

Response of tundra ecosystem in southwestern Alaska to Younger-Dryas climatic oscillation

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Abstract

Climatic warming during the last glacial–interglacial transition (LGIT) was punctuated by reversals to glacial-like conditions. Palaeorecords of ecosystem change can help document the geographical extent of these events and improve our understanding of biotic sensitivity to climatic forcing. To reconstruct ecosystem and climatic variations during the LGIT, we analyzed lake sediments from southwestern Alaska for fossil pollen assemblages, biogenic-silica content (BSiO₂%), and organic-carbon content (OC%). *Betula* shrub tundra replaced herb tundra as the dominant vegetation of the region around 13 600 cal BP (cal BP: ¹⁴C calibrated calendar years before present), as inferred from an increase of *Betula* pollen percentages from <5% to >20% with associated decreases in Cyperaceae, Poaceae, and *Artemisia*. At c. 13 000 cal BP, a decrease of *Betula* pollen from 28 to <5% suggests that shrub tundra reverted to herb tundra. Shrub tundra replaced herb tundra to resume as the dominant vegetation at 11 600 cal BP. Higher OC% and BSiO₂% values suggest more stable soils and higher aquatic productivity during shrub-tundra periods than during herb-tundra periods, although pollen changes lagged behind changes in the biogeochemical indicators before c. 13 000 cal BP. Comparison of our palaeoecological data with the ice-core δ¹⁸O record from Greenland reveals strikingly similar patterns from the onset through the termination of the Younger Dryas (YD). This similarity supports the hypothesis that, as in the North Atlantic region, pronounced YD climatic oscillations occurred in the North Pacific region. The rapidity and magnitude of ecological changes at the termination of the YD are consistent with greenhouse experiments and historic photographs demonstrating tundra sensitivity to climatic forcing.

Keywords: abrupt climatic change, North Pacific, SW Alaska, tundra ecosystem, vegetational response to climatic forcing, Younger Dryas

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Introduction

Climatic warming during the last glacial–interglacial transition (LGIT) was interrupted by abrupt reversals in at least parts of the globe (e.g. Wright, 1989; Alley, 2000; Ammann *et al.*, 2000). Understanding the causes of these reversals is necessary to improve our knowledge of the behavior of the global climate system. A crucial first step towards causal explanations is to document the geographical extent, magnitude, and character of these climatic oscillations. The YD (c. 13 000–11 600 cal BP;

Alley *et al.*, 1993) is the most prominent among the climatic oscillations of the LGIT, which has been particularly well documented in the North Atlantic region. There, numerous palaeoecological studies have shown that the YD climatic reversal resulted in pronounced ecosystem changes (e.g. Ammann *et al.*, 2000; Mayle & Cwynar, 1995). In the North Pacific region, recent climate simulations (Mikolajewicz *et al.*, 1997; Renssen, 1997) and palaeoenvironmental proxy studies (e.g. Engstrom *et al.*, 1990; Mathewes, 1993; Peteet & Mann, 1994; Hu *et al.*, 1995; Lozhkin *et al.*, 2001) also offered evidence for a YD-type climatic reversal. However, the effects of YD climatic changes on the terrestrial ecosystems of this region remain poorly understood (Brubaker *et al.*, 2001).

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We report here the results of pollen, organic-carbon, and biogenic-silica analyses of the LGIT section of a sediment core from Nimgun Lake (59°33'N, 160°46'W, 320 m asl) in southwestern Alaska. The chronology of the record is based on six AMS ^{14}C dates on plant macrofossils, and our analyses have the resolution of 35–100 years per sample for key intervals. Our data show that marked changes in terrestrial and aquatic environments occurred in response to climatic fluctuations during the YD. This study offers a high-temporal-resolution record with solid chronological controls to understand climatic and ecosystem changes during the LGIT in the North Pacific high-latitude region.

