Eocene Meridional Weather Patterns Reflected in the Oxygen Isotopes of Arctic Fossil Wood

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ABSTRACT
The spectacularly preserved Metasequoia wood excavated from the Fossil Forest site of Axel Heiberg Island (Canadian High Arctic) provides a unique window into the δ18O value of Eocene meteoric water via the analysis of fossil cellulose. Seventeen fossilized Metasequoia individuals yielded cellulose with δ18O (Vienna standard mean ocean water [VSMOW]) values ranging from 17.1‰ to 21.4‰ and with a mean value of 19.9‰—strikingly low compared to modern trees of all latitudes. Using established biosynthetic relationships for plant cellulose, we reconstructed the δ18O (VSMOW) value of Eocene meteoric water to be −15.1‰ on Axel Heiberg Island—a value similar to previous determinations of Eocene terrestrial water using varied paleoenvironmental indicators. A wholly temperature-based interpretation of these isotopic results would predict a mean annual temperature of −2.7 °C, but this is incompatible with extremely high forest productivity. Instead, a calculation of isotopic fractionation in moisture transported from the Pacific Ocean north across North America explains the simultaneous arrival of warm air and isotopically depleted moisture in the Eocene Arctic; we suggest that these meridional weather patterns were caused by the absence of a Polar Front during the ice-free Eocene.

INTRODUCTION
The sediments of Axel Heiberg Island, located in the High Arctic of Canada (Fig. 1), contain hundreds of fossil Metasequoia trees that grew at a paleolatitude of 82°N. The Fossil Forest site, near the western coast of the island, has been a focus of research since 1986 and has inspired numerous monographs on the evolutionary and biogeographic history of plants. All fossil wood recovered from Axel Heiberg Island has been of gymnosperm origin, mostly Metasequoia with rare occurrences of Picea and Larix (Jagels et al., 2001); however, significant angiosperm populations were present in Fossil Forest communities (Kalkreuth et al., 1996). The forest-bearing sediments are extensive (Fig. 2A), and contain large quantities of mummified litter, stumps, boles, roots, seeds, cones, rhizomes, soil organic matter, and fossilized resin. The excellent state of preservation, which suggests little alteration beyond drying (Fig. 2B), presents a unique opportunity to apply stable isotope techniques usually reserved for much younger substrates. Holocene trees have been used to estimate paleotemperature using relationships between δ18O value of cellulose and δ18O value of site precipitation (Burk...
and Stuvier, 1981) and between δD value of cellulose-nitrate and δD value of site precipitation (Yapp and Epstein, 1977). However, lack of well-preserved fossils has prevented application of these relationships in deep time until now.

AGE OF THE FOSSIL FOREST

The age of the Fossil Forest site on Axel Heiberg Island has been a subject of controversy. We prefer a middle-to-late Eocene interpretation of the age of *Metasequoia* fossils analyzed, but previous workers have assigned a larger age window, from middle

Eocene to early Oligocene. The most widely known age was assigned using vertebrate fossils found within the correlative Eureka Sound Group on western Ellesmere Island (Dawson et al., 1976) and elsewhere on Axel Heiberg Island; these have been used to assign a middle Eocene age for the Fossil Forest that is often assumed today (Jagels et al., 2001). Unfortunately, the vertebrate fossils in question were recovered from strata with different lithology and were at stratigraphic levels substantially below the Fossil Forest. The only vertebrate fossils that have been recovered from the Fossil Forest site itself are three tooth enamel fragments found as “float on poorly consolidated, reddish brown sandstone” directly overlying the R-S-T coal of the Fossil Forest site (Fig. 3; Eberle and Storer, 1999, p. 979). The fossils were identified as brontothere (quadrupedal herbivores that became extinct in North America during the late Eocene) teeth (Eberle and Storer, 1999). However, Eberle and Storer (1999) did not address the possibility that this float might represent the reworked debris of older sediments. Rich and diverse pollen assemblages within the Fossil Forest strata are “probably middle Eocene in age, but a late Eocene age cannot be discounted” (McIntyre, 1991, p. 83). Ricketts (1987, p. 2505) discussed a “wide range of reworked pollen, spores and dinoflagellates” of Paleocene and Cretaceous age included in the microfossil assemblages of the Fossil Forest site. Examination of sedimentary relationships suggested that the Fossil Forest site extends “perhaps into the earliest Oligocene” (Ricketts, 1991, p. 1). Plant macrofossil assemblages (*Betula, Glyptostrobus, Larix, Metasequoia, Picea, Pinus, Pseudolarix, and Tsuga*) are not temporally specific within the Paleogene. We analyzed fossils from high in the Fossil Forest section, located >30 m stratigraphically above the R-S-T coal (Figs. 2A and 3), which we believe are middle-to-late Eocene in age.

