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Millennial-scale variability during the last glacial in vegetation records from North America

Gonzalo Jiménez-Moreno[a,*], R. Scott Anderson[b], Stéphanie Desprat[c], Laurie D. Grigg[d], Eric C. Grimm[e], Linda E. Heusser[f], Bonnie F. Jacobs[g], Constancia López-Martínez[h], Cathy L. Whitlock[i], Debra A. Willard[j]

[a] *Departamento de Estratigrafía y Paleontología, Universidad de Granada, 18002 Granada, Spain*
[b] *Environmental Programs, School of Earth Sciences & Environmental Sustainability, Northern Arizona University, Flagstaff, AZ 86011, USA*
[c] *Laboratoire des Sciences du Climat et l'Environnement, 91191 Gif sur Yvette Cedex, France*
[d] *Geology and Environmental Science Department, Norwich University, VT 05663, USA*
[e] *Illinois State Museum, Research and Collections Center, 1011 East Ast St., Springfield, IL 62703, USA*
[f] *20 North Broadway, White Plains, NY 10601, USA*
[g] *Roy M. Huffington Department of Earth Sciences, Southern Methodist University, Dallas TX 75275, USA*
[h] *EPHE, UMR-CNRS 5805 EPOC, Université Bordeaux 1, Avenue des Facultés, Talence 33405, France*
[i] *Department of Earth Sciences, Montana State University, Bozeman, MT 59717, USA*
[j] *U.S. Geological Survey, 926A National Center, Reston, VA 20192, USA*

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ABSTRACT

High-resolution pollen records from North America show that terrestrial environments were affected by Dansgaard-Oeschger (D-O) and Heinrich climate variability during the last glacial. In the western, more mountainous regions, these climate changes are generally observed in the pollen records as altitudinal movements of climate-sensitive plant species, whereas in the southeast, they are recorded as latitudinal shifts in vegetation. Heinrich (HS) and Greenland (GS) stadials are generally correlated with cold and dry climate and Greenland interstadials (GI) with warm-wet phases. The pollen records from North America confirm that vegetation responds rapidly to millennial-scale climate variability, although the difficulties in establishing independent age models for the pollen records make determination of the absolute phasing of the records to surface temperatures in Greenland somewhat uncertain.

1. Introduction

High-resolution analyses of ice cores from Greenland (Svensson et al., 2006, 2008) and Antarctica (EPICA Community Members, 2006) have documented frequent rapid, high-amplitude climatic changes during the late Quaternary, antiphased between the two hemispheres (Blunier and Brook, 2001; Wolff et al., in this volume). These millennial-scale changes in climate are of two types: Dansgaard-Oeschger (D-O) cycles (Dansgaard et al., 1984), characterized by short-term warming followed by cooling, and Heinrich Stadials (HS), recorded by Heinrich layers in the north Atlantic (Heinrich, 1988) and characterized by cooling (see Sánchez Goñi and Harrison, in this volume). A key question is whether and how these rapid changes in high-latitude climates are registered by terrestrial ecosystems in temperate and tropical regions (see Sánchez Goñi and Harrison, in this volume).

Geographical proximity suggests that North American vegetation should show a response to the millennial-scale climate variations registered in Greenland ice core and North Atlantic marine records. Millennial-scale variability has been recognized in a broad range of environmental indicators from terrestrial and marine settings in and around North America during Marine Isotope Stages 2–4. Millennial-scale cold events, for example, have been recognized as intervals of lower sea-surface temperatures in records from offshore sediments along the North Pacific and North Atlantic margins (Behl and Kennett, 1996; Kennett et al., 2000; Vautravers et al., 2004), increases in terrestrial plant lipid data in marine records indicating intensified westerlies in southeastern North America (López-Martínez et al., 2006), glacier advances in the western mountain ranges (Clark and Bartlein, 1995; Benson et al., 1996; Phillips et al., 1996; Bischoff and Cummins, 2001), excursions in speleothem isotope records (Denniston et al., 2007) and in lake-level changes in the western U.S. (Allen and Anderson, 1993; Benson et al., 1996, 1998, 2003; Oviatt, 1997; Wilkins and Currey, 1997; Tchakerian and Lancaster, 2002). However, examination of vegetation changes during the Younger Dryas cold interval (YD;

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* Corresponding author. Tel.: +34 958 243347; fax: +34 958 248528.
E-mail address: gonzaloj@ugr.es (G. Jiménez-Moreno).

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Heinrich Event 0) shows that, unlike the widespread cooling registered in pollen records from Western Europe (Lowe et al., 1994; Walker, 1995; Fletcher et al., 2007), the vegetation response in North America was complex and variable. Vegetation changes consistent with a cooling are registered in the northeast but the signal becomes less pronounced and more variable toward the south and west (Peteet, 1995; Shuman et al., 2002). This may be related to the scarcity of AMS-dated high-resolution records from those areas but is clearly not an issue of sensitivity: high-resolution pollen records from North America show a rapid and sensitive vegetation response to small fluctuations in temperature and effective moisture on decadal timescales during the Holocene (see e.g. Viau et al., 2002; Brown et al., 2005; Willard et al., 2005; Jiménez-Moreno et al., 2008). Thus, it seems worthwhile to examine high-resolution pollen analysis of continuous sedimentary sequences to document the regional response of vegetation to rapid climatic changes during the last glacial.

Documentation of the vegetation response to millennial-scale climate variability during the glacial will allow comparison with other regions and a deeper exploration of the nature of regional climate changes associated with millennial-scale variability (see Harrison et al., this issue). Earlier work, for example, has highlighted the contrast between wet conditions in Florida coincident with dry conditions in the Mediterranean during Heinrich Stadials (Sánchez Goñi et al., 2002) and interpreted this asymmetry as reflecting a persistent positive mode of NAO-like (North Atlantic Oscillation; Hurrell, 1995; Barlow et al., 1997) conditions between eastern North America and southern Europe (Sánchez Goñi et al., 2002). High-resolution records from Europe and the North Atlantic suggest that Heinrich Stadials may have been divided into two phases, with an increased frequency of positive NAO during the second half of the interval (Naughton et al., 2009). Additional information from North America is required to test these interpretations.

Here, we present a synthesis of high-resolution vegetation records from North America spanning part or all of the last glacial (Marine Isotope Stage, MIS, 4–2, 73.5–14.7 cal yr BP; Tables 1 and 2; Sánchez Goñi and Harrison, in this volume) to determine whether and how regional vegetation and climates responded to the millennial-scale variability detected in Greenland and the North Atlantic. We use terminology as defined in Sánchez Goñi and Harrison (in this volume) and age assignments for D-O cycles and Greenland Interstadials (GI) derived from the ice core record from Greenland as defined by Wolff et al. (in this volume) and for Heinrich Stadials (HS) and Marine Isotope Stages (MIS) by Sánchez Goñi and Harrison (in this volume).

2. Chronological framework for recognition of millennial-scale variability in North America

Determination of whether there is a vegetation response in North America to the millennial-scale climate variability observed in Greenland, and comparisons of the nature of that response between sites in different regions, is crucially dependent on being able to erect independent age models for the pollen records. Age models for sedimentary sequences included in this study rely on three dating methods: radiometric dating (^{14}C, U–Th), tephrochronology, and oxygen isotope stratigraphy (Table 2).

Most age determinations were generated from accelerator mass spectrometry (AMS) ^{14}C dates of plant macrofossils. However, some sites include conventional or AMS dates on bulk sediment or calcareous microfossils, which may negatively affect the reliability of the chronologies (Colman et al., 2002; Grimm et al., in press). The radiocarbon dates from the published records have generally been calibrated to calendar years (1 ka = 1000 cal yr BP; Present = AD 1950): dates younger than 20 ka were calibrated to calendar years using a number of different versions of CALIB (http://calib.qub.ac.uk/calib/) and a variety of methods have been used for calibration of older dates (e.g., Bard et al., 1990; Mazaud et al., 1991; Thouveny et al., 1993; Kitagawa and van der Plicht, 1998; and Fairbanks et al., 2005: http://radiocarbon.ldeo.columbia.edu/research/radcarbcal.htm). Although the differences between the various calibrations used could pose problems for inter-site comparisons, these are likely to be minor and thus we have made no attempt to create new age models based on a single calibration. The only exception is Camel Lake: the published age model for Camel Lake is in radiocarbon years (Watts et al., 1992); we have used CALIB 5.0.2 and Fairbanks et al. (2005) to produce a calibrated age model. Chronologies from most records are built using a high number of calibrated radiocarbon dates, and the last ~40 ka are fairly well-constrained in the North American records (Table 2). For older sediments, errors in radiocarbon dates are inherently larger and calibration is less precise.

At some sites, the radiocarbon-based chronologies have been supplemented by additional dating. U–Th dating was used in the Bear Lake record (Colman et al., 2006), and tephrochronology was used to date some sequences, particularly from the Pacific Northwest. In the Carp Lake record, for example, the ages of Mount St. Helens Ye, Mazama ash, and an unnamed Mount St. Helens tephra were used, together with radiocarbon dates, to develop an age–depth model (Whitlock et al., 2000).

Stratigraphic constraints, specifically accepted ages of MIS boundaries, have been used to fine-tune age models for both continental (i.e., Carp Lake; Whitlock and Bartlein, 1997) and marine cores. In the marine records (i.e., cores W8709A-13PC and ODP Site 893A; Table 2), these constraints are based on independent oxygen isotopic records. The Carp Lake age model was refined by incorporating the ages of MIS boundary 4/5 and MIS 5e, tuning the pollen and lithologic data to SPECMAP (Whitlock et al., 2000).

The use of different calibration techniques, the broad statistical uncertainties associated with older radiocarbon dates and other radiometric techniques, and of different age-model construction methods means that there are many uncertainties associated with the use of existing chronologies to investigate millennial-scale variability. This may limit our ability to make fine-scale comparisons. Nevertheless, many records have a large number of radiocarbon dates and the age control is probably sufficient to compare events during MIS 2 and early MIS 3. For events older than 40 ka, temporal correlation is more tenuous. Nevertheless, it is still worthwhile to see whether there are vegetation changes that appear to reflect millennial-scale climate changes and to investigate whether there are coherent patterns of change through time even if the exact timing of these changes is more difficult to ascertain.

3. Registration of D-O events in pollen records

Seventy-four North American records span part or all of MIS 2 through MIS 4 (Table 1; Fig. 1) and were developed from continuous marine sediments, deep and shallow lakes, and wetlands, as well as discontinuous alluvial sediments, loess, and buried soils. Sites are located over a range of elevations from marine sites below sea level to 2,800 m elevation above sea level (Table 1). Pollen records for MIS 2 and MIS 3 are fairly abundant, but those that extend to MIS 4 are sparse (Fig. 1). Despite the large number of sites, comparatively few records are of sufficiently high resolution (<1000 years/pollen sample) to show rapid vegetation changes. South of the Last Glacial Maximum (LGM) ice sheet boundary, there are few natural lakes and wetlands that have had uninterrupted sedimentation since MIS 4. The exceptions are limited to the western United States and Florida (Fig. 1; Table 2). In addition, arid conditions during the

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Table 1

Sites from North America covering part or all of MIS 4, 3 and 2. The sites have been classified according to sampling resolution (high-resolution are sites with sampling resolution < 1000 years) and according to the length of the interval covered. Sites are organized by regions and listed in the order discussed in the text, from Northwest to the Southeast North America.

