Late Quaternary variations in tree cover at the northern forest-tundra ecotone

John W. Williams,1 Pavel Tarasov,2 Simon Brewer,3 and Michael Notaro4

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[1] Accurate land cover reconstructions are essential to understanding the past and present biogeochemical and biogeophysical interactions between the land surface and atmosphere and the impacts of these interactions on climate. Here we quantitatively reconstruct late Quaternary shifts in woody cover across the Northern Hemisphere forest-tundra ecotone, based on a synthesis of Northern Hemisphere pollen records and contemporary observations of woody cover from the advanced very high resolution radiometer sensor. Our reconstructions document the expansion of Northern Hemisphere forests following deglaciation and reveal significant hemispheric asymmetries in the Holocene position, steepness, and history of the forest-tundra ecotone. In western Canada, for example, forest expansion and infilling continued through the Holocene, while in much of northern Asia, forests reached their maximal expansion during the early Holocene, then retreated. The woody cover reconstructions are generally consistent with macrofossil-based reconstructions of northern tree line dynamics and complement them by extending study of the northern forest-tundra ecotone from the tree line limit (well mapped by macrofossils) to the entire ecotone. Using the Lund–Potsdam–Jena dynamic vegetation model, we estimate that changes in northern forest density resulted in at least a 47.7 Gt C increase in aboveground carbon sequestration between 21 and 9 ka, a 13.9 Gt C increase between 9 and 6 ka, and a 3.5 Gt C loss of aboveground carbon from northern forests after 6 ka. This trajectory is consistent with atmospheric carbon isotopic measurements for the Holocene, which suggest carbon uptake by the terrestrial biosphere until 6 ka and small carbon releases from the terrestrial biosphere afterward.


1. Introduction

[2] Accurate descriptions of the Earth’s land surface are essential to Earth system science. For the last several decades, remote sensing data are the primary source of information about land use and land cover change [DeFries, 2008]. The widespread availability, low cost, and high spatiotemporal resolution of remote sensing products have enabled, e.g., detailed studies of present vegetation distributions [DeFries et al., 2000; Loveland et al., 2000], the patterns and drivers of human land use and land cover change [Hansen et al., 2008; Schneider et al., 2003], variations in terrestrial carbon uptake [Achard et al., 2004; DeFries et al., 2002], and monitoring of tree mortality after disturbances [Giglio et al., 2006; Walder et al., 2006]. However, land cover mapping based on remote sensing is critically limited by the short duration of the remote sensing window, which prevents its application to studying land cover dynamics at time scales spanning beyond the late 1970s [Williams and Jackson, 2003].

[3] The need for accurate land cover data sets is particularly acute for the last glacial–interglacial cycle, given the critical role of surface-atmosphere feedbacks on regional climate dynamics and global biogeochemical cycles. Biogeochemical feedbacks, involving exchanges of water and energy between the land surface and atmosphere [Bonan, 2008], have tended to amplify orbitally driven climate change [Claussen, 2009], particularly at major physiographic ecotones such as the subarctic tundra–forest gradient [Betts, 2000; Foley, 1994; Notaro and Liu, 2008; Wohlfahrt et al., 2004], forest–grassland ecotones in temperate regions [Diffenbaugh et al., 2009], and the desert–grassland–savannah transition at the southern margin of the Sahara Desert [Kutzbach et al., 1996; Levis et al., 2004]. Estimating the strength of these positive feedbacks remains a key area of scientific study [Otto et al., 2009] and these positive feedbacks may have been partially counteracted by other, negative, feedbacks [Notaro et al., 2008].
Changes in forest cover also significantly affected the global carbon cycle: the early Holocene expansion of northern forests after deglaciation apparently drew down atmospheric CO₂ from 268 to 260 ppm [Indermühle et al., 1999; Joos et al., 2004], and release of carbon from the terrestrial biosphere is one of several hypothesized mechanisms for the still-puzzling 20 ppm increase in atmospheric CO₂ over the last 7,000 years [Joos et al., 2004]. Ruddiman and colleagues have proposed that anthropogenic land clearance for fuel, agriculture, and pasturing, may explain part of this atmospheric CO₂ increase (amplified perhaps by positive feedbacks in the ocean carbon cycle) and most to all of the observed Holocene increase in CH₄ [Ruddiman, 2003, 2007; Ruddiman et al., 2008]. However, the “early Anthropocene hypothesis” for atmospheric CO₂ is difficult to reconcile with evidence from carbon isotopic measurements from ice cores and carbon cycle models [Joos et al., 2004; Kleinen et al., 2010].

