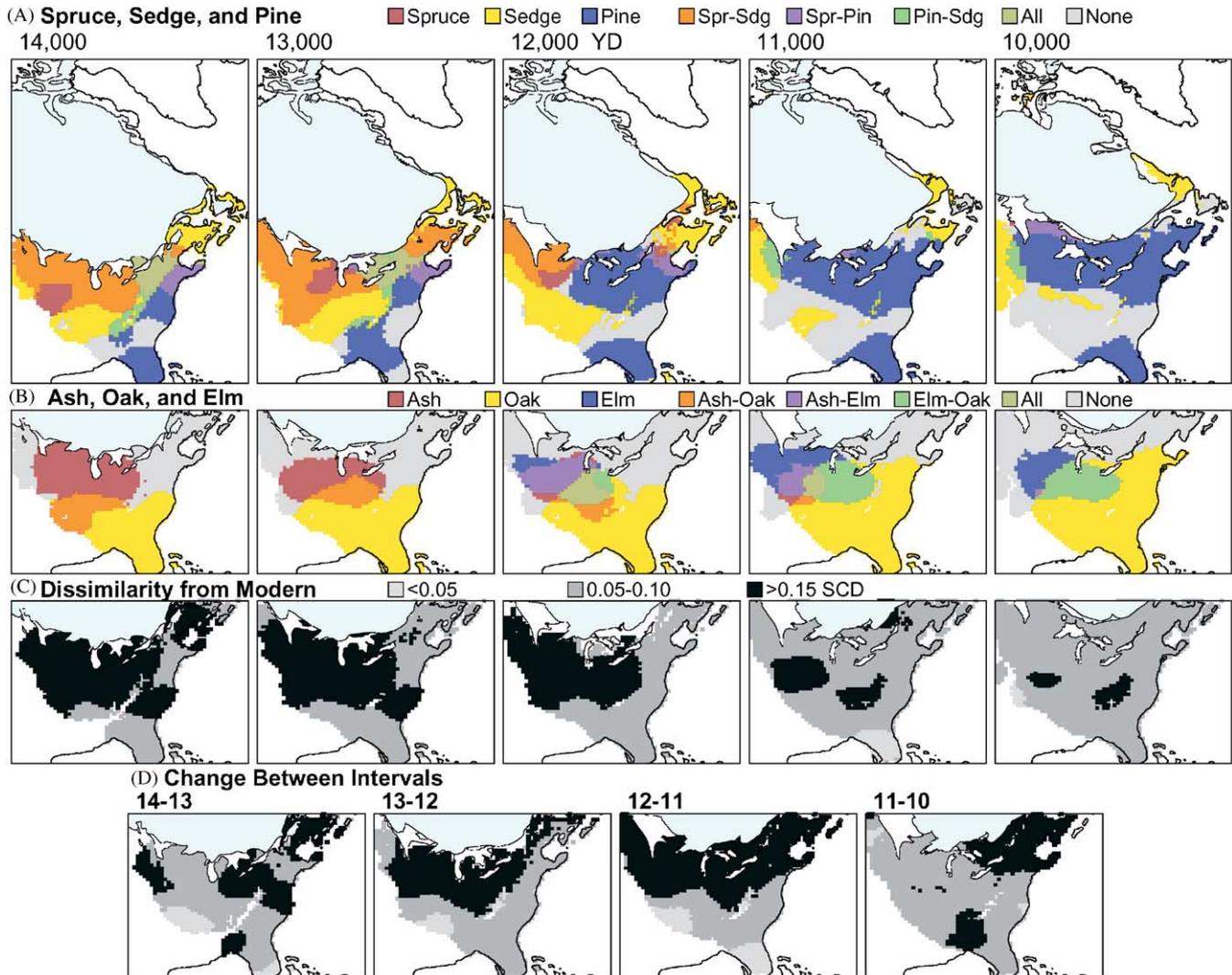


Fig. 5. Maps of plant associations and vegetation change at 1000-cal-yr intervals between 14,000 and 10,000 cal yr B.P. Different colors illustrate different vegetation assemblages. Individual plant taxa are mapped as red, yellow, or blue with overlapping ranges represented by the combinations of primary colors: orange, purple, green, or gold. Grey represents the absence of the mapped taxa, and white represents regions with no data. Two combinations of three taxa are mapped: (A) regions with greater than 20% spruce (*Picea*; red), 5% sedge (*Cyperaceae*; yellow), and 20% pine (*Pinus*; blue) pollen, and (B) regions with greater than 5% ash (*Fraxinus*; red), 15% oak (*Quercus*; yellow), and 6% elm (*Ulmus*; blue) pollen. Maps of square-chord distances (SCD) represent the dissimilarity between fossil and modern pollen assemblages (C). SCD values greater than 0.15 (black) represent pollen assemblages that have no modern equivalent. Offset maps (D) use SCDs to show the amount of change between 1000-yr intervals. High SCDs document large changes.

pollen also increased in abundance at the Stotzel-Leis site during the YDC, but the signal is local and represents a site-specific change). At other sites where spruce had been abundant before the YDC (such as Smoot Lake Bog and East Twin Lake, Ohio; Shane and Anderson, 1993; Belmont Bog, New York; Spear and Miller, 1976), spruce populations declined as pine populations expanded (Fig. 2). The range of pine extended westward (Figs. 3 and 4), but the importance of pine populations also changed throughout the former range of pine (Fig. 4). Pine populations declined at sites that had been in the interior of the pre-YDC range (such as Rogers Lake, Connecticut; Davis, 1969) (Figs. 2–4).

Given that the expansion of pine populations at the Stotzel-Leis site coincided with the expansion of spruce populations at the onset of the YDC (Shane, 1987) (Fig. 2), pine populations must have extended their range by > 300 km (possibly as much as 700–900 km) within about a century (Fig. 3A). The Stotzel-Leis site and Pretty Lake (Fig. 2) are located ~ 