Site name	Map Code	Site type	Latitude (°)	Longitude (°)	Elevation (m)	Period covered	Sampling Resolution (Yr/sample)	Reference
Vancouver Island	DW	Terrestrial	49.31	124.31	90	MIS 3 and 2	Low	Alley (1979)
Kalaloch Sea Cliff	K	Terrestrial	47.60	124.36	19	MIS 4, 3 and 2	High	Heusser (1972)
Humptulips	H	Terrestrial	47.28	123.90	100	MIS 4, 3 and 2	Low	Heusser and Heusser (1990); Heusser et al. (1999)
Davis Lake, Central Puget Lowland	DaL	Terrestrial	46.58	122.25	282	MIS 2	High but too young	Barnosky (1981)
Battle Ground Lake	BGL	Terrestrial	45.80	122.48	155	MIS 2	High but too young	Barnosky (1985)
Fargher Lake	FL	Terrestrial	45.88	122.58	200	MIS 3 and 2	High	Grigg and Whitlock (2002)
Carp Lake	CaL	Terrestrial	45.91	120.88	714	MIS 4, 3 and 2	High	Whitlock and Bartlein (1997); Whitlock et al. (2000)
Little Lake	LL	Terrestrial	44.16	123.58	217	MIS 3 and 2	High	Grigg et al. (2001)
Y7211-1	Y72	Marine	43.25	126.36	Marine	MIS 4, 3 and 2	High	Heusser (1998)
W8709A-13PC	P1	Marine	42.11	125.75	Marine	MIS 4, 3 and 2	High	Pisias et al. (2001)
W8709A-8PC	P1	Marine	42.25	127.66	Marine	MIS 3 and 2	High	Heusser (1998)
EW9504-17PC	P2	Marine	42.23	125.81	Marine	MIS 4, 3 and 2	High	Pisias et al. (2001)
ODP Site 1019	1019	Marine	41.66	124.91	Marine	MIS 4, 3 and 2	High	Pisias et al. (2001)
Tulelake	T	Terrestrial	41.88	121.51	1230	MIS 4, 3 and 2	Low	Adam et al. (1989)
Clear Lake	CL	Terrestrial	39.06	122.80	405	MIS 4, 3 and 2	Low	Adam et al. (1981)
V1-80-P3	V1	Marine	38.41	123.78	Marine	MIS 2	High but too young	Heusser (1998)
Owens Lake	OL	Terrestrial	36.36	117.95	1085	MIS 4, 3 amd 2	Low	Woolfenden (2003)
Searles Lake	SL	Terrestrial	35.71	117.35	493	MIS 4, 3 and 2	Low	Litwin et al. (1999)
F2-92-P3	F2	Marine	35.61	121.60	Marine	MIS 3 and 2	High	Heusser (1998)
ODP Site 893A	893	Marine	34.28	120.03	Marine	MIS 4, 3 and 2	High	Heusser (1998, 2000)
Diamond Valley	DV	Terrestrial	34.68	116.98	483	MIS 3	Low	Anderson et al. (2002)
F2-92-P29	F2-P29	Marine	32.90	119.73	Marine	MIS 3 and 2	High	Heusser (1998)
DSDP Site 480	480	Marine	27.90	111.66	Marine	No age model available	Low	Heusser (1982)
Hedrick Pond	HP	Terrestrial	43.75	110.60	2073	MIS 2	High	Whitlock (1993)
Bear Lake	BL	Terrestrial	41.95	111.30	1805	MIS 4, 3 and 2	High	Jiménez-Moreno et al. (2007)
Indian Cove Well	ICW	Terrestrial	41.30	112.58	1281	MIS 4, 3 and 2	Low	Davis (1998); Davis and Moutoux (1998)
Walker Lake	WL	Terrestrial	35.38	111.71	2500	MIS 3 and 2	High	Berry et al. (1982); Adam et al. (1985); Hevly (1985)
Potato Lake	PL	Terrestrial	34.45	111.33	2222	MIS 3 and 2	High	Anderson (1993)
Jacob Lake	JL	Terrestrial	34.41	110.83	2285	MIS 3 and 2	Low	Jacobs (1983)
Benny Creek	BC	Terrestrial	34.03	109.45	2865	MIS 3 and 2	Low	Merrill and Péwé (1977)
Hay Lake	HL	Terrestrial	34.00	109.50	2780	MIS 3 and 2	High	Jacobs (1985)
Willcox Playa	WiP	Terrestrial	32.21	109.81	1267	MIS 4, 3 and 2	Low	Martin (1963); Davis (1998)
Dead Man Lake	DML	Terrestrial	36.23	108.95	2780	MIS 3 and 2	High	Wright et al. (1973)
San Agustín Lake	SAL	Terrestrial	33.86	108.25	2069	MIS 3 and 2	Low	Markgraf et al. (1984)
Wolf Creek	WC	Terrestrial	46.11	94.11	375	MIS 2	Low	Birks (1976)
Biggsville Quarry	BQ	Terrestrial	40.88	90.88	190	MIS 3 and 2	Low	Baker et al. (1989)
Vandalia area	VA	Terrestrial	38.91	89.16	160	MIS 3 and 2	1300 yr	Grüger (1972a, b)
Arrington Marsh	AM	Terrestrial	39.48	95.58	280	MIS 3 and 2	Low	Grüger (1973)
Cheyenne Bottoms	CB	Terrestrial	38.46	98.66	547	MIS 3 and 2	Low	Fredlund (1995)
Ozark Springs	OS	Terrestrial	38.06	93.33	~240	MIS 3 and 2	Low	King (1973)
Powers Fort Swale	PFS	Terrestrial	36.60	90.58	91	MIS 2	Low	Royall et al. (1991)
Rayburn's Dome	RD	Terrestrial	32.46	93.16	61	MIS 2	Low	Kolb and Fredlund (1981)
Tunica Hills	TH	Terrestrial	~31.25	~91.46	~50	MIS 2	Low	Jackson and Givens (1994)
Patschke Bog	PB	Terrestrial	30.36	97.11	142	MIS 2	Low	Camper (1991)
Rogers Lake	RL	Terrestrial	41.36	72.11	10	MIS 2	Low	Davis (1967, 1969); Davis and Deavey (1964)
Tannersville Bog	TB	Terrestrial	41.03	75.26	277	MIS 2	Low	Watts (1979)
Criders Pond	CrP	Terrestrial	39.96	77.55	289	MIS 2	Low	Watts (1979)
Battaglia Bog	BB	Terrestrial	41.13	81.31	320	MIS 2	Low	Shane (1975)
Buckle's Bog	BuB	Terrestrial	39.56	79.26	814	MIS 2	Low	Maxwell and Davis (1972)
Cranberry Glades	CG	Terrestrial	38.18	80.25	1050	MIS 2	Low	Watts (1979)
Browns Pond	BP	Terrestrial	38.15	79.61	620	MIS 2	Low	Kneller and Peteet (1993, 1999)
Jackson Pond	JP	Terrestrial	37.45	85.71	250	MIS 2	Low	Wilkins et al. (1991)
Rockyhock Bay	RB	Terrestrial	36.16	76.68	6.1	MIS 3 and 2	Low	Whitehead (1981)
Bladen County	BC	Terrestrial	34.58	78.45	17	Not clear	Low	Frey (1951, 1953)
Piedmont Carolinas (4 localities)	PC	Terrestrial	35.00	82.00	300	MIS 3	Low	Whitehead and Barghoorn (1962)
Anderson Pond	AP	Terrestrial	36.03	85.50	150	MIS 2	Low	Delcourt (1979)
Pigeon Marsh	PM	Terrestrial	34.61	85.40	512	MIS 2	Low	Watts (1975)
Quicksand & Bob Black Ponds	QP, BBP	Terrestrial	34.31	84.86	285	MIS 2	Low	Watts (1970)
Green pond	GP	Terrestrial	34.31	84.86	235	MIS 3 and 2	Low	Watts (1973)
White Pond	WP	Terrestrial	34.16	80.76	90	MIS 2	Low	Watts (1980)
Clear Pond	CP	Terrestrial	33.18	81.00	42	MIS 2	Low	Hussey (1993); Watts et al. (1996)

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Table 1 (*continued*)

Site name	Map Code	Site type	Latitude (°)	Longitude (°)	Elevation (m)	Period covered	Sampling Resolution (Yr/sample)	Reference
Goshen Springs	GS	Terrestrial	31.71	86.13	105	MIS 3 and 2	Low	Delcourt (1980)
Camel Lake	CamL	Terrestrial	30.26	85.01	20	MIS 3 and 2	High	Watts et al. (1992)
Sheelar Lake	ShL	Terrestrial	29.83	81.95	47	MIS 2	High	Watts and Stuiver (1980)
Lake Tulane	LT	Terrestrial	27.58	81.50	36	MIS 4, 3 and 2	High	Grimm et al. (1993); Grimm et al. (2006)
MD02-2579	MD02	Marine	27.78	82.51	Marine	MIS 2	High but too young	Willard et al. (2007)
Joe Lake	JoL	Terrestrial	66.76	157.21	183	MIS 3 and 2	Low	Anderson (1988)
Kayak Lake	KL	Terrestrial	67.11	160.38	190	MIS 3 and 2	Low	Anderson (1985)
Imuruk Lake	IL	Terrestrial	65.58	163.25	311	MIS 3 and 2	Low	Colinvaux (1964); Colbaugh (1968)
Norton Sound Core 76-121	NS	Marine	63.88	162.70	Marine	MIS 2	Low	Ager (2003)
Zagoskin Lake	ZL	Terrestrial	63.43	162.10	7	MIS 3 and 2	Low	Ager (2003)
Tungak Lake	TL	Terrestrial	61.41	164.18	24	MIS 2	Low	Ager (1982)
Bristol Bay	BrB	Terrestrial	58.61	158.23	12	MIS 3 and 2	Low	Ager (1982)
Ongivinuk Lake	OnL	Terrestrial	59.56	159.36	163	MIS 2	Low	Hu et al. (1995)

Table 2

Chronological information for sites providing high-resolution pollen records from North America. The dating methods for each MIS are shown. Sites are organized by regions and listed in the order discussed in the text.

Site	Interval	Resolution Yr/sample	Chronological control						
			AMS	14C	U/Th	Other radiometric	Tephra	Varved	Tuning
Fargher Lake	MIS 2	510	2						
	MIS 3	270	5				1		Three dates derived from Carp Lake pollen stratigraphy and layer count
Carp Lake	MIS 2	540	3						
	MIS 3	630	3				1		
	MIS 4	660							Tuning of pollen record to MIS 4-5 boundary (73.9 ka), and the age of the peak of MIS 5e (125 ka)
Little Lake	MIS 2	215	7						
	MIS 3	260	4						
W8709A-13PC	MIS 2	380	11						
	MIS 3	430	2						Correlation $\delta^{18}O$ from benthic foraminifera to V23-81
	MIS 4								Tuning of $\delta^{18}O$ with age of MIS 3-4 boundary
EW9504-17PC	MIS 2	280	1						Correlation of benthic foraminifera $\delta^{18}O$ to W8709A-13PC
	MIS 3	460	1						
	MIS 4	600							
F2-92-P3	MIS 2	510	2						
	MIS 3	550							
ODP Site 893A	MIS 2	250	10						
	MIS 3	220	10						Correlation isotopic stratigraphy and pollen to SPECMAP
	MIS 4	230							Correlation isotopic stratigraphy and pollen to SPECMAP
F2-92-P29	MIS 2	950	3						
	MIS 3	920	1						
Bear Lake	MIS 2	650							Linear Age model (Kaufman et al., 2009). 0 mblf = 0 yr = 2000 AD), the last local glacial maximum (10.8 mblf = 17.8 ka)
	MIS 3	680							Laschamp excursion (26.5 mblf = 41 ka),
	MIS 4	620				U/Th date (66.4 mblf = 127.7 ka).			
Walker Lake	MIS 2	55	7						
	MIS 3	50	6						
Potato Lake	MIS 2	980		1					
	MIS 3	990		1					
Hay Lake	MIS 2	1000		3					
	MIS 3	960		2					
Camel Lake	MIS 2	950	2						
	MIS 3	300	1	2					
Lake Tulane	MIS 2	260	13						
	MIS 3	480	9						Correlation pollen stratigraphy to age HS5
	MIS 4	480							Correlation pollen stratigraphy to age HS6
MD02-2579	MIS 2	47	13						Correlation pollen stratigraphy to Bølling/Allerød

