Climate change and Arctic ecosystems: 1. Vegetation changes north of 55°N between the last glacial maximum, mid-Holocene, and present

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[1] A unified scheme to assign pollen samples to vegetation types was used to reconstruct vegetation patterns north of 55°N at the last glacial maximum (LGM) and mid-Holocene (6000 years B.P.). The pollen data set assembled for this purpose represents a comprehensive compilation based on the work of many projects and research groups. Five tundra types (cushion forb tundra, graminoid and forb tundra, prostrate dwarf-shrub tundra, erect dwarf-shrub tundra, and low- and high-shrub tundra) were distinguished and mapped on the basis of modern pollen surface samples. The tundra-forest boundary and the distributions of boreal and temperate forest types today were realistically reconstructed. During the mid-Holocene the tundra-forest boundary was north of its present position in some regions, but the pattern of this shift was strongly asymmetrical around the pole, with the largest northward shift in central Siberia (~200 km), little change in Beringia, and a southward shift in Keewatin and Labrador (~200 km). Low- and high-shrub tundra extended farther north than today. At the LGM, forests were absent from high latitudes. Graminoid and forb tundra abutted on temperate steppe in northwestern Eurasia while prostrate dwarf-shrub, erect dwarf-shrub, and graminoid and forb tundra formed a mosaic in Beringia. Graminoid and forb tundra is restricted today and

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does not form a large continuous biome, but the pollen data show that it was far more extensive at the LGM, while low- and high-shrub tundra were greatly reduced, illustrating the potential for climate change to dramatically alter the relative areas occupied by different vegetation types. *INDEX TERMS:* 1615 Global Change: Biogeochemical processes (4805); 1620 Global Change: Climate dynamics (3309); 1851 Hydrology: Plant ecology; 3344 Meteorology and Atmospheric Dynamics: Paleoclimatology; *KEYWORDS:* vegetation maps, mid-Holocene, last glacial maximum, Arctic ecosystems, palaeoclimate, biomization

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1. Introduction

[2] Arctic climate and ecosystems are expected to be highly sensitive to anthropogenic changes in atmospheric composition and hence radiative forcing. Early simulations of the global climatic response to CO_2 doubling indicated increases in temperature by up to 12 K in the northern polar regions [*Manabe and Wetherald*, 1975]. More recent simulations that take into account the cooling effect of sulphate aerosols show less extreme changes [*Cubasch et al.*, 2001], but it remains a robust generalization that the simulated high-latitude temperature response to increased greenhouse gas concentrations is stronger than the responses of the tropics and midlatitudes. This generalization has also been derived independently of models, by examining inferred patterns of climate change for various geological epochs [*Hoffert and Covey*, 1992]. The particular sensitivity of high-latitude climates can be explained by the operation of two powerful (and synergistic) positive feedbacks: changes in the extent and duration of sea-ice cover in the Arctic Ocean [*Ganopolski et al.*, 1998; *Braconnot et al.*, 1999; *Vavrus*, 1999], and changes in the albedo of the land surface as a consequence of changes in snow cover [*Bonan et al.*, 1992; *Foley et al.*, 1994; *Berger*, 2001]. Model experiments indicate that changes in land-surface albedo resulting from climatically induced shifts in the tundra-forest boundary play a role in the initiation of glaciations [*Gallée et al.*, 1992; *Gallimore and Kutzbach*, 1996; *de Noblet et al.*, 1996], amplification of high-latitude cooling during glaciations [*Levis et al.*, 2000], and enhancement of the direct effects of higher than present northern summer insolation during interglacial periods [*Foley et al.*, 1994; *TEMPO Members*, 1996; *Texier et al.*, 1997].

[3] The palaeorecord provides an opportunity to test the simulations of past climates and hence to evaluate the climatic and ecological sensitivity of the Arctic as indicated by models. The Palaeovegetation Mapping Project (BIOME 6000; *Prentice and Webb* [1998]) produced the first maps of vegetation distribution across the northern high latitudes at 6000 ^{14}C years B.P. (6 ka) and 18,000 ^{14}C years B.P. (18 ka) using a formal procedure (biomization; *Prentice et al.* [1996]) based on plant functional types (PFTs). The biomization procedure was applied in BIOME 6000 region by region, where the regions were defined pragmatically so as to build on pre-existing collaborative projects. The Arctic was thus fragmented among four regions, with slight overlaps between them: Beringia (Alaska and part of NW Canada plus the Russian Far East; *Edwards et al.* [2000]), Canada and Eastern North America [*Williams et al.*, 2000], Europe [*Prentice et al.*, 1996; *Tarasov et al.*, 2000], and the Former Soviet Union, excluding Beringia [*Tarasov et al.*, 1998, 2000]. Slightly different allocations of pollen taxa to PFTs, and of PFTs to biomes, were adopted by the different regional working groups. There are no apparent discontinuities at regional boundaries in the BIOME 6000 maps reconstructed from modern surface samples [see *Prentice et al.*, 2000]. This finding suggests that the differences in the regional biome schemes adopted in BIOME 6000 are not crucial, at least for the broad-scale patterns that BIOME 6000 was intended to reconstruct. However, the degree to which the reconstructed positions of transitions between steppe and tundra biomes at 18 ka have been influenced by differences in the regional biomization schemes has been questioned [*Edwards et al.*, 2000; *Tarasov et al.*, 2000; *Elenga et al.*, 2000]. Thus a re-examination of the Arctic data using a consistent biomization scheme is timely.

[4] Several additional factors motivate a reconsideration of the distribution of Arctic biomes at key times in the past. The regional biomizations made in BIOME 6000 concentrated on differentiating forest types, and forest from tundra. There was no attempt to distinguish different types of tundra. Yet tundra is highly differentiated, structurally and floristically, and the differences are closely linked to climatic gradients. Knowledge of the distribution of these different tundra vegetation types in the past could improve our understanding of regional climate changes in the high latitudes. The distinctions among tundra types are also potentially important for feedbacks involving changing water and carbon exchanges, as these vegetation types differ greatly in their biogeochemical and biophysical characteristics [*Chapin et al.*, 2000a, 2000b; *Epstein et al.*, 2001] including the height of perennial biomass and the annual net primary production (NPP). The height of perennial biomass ranges from <5 cm in cushion-forb and prostrate dwarf-shrub tundra, to nearly 2 m in high-shrub tundra near treeline. The taller shrub-dominated vegetation types present a many times rougher surface and can greatly reduce surface albedo in the presence of snow. NPP ranges from <50 g C m^{-2} yr^{-1} in cushion-forb tundra to >300 g C m^{-2} yr^{-1} in high-shrub tundra [e.g., *Christensen et al.*, 2000] implying a large range in carbon storage potential which is reinforced by slow decomposition rates in some shrub tundras. The lumping of all treeless Arctic vegetation into a single "tundra" biome for vegetation mapping and modeling purposes thus discards information about the land surface that is both ecologically and geophysically important.

[5] The international Pan-Arctic Initiative (PAIN) was set up with the goal of improving the ability of the ecological and geophysical communities to model Arctic vegetation types and their responses to environmental changes. The first part of the work carried out by PAIN was the produc-

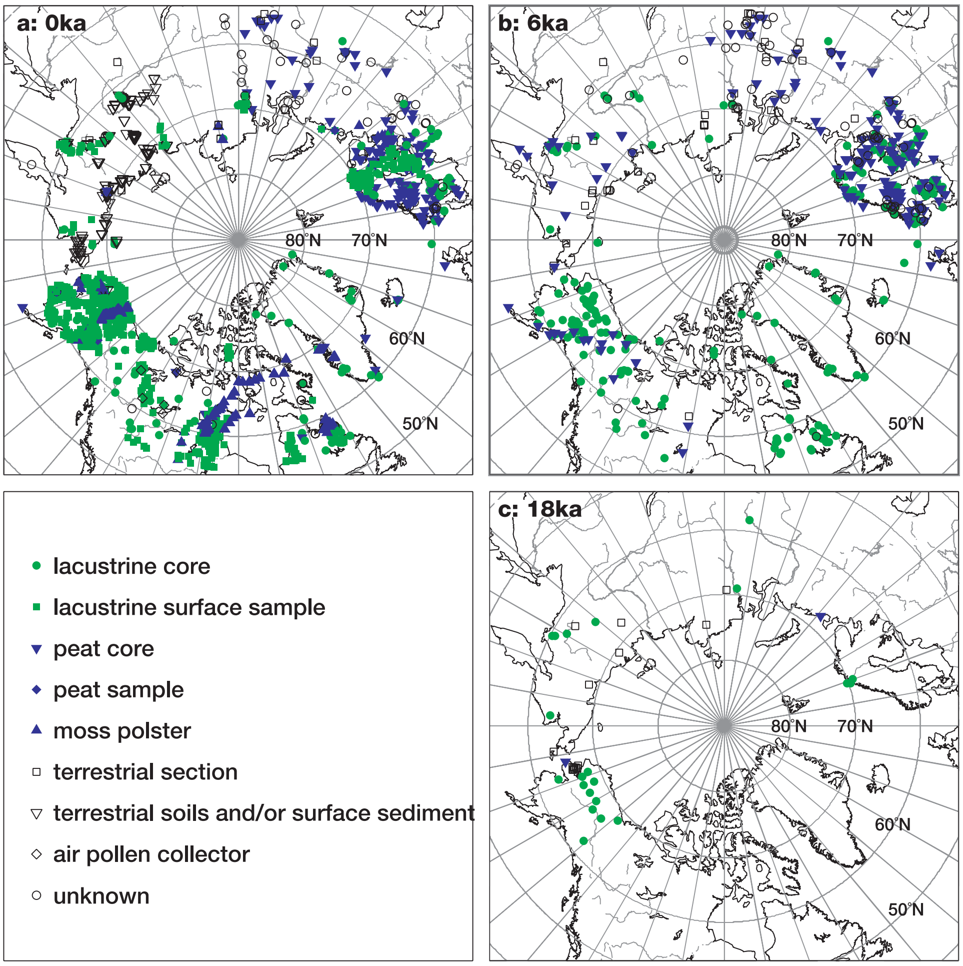

Figure 1. Types of sites providing (a) modern pollen data, (b) 6 ka pollen data, and (c) 18 ka pollen data. In cases where two or more 6 ka or 18 ka sites lie very close to one another, they have been slightly shifted in these plots to permit each site to be individually resolved.