The need for longer-term observations of land cover change, of comparable quality to contemporary land cover data sets, has spurred development of various paleovegetation reconstruction techniques. Changes in agricultural cover over the last millennium have been reconstructed by intersecting remotely sensed land cover data sets with historical agricultural data from political entities ranging from nations to counties [Klein Goldewijk, 2001; Klein Goldewijk and Ramankutty, 2004; Ramankutty and Foley, 1999a, 1999b] and human population data [Pongratz et al., 2008]. Plant macrofossil records offer definitive evidence of the presence of particular plant species [Birks and Birks, 2000] and have been used to map the shifting position of northern tree line during the Holocene [Binney et al., 2009; Lavoie and Payette, 1996; MacDonald et al., 2000, 2008] and identify previously cryptic refugia for woody species [Birks and Willis, 2008; Willis and Whitaker, 2000]. However, macrofossil records rarely provide consistent information about the relative abundance of plant species and so cannot be used to track changes in forest density or shifts in the steepness of physiognomic gradients such as the forest-tundra ecotone [Payette et al., 2001, 2002]. Fossil pollen records, conversely, are less definitive of local presence but provide quantitative indices of temporal changes in plant abundance. Common techniques for pollen-based paleovegetation reconstructions include algorithms for classifying pollen assemblages into biomes [Bigelow et al., 2003; Prentice et al., 2000], detailed local- to landscape-scale modeling of pollen production and dispersal [Hellman et al., 2008; Sugita, 2007a, 2007b], and empirical calibrations based on overlaying the spatial distribution of modern pollen abundances against remotely sensed indices of forest and canopy structure, such as percent woody cover, the normalized difference vegetation index (NDVI), and leaf area index (LAI) [D’Antoni and Schäbitz, 1995; Gonzales et al., 2008; Herszchuh et al., 2010; Tarasov et al., 2007, 2009; Williams, 2003; Williams and Jackson, 2003; Williams et al., 2008, 2009].

Here we reconstruct changes in forest cover and the position and steepness of the northern forest-tundra ecotone. Our reconstructions are based upon a synthesis of recent reconstructions of percent woody cover (%WC) for North America and Eurasia [Tarasov et al., 2007; Williams, 2003; S. Brewer, manuscript in preparation, 2011]. All reconstructions are based on networks of fossil pollen records and modern pollen data sets calibrated against woody cover maps derived from the advanced very high resolution radiometer (AVHRR) [DeFries et al., 2000]. We map woody cover and four components: broadleaved woody cover (%BWC), needleleaved woody cover (%NWC), deciduous woody cover (%DWC), and evergreen woody cover (%EWC) for five time periods: 21 ka, 9 ka, 6 ka, 1 ka, and 0 ka. We combine the woody cover reconstructions with carbon sequestration estimates from the Lund-Potsdam-Jena (LPJ) dynamic global vegetation model [Sitch et al., 2003] to reconstruct changes in aboveground carbon sequestration. These reconstructions highlight the hemispheric asymmetry in the position and steepness of the boreal forest-tundra ecotone, and the data are well suited for use with Earth system models, as assessment benchmarks or forcing scenarios [Brovkin et al., 2006]. All woody cover reconstructions are included here in the auxiliary material and have been submitted to the Neotoma Paleocommunity Database (http://www.neotomadb.org).1

2. Methods

Five time periods were chosen for mapping: the last glacial maximum (LGM; 21 ka), early Holocene (9 ka), middle Holocene (6 ka), late Holocene (1 ka), and the late 20th century (0 ka). The spatial domain is based on a synthesis of prior continental-scale analyses for North America [Williams, 2003; Williams and Shuman, 2008; Williams et al., 2009], northern Asia [Tarasov et al., 2007], and Europe (S. Brewer, manuscript in preparation, 2011). Details about the data sets and methods can be found in these papers. We summarize here the main points.

All woody cover reconstructions are based on the modern analog technique, also known as the best modern analog method [Guiot, 1990; Jackson and Williams, 2004; Overpeck et al., 1985]. The modern analog technique assumes that pollen samples with similar mixtures of pollen taxa were produced by plant communities with similar compositional and structural characteristics. Following this assumption, fossil pollen samples are compared to modern pollen samples, the closest modern analogs are identified for each fossil sample, and then the fossil pollen samples are assigned the average woody cover associated with its closest modern analogs. We use the squared chord metric of dissimilarity (SCD) to identify modern analogs; comparison of the squared chord metric to other dissimilarity metrics consistently indicate it is well able to discriminate whether pairs of pollen samples were drawn from similar or different vegetation types [Gavin et al., 2003; Overpeck et al., 1985]. The reconstructive skill of the modern analog technique is similar to other transfer functions such as weighted averaging partial least squares (WA-PLS), although analog-based cross validations for data sets with strong spatial autocorrelation may be more susceptible to inflated estimates of model performance [Tefaldo and Birks, 2005, 2009].