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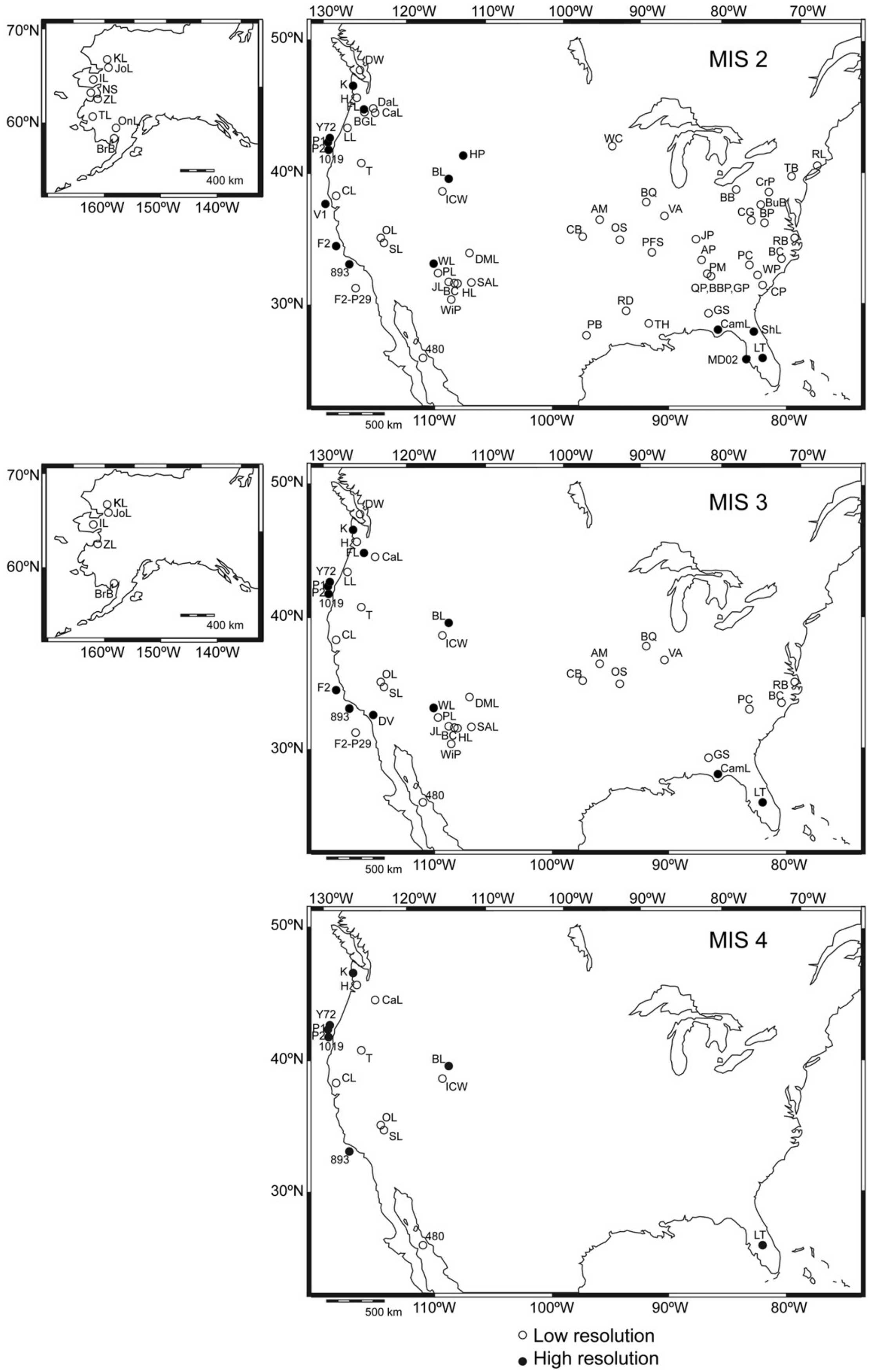

Fig. 1. Location of marine and terrestrial sites covering part or all of MIS 4, 3 and 2. The sites have been classified according to sampling resolution (high-resolution, low-resolution) and according to the length of the interval covered. High-resolution are sites with sampling resolution ≤ 1000 years. Site code names are shown in Table 1.

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Holocene have tended to desiccate basins and erode glacial sediments (Benson et al., 1990; Gill, 1996; Woolfenden, 2003).

Pollen records spanning MIS 2, 3 and 4 in North America show the strong influence of orbital-scale climate variations on vegetation change (Adam et al., 1981; Heusser and Heusser, 1990; Heusser et al., 1995; Whitlock and Bartlein, 1997; Litwin et al., 1999; Woolfenden, 2003; Jiménez-Moreno et al., 2007). These records document gradual shifts in vegetation between periods dominated by cold-climate species during glaciations and those dominated by warmer-climate species during interglaciations. With respect to the last glacial, both high- and low-resolution pollen records generally show the coldest conditions occurring during MIS 2 (including the LGM), with MIS 3 being a long and relatively warm interval, and an earlier cold period (MIS 4). MIS 4 was nevertheless warmer than MIS 2. High-resolution pollen records show millennial-scale vegetation changes (Fig. 2; Table 2) superimposed on these orbital-scale changes.

To facilitate comparisons among the different high-resolution sites, the vegetation records are summarized in terms of major biomes (or mega-biomes using the terminology of Harrison and Prentice, 2003; Table 3). The allocation of pollen types to biomes was not done in a formal way, for example following the biomization algorithm developed by Thompson and Anderson (2000). Instead, the pollen taxa have been informally grouped into major biomes, using a consistent definition of the taxa found in each vegetation type across the region (Table 3). We differentiated the following major biomes for North America: tundra, boreal forest, temperate forest, warm-temperate forest, southern pine forest, and grassland and dry shrubland. Some pollen taxa are representative of cosmopolitan species that contribute to many different biomes (e.g. *Pinus*); these species are placed in a separate category (shown as non-significant in Table 3 and on Fig. 2). Each of these biomes encompasses a range of vegetation types: the grassland and dry shrubland biome, for example, includes both chaparral and Florida scrub and represent somewhat different climates: chaparral is characteristic of regions with winter precipitation while Florida scrub occurs in regions with summer precipitation. We differentiate southern pine forest from the warm-temperate forest biome. The southern pine forest includes several pine species (including slash pine: *Pinus elliottii*, sand pine: *Pinus clausa*, longleaf pine: *Pinus palustris*, loblolly pine: *Pinus taeda*, and shortleaf pine: *Pinus echinata*) that are adapted to a climatic regime with hot, humid summers and drier winters whereas warm-temperate forests can occur over a wider range of warm climates, including those with summer drought and winter rainfall.

Fig. 2 shows the reconstructed vegetation changes, expressed in terms of these major biomes, through time for each high-resolution site from North America. Given that the response of vegetation to rapid climate changes may not necessarily involve a shift between biomes, we have also plotted changes in a taxon (or a group of taxa) that we identified by the original authors as displaying D-O variability at that site (see references for each individual site for more information). A summary of vegetation and inferred climatic changes through D-O cycles at each high-resolution site from North America are shown in Tables 4 and 5. The qualitative inferred climatic changes (Table 5) are mainly based on subjective interpretation of the observed vegetation shifts in terms of likely climate changes by the original authors.

3.1. *Pacific Northwest*

Six pollen records from the Pacific Northwest region (Kalaloch, Fargher Lake, Carp Lake, Little Lake, W8709A-13 and EW9504-17) document millennial-scale variability in vegetation and climate during all or parts of MIS 2, 3, and 4 (Heusser, 1998; Whitlock and Grigg, 1999; Pisias et al., 2001). A high-resolution pollen record from a coastal outcrop at Kalaloch on the Olympic Peninsula, Washington (Heusser, 1972, 1977) suggests open mixed boreal and temperate forest during MIS 3 and 4, with varying abundances of *Tsuga heterophylla*, *Tsuga mertensiana*, *Picea* and *Pinus*. High abundance of herbaceous taxa suggest a period of tundra between 21.5 and 15.4 ka, followed by closed boreal forest of *Pinus*, *Picea*, and *T. mertensiana* from 15.4 to 10.5 ka (Heusser, 1985). Though poorly-dated (and therefore not shown in Fig. 2), the sequence documents several fluctuations in the relative abundance of tundra and mixed boreal and temperate forest taxa between ca 70 ka and ∼17 ka. Heusser (1972) attributed these shifts to oscillations between cold and warm conditions and matched these changes with the timing of advances and retreats of the Cordilleran Ice Sheet in the Puget Lowland. The lack of a well-resolved age model precludes correlation of these changes with specific climatic events in Greenland, but nevertheless indicates that millennial-scale variability is registered by vegetation from this region.

The record from Fargher Lake in the foothills of the Cascade Range in southwestern Washington (Grigg and Whitlock, 2002) is dated using seven AMS radiocarbon dates on charcoal, terrestrial plant macrofossils, and humic acids (Grigg and Whitlock, 2002; Table 2). The age of the bottom of the core, from ca 45–58 ka, is less well-constrained and was dated using ages derived from the Carp Lake pollen stratigraphy and varve counts (Grigg and Whitlock, 2002; Table 2). This record indicates a period characterized by an open boreal forest (parkland) and colder and effectively wetter conditions than present from 58 to 44 ka, followed by a period dominated by temperate conifers and somewhat warmer conditions between 44 and 32 ka, and a mix of open boreal forest (parkland) with tundra vegetation with colder and drier-than-present conditions between 32 and 20 ka. During the early part of MIS 3 (58–45 ka), oscillations in the abundance of arboreal pollen (Table 4) record millennial-scale variability and imply shifts between cool-wet and cold-dry conditions (Table 5). The latter part of MIS 3 (45–27 ka) is characterized by repeated shifts between temperate forest conifers (mostly *T. heterophylla*) and boreal forest conifers (*T. mertensiana* and *Picea*). A decrease in arboreal taxa and an increase in non-arboreal taxa after 35 ka mark the transition to colder conditions towards the end of MIS 3 (Grigg and Whitlock, 2002). Abrupt increases in boreal and temperate forest pollen at Fargher Lake during MIS 3 occur at 1–3 ka intervals and generally correlate with the Greenland surface temperatures during GI 2, 6, 7, 8, 9–10, 11, 12, 13, 15 and 16 (Fig. 2) as well as to warm sea-surface temperatures in the Santa Barbara Basin (Grigg and Whitlock, 2002). During MIS 2, small increases in the percentages of temperate forest taxa (*T. heterophylla*, *Pseudotsuga*, and Cupressaceae) relative to those of high-elevation boreal forest taxa (*Picea*, *T. mertensiana*, and Poaceae) suggest slightly warmer conditions at 25 ka and between 23 and 21 ka. Small increases in the boreal forest conifer *T. mertensiana* at 27 and 22.5 ka also imply brief periods of increased effective moisture but do not correlate as well with ocean changes in the Santa Barbara Basin.

A ca 125 ka pollen record from Carp Lake in the southwestern Columbia Basin, Washington was also analyzed in detail to show millennial-scale variability (Whitlock and Bartlein, 1997; Whitlock et al., 2000). The age model for MIS 2–4 is fairly well-constrained and was dated using 6 AMS radiocarbon dates on bulk sediment samples, the Mt. St. Helens layer C tephra, and tuning of pollen record to the MIS 4–5 boundary (73.9 ka; Whitlock et al., 2000). The pollen record shows vegetation dominated by *Pinus* and *Artemisia* during MIS 4, with more boreal and temperate forest vegetation between 73 and 58.3 ka and more open vegetation (with more elements included in the grassland and dry shrubland biome) between 58.3 and 43.2 ka. From 43.2 to 30.9 ka, the vegetation

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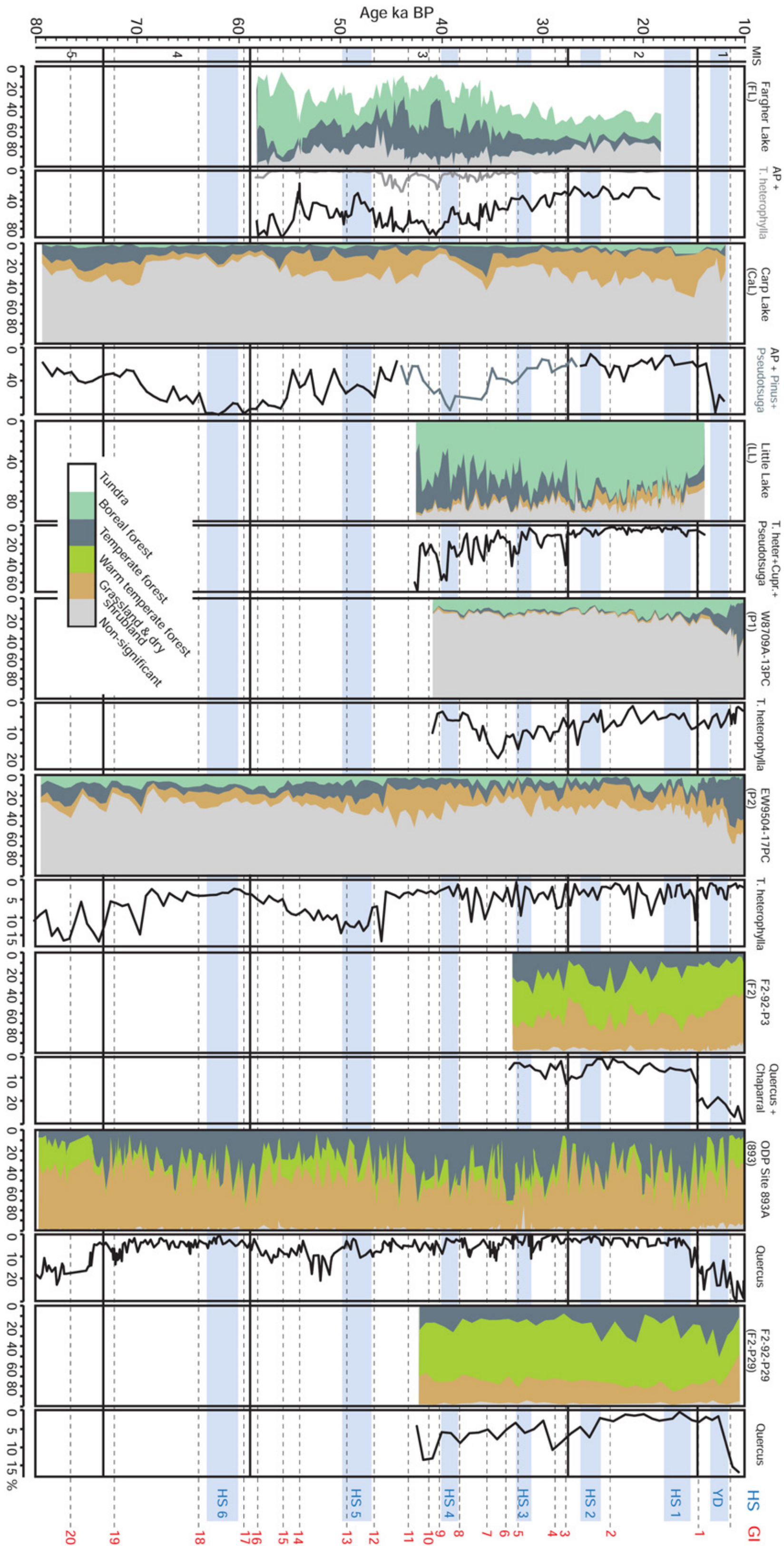