600 km from earlier populations in the Appalachian and Allegheny highlands (Spear and Miller, 1976; Watts, 1979; Kneller and Peteet, 1999) and ~ 300 km from earlier populations south of the Ohio River (Wilkins et al., 1991). Furthermore, in eastern Wisconsin (500 km northwest of the Stotzel-Leis site), the initial expansion of pine

populations at Gass Lake (Webb, 1983) also coincided with an expansion of spruce populations. Radiocarbon dates on the expansion of pine populations into central Wisconsin, from Lake Mendota (Winkler et al., 1986), Devils Lake (Maher, 1982), and Disterhalf Farm Bog (Baker, 1970), calibrate to statistically the same early YDC age (13,010–12,680 cal yr B.P.) within a 95% confidence interval (Stuiver et al., 1998). These dates may, however, be problematic due to old carbon contamination (E. Grimm, pers. comm.)

At the end of the YDC, ca 11,600 cal yr B.P., pine populations declined from Indiana to New York, but expanded at sites to the north and became important from Connecticut to Maine (Figs. 2–4). Spruce populations rapidly declined at sites across the northern United States (Fig. 2), and re-expanded in Maritime Canada (Fig. 3B). Elm populations simultaneously increased at sites from Illinois to Ohio. In Maine, where the vegetation history is ‘unidirectional,’ the expansion of pine populations marked the end of the YDC, whereas an expansion of birch populations had marked the beginning (Davis et al., 1975) (Fig. 2).

Overall, the individual sites recorded local changes that fit into a broad-scale pattern of vegetation change at the beginning and end of the YDC. Broad-scale responses included changes in the composition of the regional vegetation and changes in the distribution of taxa. New combinations of taxa developed, such as represented by the spruce-pine-fir assemblage at the Stotzel-Leis site (Fig. 2). Taxa, such as pine and spruce (Fig. 3), expanded into new areas and changed in importance across the regions where they had already been growing (Fig. 4). The pollen diagrams uniformly illustrate that vegetation during the YDC had been different from the vegetation before and after.