The woody cover values attributed to the modern pollen samples are drawn from the global tree cover data sets developed by DeFries et al. [1999, 2000] from AVHRR observations. In these land cover data sets, each 1 km pixel

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1Auxiliary material data sets are available at ftp://ftp.agu.org/apend/jg/2010jg001458. Other auxiliary materials are in the HTML.
is divided into woody vegetation, herbaceous vegetation, and bare ground, and the maximum percent woody cover per pixel is prescribed to 80% [DeFries et al., 2000]. Woody cover is parsed into deciduous and evergreen components based on seasonal variations in the AVHRR spectral bands. The proportion of needleleaved versus broadleaved woody cover is less easily determined from AVHRR observations, so DeFries et al. [1999, 2000] assumed that needleleaved evergreen and broadleaved deciduous tree taxa occupy the middle and upper latitudes, except in Siberia, which was mapped as needleleaved evergreen and needleleaved deciduous vegetation [DeFries et al., 1999]. When estimating woody cover and its components to modern pollen samples in the calibration data sets, we used a 20 × 20 km search window (25 × 25 km in Europe) based on previous cross-validation experiments that experimented with search window size [Williams and Jackson, 2003]. Both leave-one-out and h-block cross-validation exercises (in the sense of Telford and Birks [2009]) have demonstrated the ability of the modern analog technique to reconstruct contemporary continental-scale patterns of woody cover from networks of pollen data (h-block analyses [Williams and Shuman, 2008; Williams et al., 2009] and leave-one-out analyses [Tarasov et al., 2007; S. Brewer, manuscript in preparation, 2011]).

[10] We ran the modern analog technique separately for North America, Europe, and Asia (using the 60°E Meridian to distinguish Europe and Asia). The rationale for separating North America from Eurasia is clear: the two regions differ substantially in evolutionary history and hence floristic composition and pollen-vegetation relationships differ as well. Yet the pollen assemblages from these regions often are compositionally similar despite being produced by very different floras, a problem particularly acute for low-diversity assemblages dominated by a few genus-level pollen types (e.g., Betula spp., Picea spp.). These palynologically similar but floristically different assemblages can result in false analogs when using modern analog methods [Jackson and Williams, 2004]. Cross-validation experiments with the modern analog technique in North America has demonstrated improved reconstruction performance when North American surface samples are geographically split according to the different sets of species occupying eastern and western North America [Williams and Shuman, 2008; Williams et al., 2006]. The rationale for running the European and Asian analog analyses separately is more historical than ecological. The surface sample and fossil pollen data sets have been assembled separately for these regions by different flora, a problem particularly acute for low-diversity assemblages dominated by a few genus-level pollen types (e.g., Betula spp., Picea spp.). These palynologically similar but floristically different assemblages can result in false analogs when using modern analog methods [Jackson and Williams, 2004]. Cross-validation experiments with the modern analog technique in North America has demonstrated improved reconstruction performance when North American surface samples are geographically split according to the different sets of species occupying eastern and western North America [Williams and Shuman, 2008; Williams et al., 2006]. The rationale for running the European and Asian analog analyses separately is more historical than ecological. The surface sample and fossil pollen data sets have been assembled separately for these regions by different sets of researchers [e.g., Davis et al., 2003; Herzschuh et al., 2004; Peyron et al., 1998; Tarasov et al., 2000, 2007] and they have not yet been fully harmonized. Clearly a harmonization of these data sets is desirable, because the high-latitude European and Asian flora have a closely shared evolutionary history, with many common species, and because the skill of modern analog approaches generally improves with increasing size and quality of calibration data sets. Harmonizing and combining these data sets into a single Eurasian calibration data set should be a priority for future research, along with analyses to assess the degree to which complete Eurasian calibration data sets results in improved reconstructions of late Quaternary climates and vegetation.