Fig. 2. Vegetation changes through MIS 4, 3 and 2 at high-resolution terrestrial sites in North America. The pollen taxa have been grouped into major vegetation types using the mega-biomes as defined by Harrison and Prentice (2003; see also pollen site publications for complete description). For each site, the second panel shows changes in a taxon (or group of taxa, defined) that demonstrate D-O variability most clearly at that site. For the purposes of this paper we chose to use the Marine Isotope Stage (MIS) boundary ages from Martinson et al. (1987). In this respect, MIS 1 sites date from the present to 14,700 cal yr BP; MIS 2 sites date from 14,700 to 27,500 cal yr BP; MIS 3 sites date from 27,500 to 59,000 cal yr BP; and MIS 4 sites date from 59,000 to 73,500 cal yr BP. Ages of D-O warming events in Greenland ice cores are provided by dashed lines (see Wolff et al., in this volume).

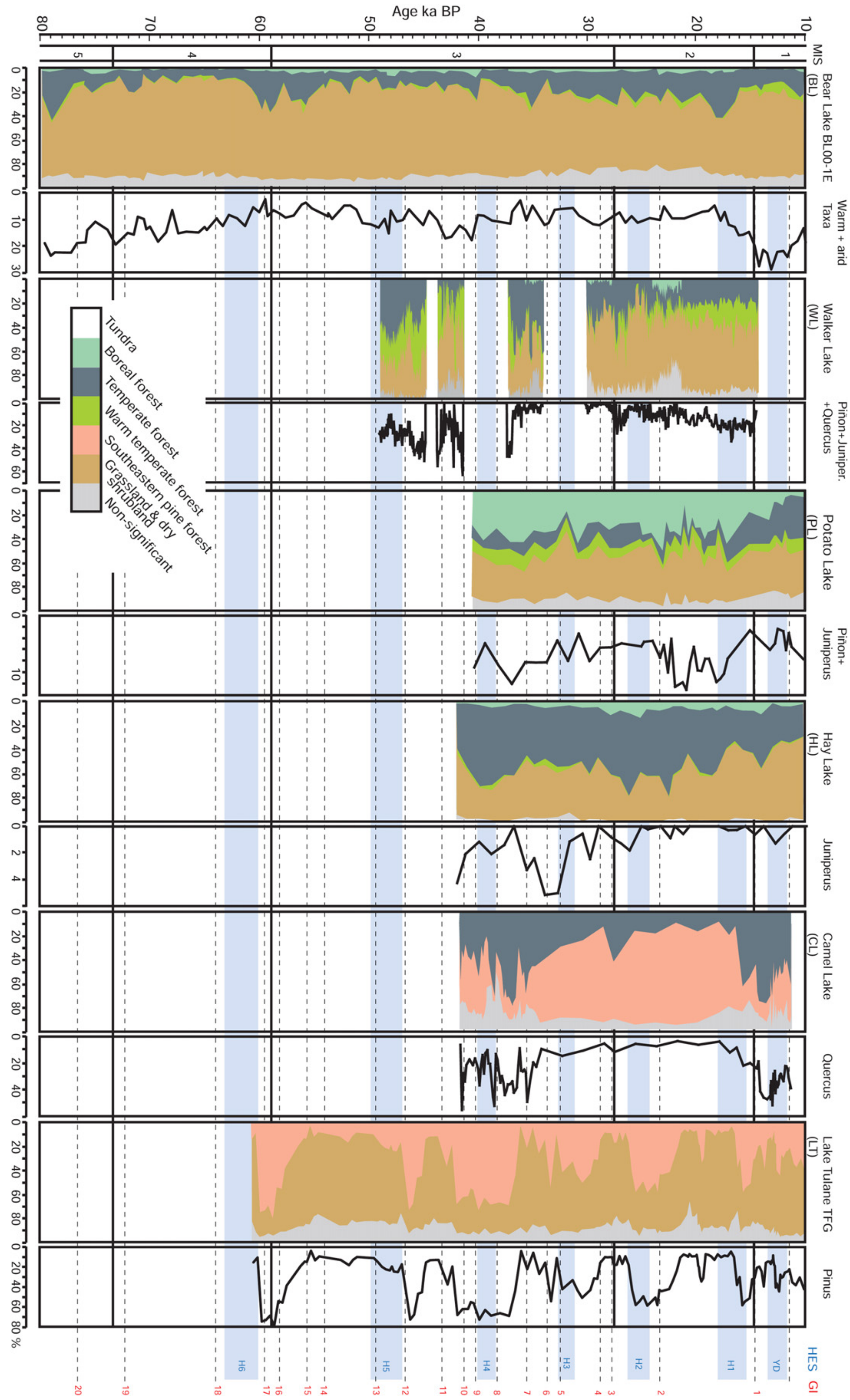

Fig. 2. (*continued*).

consisted of an open forest with a mixture of (high-elevation) boreal and (lower-elevation) temperate species (*Picea*, *Abies*, *Pinus*, *Pseudotsuga*) (Fig. 2, Table 4). It was replaced by tundra or cold steppe vegetation (here in the grassland biome) between 30.9 and 13.2 ka, and warm steppe vegetation between 13.2 and 9.2 ka. These vegetation changes show transitions in climate from (a) cooler and drier than present in MIS 4 to (b) cooler than present and relatively humid conditions in the early part of MIS 3, to (c) cooler and drier than present in the later part of MIS 3, to (d) cold and dry during MIS 2 (Table 5). Periods of greater forest cover occurred during HS 4, HS 5, and HS 6, whereas tundra vegetation prevailed at the time of YD, HS 1, HS 2, and possibly HS 3 (Whitlock and Grigg, 1999; Grigg et al., 2001). Increases in boreal forest species such as *Picea* relative to non-arboreal tundra or steppe taxa occur immediately following HS 1, HS 2, and possibly HS 3, suggesting warmer conditions most likely representing GI 4-3, 2 and 1, respectively.

The pollen record from Little Lake (Grigg et al., 2001) in the central Coast Range of Oregon spans the last 40 ka. The MIS 2 and MIS 3 chronology at Little Lake is based on eleven AMS radiocarbon dates on wood and charcoal (Table 2). A weighted, second-order polynomial equation was used to construct an age-vs-depth curve for the Little Lake core, allowing comparison of this record to the sea-surface temperatures and sediment bioturbation from the Santa Barbara Basin (Grigg et al., 2001), which was previously correlated to the GISP2 ice core record (Behl and Kennett, 1996; Hendy and Kennett, 2000). The co-occurrence of boreal (*Picea*, *T. mertensiana*) and temperate (*T. heterophylla*, *Pseudotsuga*, and Cupressaceae) forest taxa (Table 4) suggests generally cool and wet conditions prior to 27 ka. After 27 ka increases in boreal forest taxa and non-arboreal pollen indicates further cooling. Increases in temperate forest taxa relative to boreal forest taxa occur in the latter part of MIS 3 (43–27.6 ka) and suggest temperature changes that mark GI 3, 4, 5, 6, 7, 8 and 9 (Grigg et al., 2001). Increases in the boreal taxon *T. mertensiana* in MIS 2 at Little Lake suggest intervals of high effective moisture, and these occur at intervals of 1–3 ka. Increases in the temperate taxon *T. heterophylla* at 25 and 22 ka indicate brief warm periods; the latter interval is coeval with GI 2 (Grigg et al., 2001). Fluctuations in precipitation at Little Lake during MIS 2 do not correlate well with the variability recorded in marine sediments from the Santa Barbara Basin. However, cold and wetter intervals in the Pacific Northwest at 26 and 17 ka coincide well with HS 2 and HS 1 (Whitlock and Grigg, 1999; Table 5).

High-resolution pollen records and radiolarian analyses from cores W8709A-13, W8709A-8, and EW9504-17 taken from the continental margin off the coast of Oregon allow a direct correlation to be made between vegetation and oceanic changes in the Pacific Northwest region (Heusser, 1998; Pisias et al., 2001). Age models are derived from AMS-^{14}C dates on foraminifera (13 dates during MIS 2 and MIS 3 from W8709A-13) and δ^{18}O measurements on benthic foraminifera that provide a link to global stratigraphic frameworks (Table 2; Pisias et al., 2001). The pollen records show that the vegetation during MIS 3 was characterized by a mix of temperate forest taxa (*Pinus* and *T. heterophylla)* and boreal taxa (*Picea* and small amounts of *T. mertensiana*). The progressive decrease in temperate forest taxa such as *T. heterophylla* and *Sequoia* and the increase in non-arboreal taxa suggest that the composition and structure of the coastal landscape became more open, resembling high-elevation environments of the Coast Range today (Heusser, 1998; Table 4). These long-term vegetation changes suggest climate trends paralleling global temperature oscillations (i.e., MIS zonation; Heusser, 1998), with a clear MIS 3 maxima (at around 52 ka) and an oscillating progressive decrease in temperatures until the LGM (~20 ka). Millennial-scale variability in these vegetation records seems to be related mostly to changes in precipitation (Pisias et al., 2001; Tables 4 and 5). HS 6, 4, 2 and 1 are

Table 3
Definition of major biomes from North America in terms of major vegetation types, local vegetation names, and plant functional types (PFTs) and characteristic pollen taxa. Pollen types that are cosmopolitan and thus not indicative of any specific biome are included in the non-significant category.

Mega-biome	Component biomes	Equivalent local vegetation names	Component PFTs	Characteristic pollen taxa
Tundra	Cold steppe-grassland, cushion forb tundra, erect dwarf shrub tundra	High-elevation steppe, prairie	Cold- and frost-tolerant forbs and grasses	*Artemisia*, Poaceae, Cyperaceae, *Geum*, *Polygonum bistortoides*, *Betula*, *Salix*, Saxifragaceae
Boreal Forest	Cold evergreen needle-leaved forest, cold deciduous forest	Subalpine forest	Cold-tolerant evergreen needle-leaved trees, cold-deciduous broadleaved trees	*Picea*, *Abies*, *Betula*, *Tsuga mertensiana*, *Alnus*, *Populus*, *Salix*
Temperate Forest	Cool evergreen needle-leaved forest, temperate deciduous broadleaf forest, cool mixed forest	Montane forest, temperate rain forest	Cool temperate evergreen needle-leaved trees, temperate cold-deciduous broadleaved trees	*Pinus*, *Pseudotsuga*, *Tsuga heterophylla/canadensis*, *Sequoia*, *Picea*, *Abies*, *Populus*, *Carya*, *Acer*, *Quercus*, *Fagus*, *Castanea*, Cupressaceae, *Ulmus*, *Fraxinus*, *Ostrya/Carpinus*, *Betula*, *Alnus*
Warm-temperate Forest	Warm-temperate mixed forest, evergreen broadleaved forest	Savanna, woodland, coastal scrub woodland	Warm-temperate evergreen broadleaved forest, warm-temperate evergreen needle-leaved forest, warm-temperate deciduous needle-leaved forest, warm-temperate broadleaved deciduous forest	*Quercus*, *Prosopis*, *Juniperus*-type, *Pinus edulis*, *Liquidambar*, *Myrica*, *Taxodium*
Southeastern Pine Forest	Warm-temperate evergreen needle-leaved forest	Southern coniferous forest	Warm evergreen needle-leaved forest	*Pinus*
Grassland and Dry Shrubland	Cool and temperate grassland, temperate xerophytic shrubland, steppe	Prairie, desert scrub, chaparral, Florida scrub	Cool and temperate grasses, forbs, eurythermic drought-deciduous broadleaved shrubs, drought-tolerant shrubs, warm-temperate broadleaf shrubs, drought-tolerant forbs, temperate forbs, grasses	Poaceae, *Artemisia*, Amaranthaceae, Asteraceae, *Ephedra*, *Sarcobatus*, *Ambrosia*, *Quercus*, *Carya floridana*, *Ceratiola*, Rhamnaceae
Non-significant				*Pinus* undiff.