5. Mapped patterns

Maps of the pollen data (Fig. 5A–C) show continental-scale changes in vegetation pattern that were recorded as different local responses in the individual pollen diagrams (Fig. 2). The maps highlight a sharp contrast between the vegetation patterns before the YDC (14,000–13,000 cal yr B.P.) and those after the YDC (11,000–10,000 cal yr B.P.). Prior to the YDC, a large region of vegetation unlike any growing today existed in the midwestern United States (Fig. 5C), and contained populations of spruce, sedge, and ash (orange and red in Fig. 5A and B). The spruce-ash-sedge assemblage represents an open spruce-parkland (Jacobson et al., 1987; Overpeck et al., 1992), and likely reflects a combination of seasonal temperature and moisture conditions unlike any today (Williams et al., 2001). After the YDC, by 11,000 cal yr B.P., the communities became more like those growing today (Fig. 5C) with a

mixed pine forest replacing the spruce parkland. Pine populations (blue in Fig. 5A) became abundant from Minnesota to Nova Scotia (Jacobson et al., 1987), with elm and oak populations abundant to the south (green and yellow in Fig. 5B).

Patterns during the YDC (12,000 cal yr B.P.) stand out as different from both earlier and later patterns (Fig. 5) because regional vegetation changed extensively between 13,000 and 12,000 cal yr B.P., and again from 12,000 to 11,000 cal yr B.P. (Fig. 5D). The changes were more widespread than during earlier and later millennia (see also Williams et al., 2001), and were continuous across the region rather than confined to ecotones or range limits (Fig. 5D). In Maritime Canada, forest cover was temporarily reduced during the YDC due to the cooling of the North Atlantic (Mott et al., 1986; Mayle and Cwynar, 1995). This standard type of reversal in the long-term northward migration of taxa stands out in pollen diagrams as a classical North Atlantic-type oscillation (Fig. 2), but it is subtle on the maps when compared to the broad changes in vegetation in the midwestern United States during the YDC (Fig. 5A and B).

At the beginning of the YDC, the abrupt increase in pine pollen abundance from western New York to Wisconsin (blue in Fig. 5A) represents the rapid westward migration of pine populations. The spruce parkland became restricted to Minnesota and Manitoba (red, orange in Fig. 5A), and pine populations did not expand there until after the YDC (Fig. 5A). Although sites from Iowa (Kim, 1986; Baker et al., 1992) to Ohio (Shane, 1987; Shane and Anderson, 1993) record a short-lived (12,700–12,000 cal yr B.P.) expansion of spruce populations, spruce abundance had regionally declined to below the threshold mapped by 12,000 cal yr B.P. Simultaneously, however, increased abundances of some temperate deciduous taxa, such as elm (blue, purple in Fig. 5B), contributed to YDC-age assemblages, which differed in composition from both earlier and modern vegetation (Fig. 5C and D).

6. Evidence for the climatic control of the pine expansion

A shift to drier conditions at the onset of the YDC is evident in lake-level data from the southern Great Lakes region and coincided with the expansion of pine populations there (Fig. 6). Sedimentation rates were extremely low and indicate hiatuses due to low lake levels (Webb and Webb, 1988; Shuman, 2001) during the YDC at Clear Lake in northern Indiana (Bailey, 1972) and at Houghton’s Bog in western New York (Miller, 1973). In addition, lacustrine sediments changed to peat at the beginning of the YDC at Bucyrus Bog, in eastern Ohio (Shane, 1989), and at Belmont Bog, in western New York (Spear and Miller, 1976; Webb,