tion of pollen-based biome reconstructions compatible with a new global biogeography-biogeochemistry model, BIOME4, which was also developed in part within the PAIN project [*Kaplan et al.*, 2003]. This paper documents the data sets and the biomization procedure developed by PAIN. The work enabled us to make a spatially detailed and methodologically consistent reconstruction of vegetation distribution in the high northern latitudes. Our primary aims were (a) to delimit the boundary between forest and tundra now and in the past, and (b) to reconstruct changes in the distribution of tundra types. We address some specific outstanding research questions: (a) the location of the Arctic treeline in the mid-Holocene, and in particular whether its late Holocene shifts have been zonally uniform; and (b) the nature of the vegetation of northern Eurasia and Beringia during the last glacial maximum (LGM), and in particular the interface between steppe and tundra vegetation types. The steppe-tundra interface at the LGM has been controversial because of the apparent lack of convincing modern analogues for this vegetation [*Vartanyan et al.*, 1993; *Goetcheus and Birks*, 2001; *Guthrie*, 2001; *Walker et al.*, 2001; *Yurtsev*, 2001]. It is important to understand the nature of the LGM vegetation because it provided the habitat for megaherbivore populations and hence support for human populations, including those that colonized the Americas (by way of the Bering land bridge) toward the end of the last glacial period.

2. Methods

2.1. Study Region

[6] The southernmost occurrence of tundra at low elevations in the Northern Hemisphere today is at about 55°N, along the southern coast of Hudson Bay in Canada. By confining our study area to the circumpolar region north of 55°N, we could encompass the full latitudinal range of the modern lowland tundra. This latitudinal limit also enabled us to process a great deal of information concerning the past and present distribution of boreal and cool-temperate forest types that occur north of 55°N (and in Fennoscandia, even north of 70°N).

2.2. Choice of Time Slices

[7] We assembled a comprehensive pollen data set for 0 ka (i.e., core tops and surface sediment samples), 6 ka (^{14}C timescale) and 18 ka (^{14}C timescale) (Figure 1). This choice of time slices allowed comparison with previous attempts to construct pollen-based biome maps covering

different regions of the Arctic as generated by the BIOME 6000 project. These specific times were selected in BIOME 6000 in part to allow comparison with climate model simulations carried out within the framework of the Palaeoclimate Modeling Intercomparison Project (PMIP; *Joussaume and Taylor* [1995]) for 6 ka and 21 ka BP (astronomical timescale). Within the time resolution that can actually be achieved by correlating independently dated sediment cores, 6 ka ^{14}C-years is effectively the same as 6 ka astronomical years BP, and 18 ka ^{14}C-years is effectively equivalent to 21 ka astronomical years BP. The 6 ka (mid-Holocene) time period represents an interval when the total annual insolation received in the northern high latitudes was larger than today and the annual cycle of insolation was enhanced (Northern Hemisphere summer insolation was greater and winter insolation less than today). Other boundary conditions, most importantly ice sheet distributions, sea level and atmospheric greenhouse gas concentrations (CO_2, CH_4, N_2O), were not materially different from those of the pre-industrial Holocene. The 21 ka (last glacial maximum, LGM) time period represents a contrasting interval when insolation was quite similar to today, but the continental ice sheets were at a maximum and greenhouse gas concentrations were at a minimum.

2.3. Pollen Data

[8] We generally used the single pollen sample that was closest in estimated ^{14}C age to the designated time, provided it fell within a certain time range. However, because of the larger dating uncertainties and/or higher inter-sample variability characteristic of some 18 ka records, we used multiple samples from these sites. Each of these samples was independently allocated to a biome, and the reconstructed biome at the site was assumed to correspond to the biome given by the majority of the samples. Following the BIOME 6000 convention, we allowed samples that fell within 0 to 500 years for the modern sample data set, within ±500 years of 6 ka, and within ±1000 years of 18 ka. A few samples that fell just outside these designated time ranges were allowed in exceptional cases. At 0 ka, eight samples that were dated in the range 500 to 850 years B.P. were included, for comparison with fossil pollen samples from the same cores. Four mid-Holocene samples that fell beyond the designated time range but within ±700 years of 6 ka BP were included. We included one sample in the 18 ka data set that was dated to 20.7 ka because it provided critical information from the Bering Land Bridge [*Elias et al.*, 1996] and because data from other parts of Beringia suggest relatively stable vegetation and climate during the interval 21 to 18 ka BP.

[9] Pollen data were available to us either as full pollen counts, or as pollen percentages derived from summary tables or scanned from published pollen diagrams. Typically, published pollen percentage summary tables and diagrams contain only major tree, shrub and herb taxa. Digitized pollen percentage data were used extensively in earlier studies in order to ensure a reasonably dense spatial coverage. The modern pollen-based maps of Europe made by *Prentice et al.* [1996], for example, are almost entirely based on digitized pollen percentage data, and about 50% of the sites used to construct the corresponding maps for Russia were digitized [*Tarasov et al.*, 1998]. These studies, and similar studies from other regions, suggest that pollen percentage data of major taxa are generally adequate to discriminate between forest types but are less good at discriminating non-forest biomes. Since herbaceous taxa are an important diagnostic of different tundra vegetation types, we used original pollen counts to the greatest possible extent. Digitized pollen percentage data were used only from those regions (e.g., some parts of northern Fennoscandia and European Russia) from which no other data were available to us.

[10] The modern pollen data set consists of 2098 samples (Table 1), 382 of which are associated with a fossil sample at 6 ka and/or 18 ka (e.g., they are lacustrine or peat core tops, or terrestrial sections). The original pollen counts were available for most of the samples (1809). However, 289 samples (13%) were only available as pollen percentages. The samples are from a variety of site types, including lacustrine core tops (185), lacustrine surface samples (755), peat core tops (151), peat samples (19), moss polsters (596), terrestrial section tops (16), terrestrial soils and/or surface sediments (269), and air pollen collectors (7). Site information is lacking for 100 samples, 22 of which are associated with a fossil sample. The mid-Holocene data set includes 493 samples (Table 2). Original pollen counts were available for most of the samples (404). However, 89 samples (18%) were only available as pollen percentages. The samples are from lacustrine cores (230), peat cores (158) and terrestrial sections (33). Site information is lacking for 72 samples. The LGM data set includes 67 samples from 39 sites (Table 2). Original pollen counts were available for most of the samples (58). Nine samples (13%) were available only as pollen percentages. The samples are from lacustrine cores (28), peat cores (2) and terrestrial sections (37).

[11] Some sites that were used in the BIOME 6000 publications have been excluded from the PAIN data set. For example, some modern sites from Russia were excluded because they appeared to duplicate samples represented in the data for Europe (30 sites). A further 466 modern sites were excluded for one or more of the following reasons: (a) they had poor dating control, (b) they had pollen counts of <100, (c) they were based on digitized records in cases where full pollen counts have subsequently become available, or (d) key background information (e.g., about the source of the samples) was lacking. A number of fossil sites that were included in the BIOME 6000 compilation for 6 ka (117 samples) and for 18 ka (6 samples) were excluded from the current data set for the same reasons. We applied the same quality-control criteria in selecting new sites to include in the compilation.

2.4. Assignment of Pollen Samples to Biomes

[12] The "biomization" method [*Prentice et al.*, 1996] is based on the recognition that plant taxa can be grouped into functional types (PFTs) that have both identifiable sets of traits and distinctive climatic requirements. The functional characteristics are expressed in life form (e.g., tree, erect dwarf-shrub, forb), leaf morphology (e.g., needle-leaved, broad-leaved), phenology (e.g., evergreen, cold-deciduous) and mechanism of extreme cold tolerance (e.g., tropical, i.e., frost intolerant, temperate, boreal). These functional characteristics are an expression of the mechanisms whereby

Table 1 (Representative Sample). Characteristics of the Modern Pollen Samples[a] [The full Table 1 is available in the HTML version of the article.]