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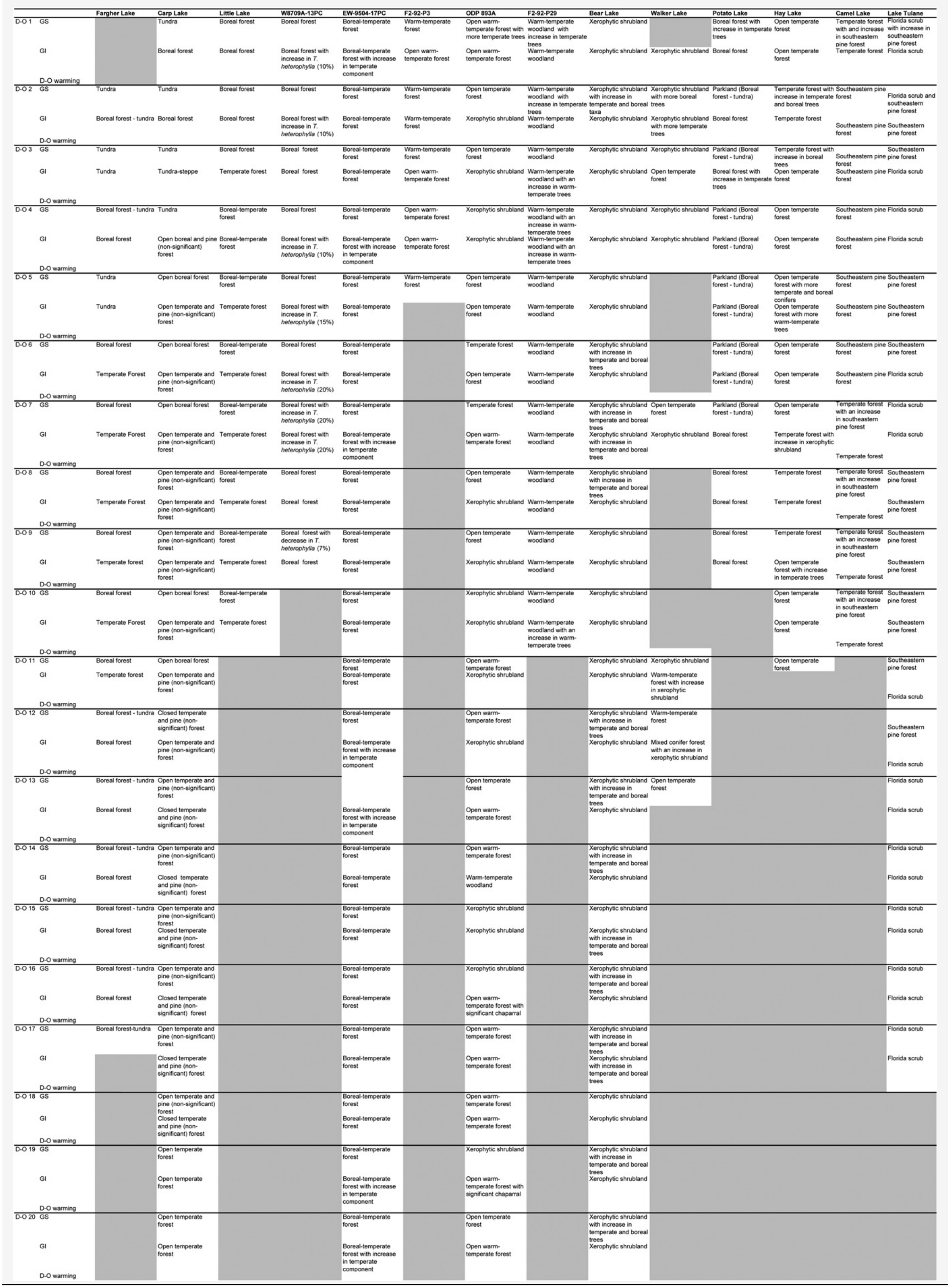
Table 4

Summary of vegetation changes through D-O cycles at individual high-resolution sites from North America. Vegetation descriptions refer to the major biomes defined in Table 3. Note that we could not distinguish between D-O warmings and GI in these records.



		Fargher Lake	Carp Lake	Little Lake	W8709A-13PC	EW-9504-17PC	F2-92-P3	ODP 893A	F2-92-P29	Bear Lake	Walker Lake	Potato Lake	Hay Lake	Camel Lake	Lake Tulane
D-O 1	GS		Tundra	Boreal forest	Boreal forest	Boreal-temperate forest	Warm-temperate forest	Open warm-temperate forest with more temperate trees	Warm-temperate woodland with increase in temperate trees	Xerophytic shrubland		Boreal forest with increase in temperate trees	Open temperate forest	Temperate forest with and increase in southeastern pine forest	Florida scrub with increase in southeastern pine forest
	GI		Boreal forest	Boreal forest	Boreal forest with increase in *T. heterophylla* (10%)	Boreal-temperate forest with increase in temperate component	Open warm-temperate forest	Open warm-temperate forest	Warm-temperate woodland	Xerophytic shrubland	Xerophytic shrubland	Boreal forest	Open temperate forest	Temperate forest	Florida scrub
	D-O warming														
D-O 2	GS	Tundra	Tundra	Boreal forest	Boreal forest	Boreal-temperate forest	Warm-temperate forest	Open temperate forest	Warm-temperate woodland with increase in temperate trees	Xerophytic shrubland with increase in temperate and boreal taxa	Xerophytic shrubland with more boreal trees	Parkland (Boreal forest - tundra)	Temperate forest with increase in temperate and boreal trees	Southeastern pine forest	Florida scrub and southeastern pine forest
	GI	Boreal forest - tundra	Boreal forest	Boreal forest	Boreal forest with increase in *T. heterophylla* (10%)	Boreal-temperate forest	Warm-temperate forest	Xerophytic shrubland	Warm-temperate woodland	Xerophytic shrubland	Xerophytic shrubland with more temperate trees	Boreal forest	Temperate forest	Southeastern pine forest	Southeastern pine forest
	D-O warming														
D-O 3	GS	Tundra	Tundra	Boreal forest	Boreal forest	Boreal-temperate forest	Warm-temperate forest	Open temperate forest	Warm-temperate woodland	Xerophytic shrubland	Xerophytic shrubland	Parkland (Boreal forest - tundra)	Temperate forest with increase in boreal trees	Southeastern pine forest	Southeastern pine forest
	GI	Tundra	Tundra-steppe	Temperate forest	Boreal forest	Boreal-temperate forest	Open warm-temperate forest	Xerophytic shrubland	Warm-temperate woodland with an increase in warm-temperate trees	Xerophytic shrubland	Open temperate forest	Boreal forest with increase in temperate trees	Open temperate forest	Southeastern pine forest	Florida scrub
	D-O warming														
D-O 4	GS	Boreal forest - tundra	Tundra	Boreal-temperate forest	Boreal forest	Boreal-temperate forest	Open warm-temperate forest	Xerophytic shrubland	Warm-temperate woodland with an increase in warm-temperate trees	Xerophytic shrubland	Xerophytic shrubland	Parkland (Boreal forest - tundra)	Open temperate forest	Southeastern pine forest	Florida scrub
	GI	Boreal forest	Open boreal and pine (non-significant) forest	Boreal-temperate forest	Boreal forest with increase in *T. heterophylla* (10%)	Boreal-temperate forest with increase in temperate component	Open warm-temperate forest	Xerophytic shrubland	Warm-temperate woodland with an increase in warm-temperate trees	Xerophytic shrubland	Xerophytic shrubland	Parkland (Boreal forest - tundra)	Open temperate forest	Southeastern pine forest	Florida scrub
	D-O warming														
D-O 5	GS	Tundra	Open boreal forest	Boreal-temperate forest	Boreal forest	Boreal-temperate forest	Warm-temperate forest	Open temperate forest	Warm-temperate woodland	Xerophytic shrubland		Parkland (Boreal forest - tundra)	Open temperate forest with more temperate and boreal conifers	Southeastern pine forest	Southeastern pine forest
	GI	Tundra	Open temperate and pine (non-significant) forest	Temperate forest	Boreal forest with increase in *T. heterophylla* (15%)	Boreal-temperate forest		Open temperate forest	Warm-temperate woodland	Xerophytic shrubland		Parkland (Boreal forest - tundra)	Open temperate forest with more warm-temperate trees	Southeastern pine forest	Southeastern pine forest
	D-O warming														
D-O 6	GS	Boreal forest	Open boreal forest	Boreal-temperate forest	Boreal forest	Boreal-temperate forest		Temperate forest	Warm-temperate woodland	Xerophytic shrubland with increase in temperate and boreal trees		Parkland (Boreal forest - tundra)	Open temperate forest	Southeastern pine forest	Southeastern pine forest
	GI	Temperate Forest	Open temperate and pine (non-significant) forest	Temperate forest	Boreal forest with increase in *T. heterophylla* (20%)	Boreal-temperate forest		Open temperate forest	Warm-temperate woodland	Xerophytic shrubland		Parkland (Boreal forest - tundra)	Open temperate forest	Southeastern pine forest	Florida scrub
	D-O warming														
D-O 7	GS	Boreal forest	Open boreal forest	Boreal-temperate forest	Boreal forest with increase in *T. heterophylla* (20%)	Boreal-temperate forest		Temperate forest	Warm-temperate woodland	Xerophytic shrubland with increase in temperate and boreal trees	Open temperate forest	Parkland (Boreal forest - tundra)	Open temperate forest	Temperate forest with an increase in southeastern pine forest	Florida scrub
	GI	Temperate Forest	Open temperate and pine (non-significant) forest	Temperate forest	Boreal forest with increase in *T. heterophylla* (20%)	Boreal-temperate forest with increase in temperate component		Open warm-temperate forest	Warm-temperate woodland	Xerophytic shrubland with increase in temperate and boreal trees	Xerophytic shrubland	Boreal forest	Temperate forest with increase in xerophytic shrubland	Temperate forest	Florida scrub
	D-O warming														
D-O 8	GS	Boreal forest	Open temperate and pine (non-significant) forest	Boreal-temperate forest	Boreal forest	Boreal-temperate forest		Open temperate forest	Warm-temperate woodland	Xerophytic shrubland with increase in temperate and boreal trees		Boreal forest	Temperate forest	Temperate forest with an increase in southeastern pine forest	Southeastern pine forest
	GI	Temperate Forest	Open temperate and pine (non-significant) forest	Temperate forest	Boreal forest	Boreal-temperate forest		Xerophytic shrubland	Warm-temperate woodland	Xerophytic shrubland		Boreal forest	Temperate forest	Temperate forest	Southeastern pine forest
	D-O warming														
D-O 9	GS	Boreal forest	Open temperate and pine (non-significant) forest	Boreal-temperate forest	Boreal forest with decrease in *T. heterophylla* (7%)	Boreal-temperate forest		Open temperate forest	Warm-temperate woodland	Xerophytic shrubland		Boreal forest	Temperate forest	Temperate forest with an increase in southeastern pine forest	Southeastern pine forest
	GI	Temperate forest	Open temperate and pine (non-significant) forest	Temperate forest	Boreal forest	Boreal-temperate forest		Xerophytic shrubland	Warm-temperate woodland	Xerophytic shrubland		Boreal forest	Open temperate forest with increase in temperate trees	Temperate forest	Southeastern pine forest
	D-O warming														
D-O 10	GS	Boreal forest	Open boreal forest	Boreal-temperate forest		Boreal-temperate forest		Xerophytic shrubland	Warm-temperate woodland	Xerophytic shrubland			Open temperate forest	Temperate forest with an increase in southeastern pine forest	Southeastern pine forest
	GI	Temperate Forest	Open temperate and pine (non-significant) forest	Temperate forest		Boreal-temperate forest		Xerophytic shrubland	Warm-temperate woodland with an increase in warm-temperate trees	Xerophytic shrubland			Open temperate forest	Temperate forest	Southeastern pine forest
	D-O warming														
D-O 11	GS	Boreal forest	Open boreal forest			Boreal-temperate forest		Open warm-temperate forest		Xerophytic shrubland	Xerophytic shrubland		Open temperate forest		Southeastern pine forest
	GI	Temperate forest	Open temperate and pine (non-significant) forest			Boreal-temperate forest		Xerophytic shrubland		Xerophytic shrubland	Warm-temperate forest with increase in xerophytic shrubland				Florida scrub
	D-O warming														
D-O 12	GS	Boreal forest - tundra	Closed temperate and pine (non-significant) forest			Boreal-temperate forest		Open warm-temperate forest		Xerophytic shrubland with increase in temperate and boreal trees	Warm-temperate forest				Southeastern pine forest
	GI	Boreal forest	Open temperate and pine (non-significant) forest			Boreal-temperate forest with increase in temperate component		Xerophytic shrubland		Xerophytic shrubland	Mixed conifer forest with an increase in xerophytic shrubland				Florida scrub
	D-O warming														
D-O 13	GS	Boreal forest - tundra	Open temperate and pine (non-significant) forest					Open temperate forest		Xerophytic shrubland with increase in temperate and boreal trees	Open temperate forest				Florida scrub
	GI	Boreal forest	Closed temperate and pine (non-significant) forest			Boreal-temperate forest with increase in temperate component		Open warm-temperate forest		Xerophytic shrubland					Florida scrub
	D-O warming														
D-O 14	GS	Boreal forest - tundra	Open temperate and pine (non-significant) forest			Boreal-temperate forest		Open warm-temperate forest		Xerophytic shrubland with increase in temperate and boreal trees					Florida scrub
	GI	Boreal forest	Closed temperate and pine (non-significant) forest			Boreal-temperate forest		Warm-temperate woodland		Xerophytic shrubland					Florida scrub
	D-O warming														
D-O 15	GS	Boreal forest - tundra	Open temperate and pine (non-significant) forest			Boreal-temperate forest		Xerophytic shrubland		Xerophytic shrubland					Florida scrub
	GI	Boreal forest	Closed temperate and pine (non-significant) forest			Boreal-temperate forest		Xerophytic shrubland		Xerophytic shrubland with increase in temperate and boreal trees					Florida scrub
	D-O warming														
D-O 16	GS	Boreal forest - tundra	Open temperate and pine (non-significant) forest			Boreal-temperate forest		Xerophytic shrubland		Xerophytic shrubland with increase in temperate and boreal trees					Florida scrub
	GI	Boreal forest	Closed temperate and pine (non-significant) forest			Boreal-temperate forest		Open warm-temperate forest with significant chaparral		Xerophytic shrubland					Florida scrub
	D-O warming														
D-O 17	GS	Boreal forest-tundra	Open temperate and pine (non-significant) forest			Boreal-temperate forest		Open warm-temperate forest		Xerophytic shrubland with increase in temperate and boreal trees					Florida scrub
	GI		Closed temperate and pine (non-significant) forest			Boreal-temperate forest		Open warm-temperate forest		Xerophytic shrubland with increase in temperate and boreal trees					Florida scrub
	D-O warming														
D-O 18	GS		Open temperate and pine (non-significant) forest			Boreal-temperate forest		Open warm-temperate forest		Xerophytic shrubland					
	GI		Closed temperate and pine (non-significant) forest			Boreal-temperate forest		Open warm-temperate forest		Xerophytic shrubland					
	D-O warming														
D-O 19	GS		Open temperate forest			Boreal-temperate forest		Xerophytic shrubland		Xerophytic shrubland with increase in temperate and boreal trees					
	GI		Open temperate forest			Boreal-temperate forest with increase in temperate component		Open warm-temperate forest with significant chaparral		Xerophytic shrubland					
	D-O warming														
D-O 20	GS		Open temperate forest			Boreal-temperate forest		Open temperate forest		Xerophytic shrubland with increase in temperate and boreal trees					
	GI		Open temperate forest			Boreal-temperate forest with increase in temperate component		Open warm-temperate forest		Xerophytic shrubland					
	D-O warming														