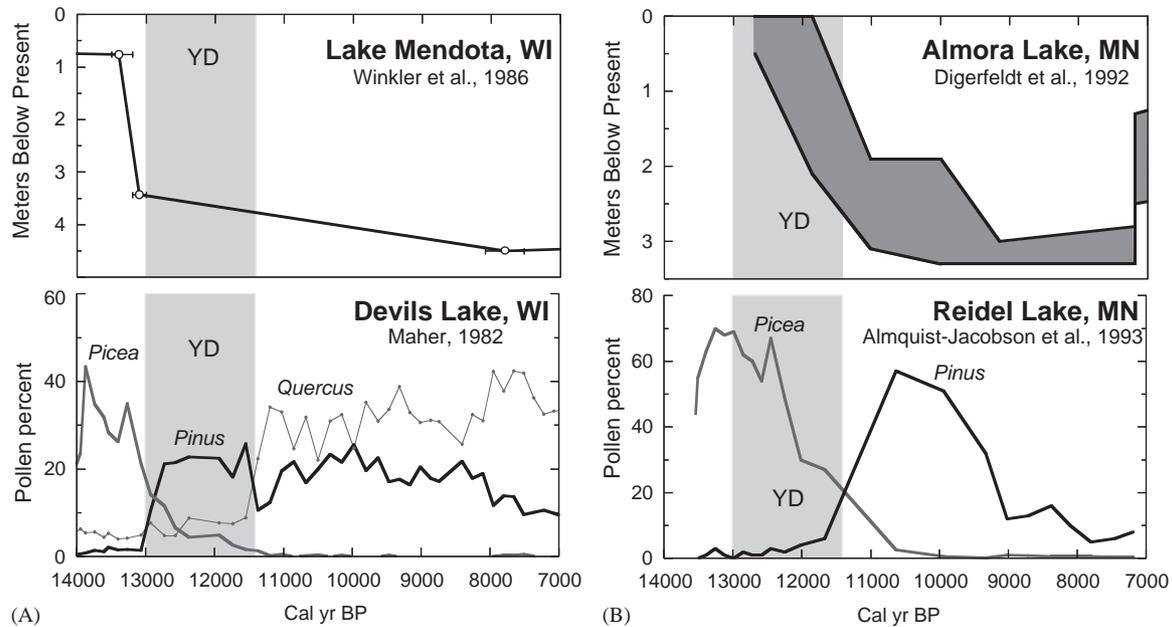


Fig. 6. Lake-level elevations and pollen percentages in Wisconsin and Minnesota from 14,000 to 7,000 cal yr B.P. Lake-level elevations at Lake Mendota, Wisconsin (A), are inferred from the elevations of radiocarbon-dated sediments (Winkler et al., 1986). Aquatic macrofossil assemblages and sediment characteristics from Almore Lake, Minnesota (Digerfeldt et al., 1992), constrain an envelope of possible water levels there (B). The lake-level data are compared to changes in the relative abundance of spruce (*Picea*), pine (*Pinus*), and oak (*Quercus*) pollen at near-by sites: (A) Devil's Lake, Wisconsin (Maher, 1982) and (B) Reidel Lake, Minnesota (Almquist-Jacobson et al., 1992).

1990). Deep-water laminated sediments were simultaneously overlain by a reducing sapropel, indicative of shallower water, at Browns Lake, Ohio (Sanger and Crowl, 1979; Harrison, 1989). At Lake Mendota, Wisconsin, radiocarbon dates below sand layers in shallow cores (Winkler et al., 1986) calibrate (Stuiver et al., 1998) to 13,400 (13,500–13,200) and 13,100 (13,200–13,000) cal yr B.P., suggesting that water levels also fell there at the beginning of the YDC (Fig. 6A). The Lake Mendota dates may be biased by contamination (E. Grimm, pers. comm.), but pollen stratigraphic correlations between shallow and deep cores at Lake Mendota indicate that pine populations expanded into central Wisconsin only after water-levels fell there (Winkler et al., 1986).

During the YDC, lake levels remained relatively high where spruce populations persisted in Minnesota and in the Northeast, but fell by ~11,000 cal yr B.P. (Digerfeldt et al., 1992; Lavoie and Richard, 2000; Newby et al., 2000; Shuman et al., 2001) as pine populations expanded northward into these regions (Jacobson et al., 1987) (Figs. 5 and 6B).