EOCENE PALEOClimATE

The Eocene (57.8–36.6 Ma) has been considered by many as an unusually warm period in Earth’s history. Latest Paleocene Thermal Maximum rocks record a methane release (Dickens et al., 1995) that prevented severe winter cooling in polar regions (Sloan et al., 1992). This event resulted in a dramatic 4–8 °C increase in deep-ocean, high-latitude, and continental temperatures (Zachos et al., 1993), marking the onset of warm conditions that extended into the Eocene.

The global plant fossil record for the Eocene (reviewed in Graham, 1999) reveals a lavishly vegetated planet Earth. Vegetation described as “subtropical” may have extended to 60°N lat, and full “tropical rainforests” occurred up to 30°N lat (Wolfe, 1985, p. 357). For this reason, we expect that the fossils of

Figure 3. Stratigraphic sequence illustrating fossiliferous sediments of Fossil Forest; sampling location for this study is highlighted, as is position of brontothere fossil teeth described by Eberle and Storer (1999).
Axel Heiberg Island result from a period of maximum primary productivity at high latitudes, and represent the upper limit of terrestrial biomass production in polar regions. However, paleontological methods used to characterize Eocene "tropicality" are based on comparison with features of modern biota, presenting inevitable complications when dealing with environments that no longer exist. Most authors recognize that the Fossil Forest of Axel Heiberg Island represents a unique ecosystem for which there is no modern analog. Both plant and animal fossils of Axel Heiberg and Ellesmere Islands have been used alternatively to characterize the Arctic paleoclimate (Basinger, 1986; Estes and Hutchinson, 1980) and to infer the environmental tolerances of the species present (Eberle and Storer, 1999; Francis, 1991). Therefore, inherent limits in paleontological methods of climate reconstruction suggest further information might be gained from isotopic techniques.

Fossil leaf margin analysis from the Bighorn Basin, Wyoming, indicated a short-lived ~8 °C temperature drop during the early Eocene (Wing et al., 2000), demonstrating variability in continental temperatures during this interval of the Cenozoic. During the early Eocene to middle Eocene transition (~52 Ma) marine isotopic records show dramatic recovery to early Paleocene values: marine bulk carbonate δ13C (Vienna Peedee belemnite [VPDB]) value returned to +1.8‰ (from +0.2‰) (Shackleton et al., 1984); and ocean water δ18O (Vienna standard mean ocean water [VSMOW]) value (as calculated from the composition of benthic foraminifera) returned to +0.0‰ (from −0.7‰) (Miller et al., 1987). These isotopic increases have been consistently interpreted as a global cooling event that occurred long after the Paleocene-Eocene warming event.

Efforts have been made to characterize the paleoclimate of the Eocene using general circulation and other models. For example, early Eocene mean global surface temperature was estimated to be at least 2 °C warmer than at present (Barron, 1987) and CO2 levels were estimated to be at least twice that of today (Berner, 1994; Sloan and Rea, 1995). Eocene cooling trends were reinforced by general circulation model results which found that ~1.0 °C of cooling in northern hemisphere mean annual surface temperature occurred during the whole of the Eocene, caused by changes in atmospheric and oceanic heat transport (Bice et al., 2000a). Despite this myriad of paleoclimate determinations, a congruent climate hypothesis remains elusive for the Eocene. Sloan and Morrill (1998) described "persistent discrepancies" between climate model results and interpretations from proxy data in the Eocene.

δ18O IN EOCENE FOSSIL CELLULOSE

We have measured oxygen isotope composition within a substrate that is extremely well characterized with respect to chemical and biological synthesis—Eocene fossil cellulose—and use these results to shed new light on the meteorologic patterns of the Eocene. Seventeen Metasequoia individuals excavated from Fossil Forest lignite layer F (Fig. 3) were analyzed in duplicate for δ18O (VSMOW) value of extracted cellulose. The purification process to obtain α-cellulose from plant tissue involved the standard technique based on Green (1963), modified by Sternberg (1989). The procedure is widely used for carbon, oxygen, and hydrogen stable isotope studies on α-cellulose (e.g., Feng et al., 1999). Five to 10 grams of bulk fossil sample were analyzed; pre-extraction of lipids was necessary because conifer tissues contain considerable amounts of resin, which is isotopically depleted relative to most plant tissues. The fluffy, white α-cellulose extracted from Fossil Forest samples is shown in Figure 4; cellulose content of extracted samples was verified using classical biochemical assay techniques (Updergraff, 1969).