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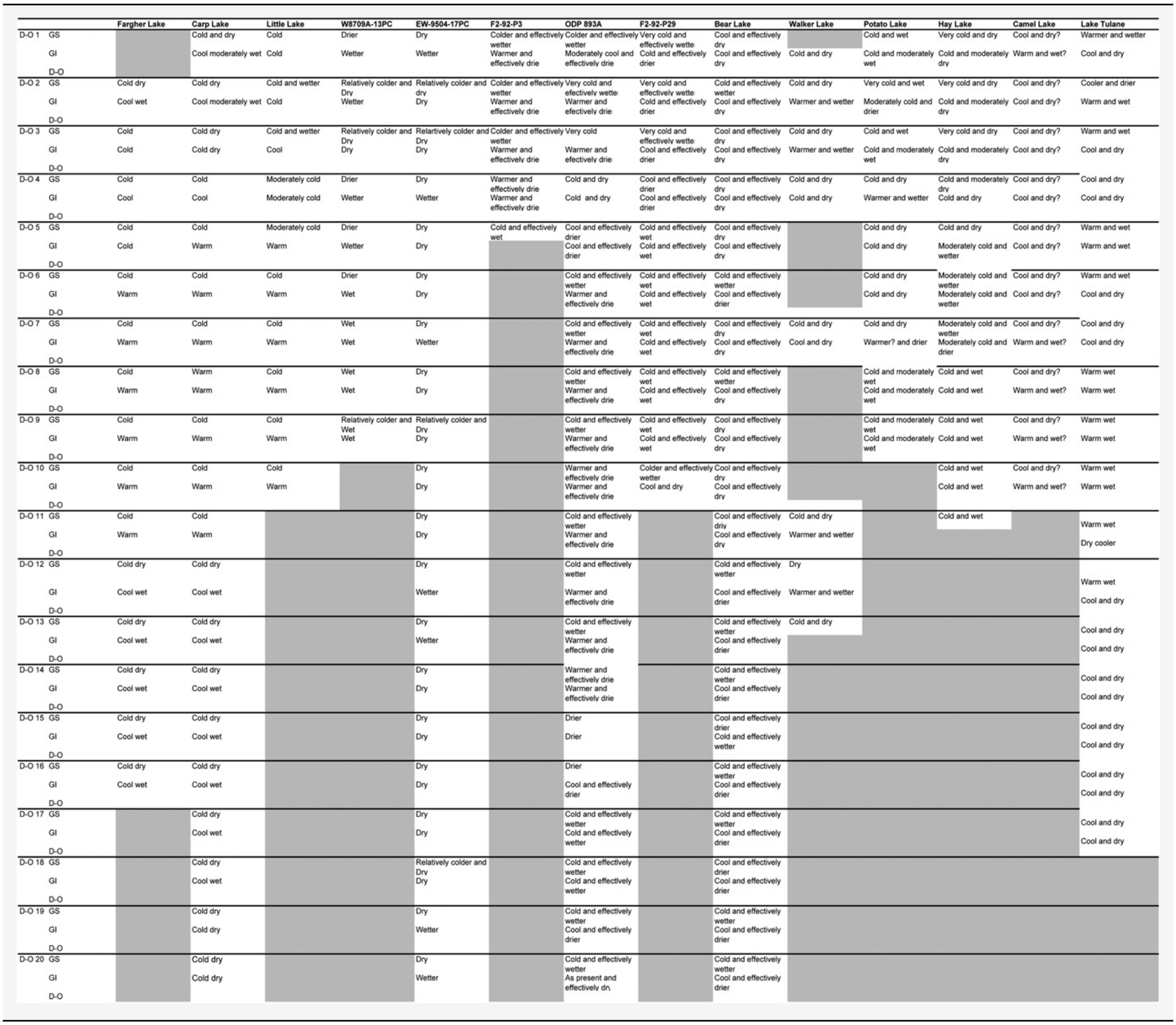
Table 5
Summary of inferred climatic changes through D-O cycles at individual high-resolution sites from North America. Note that we could not distinguish between D-O warmings and GI in these records.



		Fargher Lake	Carp Lake	Little Lake	W8709A-13PC	EW-9504-17PC	F2-92-P3	ODP 893A	F2-92-P29	Bear Lake	Walker Lake	Potato Lake	Hay Lake	Camel Lake	Lake Tulane
D-O 1	GS		Cold and dry	Cold	Drier	Dry	Colder and effectively wetter	Colder and effectively wetter	Very cold and effectively wette	Cool and effectively dry		Cold and wet	Very cold and dry	Cool and dry?	Warmer and wetter
	GI		Cool moderately wet	Cold	Wetter	Wetter	Warmer and effectively drie	Moderately cool and effectively drie	Cold and effectively drier	Cool and effectively dry	Cold and dry	Cold and moderately wet	Cold and moderately dry	Warm and wet?	Cool and dry
	D-O														
D-O 2	GS	Cold dry	Cold dry	Cold and wetter	Relatively colder and Dry	Relatively colder and dry	Colder and effectively wetter	Very cold and efectively wette	Very cold and effectively wette	Cold and effectively wetter	Cold and dry	Very cold and wet	Very cold and dry	Cool and dry?	Cooler and drier
	GI	Cool wet	Cool moderately wet	Cold	Wetter	Dry	Warmer and effectively drie	Warmer and efectively drie	Cold and effectively drier	Cool and effectively dry	Warmer and wetter	Moderately cold and drier	Cold and moderately dry	Cool and dry?	Warm and wet
	D-O														
D-O 3	GS	Cold	Cold dry	Cold and wetter	Relatively colder and Dry	Relartively colder and Dry	Colder and effectively wetter	Very cold	Very cold and effectively wette	Cool and effectively dry	Cold and dry	Cold and wet	Very cold and dry	Cool and dry?	Warm and wet
	GI	Cold	Cold dry	Cool	Dry	Dry	Warmer and effectively drie	Warmer and efectively drie	Cool and effectively drier	Cool and effectively dry	Warmer and wetter	Cold and moderately wet	Cold and moderately dry	Cool and dry?	Cool and dry
	D-O														
D-O 4	GS	Cold	Cold	Moderately cold	Drier	Dry	Warmer and effectively drie	Cold and dry	Cool and effectively drier	Cool and effectively dry	Cold and dry	Cold and dry	Cold and moderately dry	Cool and dry?	Cool and dry
	GI	Cool	Cool	Moderately cold	Wetter	Wetter	Warmer and effectively drie	Cold and dry	Cool and effectively drier	Cool and effectively dry	Cold and dry	Warmer and wetter	Cold and dry	Cool and dry?	Cool and dry
	D-O														
D-O 5	GS	Cold	Cold	Moderately cold	Drier	Dry	Cold and effectively wet	Cool and effectively drier	Cold and effectively wet	Cool and effectively dry		Cold and dry	Cold and dry	Cool and dry?	Warm and wet
	GI	Cold	Warm	Warm	Wetter	Dry		Cool and effectively drier	Cold and effectively wet	Cool and effectively dry		Cold and dry	Moderately cold and wetter	Cool and dry?	Warm and wet
	D-O														
D-O 6	GS	Cold	Cold	Cold	Drier	Dry		Cold and effectively wetter	Cold and effectively wet	Cold and effectively wetter		Cold and dry	Moderately cold and wetter	Cool and dry?	Warm and wet
	GI	Warm	Warm	Warm	Wet	Dry		Warmer and effectively drie	Cold and effectively wet	Cool and effectively drier		Cold and dry	Moderately cold and wetter	Cool and dry?	Cool and dry
	D-O														
D-O 7	GS	Cold	Cold	Cold	Wet	Dry		Cold and effectively wetter	Cold and effectively wet	Cool and effectively dry	Cold and dry	Cold and dry	Moderately cold and wetter	Cool and dry?	Cool and dry
	GI	Warm	Warm	Warm	Wet	Wetter		Warmer and effectively drie	Cold and effectively wet	Cool and effectively dry	Cool and dry	Warmer? and drier	Moderately cold and drier	Warm and wet?	Cool and dry
	D-O														
D-O 8	GS	Cold	Warm	Cold	Wet	Dry		Cold and effectively wetter	Cold and effectively wet	Cold and effectively wetter		Cold and moderately wet	Cold and wet	Cool and dry?	Warm wet
	GI	Warm	Warm	Warm	Wet	Dry		Warmer and effectively drie	Cold and effectively wet	Cool and effectively dry		Cold and moderately wet	Cold and wet	Warm and wet?	Warm wet
	D-O														
D-O 9	GS	Cold	Cold	Cold	Relatively colder and Wet	Relatively colder and Dry		Cold and effectively wetter	Cold and effectively wet	Cool and effectively dry		Cold and moderately wet	Cold and wet	Cool and dry?	Warm wet
	GI	Warm	Warm	Warm	Wet	Dry		Warmer and effectively drie	Cold and effectively wet	Cool and effectively dry		Cold and moderately wet	Cold and wet	Warm and wet?	Warm wet
	D-O														
D-O 10	GS	Cold	Cold	Cold		Dry		Warmer and effectively drie	Colder and effectively wetter	Cool and effectively dry			Cold and wet	Cool and dry?	Warm wet
	GI	Warm	Warm	Warm		Dry		Warmer and effectively drie	Cool and dry	Cool and effectively dry			Cold and wet	Warm and wet?	Warm wet
	D-O														
D-O 11	GS	Cold	Cold			Dry		Cold and effectively wetter		Cool and effectively driy	Cold and dry		Cold and wet		Warm wet
	GI	Warm	Warm			Dry		Warmer and effectively drie		Cool and effectively dry	Warmer and wetter				Dry cooler
	D-O														
D-O 12	GS	Cold dry	Cold dry			Dry		Cold and effectively wetter		Cold and effectively wetter	Dry				Warm wet
	GI	Cool wet	Cool wet			Wetter		Warmer and effectively drie		Cool and effectively drier	Warmer and wetter				Cool and dry
	D-O														
D-O 13	GS	Cold dry	Cold dry			Dry		Cold and effectively wetter		Cold and effectively wetter	Cold and dry				Cool and dry
	GI	Cool wet	Cool wet			Wetter		Warmer and effectively drie		Cool and effectively drier					Cool and dry
	D-O														
D-O 14	GS	Cold dry	Cold dry			Dry		Warmer and effectively drie		Cold and effectively wetter					Cool and dry
	GI	Cool wet	Cool wet			Dry		Warmer and effectively drie		Cool and effectively drier					Cool and dry
	D-O														
D-O 15	GS	Cold dry	Cold dry			Dry		Drier		Cool and effectively drier					Cool and dry
	GI	Cool wet	Cool wet			Dry		Drier		Cold and effectively wetter					Cool and dry
	D-O														
D-O 16	GS	Cold dry	Cold dry			Dry		Drier		Cold and effectively wetter					Cool and dry
	GI	Cool wet	Cool wet			Dry		Cool and effectively drier		Cool and effectively drier					Cool and dry
	D-O														
D-O 17	GS		Cold dry			Dry		Cold and effectively wetter		Cold and effectively wetter					Cool and dry
	GI		Cool wet			Dry		Cold and effectively wetter		Cool and effectively drier					Cool and dry
	D-O														
D-O 18	GS		Cold dry			Relatively colder and Dry		Cold and effectively wetter		Cool and effectively drier					
	GI		Cool wet			Dry		Cold and effectively wetter		Cool and effectively drier					
	D-O														
D-O 19	GS		Cold dry			Dry		Cold and effectively wetter		Cold and effectively wetter					
	GI		Cold dry			Wetter		Cool and effectively drier		Cool and effectively drier					
	D-O														
D-O 20	GS		Cold dry			Dry		Cold and effectively wetter		Cold and effectively wetter					
	GI		Cold dry			Wetter		As present and effectively dry		Cool and effectively drier					
	D-O														