7. Discussion

7.1. Responses to abrupt circulation change

The maps and time series show that dramatic vegetation changes coincided with the beginning and

end of the YDC and that these changes varied spatially, but in a coherent pattern (Figs. 2–5). The magnitude and extent of vegetation change was greater during the two millennia leading into and out of the YDC (13,000–12,000 and 12,000–11,000 cal yr B.P.) than during any other millennia of the last deglaciation (Fig. 5D) (see also Williams et al., 2001). Time series of pollen data arranged along the east–west transect demonstrate that much of the change happened during the centuries that mark the beginning and end of the YDC (Fig. 2). Although obvious ‘reversals’ in forest development resulted only in limited areas, distinctive YDC-age vegetation developed rapidly at all sites from the North Atlantic coast to the mid-continent (Fig. 2).

In contrast to locally rapid vegetation changes during other parts of the late Quaternary, which were time transgressive on the broad scale (Wright, 1968; Davis, 1981; Webb, 1982; Webb et al., 1983; Gaudreau and Webb, 1985; Davis et al., 1986), the abrupt vegetation changes at the beginning and end of the YDC were synchronous across a wide area (Figs. 2 and 3). Such widely synchronous, ‘non-reversing’ shifts in vegetation represent a style of change that likely marked the YDC in other regions of the world as well. For example, the YDC was distinguished from other periods in Chile by the sequential expansion of two key plant taxa: *Podocarpus nubigena* at the beginning of the YDC and *Tepualia stipularis* at the end of the YDC (Bennett et al., 2000). Each taxon increased simultaneously across a wide range of latitude, indicating that the changes were

abrupt rather than time-transgressive. In such regions, where insolation, ice sheets, and other regional factors (such as regional ocean and atmospheric circulation patterns) controlled climate conditions more directly than North Atlantic sea-surface temperatures, the YDC climate changes were probably not characterized by an oscillation in annual mean temperatures. Instead, as in much of eastern North America, the YDC is best characterized globally as a period of unique conditions (within the last 21,000 yr), bounded by two abrupt shifts in climatic pattern and trend, ca 12,900 and 11,600 cal yr B.P.

Because the rate of summer insolation change had slowed by 13,000 cal yr B.P. (Berger, 1978) and the Laurentide ice sheet remained extensive (Fig. 5) (Dyke and Prest, 1987), the gradual changes in these two factors alone cannot explain the dramatic changes in the pollen data at the beginning and end of the YDC. Conventions place the Pleistocene–Holocene boundary at the end of the YDC (Mangerud et al., 1974; Stuiver et al., 1995; Björck et al., 1998), but no significant (or rapid) changes in the major climate controls of insolation and ice extent coincide with the abrupt vegetation changes at that time (Berger, 1978; Dyke and Prest, 1987; COHMAP, 1988). The changes in the pollen data (Figs. 2–5), therefore, indicate that additional influences (i.e. North Atlantic circulation changes that, in turn, influence atmospheric circulation) played a key role for rapidly altering climate and vegetation patterns at the beginning and end of the YDC. The spatial patterning of YDC climates and vegetation differed from both earlier and later periods, however, because the ice sheets and insolation differed substantially from their full-glacial character, even while the North Atlantic returned to a glacial-like state during the YDC. Furthermore, the dramatic increase in atmospheric carbon dioxide concentration by the end of the YDC (Monnin et al., 2001; McElwain et al., 2002) likely played an important role in distinguishing conditions before the YDC from conditions after the YDC (Fig. 5).