Study site

Nimgun Lake is located in the southwestern flank of the Ahklun Mountains within the Togiak National Wildlife Refuge in southwestern Alaska (Fig. 1). At present, the lake is 1.0 km long and 0.4 km wide, with a surface area constituting ~15% of its total catchment area. Its bathymetry is simple with a single, 8-m-deep basin situated near its western end. The lake occupies a nearly closed basin within hummocky drift deposited during the early Wisconsin Arolik Lake advance (Briner & Kaufman, 2000). The drift was deposited in a glacial trough carved in Mesozoic siliciclastic metasedimentary rocks. The region is within the modern Transitional Zone between maritime and continental climates. Within the region, ericaceous (*Ericaceae*), willow (*Salix*), and birch (*Betula glandulosa/nana*) shrubs are the common members of the primary vegetation cover in the mountains (Gallant *et al.*, 1995). Scrub and graminoid communities dominated by willow (*Salix*), alder (*Alnus*), birch, and ericaceous species are common in valleys and lower mountain slopes. Valley bottoms near the coast to the west support tree stands of white spruce (*Picea glauca*) and balsam poplar (*Populus balsamifera*). The vegetation surrounding Nimgun Lake is shrub tundra with alder thickets on the hillsides.

Materials and methods

Two sediment cores of *c.* 5 m were recovered from the deepest part of the lake using a 7.6-cm diameter percussion corer. Subsamples were taken from the longer of the two cores for the following analyses.

One-cubic-centimeter sediment from each level was prepared for pollen analysis according to standard techniques (Faegri *et al.*, 1992) and by sieving through a 7- μm mesh to remove fine particles (Cwynar *et al.*, 1979). *Lycopodium* spore tablets were added to each sample prior to preparation. At least 300 pollen grains were counted for each level under 400X and 1000X (oil immersion) magnifications with a Nikon600 microscope. Pollen zones were delineated by CONISS, a stratigraphically constrained cluster analysis linked with the TILIA program (Grimm, 1992). Detrended correspondence analysis (DCA, an ordination technique) of the pollen data was run with PCORD software.

For the measurement of organic-carbon content (OC%), freeze-dried samples were combusted in an oxygen atmosphere to convert organic and inorganic carbon to CO_2 . CO_2 was then swept to a UIC Carbon Coulometer where it was detected by coulometric titration. Inorganic carbon was below the analytical detection limit at all levels in the Nimgun Lake sediment. Biogenic silica (BSiO_2) was extracted with 10% Na_2CO_3 and determined with a spectrophotometer (Spectronic Genesys5) following Mortlock & Froelich (1989). The percentage of mineral matter other than BSiO_2 (%MM) was calculated as $100 - \% \text{OC} - \% \text{BSiO}_2$.

Sediment samples from selective levels were washed with distilled water through a 150- μm mesh to concentrate plant macrofossils for ^{14}C dating. ^{14}C analyses were conducted at Woods Hole Oceanographic Institute (with target preparation at the Institute of Arctic and Alpine Research, University of Colorado), University of Arizona, and Lawrence Livermore National Laboratory. Seven AMS ^{14}C ages of plant macrofossils (Table 1, Fig. 2) were converted to calendar years with CALIB 4.2 (<http://Departmentswashington.edu/qil/>). We exclude the age at 419–423 cm for developing the age model

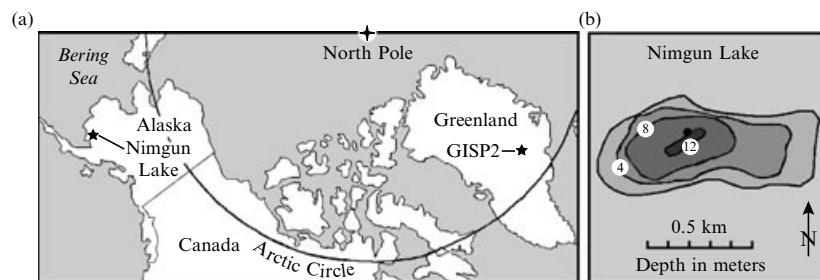


Fig. 1 (a) Map showing locations of Nimgun Lake in Alaska and GISP2 (Greenland Ice Sheet Project II) in Greenland, and (b) Bathymetry of Nimgun Lake and coring location (black dot).