Sample Code	Site Name	Sector	Latitude, deg	Longitude, deg	Elevation, m	Local Vegetation	Vegetation Formation	Sample Type	Data Type	Record Length, years	Number of ^{14}C Dates	References
N148_0k	Tårnet	Western Europe	69.67	30.10	n/a	undisturbed		peat core top	count	ca. 0–> 5000	2 + top	*Vorren* [1983]
S030	Juvjalampi	Western Europe	62.63	33.67	150	taiga dominated by *Pinussylvestris*	taiga	moss polster	unknown %	0	0	*Tarasov et al.* [1998]
S302	10 Mile Lake	Eastern Beringia (Alaska)	63.05	−145.42	n/a		alpine tundra	lacustrine surface sample	count	0	0	M. E. Edwards and A. P. Krumhardt (unpublished data, 2003)
S15-1	15/1	Labrador	55.09	−75.25	244		boreal forest	lacustrine surface sample	count	0	0	*Gajewski* [1991]
S15-2	15/2	Labrador	55.83	−75.02	305		forest tundra/ boreal forest transition	lacustrine surface sample	count	0	0	*Gajewski* [1991]
S16-1	16/1	Labrador	55.41	−75.07	285		boreal forest	lacustrine surface sample	count	0	0	*Gajewski* [1991]
S17-1	17/1	Labrador	55.07	−75.70	235		boreal forest	lacustrine surface sample	count	0	0	*Gajewski* [1991]
S17-2	17/2	Labrador	55.25	−74.93	335		boreal forest	lacustrine surface sample	count	0	0	*Gajewski* [1991]
S17-3	17/3	Labrador	55.12	−75.95	255		boreal forest	lacustrine surface sample	count	0	0	*Gajewski* [1991]
S143	6 Asseyes Lake	Eastern Beringia (Alaska)	62.65	−141.07	549	*Picea glauca* and sedge meadows	black spruce muskeg-sedge meadows	lacustrine surface sample	count	0	0	P. M. Anderson and L. B. Brubaker (unpublished data, 2003)
TA020	70 Mile Lake, Richardson Hwy	Eastern Beringia (Alaska)	61.52	−145.23	564		boreal forest	lacustrine surface sample	count	0	0	T. A. Ager (unpublished data, 2003)
S303	Ace Lake	Eastern Beringia (Alaska)	64.52	−147.56	n/a		boreal forest	lacustrine surface sample	count	0	0	M. E. Edwards and A. P. Krumhardt (unpublished data, 2003)
icp38	Adamsvatnet	Western Europe	70.53	29.45	322		tundra	lacustrine surface sample	digitized %	0	0	*Prentice* [1978]
AGE	Ageröds Mosse	Western Europe	55.83	13.42	58	pasture and arable land	nemoral forest	peat core top	count	0–9660	21 + top	*Nilsson* [1964]
S039	Ahaliorak Lake	Eastern Beringia (Alaska)	68.92	−151.32	329	*Betula* shrub tussock tundra, *Salix* present (no *Alnus*)	tundra	lacustrine surface sample	count	0	0	P. M. Anderson and L. B. Brubaker (unpublished data, 2003)
S273	Ahaliorak Lake	Eastern Beringia (Alaska)	68.91	−151.32	n/a		shrub tussock tundra	lacustrine surface sample	count	0	0	P. M. Anderson and L. B. Brubaker (unpublished data, 2003)
icp32	Ahvenjärvi	Western Europe	68.93	26.97	155.5		pine forest	lacustrine surface sample	digitized %	0	0	*Prentice* [1978]

[a]Latitude and longitude are given in decimal degrees, where N and E are conventionally positive and S and W are negative.

Table 2 (Representative Sample). Characteristics of the 6 ka and 18 ka Pollen Samples[a] [The full Table 2 is available in the HTML version of this article.]

Site Name	Latitude, deg	Longitude, deg	Elevation, m	Sample Type	Data Type	Record Length, years	Number of ^{14}C Dates	6 ka Dating Control	18 ka Dating Control	Database Source	References
Adycha Section	67.57	134.42	130	peat core	count	1000–8820	5 + top	1C	n/a	PALE	A. V. Lozhkin (unpublished data, 2003)
Ageröds Mosse	55.83	13.42	58	peat core	count	0–9660	21 + top	1C	n/a	EPD	*Nilsson* [1964]
Aholammi	61.88	25.22	114	lacustrine core	count	1480–11,552	3	2C	n/a	EPD	*Koivula* [1987]
Aiatskoe	57.00	60.08	229	peat core	digitized %	0–> = 9000	7 + top	1C	n/a		*Peterson* [1993]
Ailsa so	75.32	−19.67	88	lacustrine core	count	6000–11,500	5 (1 rejected)	1D	n/a		*Björck and Persson* [1981]
Åkerhultagöl [Tomtabaken]	57.48	14.47	303	peat core	count	6387–12,967	14	6D	n/a	EPD	*Bjelm* [1976], *Björck and Hakansson* [1982]
Akuvaara	69.13	27.68	170	lacustrine core	count	670–9434	5	1C	n/a	EPD	*Hyvärinen* [1975]
Alazeya	68.50	154.00	40	peat core	count	4000–10,000	5	2C	n/a		*Kaplina and Lozhkin* [1982]
Altersvatn	60.80	4.93	4	lacustrine core	count	ca. 2000–9000	1 (1 rejected) + pollen	7	n/a	Nordmap	*Kaland* [1984]
Alut Lake	60.30	152.31	480	lacustrine core	count	0–53,576	24 (11 rejected) + top + 1 tephra	1C	6C	PALE	P. M. Anderson and A. V. Lozhkin (unpublished data, 2003)
Andy Lake	64.65	−128.08	1360	lacustrine core	count	0–11,310	5 (1 rejected) + top	1C	n/a	NAPD	*Szeicz et al.* [1995]
Angal Lake	67.13	−153.88	853	lacustrine core	count	0–14,130	3 + top	3D	n/a	NAPD	*Brubaker et al.* [1983]
Antifreeze Pond	62.35	−140.83	706	lacustrine core	digitized %	0–>13,000	8 (1 rejected) + top + 1 tephra	2C	7C		*Rampton* [1971]
Åntu sinijarv	59.13	26.33	95	lacustrine core	count	1987–12,742	9	2C	n/a	EPD	L. Saarse (unpublished data, 2003), *Saarse and Liiva* [1995]
Arkad'evo	56.50	84.00	70	unknown	unknown %		1	2D	n/a		N. A. Berezina and P. S. Liss (personal communication to P. E. Tarasov, 1997)
Åsen	59.67	9.17	668	unknown	count	0–6000	3 + top	1D	n/a	Nordmap	*Hafsten et al.* [1979]
Ayakli	69.25	89.00	125	terrestrial section	count	ca. 11,000–20,000	2	n/a	6C		*Kind* [1974]
B. Kuropatochya	71.07	156.50	77	unknown	digitized %	6000–>/= 9000	4	1	n/a		*Peterson* [1993]
Babozero	66.37	37.52	138	lacustrine core	count	0–11,800	3 + top	3C	n/a		*Kremenetski and Patyk-Kara* [1997]
Baidara	68.85	66.90	30	unknown	count	3995–11,066	10 (3 rejected)	1C	n/a	EPD	*Andreev et al.* [1998]
Baie du Diana	60.78	−69.83	50	lacustrine core	count	250–6330	1 + top + deglaciation	2D	n/a	NAPD	*Richard* [1977]
Baird Inlet "Rock Basin Lake"	78.49	−76.78	295	lacustrine core	count	0–9000	3+ top	1C	n/a		*Hyvärinen* [1985a]
Bakkemyra	69.20	17.55	140	peat core	count	0–8800	5 + top	1C	n/a	Nordmap	*Vorren* [1979]
Banktjörn	60.12	5.47	21	lacustrine core	count	ca 2500–9000	0 + pollen	7	n/a	Nordmap	*Sønstegaard and Mangerud* [1977]
Barsebäcksmossen	55.77	12.88	1	lacustrine core	count	0–10,000	15 + top	1C	n/a	Nordmap	*Digerfeldt* [1975]
Beglianskii Riam	55.50	81.57	77	peat core	digitized %	0–6000	0 + 8 poll or strat	7	n/a		*Peterson* [1993]
Belkachi	59.15	131.98	458	unknown	digitized %	6000	0	7	n/a		*Peterson* [1993]
Bell's Lake	65.02	−127.48	580	lacustrine core	count	0–11,450	5 + top	2C	n/a	NAPD	*Szeicz et al.* [1995]
Berelyekh Section	70.58	145.00	20	terrestrial section	count	9468–31,542	4	n/a	7D	PALE	A. V. Lozhkin (unpublished data, 2003)
Bering Land Bridge	65.23	−167.42	0	peat core	digitized %	ca. 13,000–20,700	4 (+1 rejected)	n/a	7D		*Elias et al.* [1996]

[a]Latitude and longitude are given in decimal degrees, where N and E are conventionally positive and S and W are negative. The dating control (DC) follows the COHMAP scheme, as described by *Yu and Harrison* [1995].

[b]For mapping purposes, these sites, which are very close to one another, have been displaced slightly.

[c]These sites have multiple samples within the 18 ka time window; all samples have been used in the biomization procedure.

plants maximize productivity while surviving environmental stress. Plant functional types are expected to occupy a contiguous area in environmental space, even though their distribution in geographic space is typically discontinuous.

[13] In some cases, the physiological adaptations to climate stress are well established from experimental work (e.g., adaptations to extreme cold, budburst, adaptations to drought). In other situations, the mechanism is unclear although the geographic distribution of PFTs makes it abundantly clear that there are climatic limits operating. In practice, the definition of PFT distributions in climate space has relied on a mixture of known mechanistic limits and correlations of biogeographical distribution limits and climate variables. The first step in biomization is the derivation of a conceptual framework in which PFTs are arranged in climate space and biomes are identified as combinations of PFTs with particular climatic locations. ("Climate" here is interpreted in a broad sense, incorporating the idea that plants are sensitive to aspects of the environment that are modified by soil and topography.) In this study, this step has been made explicit and used a basis for model development [*Kaplan et al.*, 2003] as well as for the definitions of biomes based on taxa assigned to PFTs.

[14] The definitions of biomes adopted here are outlined in the companion paper [*Kaplan et al.*, 2003]. We aimed to distinguish as biomes those vegetation types that are recognizable throughout the region and distinctive in terms of land-surface parameters, carbon storage and climatic controls. We required that the biomes be recognisable on the modern landscape (although not necessarily occupying large continuous areas) and further that they should be able to be discriminated on the basis of modern pollen data, thus allowing their distribution to be reconstructed from the fossil record. Using these criteria, we arrived at a five-fold classification of tundra (cushion forb tundra; graminoid and forb tundra; prostrate dwarf-shrub tundra; erect dwarf-shrub tundra; low- and high-shrub tundra). For the non-tundra types we adopted the same classification as in the BIOME4 model [*Kaplan*, 2001; *Kaplan et al.*, 2003], except that we did not attempt to separate temperate deciduous broadleaf savanna from temperate deciduous broad-leaved forest (we lumped both as "forest"), nor did we attempt to separate temperate xerophytic shrubland from temperate grassland (we lumped both as "steppe"). In all, twelve biomes were recognized as occurring north of 55°N today.