expressed in the pollen record by decreases in temperate forest species such as *T. heterophylla* (Fig. 2; Table 4) showing colder conditions at that time (Table 5). However, the evidence for cycles at frequencies <3000 years (i.e. D-O variability) in the pollen record is weak (see Fig. 2). Bioturbation probably obliterated cycles at these higher frequencies (sedimentation rate for EW9504-17PC is only 10 cm/ky; Pisias et al., 2001).

3.2. Southwestern North America

Three pollen records from the southern California margin – ODP Sites 893A, F2-92-P3, and F2-92-P29 (Heusser et al., 1995; Heusser and Sirocko, 1997; Heusser, 1998, 2000) were analyzed at sufficient resolution to examine millennial-scale climate change. Age models from these cores are derived from corrected AMS-^{14}C dates on foraminifera (Table 2). Age for core ODP 893A is very well constrained, including 20 AMS-^{14}C dates during MIS 2 and MIS 3 and further dates obtained by tuning benthic foraminifera δ^{18}O from this record to SPECMAP (Ingram and Kennett, 1995). Age models for the F2-92-P3 and F2-92-P29 cores for MIS 2 and MIS 3 are less well constrained with only 2 and 4 AMS-^{14}C dates respectively (Table 2). These records document fluctuations in the relative abundance of an open warm-temperate forest with *Quercus* as the main representative (warm-temperate *Quercus* woodland) and conifers typical of temperate forests during the past 160 ka (Heusser et al., 1995; Fig. 2; Table 4). Temperate conifer forests, which today occur at high elevations, dominated the vegetation at lower elevations during the Last Glacial Maximum and other cold intervals of the last glacial period. These three records show the coldest conditions occurring during HS 3, 2 and 1 (Fig. 2; Table 5). Warm-temperate *Quercus* woodland, which today occurs in low elevation foothills, was well represented in the pollen spectra during interglacials and interstadials and probably had a more extended distribution uphill. During the Last Interglacial and many GI, increases in *Quercus* pollen in ODP 893A are correlated with decreases in paleo-oxygenation (bioturbation index) and warm surface waters (Behl and Kennett, 1996; Heusser, 1998; Hendy and Kennett, 2000).

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Heusser (1998) documented a high correspondence between upland vegetation in areas drained by streams flowing into the Santa Barbara Basin, high-amplitude fluctuations in the characteristics of Santa Barbara Basin bottom waters, and the Greenland $\delta^{18}O$ record, particularly in GI 8, 12, 14 and 16.

3.3. Interior mountains and plateaus

Five records from the interior uplands of North America provide adequate temporal resolution for the last glacial: Bear, Potato, Walker, Hay, and Dead Man lakes (Figs. 1 and 2). Bear Lake provides the longest high-resolution pollen record from this region, spanning the past 225 ka (Jiménez-Moreno et al., 2007) but is poorly dated. The age model is based on the registration of the Laschamp paleomagnetic excursion (41 ka) and a U/Th date of 127.7 ka (Table 2). Nevertheless, the record show rapid fluctuations between high percentages of boreal forest taxa found today at elevations between 2900 and 3400 m (e.g., *Picea*), and high percentages of xerophytic shrubland or steppe taxa (Amaranthaceae, *Sarcobatus*, and *Ambrosia)* and warm-temperate mixed forest taxa (e.g., *Juniperus* and *Quercus*) that are dominant at elevations below ~2100 m. The pollen record shows decreases in xerophytic shrubland and warm-temperate mixed forest taxa (Table 4), which suggest cold events similar in timing to HS 1 through 6 (best documented for HS 4, 5 and 6; Fig. 2). The pollen record also shows increases in xerophytic shrubland taxa and warm-temperate mixed forest taxa that may correspond to GI 5-6, 8-12, 13-14, 16-17. Particularly marked intervals correspond to GI 19, 20, and 21 (Fig. 2).

Pollen records from the Colorado Plateau (Anderson et al., 2000) also show millennial-scale vegetation and climatic variability. Even though these records are rather poorly dated, with only a few conventional bulk radiocarbon dates for each core (Table 2), they show interesting vegetation changes previously discussed by Anderson et al. (2000) (Table 4). The record from Potato Lake (Anderson, 1993) is characterized by high values of *Artemisia,* here interpreted as xerophytic shrubland, and low abundances of the boreal forest conifers *Picea* and *Pinus* during HS 3. The assemblages during HS 2, HS 1 and HS 0 are characterized by less *Artemisia* and higher abundances of subalpine boreal trees (*Picea*, *Pinus* and *Abies*). The abundance of *Artemisia* in HS 3 is interpreted as indicating cold and dry conditions; the abundance of boreal forest conifers as indicating cold and wet conditions (Table 5). Therefore, it seems that climate during HS 2, 1 and 0 is less dry (Anderson et al., 2000). There are hiatuses in deposition at Walker Lake (Berry et al., 1982; Adam et al., 1985; Hevly, 1985) corresponding to the intervals of HS 4 and HS 3 (Fig. 2), but HS 5, HS 2 and HS 1 are all characterized by high abundances of *Artemisia*, characteristic of xerophytic shrublands, and *Pinus*, with low representation of *Picea* and *Abies*, and Poaceae. These assemblages suggest cold and dry conditions rather than the cold and wet conditions registered at Potato Lake (Table 5). At Hay Lake (Jacobs, 1985; Fig. 2), each HS is characterized by abundant *Artemisia*, suggesting relatively dry conditions, but there is no consistent pattern in the abundance of arboreal species other than predominance of *Pinus edulis*, *Pinus flexilis* and *Pinus aristata* during MIS 3 (Jacobs, 1985). The near disappearance of *P. edulis* pollen at the onset of MIS 2 (and HS 2), is interpreted as a change to colder and drier conditions. High percentages of *Artemisia* are also recorded during HS 1 at Dead Man Lake (Wright et al., 1973). The expression of millennial-scale climatic variability and the HS in the pollen records from the Colorado Plateau (Anderson et al., 2000) differs from site to site. This may be a function of inadequate dating and differences in sampling resolution, or may reflect local heterogeneity in the response to regional climate forcing.

3.4. Southeastern North America

Three sites in southeastern North America document climate fluctuations during the last 60 ka, Lake Tulane, Camel Lake and Tampa Bay (Fig. 1). The longest record was obtained from Lake Tulane in Florida (Grimm et al., 2006). Twenty-two AMS radiocarbon dates were used in order to construct the age model for the MIS 2–3 part of the Lake Tulane record (Grimm et al., 2006; Table 2). Although a number of these AMS dates were obtained from bulk sediment samples, and could therefore be subject to an error of between 500 and 2000 yr (see Grimm et al., in press), the bulk dates seem to be reliable as there is no apparent offset between dates obtained from bulk sediments and macrofossils (Grimm et al., 2006, in press). The bottom part of the record, beyond the range of radiocarbon dating, was dated by assuming that the observed correlation of HS 1 through 4 with major peaks in *Pinus* would have held for earlier intervals: peaks 5 and 6 of *Pinus* were therefore assumed to correlate with HS 5 and 6 (Grimm et al., 2006). The Lake Tulane record shows fluctuations between intervals dominated by *Pinus* (representing southeastern pine forests) and those dominated by *Quercus*, *Ambrosia*, and Poaceae, which indicate open xerophytic shrubland or Florida scrub (Fig. 2; Table 4). Southeastern pine forest phases indicate periods of warmer and wetter climate, and are correlated with HS and GS (Grimm et al., 2006). Florida scrub phases indicate periods of drier climate and are correlated with GI (including GI 17-14, 12-11, 7-6, and 3-4; Table 5). Higher values of *Carya* pollen, which includes the endemic Florida scrub species *Carya floridana*, together with other scrub taxa such as *Ceratiola* imply drier conditions than today. The similarity of the *Pinus* zones during the glacial with the late-Holocene pollen assemblages implies a warm-wet climate similar to today, consistent with macrofossil evidence (Grimm et al., 2006). Periods of high *Pinus* percentages at Lake Tulane during the glacial were interpreted as being synchronous with weakened North Atlantic Deep Water (NADW) production. HS 4, 3, and 2 probably terminated long periods of cooling and weakened NADW production in the North Atlantic (Bond et al., 1993; Oppo and Lehman, 1995) and are correlated with long *Pinus* phases (Grimm et al., 2006).

