Quaternary Science Reviews 34 (2012) 66–80

Contents lists available at SciVerse ScienceDirect

Quaternary Science Reviews

journal homepage: www.elsevier.com/locate/quascirev

Climatic and megaherbivory controls on late-glacial vegetation dynamics: a new, high-resolution, multi-proxy record from Silver Lake, Ohio

Jacquelyn L. Gill[a,*], John W. Williams[a], Stephen T. Jackson[b], Jeffrey P. Donnelly[c], Grace C. Schellinger[a]

[a] University of Wisconsin, Department of Geography, 550 North Park St., Madison, WI 53713, USA
[b] University of Wyoming, Department of Botany, 3165, 1000 E. University Ave., Laramie, WY 82071, USA
[c] Woods Hole Oceanographic Institution, Mail Stop 22, Woods Hole, MA 02543, USA

ARTICLE INFO

Article history:
Received 26 September 2011
Received in revised form
9 December 2011
Accepted 10 December 2011
Available online 24 January 2012

Keywords:
Fire
Late-glacial
Megafauna
No-analog communities
Ohio
Pleistocene extinctions
Pollen
Sporormiella
X-ray fluorescent spectroscopy

ABSTRACT

Novel plant assemblages are a long-recognized feature of late-glacial North America, but identifying their causes has been hampered by inaccurate radiocarbon chronologies and the multiplicity of ecological and climatic events during the late Pleistocene. Recently we reported that the formation of no-analog vegetation may have been linked to declines in Pleistocene megafaunal communities, based on pollen and spores from the coprophilous fungus *Sporormiella* at sites in Indiana and New York. We present a new, multi-proxy analysis from Silver Lake, OH, which 1) updates the radiocarbon chronology of a classic pollen record with a well-established zone of no-analog vegetation, 2) combines a new sub-centennial pollen record with charcoal, *Sporormiella*, and x-ray fluorescence (XRF) spectroscopy analyses for an integrated record of landscape change before, during, and after the period of no-analog vegetation, and 3) replicates both the absolute and relative temporal patterns of landscape change at Appleman Lake, IN. At Silver Lake, the decline in *Sporormiella* at 13.9 ka BP was immediately followed by the formation of novel plant assemblages, as well as the highest-magnitude charcoal peak in the record. Increased Ca and Sr concentrations during the no-analog interval indicate either increased moisture, increased input of nutrients from deciduous litter, or both. The duration of the no-analog assemblages (13.9–11.8 ka BP) roughly corresponds to the period of peak insolation dissimilarity, but is more temporally constrained than previously reported in subcontinental-scale syntheses (17–11 ka BP). We propose a hierarchy of controls on late-glacial plant communities, where biotic interactions such as megaherbivory mediate climate-driven vegetation change.

1. Introduction

Pollen assemblages with no modern analog are a long-recognized feature of late-glacial paleoecological records in eastern North America (Wright et al., 1963; Cushing, 1967; Jackson and Williams, 2004). Relative to modern pollen samples, no-analog assemblages include unusual combinations of boreal (e.g. *Picea*, *Larix*) and temperate deciduous taxa (e.g., *Quercus*), low abundances of other taxa common to modern boreal forests (e.g. *Pinus*, *Betula*, *Alnus*), anomalously high abundances of certain deciduous taxa (e.g. *Fraxinus, Ostrya*-type), and low to moderate abundances of herbaceous taxa such as *Artemisia* and *Ambrosia* (suggesting parkland-like conditions) (Winter, 1962; McAndrews, 1966; Ogden, 1966; Davis, 1967, 1969; Wright, 1967). The lack of modern analogs has complicated the interpretation of these assemblages. Early explanations invoked the differential rates of response among taxa (migration lags), but these hypotheses have been discarded (Jackson and Williams, 2004), due to 1) evidence that at a sub-continental scale the formation of no-analog communities preceded the period of fastest climate change (Williams et al., 2001) and 2) the presence of macrofossil evidence for temperate hardwoods in the late-glacial upper Midwest (Jackson and Williams, 2004). Most recent explanations for the formation and maintenance of late-glacial no-analog vegetation invoke various climate factors (Williams et al., 2001; Grimm and Jacobson, 2004; Jackson and Williams, 2004; Gonzales and Grimm, 2009), but new evidence from lake-sediment records from Appleman Lake, IN, and sites in New York links the development of no-analog vegetation to declining megafaunal population abundances and altered fire regimes, indicating that top-down trophic processes also may have shaped novel plant communities (Gill et al., 2009). In this paper, we improve understanding of the late-glacial no-analog communities