[15] As the biomization method requires the maximum use of floristic information in pollen records, it is usually necessary to define a larger number of PFTs for this purpose than can practically be used in a modeling context. Here we have defined 29 PFTs (Table 3). We adopted the classification for arboreal PFTs that has been used in previous biomizations [e.g., *Prentice et al.*, 1996; *Tarasov et al.*, 1998; *Edwards et al.*, 2000], retaining just those that occur in the northern high latitudes. Thus we recognised 11 arboreal PFTs. We modified their names in order to make the classification according to bioclimate, phenology, leaf morphology and life form more explicit.

[16] Non-arboreal PFTs have been treated in a highly simplified way in previous biomizations. We devised a new functional classification, paying special attention to the diversity of shrub life forms that characterizes the vegetation of the Arctic. We divided shrubs into three primary categories according to stature: prostrate dwarf-shrubs are less than 5 cm tall; erect dwarf-shrubs are between 5 and 25 cm tall; and low- and high-shrubs are greater than 25 cm, but less than 200 cm tall. The shrubs are then further divided according to differences in bioclimatic range, leaf morphology and phenology. In this way, we define 11 shrub PFTs. Among forbs, we distinguished three PFTs: rosette or cushion forb, arctic forb, and drought-tolerant boreal or temperate forb. The characteristic shape of rosette and cushion forbs enables them to trap air close to the leaf surface and thus to survive extremely low air temperatures through thermal enhancement [*Sonesson and Callaghan*, 1991]. Typical examples are *Draba* spp. and *Silene aucaulis*. Arctic forbs do not have a unique growth form but characteristically survive extreme winter air temperatures by being snow covered and have a rapid growth cycle once the snow melts [*Bliss*, 1962]. Typical examples include *Polemonium* spp., *Pedicularis* spp., *Gentiana* spp. and *Oxyria digyna*. The drought-tolerant boreal or temperate forbs show no characteristic adaptations to temperature stress but rather have adaptations that enable them to survive drought conditions, such as succulence and early senescence. Characteristic taxa include *Sarcobatus* spp. and *Atriplex* spp. Two additional forb PFTs (boreal forbs and temperate forbs) were recognised but not used in previous biomizations because they appear to lack diagnostic value [e.g., *Edwards et al.*, 2000]. Most of the taxa that could be allocated to boreal or temperate forbs can tolerate a wide range of bioclimatic conditions. The relatively few forbs that occur uniquely in boreal or temperate environments are encountered only rarely in the pollen data. We therefore followed previous work in excluding boreal or temperate forbs from our analysis. The PFTs grass (Poaceae) and sedge (Cyperaceae) were retained, and bog moss (*Sphagnum* spp.) and rushes (Juncaceae) were further identified as distinct PFTs because of their potential discriminatory power in the Arctic. Following previous work, we excluded ferns and aquatics from our analysis.

[17] On the basis of the definitions of the biomes as presented in Table 4, Table 5 indicates the characterization of each biome in terms of constituent PFTs. Table 6 gives the assignments of pollen taxa to PFTs. The information in Tables 5 and 6 allows each pollen sample to be assigned uniquely to the most likely biome according to its numerical affinity score, following the biomization method of *Prentice et al.* [1996]. Pollen taxa that are present but constitute less than 0.5% of the pollen sum do not contribute to the calculation of the affinity score. We applied a weighting (×15) to the pollen percentages of *Larix* prior to calculating the affinity score (including the square root transformation of pollen percentages used in this calculation) in order to compensate for the known low pollen production characteristic of this taxon. This weighting was chosen because it resulted in the most realistic modern distribution of cold deciduous forest in Siberia. In the case when equal affinity scores were obtained for more than one biome, biomes were assigned in the order shown in Table 5. We varied the standard biomization method in one respect: namely, to perform the biomization in two steps. At the first step, a composite biome "tundra" was distinguished. The composite biome was defined as the union of all of the tundra

Table 3. Definition of Plant Functional Types Used in the Biomization Procedure[a]

Biome 6000 Code	New Code	PFT Name	Characteristic Taxa
sp	m	bog moss	*Sphagnum*
g	g	grass graminoid	Poaceae
s	s	sedge graminoid	*Carex*
r	r	rush graminoid	*Juncus*
crc	rcfb	rosette or cushion forb	*Draba, Silene aucaulis*
af	ar.fb	arctic forb	*Polemonium, Pedicularis*
sf	bo/te-dt.fb	boreal or temperate drought-tolerant forb	*Sarcobatus, Atriplex*
dpms	ar.cd.mb.pds	arctic cold-deciduous malacophyll broad-leaved prostrate dwarf shrub	*Salix arctica*
eps	ar.e.mb.pds	arctic evergreen malacophyll broad-leaved prostrate dwarf shrub	*Diapensia, Dryas*
juni	ab.e.n.pds	arcto-boreal evergreen needle-leaved prostrate dwarf shrub	*Juniperus*
dds	ab.cd.mb.eds	arcto-boreal cold-deciduous malacophyll broad-leaved erect dwarf shrub	*Betula nana*
eds	ab.e.mb.eds	arcto-boreal evergreen malacophyll broad-leaved erect dwarf shrub	*Empetrum, Cassiope, Vaccinium vitis-idaea*
dlhs	ab.cd.mb.lhs	arcto-boreal cold-deciduous malacophyll broad-leaved low or high shrub	*Alnus crispa*
elhs	ab.e.mb.lhs	arcto-boreal evergreen malacophyll broad-leaved low or high shrub	*Calluna, Ledum*
cbc	ab.e.n.lhs	arcto-boreal evegreen needle-leaved low or high shrub	*Pinus pumila*
bss	bo.cd.mb.lhs	boreal cold-deciduous malacophyll broad-leaved low or high shrub	*Alnus incana, Myrica*
bes	bo.e.mb.lhs	boreal evergreen malacophyll broad-leaved low or high shrub	*Chamaedaphne*
ss	bo/te-dt.cd/e.mb.lhs	boreal or temperate drought-tolerant cold-deciduous or evergreen malacophyll broad-leaved low or high shrub	*Euphorbia*
bec	bo.e.n.t	boreal evergreen needle-leaved tree	*Picea abies*
cdc	bo.cd.n.t	boreal cold-deciduous needle-leaved tree	*Larix*
bst	bo.cd.mb.t	boreal cold-deciduous malacophyll broad-leaved tree	*Populus*
ec	eu.e.n.t	eurythermic evergreen needle-leaved tree	*Pinus sylvestris*
ctc	te.e.n.t	temperate evergreen needle-leaved tree	*Tsuga canadensis, Tsuga heterophylla, Thuja*
ctc1	ma.e.n.t	maritime evergreen needle-leaved tree	*Taxus*
ctc2	c-te.e.n.t	cool-temperate evergreen needle-leaved tree	*Tsuga mertensiana*
ts	te-fa.cd.mb.t	temperate (spring-frost avoiding) cold-deciduous malacophyll broad-leaved tree	*Quercus* (deciduous), *Acer*
ts1	te-ft.cd.mb.t	temperate (spring-frost tolerant) cold-deciduous malacophyll broad-leaved tree	*Tilia cordata, Fagus grandifolia*
ts2	te-fi.cd.mb.t	temperate (spring-frost intolerant) cold-deciduous malacophyll broad-leaved tree	*Juglans, Castanea*
wte1	te.e.mb.wp	temperate evergreen malacophyll broad-leaved woody plants	*Ilex, Hedera*

[a]We have adopted PFT names and codes that make the relationship to bioclimate, phenology, leaf morphology, and life form explicit. We include the PFT codes used in the BIOME 6000 project for information and to facilitate cross-comparison with earlier biomization schemes.

biomes; that is, it was defined by the presence of PFTs assigned to any tundra biome. The separate tundra biomes were identified in a second step. This two-step procedure was adopted because it was found to allow a slightly more accurate reconstruction of the modern tundra-forest boundary.

2.5. Modern Vegetation at the Surface Pollen Sites

[18] In order to assess the accuracy of present-day vegetation reconstructions based on pollen data, we required a way to assign each pollen sample to a modern biome independently, based on the present-day distribution of the biomes. In principle this can be done in two ways, which do not necessarily agree. Both are approximations of what the pollen samples actually "see."

[19] 1. On the one hand, we had access to information from field notes about the vegetation surrounding most of the surface pollen samples in Beringia, and a proportion of the samples from other regions. Field notes indicate the local (i.e., within 1–2 km) vegetation immediately around the sampling site, which can be influenced by local soil, orography and drainage patterns.

[20] 2. On the other hand, we could estimate the regional vegetation around each site from a contemporary biome map. We constructed this map using the observation-based gridded (0.5°) map of potential natural vegetation map of *Haxeltine and Prentice* [1996] as a starting point (see Table 7). This map itself was derived from a variety of existing regional and global maps. We overlaid the map of *Walker* [2000] digitized at the same (0.5°) resolution to provide further information on regional tundra types. Data from *Haxeltine and Prentice* [1996] were retained for all grid cells for which *Walker* [2000] does not provide a classification including the whole of the forested area. The regional vegetation around each pollen sample was assumed to be the potential natural vegetation of the grid cell in which the sample is located. In cases where a sample fell in a grid cell not covered by the map (for example some coastal sites), the most prevalent biome in immediately adjacent grid cells was used. The biomes assigned in this way form the basis for the actual vegetation assignments plotted in Figure 2b, and used in the construction of Table 8.