7.2. *Younger Dryas climate patterns*

The seasonal temperature patterns qualitatively estimated from the pollen data (many of which lack modern analogs) match well with spatial patterns simulated by climate model experiments (e.g. Rind et al., 1986) (Fig. 1). Spruce populations shifted southward as annual mean temperatures near the North Atlantic coast became colder than before because of the direct impact of cold sea-surface temperatures (Fig. 3B). Increases in spruce, fir, and birch populations as far as Illinois at the onset of the YDC (Fig. 2) indicate that the cooler-than-previous conditions extended well inland at least during YDC winters. The mapped increases in the abundance of elm and oak by 12,000 cal yr B.P. (Fig. 5B)

show, however, that higher-than-previous summer temperatures were simultaneously important in the mid-continent. Today, elm pollen reaches >6% only where mean July temperatures exceed 18°C (Fig. 1D), and >20% oak pollen exists only above 23°C (Webb et al., 1993). Therefore, the replacement of the spruce parkland by a mixed forest that included even relatively low percentages of elm (Fig. 5B) probably resulted from an increase in growing season temperatures.

The end members of the east–west transect of selected pollen stratigraphies (Fig. 2) illustrate the contrast between continental and coastal climates. The classic type of oscillation between arboreal and non-arboreal environments, recorded at the northeastern-most site (Splan Pond, NB) and elsewhere in Maritime Canada (Mayle and Cwynar, 1995; Mott et al., 1986), indicate cooler-than-previous summers and winters during the YDC (like location 2 in Fig. 1). At the southwestern end, at Chatsworth Bog, Illinois (King, 1981), warm-tolerant elm and oak populations increased and, in combination with low abundances of cold-tolerant spruce, fir, and birch populations, reflect amplified seasonality there during the YDC (like location 4 in Fig. 1). Colder-than-previous winters (about -10°C) coincided with warmer-than-previous summers ($>23^{\circ}\text{C}$). These highly seasonal conditions during the YDC have no modern equivalent in North America (Figs. 1C and 5D).

After the YDC, seasonality in the mid-continent decreased as winters warmed again (see Shane and Anderson, 1993), favoring elm populations over spruce, fir, and pine (Figs. 2 and 5). Spruce populations, which had shifted southward along the Gulf of Maine (Figs. 2 and 3B) and into parts of the southern Great Lakes region (Fig. 2), decreased across most of eastern North America because the optimal climate conditions for spruce had rapidly shifted northward into western Canada (Ritchie and MacDonald, 1986).

7.3. *Regional differences and climate controls*

The spatial patterns of climate change fit well with the regional differences in climatic controls. Upstream of the direct influence of the North Atlantic, insolation continued to heavily influence the temperature of the mid-continent (Rind et al., 1986). The high seasonality was then rapidly amplified during the YDC, because the cold North Atlantic altered atmospheric circulation patterns, potentially causing a pronounced ridge in the westerlies to develop over the mid-continent (Schiller et al., 1997). The associated northward-advection of relatively warm air masses added to the radiative heating there, causing conditions during the YDC summers to be warmer than the influence of insolation alone could have produced (Fig. 1). Such a circulation pattern may result from the development of anomalous

low pressure over the cold North Atlantic, and become intensified by the steeper-than-earlier temperature gradient between the insolation-heated continent and the colder-than-earlier North Atlantic. Climates (and vegetation) that developed in many regions during the YDC lacked earlier or modern equivalents (Figs. 1C and 5D), but conditions after the YDC likely had modern analogs (Fig. 5C) because the extreme seasonality of the YDC was reduced (see also Williams et al., 2001) and atmospheric carbon dioxide reached Holocene concentrations. On the regional scale, additional variability stems from surface feedbacks, like lake effects, that were also an important factor (see below; Hostetler et al., 2000).