Table 1 Radiocarbon Dates, Nimgun Lake

Depth (cm)	¹⁴ C age (yr BP)	Calibrated age (cal yr BP; midpoint & 1 σ range)	Laboratory number	Dated material
344	7620 ± 50	8381 (8406) 8417	NSRL 10557	Wood
379	9030 ± 85	10156 (10212) 10238	AA 26594	Wood
401	9370 ± 50	10503 (10565) 10672	CAMS 73100	Twig
406–407	9380 ± 110	10428 (10623) 10735	CAMS 76365	Mixed plant tissue
419–423	10500 ± 80	12330 (12472) 12817	NSRL 11551	Graminoid fragments & seeds
465–467	11070 ± 60	12988 (13094) 13154	NSRL 11552	Twig & moss fragments
493–495	12110 ± 85	13853 (14103) 15115	AA 10557	Moss & graminoid fragments

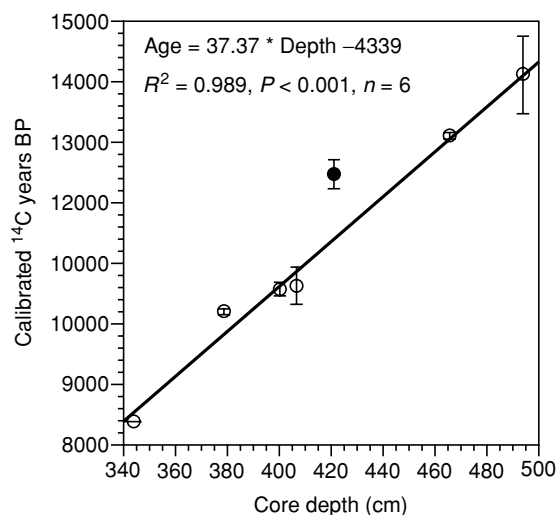


Fig. 2 Age–depth model of the sediment core from Nimgun Lake. Error bars indicate 1-sigma ranges of calibrated calendar-year dates. Age represented by solid symbol was excluded in calculating the age model (see text).

because the macrofossil-poor sediment yielded insufficient carbon mass for a standard AMS analysis. Furthermore, it deviates from the linear trend defined by the other six ages. We fit a linear regression model through the remaining six dates:

$$\text{Age (cal yr BP)} = 37.37 * \text{depth (cm)} - 4339$$

$$(R^2 = 0.989, P < 0.001, n = 6)$$

This model was applied to estimate age scales for all proxy records (Figs 3 and 4). As with all ¹⁴C chronologies, the accuracy of the modelled ages depends on various factors, including analytical errors (Table 1), uncertainties related to ¹⁴C plateaus (Lotter *et al.*, 1992), and differences between the modelled and actual sedimentation rates.

Ecosystem and climatic reconstruction

In this section, we use pollen-assemblage data (Fig. 3) to infer past vegetation and climate. Pollen accumulation

rates (PARs; not presented) show patterns similar to those of pollen percentages except where noted, and we do not discuss PARs in detail. The vegetational and climatic inferences are supplemented by stratigraphic changes in BSiO₂% and OC% (Fig. 4). BSiO₂% primarily reflects changes in the productivity of diatoms, which are the main primary producers in many lakes (Wetzel, 1983). OC% is potentially related to aquatic productivity. However, the detailed patterns of the BSiO₂% and OC% profiles differ substantially, suggesting that aquatic production was not the main driver of OC% changes. We use decreased OC% values as a proxy indicator of increased soil erosion, possibly resulting from increased soil solifluction, increased eolian mineral input, and decreased vegetation cover (Engstrom & Wright, 1984; Mayle & Cwynar, 1995).