[21] This procedure does not assign any modern sites to graminoid and forb tundra, because this tundra type does

Table 4. Definition of the Biomes Used in the Biomization Procedure

Biome Code	Biome Name in BIOME4	Definition	Characteristic Species or Assemblages in NH Arctic	Equivalents
STEP	temperate grassland	Treeless vegetation dominated by drought-tolerant forbs and grasses	Grasses, Chenopodiaceae, Asteraceae, Liliaceae	prairie (North America); steppe (Ukraine, North China)
STEP	temperate xerophytic shrubland	Treeless vegetation dominated by drought-tolerant, and locally salt-tolerant, shrubs with grasses	*Artemisia, Purshia, Chrysothamnus, Hippophae*, and grasses	sagebrush steppe of North American Great Basin, cold semi-desert in central Asia
CUSH	cushion-forb tundra	Discontinuous treeless vegetation characterised by high-arctic rosette or cushion forbs, grasses, mosses, lichens	Saxifragaceae, Caryophyllaceae, *Papaver, Draba*	polar desert, cold semi-desert
DRYT	graminoid and forb tundra	Treeless and predominantly herbaceous vegetation dominated by arctic forbs, graminoids, true mosses, and lichens	*Artemisia, Kobresia*, Brassicaceae, Asteraceae, Caryophyllaceae, grass, true mosses	*Yurtsev*'s [2001] cryoxeric vegetation, *Kobresia* meadows
PROS	prostrate dwarf-shrub tundra	Treeless vegetation dominated by arcto-boreal prostrate dwarf shrubs, grasses, arctic forbs, true mosses, lichens	*Salix, Dryas, Pedicularis*, Asteraceae, Brassicaceae, grass and sedge	northern Arctic tundra
DWAR	erect dwarf-shrub tundra	Treeless vegetation dominated by arcto-boreal dwarf shrubs, with graminoids, true mosses, and lichens	*Betula, Salix, Vaccinium, Empetrum, Cassiope*, grass and sedge	low Arctic tundra, tussock tundra
SHRU	low- and high-shrub tundra	Treeless vegetation dominated by arcto-boreal deciduous or evergreen low and high shrubs, sometimes with tussock-forming graminoids and true mosses, bog mosses, and lichens	*Alnus, Betula, Salix, Pinus pumila, Eriophorum, Sphagnum*	shrub tundra
CLDE	cold deciduous forest	Forest dominated by boreal broad-leaved or needle-leaved deciduous trees, sometimes with significant component of arcto-boreal evergreen needle-leaved shrubs	*Larix, Betula* or *Populus* subg. *tremula/tremuloides*, with *Pinus pumila*	E. Siberian larch forests; aspen parkland (North America); maritime birch forests
TAIG	cold evergreen needle-leaved forest	Forest dominated by boreal evergreen needle-leaved trees, with boreal deciduous or needle-leaved trees	*Picea* and *Abies*, with some *Pinus, Betula, Populus* or *Larix*	dark taiga (Russia); boreal forest (North America)
COCO	cool evergreen needle-leaved forest	Forest dominated by boreal and temperate evergreen needle-leaved trees	*Pinus strobus, Pinus resinosa, Picea glauca, Pinus banksiana, Abies balsamea, Acer saccharum*	southern boreal forest (Europe); cool conifer forest (south-central Ontario-Quebec)
CLMX	cool-temperate evergreen needle-leaved forest	Forest lacking boreal evergreen needle-leaved trees, with boreal deciduous broad-leaved trees and evergreen needle-leaved trees	*Tsuga* and *Picea sitchensis, Pinus* with *Betula, Pinus* with *Betula* and *Populus*	*Pinus-Betula* forests (W. Norway & Scotland); *Pinus-Populus-Betula* woodland (Central Asia)
TEDE	temperate deciduous forest	Forest dominated by temperate deciduous broad-leaved trees	*Quercus, Fagus, Carya, Ulmus, Castanea*	temperate deciduous forest (eastern North America); nemoral forest (western Europe)
COMX	cool mixed forest	Forest with boreal and temperate evergreen needle-leaved trees and deciduous broad-leaved trees	*Picea, Pinus, Quercus, Acer, Ulmus*	North American northern hardwoods; Scandinavian boreo-nemoral forest

Table 5. Assignment of Plant Functional Types to Biomes[a]

	Biome	m	rcfb	ar.fb	g	s	r	ar.cd. mb.pds	ar.e. mb.pds	ab.cd. mb.eds	ab.e. mb.eds	ab.cd. mb.lhs	ab.e. mb.lhs	ab.e. n.lhs	eu.e. n.t	ab.e. n.pds	bo.cd. n.t	bo.e. n.t	bo.cd. mb.t	bo.e. mb.lhs	te.e. n.t	ma.e. n.t	c-te. e.n.t	te-ft. cd.mb.t	te-fa. cd.mb.t	te-fi. cd.mb.t	te.e. mb.wp	bo/te- dt.fb	o/te-dt.cd/ e.mb.lhs	bo.cd. mb.lhs
1	STEP	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
2	CUSH	0	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	DRYT	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	PROS	0	1	1	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	DWAR	0	0	0	1	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6	SHRU	1	0	0	0	1	0	1	1	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7	CLDE	1	0	0	0	0	0	0	0	1	1	1	1	1	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	1
8	TAIG	1	0	0	0	0	0	0	0	1	1	1	1	0	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	1
9	COCO	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	1	1	0	1	0	0	0	0	0	0
10	CLMX	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	1	1	1	0	0	0	0	0	0
11	TEDE	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	1	1	1	1	0	0	0
12	COMX	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	1	0	0	1	1	0	0	0	0	0

[a]The PFT codes are given in Table 3, and the BIOME codes are given in Table 4.

not form the dominant regional vegetation today in any region north of 55°N but rather occurs only in topographically suitable habitats [*Kaplan et al.*, 2003]. However, some samples were assigned to this biome on the basis of their pollen assemblage and/or local site description.

3. Results

3.1. Biome Reconstructions for the Present-Day

[22] The biomization procedure is able to capture the large-scale patterns of vegetation distributions across the Arctic (Figure 2 and Table 8). The tundra-forest boundary is correctly placed in all regions, and the distribution of different forest and tundra vegetation types is in good agreement with observations.

[23] We do not reconstruct the occurrence of cushion forb tundra today because the surface pollen data set is deficient in sites from the appropriate regions, such as Svalbard and north-central Greenland. We reconstruct a number of occurrences of graminoid and forb tundra. In some cases, this classification correctly reflects the local occurrence of this vegetation type, e.g., on the islands and coast of Chukotka (western Beringia), and in the Canadian Arctic archipelago. One location (Sommersø) in northeast Greenland, in cushion forb tundra, is incorrectly assigned to graminoid and forb tundra because of the local presence of sedges. A few sites from the western Beringia coast are misclassified as steppe although the vegetation is graminoid and forb tundra.

[24] Although the overall placement of the tundra-forest boundary is rather good, there are nevertheless some biases in the reconstruction. In eastern Beringia (i.e., Alaska) and western Beringia (i.e., Eastern Siberia, east of 130°E, and Chukotka), 18% and 43% of the sites, respectively, are misclassified (tundra as forest, or vice versa). Most of these misclassifications (17% and 35%) are of sites that are in forest but have been classified as tundra. The treeline in western Beringia is composed of *Larix* spp., which is a low pollen producer. Although low pollen production does not appear to impact significantly on the geographical patterning of forests (the pollen-based reconstruction of the distribution of cold deciduous forests dominated by *Larix* is realistic), it nevertheless apparently increases the chance of individual sites being misclassified as tundra and hence impacts on our numerical assessment of the success of the biomization procedure. The treeline in eastern Beringia is composed of *Picea glauca*, which is not a particularly low pollen producer. In this case, it would appear that the bias in our reconstructions is a result of the importance of *Alnus* spp. in the forests and (in its shrub form) in the tundra. Misclassification of sites in the modern tundra as forest is common in Keewatin (21%) and Labrador (20%). This misclassification is due to the prevalence of long-distance transport of pollen of trees that are prolific pollen producers, including *Pinus* spp., from nearby forested regions. We assume that these biases with respect to treeline operated in a similar manner in the past, so regional assessments of the change in the treeline position compared to present should be more accurate than the exact placement of the treeline.

[25] Among tundra types, the reconstruction shows erect dwarf-shrub tundra as being too extensive at the expense of prostrate dwarf-shrub tundra, for example in Greenland. The