[11] For North America, the modern calibration pollen data are drawn from the North American modern pollen database [Whitmore et al., 2005], version 1.72 (http://www.lpc.uottawa.ca/data/index.html). The fossil pollen data are mostly from the North American Pollen Database, now incorporated into the Neotoma Paleocommunity Database (http://www.neotomadb.org); Data Set S1 lists all fossil pollen sites and their sources. Radiocarbon dates were converted to calendar years before present (BP) using the IntCal04 calibration data set. Age models for the North American data were built by linearly interpolating between age controls, and pollen abundances were linearly interpolated between bracketing samples to the target time intervals [Williams et al., 2004]. All European pollen data (modern and fossil) were obtained from the data set compiled by Davis et al. [2003] for climate reconstructions, and use the radiocarbon year to calendar year conversions described above. Anthropogenic effects on vegetation are more pervasive and longer lasting in Europe than in North America and northern Eurasia, so anthropogenic pollen assemblages were transformed in plant functional types [Prentice et al., 1996], prior to calculating analog distances, in order to reduce the sensitivity of the method to ecological changes caused by anthropogenic modification of the modern landscape [Davis et al., 2003]. Aggregating pollen types to plant functional types is a partial solution only, because it will reduce the sensitivity of the method to anthropogenically caused shifts in taxonomic abundances within plant functional types, but does not correct for anthropogenic influences on the relative abundance of plant functional types. The northern Asian surface pollen samples are based on a compilation of surface-pollen spectra from Eurasia begun during the BIOME 6000 project [Prentice et al., 2000] and continued afterward. This data set includes 1173 pollen spectra from the former Soviet Union and Mongolia, 63 spectra from northwestern China and 505 spectra from unpublished sources compiled here from Siberia, Sakhalin, Hokkaido, and northern China (see Tarasov et al. [2007] for references). The late Quaternary fossil pollen records from northern Asia are available in the Neotoma database and the European Pollen Database (http://www.europeanpollendatabase.net). For each northern Asian record the radiocarbon dates were converted to calendar years before present (BP) using CalPal ver.1.4 (http://www.europeanpollendatabase.net), while the analog reconstructions were performed using Polygon 1.5 (http://dendro.naruto.ac.jp/~nakagawa/).

[12] Spatial and temporal patterns in woody cover and its components are summarized as maps (Figures 1–3 and auxiliary material) and as gradients in woody cover along latitudinal transects (Figures 4–5) for six regions of the Northern Hemisphere (Figure 4): western Canada (WCAN),
Figure 1
Figure 2. As Figure 1 but for needleleaved tree cover.
Figure 3. As Figure 1 but for broadleaved tree cover.
eastern Canada (ECAN), Europe (EUR), northwestern Asia (ASIA NW), north-central Asia (ASIA NC), and northeastern Asia (ASIA NE). Woody cover values are mapped as original values and as differences from 0 ka. For the difference maps, woody cover was spatially interpolated to a 0.5° grid prior to differencing because some fossil pollen records do not extend to present, so the interpolation allows anomalies to be calculated if a modern site is nearby. A tricubic spline \cite{Huntley et al., 1989} with a search radius of 250 km was used to spatially interpolate woody cover. To characterize the latitudinal gradient in woody cover, we sort the woody cover site level data by latitude for each region, then ran a loess smoother with a span of 0.25 and a power of one.

We estimate the effects of changing forest density upon terrestrial aboveground carbon sequestration, using the LPJ dynamic global vegetation model \cite{Sitch et al., 2003}. We ran LPJ offline, driving it with 20th-century historical climates, CO$_{2}$ atm fixed at 280 ppm, and an initial spinup of 1000 years. We then calculated a 30 year average for woody cover and total aboveground carbon. This analysis was restricted to grid cells north of 50°N, and used the last 30 years of the simulation. The simulated woody cover and aboveground carbon data were then used to calibrate a fifth-order polynomial predicting aboveground carbon ($C_{VL} =$ the sum of the vegetation and litter carbon pools) as a function of woody cover (WC): $C_{VL} = 2.313 \times 10^{3} + 3.871 \times 10^{4} \times WC - 4.140 \times 10^{5} \times WC^{2} + 1.661 \times 10^{6} \times WC^{3} - 2.671 \times 10^{7} \times WC^{4} + 1.502 \times 10^{8} \times WC^{5}$. See Figure S4 for the plotted woody cover and aboveground carbon data and the fitted polynomial.

Woody cover is expressed here as fractional area and the carbon units are g C/m$^{2}$. The percent variance explained, root mean squared error (RMSE), and mean average error

**Figure 4.** Map of the four transects used to plot the latitudinal gradient in tree cover (Figure 5). Dots show locations of fossil pollen sites at 9 ka. Note that in this polar projection, the southern and northern latitudinal limits of the wedges are in fact arcs rather than the lines shown here. The eastern and western bounds are drawn accurately. The boundaries for each region are as follows: (1) WCAN, 50 to 75°N, 100 to 120°W; (2) ECAN, 45 to 75°N, 50 to 80°W; (3) EUR, 45 to 75°N, 10 to 45°E; (4) ASIA NW, 45 to 75°N, 45 to 85°E; (5) ASIA NC, 45 to 75°N, 85 to 130°E; and (6) ASIA NE, 45 to 75°N, 130 to 180°E.
The MAE of the polynomial are 0.834, 1.711 g C/m², and 1.373 g C/m², respectively. We then applied this polynomial to the smoothed latitudinal transects of woody cover for WCAN, ECAN, EUR, ASIA NW, and ASIA NC (leaving out ASIA NE due to low site density), thereby estimating zonal and total carbon sequestration for each region and time period.