A pollen record from Camel Lake in northern Florida (Watts et al., 1992) documents millennial-scale climatic variability during the last glacial, shown by the alternating dominance of southeastern pine forests and deciduous temperate forests. The age model for this core during the last glacial is based on three AMS of vegetal remains and two conventional radiocarbon dates on bulk sediment samples (Watts et al., 1992; Table 2). The poorly-dated basal portion of the core >37 ka (Table 2) has a mixture of *Pinus* and temperate deciduous taxa. A diverse temperate forest, with *Quercus, Liquidambar, Fagus*, and *Castanea,* dominated from ~37 to 34.5 ka. This assemblage indicates relatively wet conditions. *Pinus* dominates the record between 34.5 and 16 ka, but several sharp breaks in sediment lithology suggest significant hiatuses in the record and LGM sediments are probably missing as they in other similar shallow Florida lakes. The coldest conditions are indicated between 16 and 12 ka, with a spike of *Picea* followed by mesic deciduous taxa, *Quercus, Carya, Ostrya/Carpinus and Fagus*. Watts et al. (1992) interpreted this vegetation as similar to the vegetation found today in Quebec. However, Jackson and Weng (1999) and Jackson et al. (2000) have argued that the *Picea* is probably the now extinct *Picea critchfieldii*, a species that occurred across the Southeast in the Pleistocene and appears to be characteristic of temperate to cool-temperate climates (Jackson and Weng, 1999; Jackson et al., 2000). Thus, the presence of this species suggest climate conditions warmer than Quebec but cooler than today during GS 2 and HS 1. This cool signal is opposite to the signal indicated by the Lake Tulane record from farther south on the Florida peninsula. The GS 3

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sediments are probably missing at Camel Lake, and no information is available for the LGM. The occurrence of mesic temperate forest during GI 1 indicates a very wet climate, because very high precipitation would be necessary to support mesic forest on such sandy soils. Wet conditions persist through GS 1. Pollen spectra coeval with GS 1 are not particularly distinguished from those of GI 1, and the temperature signal is unclear. A sharp lithologic break occurs at the end of GS 1, followed by a 3 ka sedimentary hiatus, probably indicative of drier conditions at onset of the Holocene.

A shorter record of lacustrine/wetland sedimentation from Tampa Bay on the west coast of the Florida peninsula provides multidecadal resolution throughout the 21–11 ka interval (Willard et al., 2007; not plotted in Fig. 2 because of its short duration but worth discussing here as it shows vegetation patterns that differ from Lake Tulane record for the latest Pleistocene). The age control of this record comes from thirteen AMS radiocarbon dates taken from shells and pollen preserved through the core (Table 2). No reservoir correction was applied to the shell dates as dates obtained from pollen fell within 50-yr of age-depth lines interpolated between mollusk dates (Willard et al., 2007). Intervals dominated by *Pinus* (indicating development of southeastern pine forest), and when moisture availability was sufficient to maintain a lacustrine system, alternate with intervals dominated by Amaranthaceae (typical of Florida scrub) and when wetlands and seasonal ponds occupied the site. Rapid vegetation response to climatic changes occurred over <50 yr and dry intervals are correlated with the Oldest Dryas (GS 2), Older Dryas (GI 1d), and part of the Younger Dryas (GS 1) chronozones. Unlike the Lake Tulane record, Tampa Bay assemblages are interpreted as indicating warmer, wetter conditions with high *Pinus* during the B-A (GI 1) and drier conditions during at least part of the YD.

4. Discussion

High-resolution pollen records from North America show changes in vegetation on multiple timescales during the last glacial (MIS 2-4). The vegetation response to climate variations during D-O cycles and HS can be relatively subtle, and their interpretation requires an understanding of the broader-scale changes in vegetation on Milankovitch timescales (Whitlock and Grigg, 1999).

Many of the pollen taxa from North America have high species diversity, and the individual species may have a very wide range of climate tolerance. Thus, the climatic interpretation of changes in the pollen record will necessarily vary regionally, and may indeed vary through time, depending on the base state of the vegetation (including which species are represented within the pollen taxon) and the direction of the climate change. For example, increases in the typically temperate species *T. heterophylla* and *Quercus* imply warming conditions in coastal Washington, Oregon and northern California (Heusser, 1998; Grigg and Whitlock, 2002), but the presence of *Quercus* in records from the Pacific Northwest is evidence of effectively drier conditions than *T. heterophylla*. In this area, increases in boreal *Picea* during MIS 2, when the overall climate conditions were cold and dry, indicate replacement of tundra or cold steppe by high-elevation boreal forests consistent with a warming interval. During the somewhat milder conditions characteristic of MIS 3, increases in *Picea* indicate an expansion of high-elevation boreal forests at the expense of lowland temperate forest and thus cooling conditions. Thus, vegetation-inferred climate variations should be made taking into account shifts in assemblages and not individual taxa and they seem to be regionally specific: in the more mountainous regions of the west, climate changes are primarily evidenced as temperature-dependent shifts in the elevation limits of species distribution. In non-mountainous regions, such as the southeastern U.S., plant species distributions underwent dramatic latitudinal shifts as a result of temperature and hydrological changes (Jackson et al., 2000).

Most of the records examined here appear to exhibit greater variability during MIS 3 and 4 than during MIS 2 (Fig. 2; Table 4). The records in the Pacific Northwest (e.g. Carp Lake, Little Lake) are an exception, in showing considerable variability during MIS 2 with shifts between forest and parkland registered during HS 1 and 2 (Whitlock and Grigg, 1999; Grigg et al., 2001; Table 4). More muted changes in vegetation during MIS 2 most likely reflect a reduction in the amplitude of climate change (Grootes et al., 1993; Hendy and Kennett, 2000; Wolff et al., in this volume). Alternatively, the more muted variability during MIS 2 at other sites may be an issue of detection, since glacial pollen assemblages are characterized by relatively fewer taxa and are therefore, perhaps, less sensitive to climate change.

The records studied here (Fig. 2) generally show vegetation changes indicating warmer conditions during GI than during GS and HS. However, the Lake Tulane record is characterized by vegetation changes that indicate relatively cooler conditions during most of the GI and warmer conditions during HS. This appears to indicate an antiphase temperature relationship between southern Florida peninsula and the North Atlantic region (Grimm et al., 2006; Donders et al., in press; Table 5). Many of the pollen records (i.e., most pollen records from the Pacific Northwest and the Colorado Plateau) show D-O warming events and GI are characterized by increased precipitation (Table 5) whereas GS and HS are characterized by decreased precipitation relative to GI. Again, the Lake Tulane record shows an opposite pattern with wetter HS and GS (Grimm et al., 2006). The discrepancy between the record of vegetation-inferred climate changes from Lake Tulane and sites from other regions of North America, including other parts of Florida (e.g. Camel Lake, Tampa Bay), could be due to chronological uncertainties coming from dating bulk sediment samples (see above; Grimm et al., 2006). However, a new, and better-dated record from Lake Annie in central Florida Annie shows quantitatively similar changes to those inferred from the Tulane record (Donders et al., in press). Furthermore, the idea that there is an opposition between the signals registered on the Florida peninsula and regions further north including Greenland is supported by a climate-model sensitivity analysis (Donders et al., in press). Recent studies indicate that sea-surface temperature in the northern Gulf of Mexico were out of phase with Greenland climate (Flower et al., 2004; Ziegler et al., 2008), a feature which is consistent with weakened thermohaline heat transport (Flower et al., 2004). Thus, the apparent antiphase between vegetation-inferred climate changes in southern Florida and the rest of the continent may be a real feature of millennial-scale climate changes, although this does not preclude the need for additional research to improve the geochronology of these sites.

The reconstruction of changes in moisture balance from vegetation records is less easy than inferring temperature changes. The simplest interpretation of the pollen records from most North American sites suggests that D-O warming events and GI are characterized by increases in precipitation and that GS and HS are characterized by decreases in precipitation. However, different regions appear to show different precipitation patterns. Increases in xerophytic vegetation at Bear Lake and in the southwestern U.S. indicate decreased effective precipitation during GI and decreases in xerophytic vegetation during GS and HS indicate increased effective precipitation (Heusser, 1998; Jiménez-Moreno et al., 2007). Even though the records from the Pacific Northwest generally show dry conditions during HS and GS (Table 5), the records from Little and Fargher Lakes have also been interpreted as a response to increased effective moisture during the cold intervals of HS 1, HS 2, and other HS (Grigg and Whitlock, 2002). The climate

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changes inferred from vegetation changes at some of the sites in the Pacific Northwest is opposite that inferred from lake levels in the Great Basin where GI correspond to warm-wet periods (Benson et al., 2003). The difference in the climate signals between these two regions is not unlike the modern climate differences between the Pacific Northwest and the Great Basin, and, like present day, probably reflects geographic differences in atmospheric circulation, including the position of jet stream (Thompson et al., 1993). Moreover, certain records probably register the effect of effective precipitation on vegetation, while levels of large lakes may be dominated by the runoff to those lakes. Resolution of these differences recording precipitation between different proxy records will require more data on seasonality of precipitation, water sources of rivers feeding pluvial lakes, and the effect of vegetation itself on evapotranspiration and runoff (Hostetler et al., 1999).

Paleoclimate model simulations for the LGM could tentatively be used to provide an analogue for atmospheric circulation patterns during GS. These simulations would suggest that cold intervals, like the GS, were likely to have been characterized by stronger westerlies than today along the Pacific coast, essentially mimicking present conditions further north today (Bartlein et al., 1998; Hostetler et al., 1999). Similarly, the LGM simulations would suggest that the GS would be characterized by colder winters and summers than at present, and greater winter precipitation in southwestern North America. According to these simulations, monsoonal flow was inhibited by (1) the southerly position of the jet stream in summer, blocking the development of high pressure over the midcontinent; (2) a heavy spring snowpack over the Plateau and the southern Rockies preventing summertime heating and thermally induced low pressure upstream; and (3) lower sea level in the Gulfs of Mexico and California, and a colder tropical ocean.

Atmospheric circulation changes have also been invoked to explain climate patterns over North America during GI. Benson et al. (2003), for example, suggested that the mean position of the jet stream shifted north (between 35° and 43°N) during GI, greatly increasing the amount of precipitation received by most of western US surface-water systems (Benson et al., 2003). In addition, they suggest that warmer temperatures associated with the southern boundary of the jet stream aided the retreat of Sierran alpine glaciers during GI (Benson et al., 2003).

Other modeling results have also shown a role for changes in North Atlantic thermohaline circulation and attendant changes in Atlantic sea-surface temperature gradients on Pacific El Niño-Southern Oscillation (ENSO) variability (Dong et al., 2006; Dong and Sutton, 2007; Timmermann et al., 2007). The Atlantic Multidecadal Oscillation (AMO) may be another factor modulating large-scale patterns of precipitation variability in the western US, including summer precipitation and winter precipitation variability associated with ENSO (Enfield et al., 2001; McCabe et al., 2004). One possible explanation for the strong antiphase relationship in temperature between the Florida peninsula and the North Atlantic region (Grimm et al., 2006) is diminution of Atlantic Meridional Overturning Circulation (AMOC) before and during HS which would reduce northward heat transport and retain warmth in the subtropical Atlantic and Gulf of Mexico (Grimm et al., 2006). This interpretation is still controversial, and Ziegler et al. (2008) have showed that there was no cooling in the Gulf of Mexico during HS because of the invariable position of the Atlantic Warm Pool and Intertropical Convergence Zone during boreal summer and not because of the accumulation of heat in the tropics and subtropics related to the reduction in AMOC. The atmospheric circulation associated with a NAO-like mechanism can explain the asymmetry between the SE USA and Europe (Naughton et al., 2009).

5. Future perspectives

Even though there is an enormous potential to generate long, continuous, high-resolution vegetation records from continental North America, there are only isolated records from vast areas, which greatly hampers our ability to interpret regional patterns in climate. Several long records have already been obtained from western North America (i.e. Clear Lake: 130 ka, Adam et al., 1981; San Agustin Lake: 1.6 Ma, Markgraf et al., 1984; Tulelake: 3 Ma, Adam et al., 1989; Indian Cove Well: 1.5 Ma, Davis, 1998; Searles Lake: 230 ka, Litwin et al., 1999), but they lack high-resolution sampling necessary to examine the vegetation response to millennial-scale climate variations during MIS 2-4. Pollen records from marine cores along the continental margin also provide long vegetation histories (see e.g. Fletcher et al., in this volume; Hessler et al., in this volume), but marine cores taken from the continental margins off North America have been little studied in this regard, and should provide excellent records, especially from sites with generally high sedimentation rates where high-resolution studies can be performed. Such records have great potential for linking the observed vegetation changes from terrestrial environments to climate changes as recorded in paleoceanographic records.

One place where such records would be most useful is to investigate the apparent antiphase relationship in temperature between Florida and the rest of North America. Marine cores off the coasts of North Carolina (MD99-2203; López-Martínez et al., in progress), South Carolina (KNR140-2 GGC39; Desprat et al., in progress) and Georgia (ODP site 1059; note that L. Heusser already studied pollen from stage 5e; Heusser and Oppo, 2003) will improve our understanding of the oceanic and atmospheric processes in modulating and propagating abrupt climatic changes in this region. But only with analysis of additional long, high-resolution records will our understanding of rapid and short-term climate change come into better focus. Such high-resolution studies are necessary in order to predict for vegetation changes and their impact on human activity caused by projected future climate change.

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