7.4. Rapid changes in the abundance of pine

Rapid changes in the distribution of pine populations illustrate that the apparently 'unidirectional' vegetation changes at some sites (Fig. 2) were, in fact, the local expression of a broader-scale YDC 'oscillation' (Fig. 4). Pine populations expanded into the southern Great Lakes region only during the YDC, but were abundant to the northeast (i.e. southern New England) before and after the YDC (Figs. 3A and 4). In Connecticut and Massachusetts, renewed spruce populations replaced pine populations (Figs. 2 and 3) as temperatures there declined to below 18–20°C during YDC summers and to below about –10° C in YDC winters. To the west, however, pine populations became more abundant than spruce populations in the southern Great Lakes region (Fig. 2). Warmer-than-earlier summers during the YDC favored pine populations over spruce, even though cooler-than-earlier winters had increased spruce abundance and caused ash populations to decline. Temperatures during the YDC in the region of pine expansion (New York, Ohio, and Indiana) were probably relatively warm (20–23° C) in summer, but like sites in New England, had declined below –10° C in winter (Fig. 1; see also Shane and Anderson, 1993). After the YDC, relatively warm summer and winter conditions favored the expansion of pine to the north with increased abundances in New England (Figs. 2–4).

Moisture availability also closely controlled the westward expansion of pine populations (Fig. 6), because pine populations favor drier conditions than spruce (Webb et al., 1993; Thompson et al., 1999). The lake-level data document a shift towards drier conditions from western New York to Wisconsin, which favored pine populations there at the onset of the YDC (Fig. 6A). The expansion continued only as far as was climatically feasible for pine populations to flourish. Pine populations did not expand further west during the YDC because relatively moist conditions prevailed in Minnesota (Fig. 6B). The lake effect of Lake Agassiz, which supplied moisture for the readvance of the

Superior Lobe of the Laurentide Ice Sheet during the YDC (Hu et al., 1997; Hostetler et al., 2000), may have been an important source of additional moisture across the upper Midwest until after 10,900 cal yr B.P. (Bartlein and Whitlock, 1993). Thus, vegetation patterns changed not only in response to new combinations of seasonal temperatures (Fig. 1) but also due to changes in moisture balance.

The rapidly changing distribution of pine also demonstrates that plant taxa can respond to abrupt climate change by expanding their ranges at rates (> 300 km/century) that greatly exceed the average pace of late-Quaternary migrations (10–100 km per century; Davis, 1981, 2001; Huntley and Birks, 1983; Huntley and Webb, 1988). Although most seeds only fall a few meters from their parent tree, the observation that pine populations spread rapidly when conditions became favorable is consistent with the recent assessment that long-distance dispersal events are rare, but not unlikely (Clark et al., 1998).

7.5. Vegetation dynamics and sensitivity

Vegetation was widely sensitive to the abrupt climate changes at the beginning and end of the YDC. The vegetation changes differed, however, according to spatially varied patterns of climate change, and were not accentuated in particular biotic zones, such as ecotones or range limits (Figs. 4 and 5D). The varied vegetation responses match well with the conceptual model of pollen abundance (or plant population size) in which responses follow Gaussian-like response surfaces (Fig. 1). For example, as predicted by the spruce response surface (Fig. 1D), spruce abundance changed in opposite directions in Massachusetts and Maritime Canada (Fig. 3B), even though the direction of the climate change was the same in both places. Due to progressive warming prior to the YDC, spruce populations increased at sites in Maritime Canada, while simultaneously declining to the south (Fig. 3B). At the onset of the YDC, dramatic cooling rapidly decimated spruce populations in Maritime Canada, and shifted the optimal conditions for spruce south again into Massachusetts. Conditions in Canada were colder than spruce populations could tolerate, but spruce remained at intermediate abundances in Maine, because conditions there were tolerable, although colder than optimal (Fig. 3B). The changes across the range of pine (Figs. 3A and 4) similarly demonstrate that taxa-tracked dramatic climate shifts by changing local abundances in accordance with their unimodal response surfaces (Fig. 1D).