3. Results

3.1. Spatial Patterns of Woody Cover

At the LGM (21 ka), tree cover was substantially reduced relative to present across the Northern Hemisphere (Figures 1a and 1f). Woody cover values above 40% are found only in eastern North America, where *Picea* and *Pinus* were abundant, and at scattered Eurasian sites. Reconstructed woody cover in the Mediterranean is generally < 20%, although a few sites in eastern Europe have woody cover values close to 30%. While the finding of substantial woody cover in eastern Europe is consistent with recent arguments for northerly tree refugia at the LGM [Birks and Willis, 2008], it is largely based on undifferentiated birch pollen at these sites, and may be biased toward too-high woody cover reconstructions by high abundances of shrub birch (*Betula nana*). Dense forests (WC > 70%) are reconstructed in eastern Asia at the Pacific coast, based on one site at Headwaters Opasnaya River (Core 10 [Anderson and Lozhkin, 2002]). The authors noted that at this mountain site pollen

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**Figure 5.** Plots showing the shifting position and steepness of the northern forest-tundra ecotone for the six regions shown in Figure 4. Curves are the upper limit surfaces fitted to the woody cover data and approximate the relationship between latitude and maximal woody cover (see section 2). For purposes of comparison, the northern range limits of boreal tree species are also shown below each plot for the early/middle Holocene (based on plant macrofossils) and for the present (based on modern observations). Northern range limits are indicated by the numbers below each plot, where 9 indicates 9 ka, 6 indicates 6 ka, and 0 indicates 0 ka and La indicates *Larix*, Be indicates *Betula*, Pin indicates *Pinus*, and Pic indicates *Picea*. The northern range limit data were obtained from Binney et al. [2009] for Europe and Asia and from Jackson et al. [1997] and Payette et al. [2001] for eastern Canada.
spectra older than 9,930 14C yr BP might be contaminated. Therefore, this reconstruction must be taken with great care. Needleleaved trees dominated LGM forests (Figure 2); broadleaved trees were present only in low abundances (Figure 3).

[15] Early Holocene forests (9 ka) are much denser than LGM forests and the global distribution of woody cover by the early Holocene broadly resembles modern patterns (Figures 1b and 1g). However, at regional scales, substantial differences exist between early Holocene and modern forests (Figures 1b and 1g). The largest differences are reconstructed for western Canada and Alaska, where woody cover was lower than present. Western Canada had recently deglaciated [Dyke, 2004], and the best modern analogs for these early Holocene pollen samples come from tundra sites with low local pollen productivity and a substantial proportion of nonlocal Picea pollen [Williams et al., 2009]. Forest density was also lower than present across much of Europe, with the highest values in the southwest. This is due to the early expansion of broadleaved types in this region, in particular the rapid migration of Quercus from the Iberian Peninsula [Brewer et al., 2002; Huntley and Birks, 1983]. Needleleaved trees have a much wider distribution, reaching from the northeast into the southwest to form mixed forest. In northern Asia, forest density was similar to present, but tree line was north of its present position, reaching as far as the Arctic coastline near the Taymyr Peninsula and south of Novaya Zemlya. The northward shift of tree line in Asia relative to present is supported by tree macrofossil data, which suggests that boreal forests were near the Arctic coastline between 10 and 8 ka [Kremenetski et al., 1998; MacDonald et al., 2000]. Radiocarbon-dated larch macrofossils and pollen data from the western foreland of the Verkhoyansk Mountains in East Siberia provide the first unequivocal evidence for the local larch growths ~170 km south of the Arctic Circle during the Younger Dryas [Werner et al., 2010] and helps to explain the quick reforestation of eastern Siberia in the early Holocene [Tarasov et al., 2009]. The anomaly maps for woody cover closely resemble those for needleleaved woody cover (Figures 1 and 2), suggesting that changing densities of needleleaved trees explain most of the differences between early Holocene and modern forest density. However, in the eastern U.S., broadleaved tree cover was higher than present in the southeastern U.S. and lower than present along the prairie-forest ecotone.

[16] By the middle Holocene, tree cover had increased in western Canada but was still lower than present (Figure 1). A zonal band of higher-than-present broadleaved tree cover is apparent in southeastern Canada (Figures 1 and 3). This band corresponds to higher-than-present pollen abundances of Acer, Fagus, and Pinus strobus [Williams et al., 2004], suggesting that areas today occupied by northern needleleaved forests were more of a mixed hardwood-conifer forests in the middle Holocene. In Europe, mid-Holocene tree cover was generally similar to present, although the tree line was extended slightly to both the north and south. The higher-than-present woody cover in western Europe likely signals the ensuing decreases in forest cover due to historic land clearance in the late Holocene [Litt et al., 2009]. In northern Asia, woody cover had begun to decline from early Holocene maxima and several sites suggest similar-to-present or lower-than-present values.