Table 6. Assignment of Pollen Taxa to Plant Functional Types

PFT Name	PFT Code	Taxa
bog moss	m	*Sphagnum*
grass graminoid	g	Gramineae, Poaceae
sedge graminoid	s	*Carex*-type, Cyperaceae
rush graminoid	r	Juncaceae undiff.
rosette or cushion forb	rcfb	Caryophyllaceae undiff., *Draba, Saxifraga hirculus*-type, Saxifragaceae undiff., *Saxifraga caesia, Saxifraga cernua*-type, *Saxifraga hieracifolia*-type, *Saxifraga nivalis*-type, *Saxifraga nelsoniana, Saxifraga oppositifolia, Saxifraga tricuspidata*-type, *Saxifraga, Silene*-type
arctic forb	ar.fb	*Achillea*-type, *Achillea, Aconitum*, Alliaceae, *Allium, Androsace, Anemone*-type, *Anemone, Angelica*-type, *Angelica, Antennaria*-type, Apiaceae, *Arnica, Artemisia*, Asteraceae subf. Asteroideae, Asteraceae subf. Asteroideae (thick spines), Asteraceae subf. Carduoideae, *Aster*, Asteraceae undiff., *Astragalus*-type, Brassicaceae, Brassicaceae-type undiff., *Caltha*, Campanulaceae, *Campanula*-type, *Cardamine, Cerastium*-type,Asteraceae subf. Chichorioideae, *Claytonia acutifolia, Claytonia, Claytoniella vassilievii*, Asteraceae (high spine), *Corydalis*, Crassulaceae, Caryophyllaceae undiff., *Dodecatheon*-type, *Epilobium angustifolium, Epilobium*, Fabaceae, Fabaceae undiff., *Galium, Galium*-type, Gentianaceae, *Gentiana* undiff., *Geum, Hedysarum*-type, *Koenigia, Koenigia islandica*, Liliaceae, *Lloydia, Lychnis dianthus*-type, Onagraceae, *Oxyria digyna, Oxyria, Oxytropis*, Papaveraceae, *Papaver, Parnassia palustris, Parnassia, Pedicularis, Pedicularis langsdorfii, Pedicularis lanceolata, Pedicularis verticillata, Phlox, Phlox sibirica, Plantago* undiff., *Plantago canescens*-type, Plantaginaceae, Polygonaceae, Polemoniaceae undiff., *Polemonium, Polygonum, Polygonum bistorta*-type, *Polygonum viviparum, Polygonum aviculare, Polygonum aviculare*-type, Polygonaceae, *Polygonum sect. Bistorta*, Portulacaceae, *Potentilla, Potentilla*-type, Primulaceae, *Pyrola*, Pyrolaceae, *Ranunculus* undiff., Ranunculaceae undiff., *Ranunculus acris*-type, Ranunculaceae *type 1*, Ranunculaceae *type 2*, Rosaceae undiff., Rubiaceae undiff., *Rubus, Rubus arcticus, Rumex* Subgen. *Acetosa/R*. Subgen. *Acetosella, Rumex, Rumex acetosa, Rumex/Oxyria digyna, Rumex/Oxyria, Rumex*-type, *Sagina, Sanguisorba, Sanguisorba officinalis, Saussurea alpina, Saussurea, Saxifraga hirculus*-type, Saxifragaceae undiff., *Saxifraga caesia, Saxifraga cernua*-type, *Saxifraga hieracifolia*-type, *Saxifraga nivalis*-type, *Saxifraga nelsoniana, Saxifraga oppositifolia, Saxifraga tricuspidata*-type, *Saxifraga*, Scrophulariaceae, *Senecio*-type, *Sedum, Silene*-type, *Solidago*-type, *Spiraea, Stellaria, Taraxacum, Taraxacum*-type, *Thalictrum, Tofieldia, Trientalis europaea, Trollius europaeus*, Umbelliferae undiff., *Valeriana*, Valerianaceae, *Veratrum*, Violaceae
boreal or temperate drought-tolerant forb	bo/te-dt.fb	*Achillea*-type, *Achillea*, Alliaceae, *Allium, Amarantha, Ambrosia*-type, *Antennaria*-type, *Anthemis*-type, Apiaceae, *Artemisia*, Asteraceae subf. Asteroideae, Carduoideae, Asteraceae undiff., *Astragalus*-type, *Atriplex nudicaulis*, Boraginaceae, Brassicaceae, Brassicaceae-type undiff., *Bupleurum*, Campanulaceae, *Campanula*-type, *Centaurea, Centaurea cyanus, Centaurea cyanus*-type, *Centaurea jacea, Cerastium*-type, Chenopodiaceae, Chenopodiaceae/Amaranthaceae,Asteraceae subf. Chichorioideae, Asteraceace (high spine), Crassulaceae, Cruciferae, Caryophyllaceae undiff., Dipsacaceae, *Euphorbia*, Fabaceae undiff., *Galium, Galium*-type, Gentianaceae, *Hedysarum*-type, Iridaceae, *Iris, Kochia laniflora*, Labiatae undiff., Lamiaceae, Liguliflorae, Liliaceae, Onagraceae, *Oxytropis*, Papaveraceae, *Papaver, Phlox, Plantago* undiff., *Plantago canescens*-type, Plantaginaceae, Plumbaginaceae, *Polygonum*, Polygonaceae, Portulacaceae, *Potentilla, Potentilla*-type, Primulaceae, *Ranunculus* undiff., Ranunculaceae undiff., *Ranunculus acris*-type, Ranunculaceae type 1, Ranunculaceae type 2, Ranunculaceae, Rosaceae undiff., Rubiaceae undiff., *Rumex, Rumex/Oxyria digyna, Rumex/Oxyria, Rumex*-type, *Sanguisorba, Sanguisorba officinalis, Sarcobatus vermiculatus, Sarcobatus vermiculatus*, Scrophulariaceae, *Senecio*-type, *Sedum, Silene*-type, *Solidago*-type, *Spergula arvensis, Sphaeralcea, Spiraea, Stellaria, Taraxacum, Taraxacum*-type, *Thalictrum, Thymus*, Umbelliferae undiff., *Valeriana*, Valerianaceae

Table 6. (continued)

PFT Name	PFT Code	Taxa
arctic cold-deciduous malacophyll broad-leaved prostrate dwarf shrub	ar.cd.mb.pds	*Arctostaphylos, Salix, Salix herbacea*-type, *Salix cf. herbacea, Salix vestita*-type
arctic evergreen malacophyll broad-leaved prostrate dwarf shrub	ar.e.mb.pds	*Arctostaphylos, Diapensia, Dryas, Dryas*-type
arcto-boreal evergreen needle-leaved prostrate dwarf shrub	ab.e.n.pds	Cupressaceae, *Juniperus*-type, *Juniperus communis*
arcto-boreal cold-deciduous malacophyll broad-leaved erect dwarf shrub	ab.cd.mb.eds	*Arctostaphylos, Betula sect. nanae, Betula nana*-type, *Betula* undiff., *Betula* corroded, *Betula exilis, Betula* small, Ericaceae undiff., *Ericales, Salix, Salix herbacea*-type, *Salix cf. herbacea, Salix vestita*-type
arcto-boreal evergreen malacophyll broad-leaved erect dwarf shrub	ab.e.mb.eds	*Arctostaphylos, Cassiope, Empetrum*, Ericaceae undiff., Ericaceae undiff., *Ericales, Vaccinium*-type, *Vaccinium vitis-idaea*
arcto-boreal cold-deciduous malacophyll broad-leaved low or high shrub	ab.cd.mb.lhs	*Alnus crispa, Alnus viridis ssp. crispa*-type, *Alnus viridis ssp. fruticosa, Duschekia fruticosa, Alnus viridis ssp. sinuata*-type, *Alnus viridis, Alnus viridis*-type, *Alnaster, Alnus fruticosa*-type, *Alnaster, Alnus* undiff., *Betula sect. nanae, Betula nana*-type, *Betula* undiff., *Betula* corroded, *Betula exilis, Betula fruticosa, Betula humilus, Betula* small, Betulaceae, Ericaceae undiff., *Ericales, Salix, Salix vestita*-type, *Vaccinium*-type, *Vaccinium uliginosum*-type
arcto-boreal evergreen malacophyll broad-leaved low or high shrub	ab.e.mb.lhs	*Calluna vulgaris, Calluna*, Ericaceae undiff., *Ericales, Ledum palustre, Ledum*-type, *Rhododendron, Rubus chamaemorus*
arcto-boreal evegreen needle-leaved low or high shrub	ab.e.n.lhs	*Pinus pumila*
boreal cold-deciduous malacophyll broad-leaved low or high shrub	bo.cd.mb.lhs	*Alnus crispa, Alnus incana, Alnus incana*-type, *Alnus viridis ssp. crispa*-type, *Alnus viridis ssp. fruticosa, Duschekia fruticosa, Alnus viridis ssp. Sinuata*-type, *Alnus viridis, Alnus viridis*-type, *Alnus fruticosa*-type, *Alnaster, Alnus* undiff., *Betula* undiff., *Betula* corroded, Betulaceae, Caprifoliaceae undiff., Cornaceae, *Cornus, Cornus alba, Cornus canadensis, Cornus mas/C. svecia, Cornus sericea, Cornus suecica*-type, *Linnea, Lonicera, Myrica, Myrica gale, Ribes, Salix, Sambucus, Shepherdia, Shepherdia canadensis, Viburnum, Vibirnum opulus*
boreal evergreen malacophyll broad-leaved low or high shrub	bo.e.mb.lhs	*Chamaedaphne calyculata*
boreal or temperate drought-tolerant cold-deciduous or evergreen malacophyll broad-leaved low or high shrub	bo/te-dt.cd/e.mb.lhs	*Euphorbia*, Fabaceae undiff.
boreal evergreen needle-leaved tree	bo.e.n.t	*Abies, Abies sibirica*, bi-saccate pollen, *Picea abies ssp. obovata, Picea abies, Picea* abnormal, *Picea eupicea, Picea glauca, Picea mariana, Picea*
boreal cold-deciduous needle-leaved tree	bo.cd.n.t	*Larix, Larix gmelinii, Larix lariana, Larix siberica, Larix dahurica*
boreal cold-deciduous malacophyll broad-leaved tree	bo.cd.mb.t	*Alnus glutinosa, Alnus incana, Alnus incana*-type, *Alnus viridis ssp. sinuata*-type, *Alnus* undiff., *Alnus hirsuta, Betula arbor s. albae, Betula albae, Betula* undiff., *Betula arbor., Betula* corroded, *Betula pendula, Betula platyphylla, Betula pubescens, Betula tortuosa*, Betulaceae, *Chosenia, Corylus, Corylus*-type, *Populus, Populus balsamifera, Populus tremuloides, Populus tremula, Salix, Salix vestita*-type, *Sorbus*
eurythermic evergreen needle-leaved tree	eu.e.n.t	Bi-saccate pollen, Cupressaceae, *Juniperus*-type, *Juniperus communis, Pinus diploxylon*-type, *Pinus haploxylon, Pinus, Pinus banksiana*-type, *Pinus contorta, Pinus subg. Pinus, Pinus sect., Pinus sibirica, Pinus subg. Strobus, Pinus* undiff., *Pinus sylvestris*
temperate evergreen needle-leaved tree	te.e.n.t	*Abies, Picea* abnormal, *Picea eupicea, Picea omorica, Picea, Thuja, Tsuga, Tsuga canadensis, Tsuga diversifolia, Tsuga heterophylla*
maritime evergreen needle-leaved tree	ma.e.n.t	*Taxus*
cool-temperate evergreen needle-leaved tree	c-te.e.n.t	*Tsuga mertensiana*
temperate (spring-frost avoiding) cold-deciduous malacophyll broad-leaved tree	te-fa.cd.mb.t	*Acer, Acer saccharum, Acer spicatum, Alnus glutinosa, Alnus* undiff., Caprifoliaceae undiff., *Carya, Carya ovata*, Cornaceae, *Cornus, Cornus alba*, Fabaceae undiff., *Fraxinus americana*-type, *Fraxinus nigra*-type, *Fraxinus pennsylvanica*-type, *Lonicera, Populus, Prunus pennsylvanica, Quercus* (deciduous), *Quercus, Salix, Salix vestita*-type, *Sambucus, Sorbus, Viburnum, Vibirnum opulus*
temperate (spring-frost tolerant) cold-deciduous malacophyll broad-leaved tree	te-ft.cd.mb.t	*Carpinus betulus, Carpinus, Corylus, Corylus avellana, Corylus cornuta, Corylus*-type, *Fagus, Frangula, Frangula alnus, Fraxinus excelsior*-type, *Ostrya/Carpinus, Ribes, Tilia, Tilia cordata, Ulmus, Ulmus glabra*
temperate (spring-frost intolerant) cold-deciduous malacophyll broad-leaved tree	te-fi.cd.mb.t	*Carpinus, Castanea, Castanea dentata, Juglans, Ostrya, Ostrya*-type, *Ostrya/Carpinus, Platanus, Rhamnus, Ulmus*
temperate evergreen malacophyll broad-leaved woody plants	te.e.mb.wp	*Genista, Hedera, Hedera helix, Ilex, Rhododendron*