At any given time, the abundance of each taxon peaked in certain, presumably optimal regions (Figs. 2–4). Away from these optimal regions, percentages progressively declined, as the percentages of other taxa

increased (Fig. 2). As conditions changed, distributions shifted, but remained unimodal (Fig. 4). Peak abundances, like range limits, shifted (Fig. 4) because they tracked the optimal climate conditions for high seedling survivorship, adult longevity and competitiveness, and large metapopulations. Local responses, therefore, included the local arrival or extinction of taxa, as well as changes in the abundance of taxa that were already present (Webb, 1986) (Fig. 2). Such changes affected all sites in accordance with local climate and edaphic conditions (Graumlich and Davis, 1993). Yet, biotic processes, such as seed dispersal, did not significantly delay the vegetation responses (see also Ammann et al., 2000; Tinner and Lotter, 2001), even though the rates of climate reorganization at the beginning and end of the YDC (Ruddiman and McIntyre, 1981; Stuiver et al., 1995) far exceeded the rates of orbitally forced climate change (COHMAP, 1988; Webb et al., 1993; Bartlein et al., 1998).

8. Conclusions

The YDC has been identified as a period when a ‘climatic oscillation’ (or specifically an alternation between relatively warm and cold annual mean temperatures) is widely evident in paleoclimatic data (Broecker et al., 1985; Rind et al., 1986; Peteet, 2000; Rutter et al., 2000). The pollen data from eastern North America show, however, that other types of climate change also occurred during the YDC. Rapid shifts in the seasonal temperature and moisture-balance gradients at the beginning and end of the YDC were manifested as ‘climatic oscillations’ only in limited regions, even though conditions were rapidly modified elsewhere as well. Progressive, non-reversing changes may be more extensive than previously thought. Such changes may, in fact, be the modal pattern of climate change during the YDC. Widespread, non-reversing changes resulted in the mid-continent from increased seasonality (summers became warmer than before and winter became colder), due to altered atmospheric circulation patterns that reinforced the influence of insolation. Thus, the changes in eastern North America exhibit a range of climate and vegetation responses that may have also occurred in other parts of the world during the YDC.

The vegetation responses also show evidence of pervasive vegetation sensitivity to rapid climate change. Regional differences in the vegetation responses resulted from (1) different combinations of seasonal temperature and moisture-balance change and (2) the unimodal distributions of most taxa along climate gradients. Vegetation responses included rapid long-distance range shifts (> 300 km/century), as well as local changes in abundance. Future climate changes may likewise trigger

broad-scale reorganization of terrestrial ecosystems, because biotic factors do not appear to limit the sensitivity of the vegetation.

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Appendix A

The Younger Dryas chronozone

We use the term, “Younger Dryas”, here strictly in a chronostratigraphic sense (i.e. as an adjective as opposed to a noun). The “younger *Dryas*” first referred to an interval in Danish sediments (Iversen, 1954), and became defined as a biostratigraphic term, based on the presence of *Dryas octopetala* macrofossils. Further work correlated the plant fossils and sediments of the original younger *Dryas* interval with broader evidence of colder-than-previous climates in Europe, such as tundra-like pollen assemblages (Watts, 1977; Björck and Möller, 1987) and glacial readvances (Gray and Lowe, 1977). Radiocarbon dating placed the interval between 11,000 and 10,000 ¹⁴Cyr B.P., which Mangerud et al. (1974) designated as the Younger Dryas chronozone (YDC). With calibration (Stuiver et al., 1998), the chronozone dates from ca 12,900 to ca 11,100 cal yr B.P., and well-dated, high-resolution records in Greenland and Europe have constrained the age of the cold North Atlantic conditions to between 12,600 ± 200 and 11,550 ± 90 cal yr B.P. (Brauer et al., 1999). The INTIMATE group (Björck et al., 1998) has recommended age boundaries of 12,650 and 11,500 cal yr B.P., as well as a revised event terminology based on numbered stadials and interstadials in the Greenland ice cores. For simplicity, we have designating the cold interval from 12,900 to 11,600 cal yr B.P. in the GISP2 ice core (Stuiver et al., 1995) as the YDC for this paper, and we note that the age discrepancies of several centuries between definitions of the YDC are indistinguishable at the level of radiocarbon age control considered here. Similarly, the age of the Bölling warming in the GISP2 record, 14,600 cal yr B.P., is indistinguishable from

14,700 cal yr B.P. (Björck et al., 1998) and ca 15,000 cal yr B.P. used here.

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