[17] By 1 ka, reconstructed woody cover in the Northern Hemisphere is similar to or higher than late 20th-century values (Figures 1d and 1i). In North America, woody cover and broadleaved woody cover are still higher than present in southeastern Canada, but are reduced from mid-Holocene values. Anomaly maps for woody cover for the western U.S. and southwestern Canada suggest higher-than-present values, but this is in an area of high topographic complexity and lower site density, so the spatially interpolated anomaly maps here should be viewed with caution. In Europe, woody cover is higher than present in western Europe and slightly lower than present in northern Europe. By contrast, only a few scattered sites in northern Asia show higher-than-present woody cover; here the dominant regional pattern is mostly similar to present, or lower than present in eastern and central Kazakhstan. This pattern suggests that in parts of central Asia, boreal forest has expanded over the last millennium [Tarasov et al., 2007].

3.2. Holocene History of the Forest-Tundra Ecotone

[18] The position, steepness, and history of the forest-tundra ecotone vary widely around the Northern Hemisphere (Figure 5). Western Canada (Figure 5a) shows the most pronounced northward shift of the forest-tundra ecotone, with tree cover increasing since 9 ka at all latitudes north of 55°N. In Eastern Canada, tree cover increased between 9 ka and 6 ka, reflecting the final melting of the Laurentide Ice Sheet [Dyke, 2004], but has been stable since 6 ka (Figure 5b). Tree cover is consistently lower in eastern Canada relative to comparable latitudes in other Northern Hemispheric regions. In western Europe (Figure 5c), tree cover also has progressively increased during the Holocene, although the increase is less pronounced than in western Canada and is mainly confined to latitudes between 50 and 65°N. Prentice et al. [2000] indicate a northward shift of the tree line in Europe at the mid-Holocene. Although this shift is not clearly shown in Figure 5, Figure 1 shows positive tree anomalies in northernmost Europe at 6 ka. By contrast, in northwestern Asia (Figure 5d), tree cover reached a maximum during the early to middle Holocene and has decreased since 6 ka. In north-central Asia, the apparently high values north of 65°N and the apparent steep gradient ~73°N is an artifact caused by fitting the upper surface curve to a region with low site density (Figures 4 and S3). At the spatial scale of the reconstructions shown here, the forest-tundra ecotone in north-central Asia (Figure 5e) appears to have been fairly stable during the Holocene. However, detailed mappings of tree line limit based on macrofossils of Betula, Larix, Picea, and Pinus suggest that tree line was at or near the northern Arctic coastline between 9 and 7 ka, and retreated to its present position between 7 and 3 ka [MacDonald et al., 2000]. Similarly, there is no clear trend in the position of the forest-tundra ecotone in northeast Asia (Figure 5f), which may be caused by the fairly low density of sites in this region (Figure 4).

3.3. Carbon Sequestration

[19] As northern forests expanded between 21 ka and 9 ka, aboveground carbon sequestration rose rapidly, increasing from 9.1 to 56.8 Gt C (Table 1 and Figure 6). Northern forests continued to be a long-term carbon sink until the mid-Holocene (Table 1), absorbing an additional
13.9 Gt C between 9 and 6 ka. Between 6 ka and 0 ka, declines in woody cover caused a net release of 3.5 Gt C carbon to the atmosphere. The trajectories for individual regions are generally similar, although with some subtle differences: for eastern Canada, northwestern Asia, and north-central Asia, aboveground carbon follows the hemispheric trend by peaking at 6 ka, but in northern Europe carbon sequestration is largely unchanged after 6 ka, while in western Canada carbon sequestration continues to increase until 1 ka (Table 1 and Figure 6).

4. Discussion
4.1. Holocene Dynamics of the Northern Tundra-Taiga Ecotone

These reconstructions offer a new perspective on Holocene forest dynamics in the high northern latitudes, one that is complementary to and generally consistent with previous macrofossil-based studies of tree line history [Binney et al., 2009; MacDonald et al., 2000, 2008; Payette et al., 2002]. Macrofossil-based studies are preferable for precisely mapping the shifting northern range limits of individual species, while these pollen-based woody cover reconstructions provide quantitative estimates of changes in tree cover density.

For the regional analyses shown here, the pollen-based woody cover reconstructions and macrofossil-based reconstructions of northern tree line are in quite good agreement (Figure 5). The latitudinal limits of tree species (based on macrofossils) usually agree to within a few degrees of the latitudes where reconstructed woody cover decreases to zero. In northwestern and north-central Asia, both woody cover reconstructions and macrofossil data indicate a decline in tree extent and density after the early Holocene (Figures 1 and 5) [MacDonald et al., 2000, 2008], although the upper surface curve fitting algorithm does not reproduce this well for north-central Asia (Figures 5e and S3). Other regions, such as Europe and northeastern Asia, show relatively little change in northern extent and density during the Holocene, although the range and abundance of individual tree species may have changed significantly (Figures 2, 3, and 5). In particular, broadleaved deciduous trees appear to have been relatively abundant in eastern Siberia and Alaska during the early Holocene, and declined thereafter [Binney et al., 2009; Edwards et al., 2005].