Between *c.* 15000 and 13600 cal BP (pollen zone NG1), the dominance of Cyperaceae (40–65%), Poaceae (10–35%), and *Artemisia* (Fig. 3) in the pollen assemblages suggests that herb tundra prevailed over the landscape around Nimgun Lake. The presence of several minor pollen/spore taxa (e.g. Tubuliforae, *Thalictrum*, Chenopodiaceae, and *Encalypta*) indicates that vegetation cover was sparse and that soil disturbance was frequent (Hulten, 1968; Cwynar, 1982; Oswald *et al.*, 1999; Oswald, 2002). The regional climate was likely too severe to support shrub communities. However, during this period, OC% and BSiO₂% increased from 0.12 to 3.25% and from 4.58 to 18.56%, respectively. These increases suggest decreased soil erosion and increased aquatic productivity, probably as a result of climatic warming.

Around 13600 cal BP (beginning of pollen zone NG2), the sharp rise of *Betula* pollen from 2 to 25% and the decrease of Cyperaceae pollen from 66 to 37% indicate an abrupt transition of herb tundra to shrub tundra dominated by *Betula glandulosa/nana*. This vegetation interpretation is based on modern pollen-vegetation relationships from the North American Arctic (Anderson *et al.*, 1991). The establishment of shrub tundra at this time probably resulted from regional climatic warming

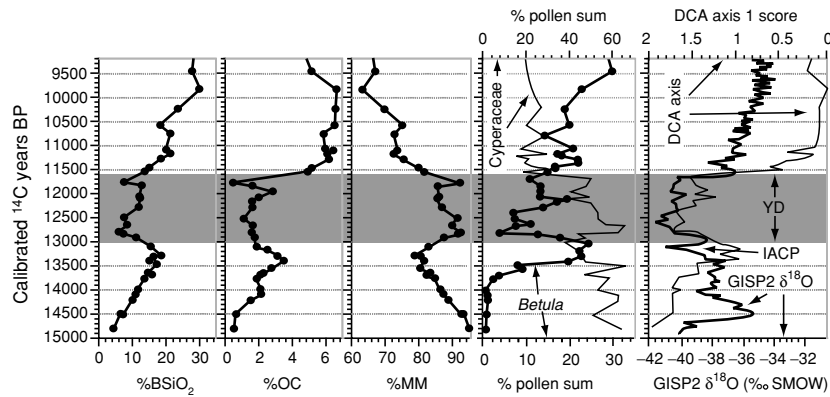


Fig. 4 Comparisons of biogenic silica (BSiO₂), organic carbon (OC), total mineral matter other than biogenic silica (MM), selective pollen types, and pollen DCA axis 1 scores from Nimgun Lake with the $\delta^{18}\text{O}$ record from GISP2 (Stuiver *et al.*, 1995).

At *c.* 11 600 cal BP (beginning of pollen zone NG4), an abrupt decrease in Cyperaceae pollen from 50 to 18% along with increased *Betula* pollen suggests that shrub tundra replaced herb tundra to resume its dominance of the regional landscape. Multivariate analyses (DCA and CONISS) show that the composition of plant communities changed more at this boundary than at any other zone boundaries (Figs 3 and 4). The transition does not appear to be a mere recovery to the pre-YD vegetational composition of *c.* 13 600–13 000 cal BP. In particular, the increase of *Betula* pollen percentages is more gradual than its decline at the onset of the YD and appears to be part of the overall recovery that began during the YD. However, *Betula* PARs increase abruptly by ~ 4 fold (from 204–784 grains $\text{cm}^{-2}\text{yr}^{-1}$) to reach values higher than at any other older levels, suggesting the rapid expansion of its populations at this time. Poaceae also expanded markedly at this time; similar Poaceae peaks have also been observed at other sites in southwestern Alaska (Axford, 2000; Brubaker *et al.*, 2001). The climatic and ecological significance of these Poaceae peaks is unclear, although glacial geomorphic data from that region (Axford, 2000) indicate glacial retreat corresponding to the Poaceae peak, suggesting warm and/or dry climatic conditions. The increases in shrub taxa (e.g. *Betula*, Ericales) along with major increases in the pollen/spore abundances of Polypodiaceae, *Sphagnum*, and Apiaceae within this zone all clearly indicate climatic warming and increased moisture availability *c.* 11 600 cal BP, marking the end of the YD and the onset of the Holocene. Corroborating this climatic interpretation, soil stability and aquatic productivity increased, as indicated by the major increases of OC% and BSiO₂%.