Table 7. Equivalences Between Biome Classifications Used in the BIOME4 Model, in the Pollen-Based Mapping Scheme; by *Haxeltine and Prentice* [1996], and by *Walker* [2000]

BIOME4[a]	Pollen-Based Mapping Scheme[a]	*Haxeltine and Prentice* [1996]	*Walker* [2000]
temperate deciduous broadleaf forest	temperate deciduous broadleaf forest[b]	temperate deciduous forest	
cool mixed forest	cool mixed forest	temperate/boreal mixed forest	
cool evergreen needleleaf forest	cool evergreen needleleaf forest	temperate conifer forest	
cool-temperate evergreen needleleaf forest	cool-temperate evergreen needleleaf forest	boreal evergreen forest/woodland or temperate conifer forest	
cold evergreen needleleaf forest	cold evergreen needleleaf forest	boreal evergreen forest/woodland	
cold deciduous forest	cold deciduous forest	boreal deciduous forest/woodland	
temperate xerophytic shrubland	temperate grassland and xerophytic shrubland (steppe)[c]	tall grassland or short grassland	
temperate deciduous broadleaf savanna	temperate deciduous broadleaf forest[b]	moist savanna	
temperate grassland	temperate grassland and xerophytic shrubland (steppe)[c]	tall grassland or short grassland	
graminoid and forb tundra	graminoid and forb tundra		
low- and high-shrub tundra	low- and high-shrub tundra		oceanic evergreen low-shrub and low-shrub subzones
erect dwarf shrub tundra	erect dwarf shrub tundra		oceanic herb, dwarf-shrub and dwarf-shrub subzones
prostrate dwarf shrub tundra	prostrate dwarf shrub tundra		prostrate-shrub subzone
cushion forb lichen and moss tundra	cushion-forb tundra		lichens, moss subzone

[a]The BIOME4 model and pollen-based mapping scheme are given by *Kaplan et al.* [2003].
[b]We did not attempt to separate temperate deciduous broadleaf savanna from forest.
[c]We did not attempt to separate temperate shrubland from grassland.

reconstructed presence of low- and high-shrub tundra in the Canadian archipelago is incorrect and is caused by long-distance transport of pollen of *Alnus viridis* from farther south. We assume this would not be an issue at LGM, when shrub tundra was restricted.

[26] The ability to successfully reproduce the regional vegetation is dependent on the nature of the samples used. Lacustrine surface samples yield reconstructions in better agreement with the regional vegetation (61% correct allocations) than moss polsters (54%). However, when compared to descriptions of local vegetation (as given by the original investigators' field notes), moss polsters give a better representation than lacustrine samples. These differences are consistent with the general empirical finding, explained by pollen transport theory [*Prentice*, 1985, 1988], that lake sediments have a wider source region than peat or other terrestrial pollen sampling sites. Samples derived from terrestrial soils and/or surface sediments yield considerably worse reconstructions (43% correct) than either lake or peat samples. This probably reflects differential oxidation of the components of the original pollen assemblage. Samples obtained in geological contexts (lacustrine core tops, peat core tops or terrestrial section tops) are systematically less successful in reproducing the observed modern vegetation than other samples from the same type of environment. Thus predictions of the modern vegetation using lacustrine core tops are successfully in only 55% of all cases (compared to 61% for lacustrine surface samples), peat core tops in 46% of all cases (compared to 54% for moss polsters), and section core tops in 38% of all cases (compared to 43% for surface soils/sediments). In some regions (e.g., Beringia, western Europe) it would be possible to reconstruct modern vegetation patterns on the basis of only lacustrine surface samples or moss polsters; this would not be possible for central Siberia or western Beringia. Furthermore, it would appear that although the biases due to site type impact on our numerical assessment of the success of the biomization procedure, it does not affect the ability of the biomization technique to successfully reproduce the geographic patterns of vegetation. We have therefore made both modern and palaeo-vegetation reconstructions using all types of sample, and have checked to see that the conclusions drawn from comparisons of these maps are not affected by site-type (or other) biases.

3.2. Biome Reconstructions for 6 ka

[27] The biome reconstructions for 6 ka show systematic changes from present (Figure 2c and Table 9). Table 9 shows the frequency of transitions, based only on sites where both 6 ka and present biomes have been reconstructed from samples in one core. The reconstructed treeline was farther north than present (Table 10) in Fennoscandia (western Europe) and central Siberia (e.g., Taimyr peninsula). In contrast, Beringia shows little or no change from present, and treeline was south of its present position in Labrador and Keewatin. These results are consistent with the preliminary synthesis by *TEMPO Members* [1996], subsequent studies using biomization (as summarized by *Prentice et al.* [2000]), and with the reconstructions based on subfossil tree remains by *MacDonald et al.* [2000]. They do not support the con-

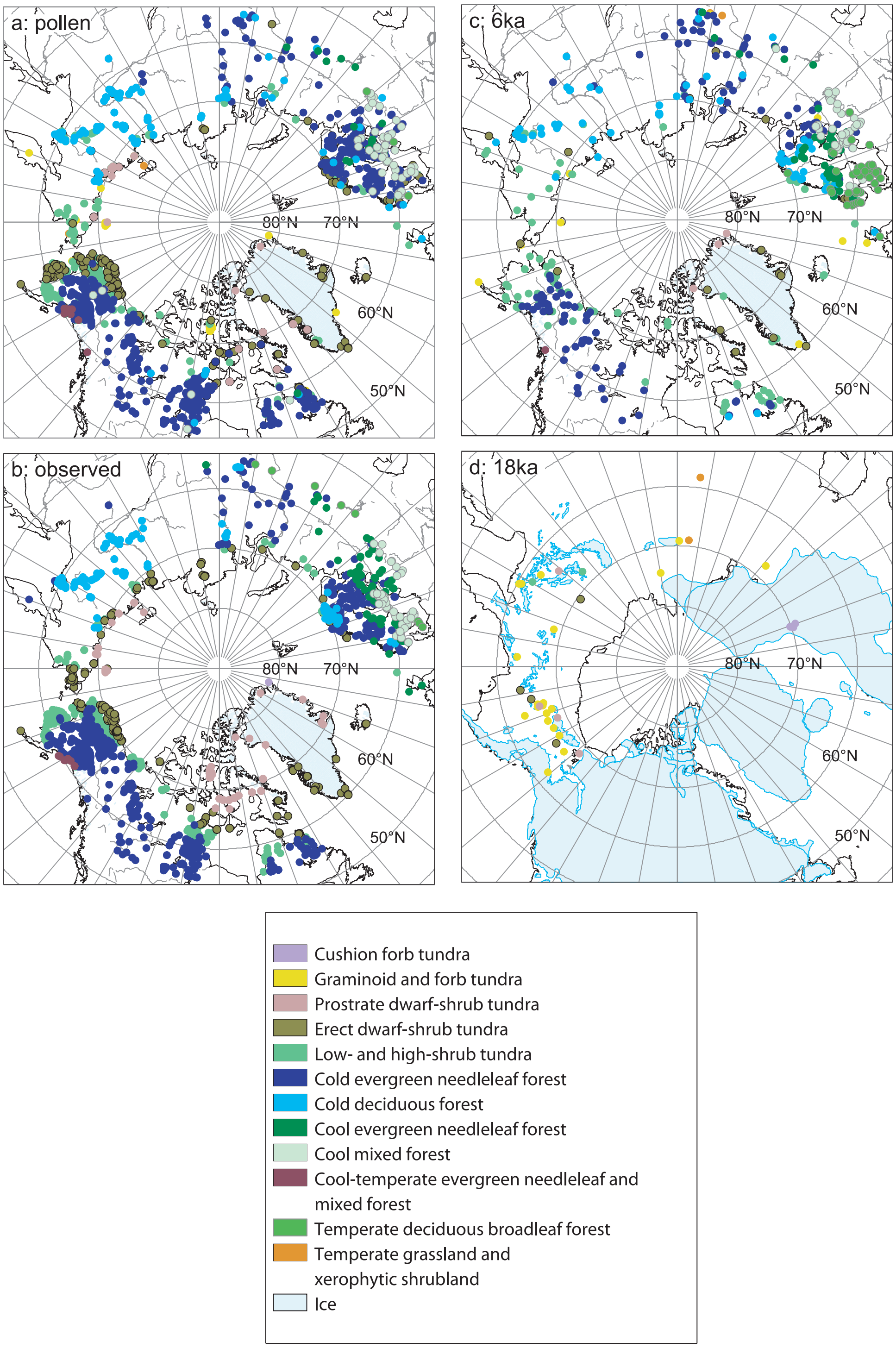

Figure 2. Biomes (a) reconstructed from modern pollen data, compared to (b) modern vegetation at the pollen data sites, and biomes reconstructed from fossil pollen data at (c) 6 ka and (d) 18 ka. In cases where two or more 6 ka or 18 ka sites lie very close to one another, they have been slightly shifted in these plots to permit each site to be individually resolved. The sites that have been shifted are indicated in Table 2.