* Corresponding author. Tel.: +1 608 890 1188 (work), +1 608 354 6874 (cell); fax: +1 608 259 3991.
E-mail addresses: jlgill@wisc.edu (J.L. Gill), jww@geography.wisc.edu (J.W. Williams), Jackson@uwyo.edu (S.T. Jackson), jdonnelly@whoi.edu (J.P. Donnelly), schellinger@wisc.edu (G.C. Schellinger).

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doi:10.1016/j.quascirev.2011.12.008

and their primary drivers by comparing temporal changes in pollen assemblages with other physical and biological changes, including fire regimes, megafaunal population change, chemostratigraphy, and physical characteristics of lake sediments. Our study updates previous work at Silver Lake, OH (Table 1), a site with a classic record of late-glacial vegetation history and formation of no-analog plant associations (Ogden, 1966).

Late-glacial and early Holocene climates were strongly influenced by higher-than-present insolation, lower-than-present CO_2 concentrations, and the effects of the nearby Laurentide Ice Sheet (LIS) on regional radiative budgets and surface atmosphere circulation patterns (Ruddiman, 2007). Early climatic hypotheses for late-glacial no-analog vegetation invoked lower-than-present seasonal temperature ranges to allow for the co-existence of temperate and boreal taxa. Bryson and Wendland (1967) proposed that the LIS blocked the southern incursion of Arctic air, and adiabatically warming air off the ice sheets resulted in warmer and drier winters. However, Williams et al. (2001) reported that periods of no-analog community formation corresponded to increased temperature seasonality and dryer-than-present climates during the late-glacial to early-Holocene transition, based on paleoclimatic simulations. The high abundance of pollen from *Fraxinus nigra* (black ash), which grows in mesic to hydric conditions today (Wright and Rauscher, 1990), indicates that conditions in the Midwest were much wetter than present (Grimm and Jacobson, 2004). Gonzales et al. (2009), using an expanded response surface method, argued for wetter-than-present winters with no change in temperature seasonality. However, the expanded response surface method is based on the assumption that the distribution of pollen abundances along environmental gradients are stable over time, when in fact they may have varied at glacial–interglacial timescales (Veloz et al., in press). Amidst these differing explanations, perhaps the most plausible climatic interpretation for the no-analog communities of the upper Midwest is that insolation regimes and temperatures were more seasonal and moisture availability was regionally higher than at present, either due to enhanced precipitation (Gonzales and Grimm, 2009) or because these landscapes were newly deglaciated and poorly drained (Yansa, 2006).

In addition to novel climates and plant associations, late-glacial and early Holocene landscapes also experienced unprecedented disruptions to their faunal communities. While the causes of the extinction of 34 genera of megafaunal browsers, grazers and their predators have been much-discussed (Koch and Barnosky, 2006), the influence of Pleistocene megaherbivores in shaping late-glacial vegetation dynamics remains poorly understood. A recent paleovegetation record from Appleman Lake, IN, (Gill et al., 2009) suggests that the increased abundances of broadleaved deciduous trees during the interval of peak no-analog vegetation may have resulted from herbivory release following the collapse of megaherbivore populations. The Appleman Lake study combined traditional pollen and charcoal records with the analysis of spores from the dung fungus *Sporormiella*, which was used as a qualitative proxy for the functional extinction of megaherbivores (Davis and Shafer, 2006). The results at Appleman indicated that megaherbivores influenced vegetation composition, ecosystem structure, and ecosystem function, and that their local extinction allowed for the expansion of broad-leaved deciduous trees and the buildup of landscape fuel loads. These findings are consistent with the results of modern megaherbivore studies, such as hardwood suppression by moose (*Alces alces*) on Isle Royale (McInnes et al., 1992), documented impacts of megaherbivores on sapling recruitment (Hester et al., 2000), and effects of herbivores and fire on tree-grass coexistence in savannas (Sankaran et al., 2005).