In these woody cover reconstructions, the timing of Holocene forest expansion in the high northern latitudes was asymmetrical, with the strongest contrast apparent between northwestern Eurasia and western Canada (Figures 5a and 5d). In northwestern Eurasia, maximum forest expansion occurred between 9 ka and 6 ka, and forest cover declined after 6 ka. In contrast, in western Canada forest density increased through the Holocene. In western Canada, low charcoal influx values from suggest low fuel loads during the Holocene, while pollen influx values indicate that Picea glauca densities increased rapidly soon after its early Holocene arrival, but that Picea mariana expanded more slowly and continued expanding until 5 ka [MacDonald, 1987; Moser and MacDonald, 1990]. This hemispheric asymmetry in the dynamics of the northern forest-tundra ecotone has been reported in previous syntheses [Payette et al., 2002], but this is the first quantitative analysis of the phenomenon.

The hemispheric asymmetry in tree cover history is also consistent with syntheses of Holocene high-latitude paleoclimatic data [Kaufman et al., 2004], which show that the Holocene Thermal Maximum was time transgressive.

### Table 1. Estimated Aboveground Carbon for Five of the Six Regions Shown in Figure 4 and a Sum Across Regions

<table>
<thead>
<tr>
<th>Time</th>
<th>WCan</th>
<th>ECan</th>
<th>Europe</th>
<th>AsiaNW</th>
<th>AsiaNC</th>
<th>Sum</th>
<th>Change</th>
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<td>6.5</td>
<td>10.3</td>
<td>16.9</td>
<td>14.7</td>
<td>18.7</td>
<td>67.2</td>
<td>3.4</td>
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<tr>
<td>1 ka</td>
<td>7.3</td>
<td>9.2</td>
<td>16.8</td>
<td>11.6</td>
<td>18.9</td>
<td>63.8</td>
<td>−6.9</td>
</tr>
<tr>
<td>6 ka</td>
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<td>12.1</td>
<td>16.5</td>
<td>16.9</td>
<td>19.8</td>
<td>70.7</td>
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<tr>
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<td>8.8</td>
<td>11.8</td>
<td>13.4</td>
<td>18.7</td>
<td>56.8</td>
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<td>0.0</td>
<td>2.6</td>
<td>6.2</td>
<td>0.3</td>
<td>9.1</td>
<td></td>
</tr>
</tbody>
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*Units are Gt C. “Change” shows the difference between each time period and the preceding one.*

![Figure 6](image-url)  
**Figure 6.** Histograms showing reconstructed aboveground carbon for western Canada, eastern Canada, Europe, northwestern Asia, and north-central Asia and for the sum of all five regions for 21 ka, 9 ka, 6 ka, 1 ka, and 0 ka.
around the western Arctic, occurring between 12 and 10 ka in Alaska and eastern Siberia, between 6 and 5 ka in western Canada, and as recently as 3 ka in Quebec and Labrador. (Note that the temperature reconstructions by Kaufman et al. [2004] are based on many paleoclimatic proxies, including fossil pollen, and so are only partially independent of the pollen-based woody cover reconstructions presented here.) This spatial asymmetry in temperature is believed to result from the interacting climatic effects of orbitally driven summer insolation, which peaked 11,000 years ago [Berger and Loutre, 1991] and the melting Laurentide Ice Sheet, which melted first in western Canada and later in the east [Dyke, 2004]. This agreement between Holocene temperature and tree cover is expected, given that tree extent and density are highly temperature sensitive in the high latitudes [Payette, 2007; Payette et al., 2001], and given that northern tree line also regulates surface air temperature, via positive albedo feedback loops are associated with shifts in tree density [Bonan, 2008; Claussen, 2009; Foley, 1994]. Thus, the spatial asymmetry in tree cover history presumably resulted from and reinforced the asymmetric patterns in surface air temperature.

[24] Many of the differences between early Holocene (1 ka) and modern (0 ka) forest cover can be attributed to intensified human land use and deforestation over the last millennium. However, climatic variations may also play a role. Northern Hemisphere temperatures at 1 ka were approximately 0.5°C higher than temperatures at the start of the 20th century [Mann et al., 2008]. Higher-than-present temperatures and summer insolation may have contributed to higher-than-present tree cover in areas where moisture availability was similar to present. In semiarid regions such as the southern tree line in Eurasia, reconstructions of lower-than-present woody cover despite generally warmer temperatures suggests an increase in moisture availability over the last millennium [Tarasov et al., 2007].