Discussion

Evidence is accumulating that a YD-type climatic reversal occurred in the high-latitude regions of the North Pacific (e.g. Engstrom *et al.*, 1990; Peteet & Mann, 1994; Epstein,

1995; Hu *et al.*, 1995; Hajdas *et al.*, 1998; Brubaker *et al.*, 2001; Lozhkin *et al.*, 2001). Most of these studies, however, did not offer detailed patterns of YD-related environmental changes because they lacked adequate temporal resolution and/or secure chronological controls. For example, at two other sites in southwestern Alaska, ~ 100 km east of Nimgun Lake, pollen analysis showed a decline in *Betula* shrubs in favour of herbaceous taxa at the onset of the YD, but the chronology of those records was problematic (Hu *et al.*, 1995). Within the limit of ¹⁴C dating accuracy, our data from Nimgun Lake offer new compelling evidence for ecosystem and climatic changes coincident with the YD climatic reversal. These data support recent GCM modelling results indicating a YD climatic cooling in the North Pacific region (Mikolajewicz *et al.*, 1997; Renssen, 1997). Mikolajewicz *et al.* (1997), for example, estimated that a 2–4 °C cooling occurred during the YD in the North Pacific region, resulting both from decreased sea-surface temperatures and from altered patterns of atmospheric circulation.

The ice-core records from Greenland offer important insights into abrupt climatic changes in the North Atlantic region (Alley *et al.*, 1993; Stuiver *et al.*, 1995; Alley, 2000). Comparison of ecosystem changes at Nimgun Lake with YD climatic oscillations in Greenland shows both similarities and discrepancies (Fig. 4). In particular, pollen DCA axis 1 values at Nimgun Lake and GISP2 $\delta^{18}\text{O}$ data exhibit strikingly consistent patterns for the onset at 13 000 cal BP through the termination at 11 600 cal BP of the YD. At GISP2, the YD was characterized by a relatively gradual onset and an extremely rapid termination (Alley, 2000; Alley *et al.*, 1993; Taylor *et al.*, 1997). Our pollen DCA axis 1 profile from Nimgun Lake also shows this pattern. Although our sample resolution and chronology are inadequate for determining the rates of ecological changes, the rapidity and magnitude of the changes in OC% and vegetation at Nimgun Lake were remarkable at the end of the YD. Between two samples ~ 150 years apart, OC% values more than doubled,

Cyperaceae pollen percentages decreased by three fold, and DCA axis 1 exhibited the most change in the entire record. No depositional hiatus exists in the sediment core to cause these abrupt changes in our pollen and geochemical records. These rapid ecosystem changes reflected abrupt climatic warming and a marked increase in effective moisture at the termination of the YD. Our data thus suggest that, as in the North Atlantic region, pronounced environmental oscillations occurred in the North Pacific region during the LGIT.