The data at Appleman Lake, however compelling, represent a single site that may be complicated by age-model errors and sedimentological variations, including sand and gravel layers in the deeper horizons (Gill, 2008; Gill et al., 2009). Here, a new multi-proxy, well-dated, high-resolution record from Silver Lake presents an opportunity to test the hypotheses raised by Gill et al. (2009). Silver Lake, OH (Ogden, 1966) is located in the heart of the no-analog communities (Shane, 1987; Williams et al., 2001; Grimm and Jacobson, 2004) (Fig. 1), with a previously identified no-analog interval (Table 1); Ogden (1966) concluded that for Zone 2, “no modern equivalent vegetation type has been found.” Our new Silver Lake record improves upon Ogden’s chronology, which utilized widely spaced bulk-sediment ^{14}C dates that may have had millennial-level offsets due to carbon sourced from Paleozoic carbonates (Ogden, 1966). We analyzed the Silver Lake sediments for pollen, *Sporormiella*, macroscopic charcoal, loss-on-ignition, and X-ray fluorescence (XRF) spectroscopy analyses to better understand the ecological and climatic history of the landscape around Silver Lake before, during, and after the megafaunal declines and formation of the no-analog plant associations. This record contributes to a new generation of high-resolution, well-dated records from the upper Midwest (e.g. Nelson et al., 2006; Umbanhowar et al., 2006; Gonzales and Grimm, 2009) that can be used to study species responses to abrupt climate change, map spatiotemporal patterns of the rise and decline of the no-analog plant communities, and study the interacting effects of climate change, human arrival (Waters et al., 2011), and megafaunal declines on late-glacial vegetation dynamics (Johnson, 2009).

2. Material and methods

2.1. Site description

Silver Lake (Fig. 1) (Logan County, OH, 40°21′15″ N, 83°48′45″W, 332 m MSL) is a compound kettle located on the Central Lowland Till Plain, and was formed when the Miami Sublobe of the Lake Erie Lobe of the Laurentide Ice Sheet retreated from what is now the Farmersville Moraine (Ogden, 1966; Ekberg et al., 1993). The lake is bordered by YMCA Camp Willson to the east and a raised railroad bed to the north. Silver Lake has an apparently man-made outlet channel on the west side (steep sides, uniform, <1 m deep). Marl

Table 1
Pollen Zones from Ogden (1966) and this paper, including age estimates and relevant phenomena. All ages are calendar ka BP.

Ogden, 1966				This paper		
Zone	Climate interpretations	Vegetation	Calibrated age interval	Zone	Phenomena	Age
1	cold to cool, moist	*Picea–Abies* maximum	Est. 14 ka–11 ka	A	High *Picea*, *Sporormiella*	18.5 ka–13.9 ka
2	dry, warmer	*Pinus* max, *Quercus*, no-analog	Est. ∼11 ka–9.8 ka	B	High *Fraxinus*, *Ostrya*, no-analog	13.9 ka–12.7 ka
				C1, C2	High *Pinus*, *Abies*, 2nd *Picea* peak	12.7 ka–10.9 ka
3a	warm, wetter	deciduous forest, *Fagus* max (6 ka)	9.8 ka to ∼4 ka	D	High *Quercus*, *Ulmus*, *Carya*,	10.9 ka–8.2 ka
3b	warm, drier	*Quercus–Carya* max, *Fagus* min	4 ka–1.3 ka		*Not recorded*	
3c	cooler, moister	modern	1.3 ka–260			
3d	as present	sharp rise in *Ambrosia*	260–present			