4.2. Northern Forest Growth and the Holocene Carbon Cycle

[25] The drivers of Holocene variations in the carbon cycle remain a critical puzzle, particularly with respect to the observed 20 ppm increase in atmospheric CO$_2$ over the last 8,000 years [Indermühle et al., 1999]. Proposed mechanisms [reviewed in Joos et al., 2004] include release from terrestrial vegetation, a delayed release of carbon from the oceans following an early Holocene pulse in terrestrial carbon uptake, growth of coral reefs, other changes in ocean carbon cycle, and early anthropogenic land use [Ruddiman, 2003, 2007].

[26] Our estimation of a 13.9 Gt C net sequestration by northern forests (for the five regions listed in Table 1) between 9 and 6 ka is equivalent to a 6.3 ppm drawdown from the atmosphere. This corresponds closely to the 8 ppm decrease in atmospheric CO$_2$ observed between 10.5 and 8.2 ka, and hence reinforces prior hypotheses that the early Holocene decline in atmospheric CO$_2$ is caused by the expansion and infilling of northern forests [Indermühle et al., 1999]. However, the estimate of 6.3 ppm drawdown from the atmosphere comes with two opposing caveats. On the one hand, the total hemispheric uptake by northern forests should be larger than 13.9 Gt C, because this estimate represents only the five regions listed in Table 1. Furthermore, these estimates are for aboveground carbon only and so do not include the drawdown caused by expansion of boreal peatlands [Gajewski et al., 2001; Turunen et al., 2002]. On the other hand, drawdown of CO$_2$ from the atmosphere by northern forests likely would have been partially buffered by releases of CO$_2$ from the ocean and other reservoirs to the atmosphere [Joos et al., 2004], reducing the net change in atmospheric CO$_2$. Nonetheless, our estimates strongly suggest that the growth and expansion of northern forests are indeed a primary cause for the early Holocene decrease in atmospheric CO$_2$.

[27] Our results suggest that the northern forests are at most only a minor contributor to the observed 20 ppm rise in atmospheric CO$_2$ between 8 ka and 2 ka [Indermühle et al., 1999], for several reasons. First, atmospheric CO$_2$ begins to rise at 8 ka, whereas these reconstructions suggest that the northern afforestation continues to draw down carbon from the atmosphere until 6 ka. Second, the reconstructed loss in aboveground carbon between 6 ka and 1 ka is small (6.9 Gt C, or ~3 ppm) relative to the observed (20 ppm) increase in atmospheric CO$_2$. Our reconstructed history of carbon balance in northern forests (i.e., uptake until 6 ka and a small carbon release thereafter) is in good agreement with δ^13C ice core records, which show a shift toward isotopically heavier carbon in the atmosphere until 6 ka, and a slight trend toward lighter values afterward [Elsig et al., 2009]. Therefore, the source of carbon must be found elsewhere, mostly likely in changes in the marine carbonate cycle [Elsig et al., 2009; Joos et al., 2004; Kleinen et al., 2010]. Our results do not directly bear on the early Anthropocene hypothesis [Ruddiman, 2007], except to rule out northern forests as an area of substantial land clearance and carbon release to the atmosphere.

5. Conclusions

[28] Quantitative reconstructions of late Quaternary land cover dynamics are essential to a wide range of scientific applications, including carbon dynamics, surface-atmosphere feedbacks, human land use history, and habitat drivers of range shifts for other species. The reconstructions presented here provide a newly detailed history of the northern tundra-taiga ecotone, and highlight hemispheric asymmetries in its position and dynamics. The largest difference is seen between western Canada, which shows continued expansion through the Holocene, and northwestern Asia, which shows a maximal forest expansion during the early and middle Holocene, and retreat thereafter. These pollen-based quantitative reconstructions of tree cover are complementary to and consistent with macrofossil-based estimates of northern tree line. Overall, afforestation in the northern high latitudes resulted in a drawdown of carbon from the atmosphere between 21 ka and 6 ka, while forest retreat in some areas after 6 ka appears to have caused a net release of carbon to the atmosphere after 6 ka. These woody cover reconstructions have particular value as a benchmark for terrestrial vegetation models.

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S. Brewer, Department of Botany, University of Wyoming, 1000 E. University Ave., Laramie, WY 82071, USA.

M. Notaro, Center for Climatic Research, University of Wisconsin–Madison, Madison, WI 53706, USA.

P. Tarasov, Institute of Geological Sciences, Palaeontology Department, Free University, Berlin D-12249, Germany.

J. W. Williams, Department of Geography and Center for Climatic Research, University of Wisconsin-Madison, Madison, WI 53706, USA. (jww@geography.wisc.edu)