ventional idea that the Arctic treeline was consistently north of its present position in a circumpolar sense [e.g., *Foley et al.*, 1994]. More extensive geographic changes are seen in the boundaries among forest types south of the Arctic treeline, including a northward displacement of temperate deciduous forest in eastern North America (south of our study region) and especially Fennoscandia (western Europe), and a more restricted distribution of cold evergreen needle-leaved forest toward the western edges of the continents (western Europe and eastern Beringia).

Table 8. Observed Versus Reconstructed Biomes Using the Modern Pollen Data Set[a]

	Reconstructed Biomes													
Observed	STEP	CUSH	DRYT	PROS	DWAR	SHRU	CLDE	TAIG	COCO	CLMX	TEDE	COMX	Observed	Percent Correct
STEP													0	
CUSH			1										1	0.0
DRYT													0	
PROS	1		44	**16**	46	20		3					130	12.3
DWAR	2		26	17	**110**	89	15	16					275	40.0
SHRU	1		11	9	74	**258**	18	109				1	481	53.6
CLDE	3		4	1	7	77	**123**	34					249	49.4
TAIG			2	2	19	132	25	**596**	5	7		15	803	74.2
COCO			1	1		2	4	61	**8**		2	13	92	8.7
CLMX				1		3		5	1	**2**			12	16.7
TEDE					2	1	1	2	2				8	0.0
COMX					2		2	19	2		1	**21**	47	44.7
Total	7	0	89	47	260	582	188	845	18	9	3	50	**2098**	

[a]The definitions of the BIOME codes are given in Table 4.

[28] North of the treeline, a few samples north of 75 °N in Greenland are assigned to low- and high-shrub tundra at 6 ka. This indicates that low- and high-shrub tundra may have been present >500 km farther north at 6 ka than today. Even if the classification reflects long-distance pollen transport of shrub pollen, the presence of this pollen at very high latitudes implies that the pollen source was substantially farther north than today. However, there is no evidence in the data for systematic shifts in the distribution of the more cold-tolerant tundra types. The boundary between erect and prostrate dwarf-shrub tundra was apparently located near its present position.

3.3. Biome Reconstructions for the LGM

[29] The LGM reconstruction (Figure 2d) suggests that forests were absent (or at least, highly restricted) north of 55°N. Low- and high-shrub tundra was reconstructed at a single site on the Beringian land bridge, and two sites in what is now the *Larix* forest region of eastern Siberia. Cushion forb tundra was identified on the basis of samples of LGM age from three small lakes on Andøya, northwest Norway, which lay at the very edge of the Scandinavian ice sheet at its maximum extent [*Vorren*, 1978]. Elsewhere, the data indicate that the landscape consisted of a mosaic of tundra biomes. In Beringia the dominant biomes were erect dwarf-shrub tundra, prostrate dwarf-shrub tundra, and graminoid and forb tundra. Farther west, in western and central (Taimyr) Siberia, the dominant biomes were graminoid and forb tundra and temperate grassland or xerophytic shrubland (steppe), suggesting the prevalence of very dry conditions downwind of the Scandinavian ice sheet [cf. *Siegert and Marsiat*, 2001]. The data, although sparse, suggest that there may have been a transition in central Siberia from graminoid and forb tundra north of about 65°N, to true temperate steppe farther south. This steppe was distinguished by the occurrence of drought-tolerant forbs or shrubs, in place of arctic forbs (Table 5).

4. Discussion and Conclusions

[30] The comprehensive data set of mid-Holocene and LGM pollen data north of 55°N, and the biome reconstructions made using these data based on a unified circumpolar classification of plant functional types and biomes, represent a key resource for understanding and modeling changes in northern-high latitude vegetation and climate in response to changing global boundary conditions between glacial and interglacial states. Given the success of the biome reconstruction method in reconstructing the tundra-forest boundary and the distributions of major forest and tundra biomes from surface pollen data, we can now make more confident statements about the large-scale, climatically induced changes in vegetation distribution between the LGM, mid-Holocene and present.

Table 9. Changes in Biome Assignments Between 0 ka and 6 ka[a]

Reconstructed	Reconstructed Modern Biomes												
6k Biomes	STEP	CUSH	DRYT	PROS	DWAR	SHRU	CLDE	TAIG	COCO	CLMX	TEDE	COMX	Total
STEP								1					1
CUSH													0
DRYT				1	2	1		1					5
PROS			1	**2**									3
DWAR					**7**	3							10
SHRU			3		10	**35**	1	17					66
CLDE					2	5	**14**	20					41
TAIG					1	7	5	**64**				1	78
COCO					1		1	19	**6**			2	29
CLMX										**1**			1
TEDE					2	1	3	10	1		**1**	11	29
COMX					1			10	2			**12**	25
Total	0	0	4	3	26	52	24	142	9	1	1	26	**288**

[a]The definitions of the BIOME codes are given in Table 4.

Table 10. Approximate Changes in the Position of Arctic Treeline at 6 ka Compared to Present Shown by Pollen Data

Sector	Change
Mackenzie Delta	100 km N
Keewatin	280 km S
Labrador	170 km S
Greenland	no evidence for treeline
Atlantic	no evidence for treeline
Western Europe	70 km N
Eastern Europe	insufficient data
Western Siberia	insufficient data
Central Siberia (Taimyr)	180 km N
Central Siberia (Lena)	70 km N
Western Beringia (Eastern Siberia)	no change
Western Beringia (Chukotka)	no evidence for treeline
Eastern Beringia (Alaska)	no change

[31] Our findings confirm the conclusions of the BIOME 6000 studies [*Prentice et al.*, 1996; *Tarasov et al.*, 1998; *Edwards et al.*, 2000; *Williams et al.*, 2000] concerning the mid-Holocene to present changes in the location of the Arctic tree limit, now based on a much larger set of modern and 6 ka pollen samples and a unified biomization scheme applied across the entire circumpolar region. These results establish that the shift in the forest limit between 6 ka and present was characterized by a strong circumpolar asymmetry, with the largest poleward shifts in central Siberia, little or no change in Beringia, and treeline south of present in eastern Canada. This pattern was first documented by *TEMPO Members* [1996] and is also shown in estimates of relative warming, using a rule-based interpretation of pollen data, made by *CAPE Project Members* [2001]. A small residual ice sheet was still present in Labrador around 6 ka, and this presumably accounts for the anomalous treeline situation there [*Richard*, 1995; *Williams et al.*, 2000]. The treeline in this region reached its maximum northward extension after 6 ka [*Payette*, 1992; *Richard*, 1995]. In the rest of the circum-polar region, it remains a challenge to deduce how a zonally uniform pattern of increased summer and annual insolation, due to the greater-than-present tilt of the Earth's rotational axis, could produce a strongly asymmetrical response in the location of the Arctic treeline. Recent climate simulations using a model with sea-ice dynamics [*Vavrus and Harrison*, 2003] suggest that the explanation may lie in the modulation of the orbital forcing through sea-ice dynamics. Modern sea ice is thinnest and least compact in the eastern Arctic Ocean and thickest and most compact in the western Arctic Ocean, largely as a result of the climatological drift of ice from the Siberian to the North American coast. In a warmer climate, sea ice melts more easily in the eastern part of the basin where ice divergence occurs, but tends to persist in the western sector because of ice convergence. Simulated changes in ice concentration at 6 ka show a dipole spatial pattern, with large reductions in the east and little or no change in the west, and these spatial differences in the change in ice coverage lead in turn to larger increases in surface temperature in central Siberia than elsewhere [*Vavrus and Harrison*, 2003].

[32] At LGM, conditions are generally assumed to have been far colder and drier than present throughout the high latitudes. This is confirmed by the extreme southward displacement of the forest belts [*Peyron et al.*, 2000] and supported by geomorphological evidence that indicates cold, dry conditions in the unglaciated part of Beringia [*Hopkins et al.*, 1982]. Our data also indicate a major change in the relative importance of different tundra biome types between LGM and present. Thus low- and high-shrub tundra was extremely restricted in extent and, in contrast, there was a major extension of graminoid and forb tundra and an intergradation of steppe and tundra in the north Eurasian interior. It seems likely that dryness (lack of snow cover) contributed to this change. The contrasting fates of low- and high-shrub tundra, and graminoid and forb tundra, during the LGM illustrate how an altered climate regime can cause dramatic shifts in the relative areal extent of different biomes.

[33] Investigating the mechanisms behind regional patterns of vegetational change on orbital timescales requires the use of climate and vegetation models with altered boundary conditions. In the companion paper [*Kaplan et al.*, 2003] we use the data from the present paper as a benchmark for models of the mid-Holocene and LGM environments. In doing so, we provide physically possible explanations for the major features of the 6 ka and 18 ka palaeovegetation maps.

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