In contrast to the consistency described above, the initial establishment of *Betula* shrub tundra c. 13 500 cal BP at Nimgun Lake lagged behind climatic warming at GISP2 by at least 1000 years (Fig. 4). The exact length of this time lag is uncertain, because the ^{14}C date of $12\,110 \pm 85$ BP sits on a ^{14}C plateau, which yields multiple calibrated ^{14}C dates with a 1-sigma range of 1262 years. Nevertheless, a time lag in vegetational response indeed occurred; soil stabilization and increased lake productivity, as inferred from increased OC% and BSiO₂%, both occurred before the pollen-inferred transition from herb tundra to shrub tundra at 13 600 cal BP. Similarly, the vegetational reversal from shrub tundra to herb tundra at 13 000 cal BP lagged behind reductions in soil stability and aquatic productivity by up to 400 years (Fig. 4).

Our data from Nimgun Lake thus show a rapid vegetational change at the termination of the YD and significant vegetational lags behind climatic change at and before the onset of the YD. Ecological and climatic factors responsible for this contrast are difficult to decipher. The rapid shrub expansion during the 20th century warming on the North Slope of Alaska (Sturm *et al.*, 2001) would argue against any inherent rate limitations for shrubs to invade herb tundra. The time lag of the initial *Betula* expansion at 13 600 cal BP might have been caused by the lack of suitable soil conditions for the establishment of *Betula* shrub tundra, whereas the time lag of the subsequent decline at 13 000 cal BP was probably related to the inertia of established *Betula* populations. The rapid shift from herb tundra back to shrub tundra at 11 600 cal BP probably reflected the local availability of *Betula* seeds and existence of suitable soil conditions.

The rate of vegetational response to abrupt climatic change remains a controversial issue. High-resolution studies of annually laminated lake sediments provide evidence that terrestrial vegetation responded to past climatic fluctuations without any time lag (Brauer *et al.*, 1999; Ammann *et al.*, 2000; Tinner & Lotter, 2001). For example, Tinner & Lotter (2001) showed that deciduous forests changed rapidly with a pronounced climatic reversal at 8200 cal BP in central Europe. In contrast, time lags of several decades to several centuries in

vegetational response to climatic forcing have been documented by other palaeoecological analyses (Pennington, 1986; Mayle *et al.*, 1993) and ecological simulations (Chapin & Starfield, 1997). For example, detailed pollen data of the YD in maritime Atlantic Canada (Mayle & Cwynar, 1995) suggest that the response of some taxa, especially dwarf birch, lagged behind the onset of the climatic change by ~50 years.

An alternative interpretation for the differences in the timing of pollen, OC%, and BSiO₂% is that terrestrial vegetation, soil stability, and lake productivity responded to different climatic events. For example, the declines of OC% and BSiO₂% that took place prior to the reversal of *Betula* shrub tundra to herb tundra 13 500–13 000 cal BP might have resulted from climatic cooling near the end of the Bolling-Allerod warm period before the YD, which included the abrupt but brief Inter-Allerod Cold Period (IACP; Alley *et al.*, 1993; Stuiver *et al.*, 1995). The magnitude and/or duration of these pre-YD cooling events may have been inadequate to induce a major terrestrial vegetational change. In fact, *Betula* appeared to have reached peak population density at Nimgun Lake during IACP (Fig. 4), possibly responding to adequate warmth along with increased effective moisture. However, our chronology is not secure enough for such precise comparisons.

A confounding factor in the comparison of our record from southwestern Alaska with the GISP $\delta^{18}\text{O}$ data is the sea-level history of the Bering Sea, which must have exerted major controls over the regional climate of southwestern Alaska during the LGIT (Bartlein *et al.*, 1991). Eustatic sea level was lower during the Late Glacial than at present, and large areas of Beringia that are now flooded were exposed (Hopkins, 1982; Elias *et al.*, 1996). These conditions would have resulted in a dry, continental climate in the present coastal areas of southwestern Alaska. The time lag of vegetational change at Nimgun Lake behind climatic warming recorded at GISP2 thus may have resulted from the lack of effective moisture for the establishment of shrub tundra because of lower sea level and greater continentality. This factor, however, cannot be rigorously assessed until we know the detailed flooding history of the Bering Land Bridge (Hopkins, 1982).

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