We quantitatively converted oxygen in cellulose into pure CO2 using the procedure described by Sternberg (1989) with a modification of the HCl removal step (Sauer and Sternberg, 1994). Resulting CO2 gas was then analyzed on a VG Isogas Prism dual-inlet isotope ratio mass spectrometer at the University of Miami. δ18O (VSMOW) variability within each individual was found to be 0.5‰; total uncertainty in value of each sample (conservatively calculated as the total of field variability and instrumental uncertainty) was found to be 1.0‰. The total range of δ18O (VSMOW) values found in these fossil samples (n = 17) was 17.1‰–21.4‰ with a mean value of 19.9‰. These are strikingly low oxygen isotope values compared to published δ18O values of modern tree cellulose (Fig. 5).

The δ18O value of tree cellulose can be used to estimate the δ18O value of meteoric water used by the plant; however, processes of isotopic fractionation during cellulose synthesis are complex. The biosynthesis of wood cellulose in trees can be understood by the following sequence of events. (1) Leaf water is isotopically enriched relative to stem water by the process of transpiration; this enrichment is a function of both relative humidity and leaf characteristics. (2) Carbohydrates synthesized in the leaf during photosynthesis and then transported to stem and roots have the oxygen isotopic signature of leaf water (i.e., δ18O_carbohydrate = δ18O_leaf water + 27‰). (3) During cellulose synthesis in the stem, ~30%–40% of oxygen atoms in carbohydrate exchange with stem water via the carbonyl-hydration reaction. Therefore, some cellulose oxygen atoms retain their isotopic signature from previous equilibration with leaf water, while others show isotopic ratios consistent with stem water equilibrum. For this reason, we expect the δ18O value of stem cellulose to be higher than δ18O_meteoric water + 27‰. We use
here the empirically observed fractionation for modern *Metasequoia* grown under controlled conditions in Japan (Table 1). Taking this observed value, $\Delta = \delta^{18}O_{\text{cellulose}} - \delta^{18}O_{\text{plant water}} = 35\%$, in conjunction with the $\delta^{18}O$ (VSMOW) mean value of Fossil Forest cellulose of 19.9\%, we reconstructed an oxygen isotope composition of Eocene meteoric water equal to $-15.1\%$ on Axel Heiberg Island.

**THE SOURCE OF LOW-$\delta^{18}O$ VALUES IN EOCENE METEORIC WATER**

Other studies have also documented low-$\delta^{18}O$ values in Eocene terrestrial substrates, and inferred $^{18}O$-depleted meteoric water. Norris et al. (1996) observed $\delta^{18}O$ values as low as $-16\%$ (VPDB) in Eocene lacustrine carbonates and calculated source waters as low as $\delta^{18}O$ (VSMOW) $= -19.8\%$ for the Green River Basin, perhaps representative of paleosnowfall. $\delta^{18}O$ values of Fe-oxides from early Eocene rocks of the Bighorn Basin suggested a change in surface water $\delta^{18}O$ (VSMOW) value, $\Delta = -3.25\%$, in the earliest Eocene (Wing et al., 2000). Based on the oxygen isotope value of soil carbonates and fossil teeth, Koch et al. (1995) concluded that Paleocene-Eocene meteoric water was "significantly" $^{18}O$ depleted, with values as low as $\delta^{18}O$ (VSMOW) $= -14\%$.

One explanation for low-$\delta^{18}O$ values would be cold temperatures. An empirical (modern) relationship

$$\delta^{18}O_{\text{cellulose}} = 21 + 0.4 \times (°C \text{ MAT}) \quad \text{R}^2 = 0.71$$

between $\delta^{18}O$ in tree cellulose and site mean annual temperature has been observed, based on analyses of a large set of tree species across 50° of latitude (Epstein et al., 1977). When we used this to estimate Eocene paleotemperature from our Axel Heiberg fossil wood $\delta^{18}O$ results, we obtained predicted mean annual temperature for the site equal to $-2.7 °C \pm 2.5$. For comparison, mean annual temperature in Dawson, Yukon, Canada, is $-4.7 °C$; Godthåb, Greenland, is $-1.1 °C$; and Whitehorse is $-0.9 °C$. Thus, paleotemperature predicted for Axel Heiberg Island using equation 1 would have been similar to modern Arctic regions. However, we reject a wholly temperature-based interpretation of our isotopic results: The Arctic could not have had below-zero mean annual temperature during the Eocene based on climate models and also based on the apparent high bioproductivity of the Fossil Forest during the Eocene. Koch et al. (1995) similarly rejected a cold-climate interpretation of low-$\delta^{18}O$ values in Eocene soil carbonates and fossil teeth and suggested an isotopic “rain-out effect” as more likely.

Our preferred explanation for the low-$\delta^{18}O$ values involves changing weather patterns. For example, altered meteoric transport patterns have been proposed to control $\delta^{18}O$ values in the ice-core (Hendricks et al., 2000), marine carbonate (Wolff et al., 1998), and soil carbonate (Amundson et al., 1996) paleorecords. As clouds travel across continents, the moisture they carry becomes isotopically lighter as $^{18}O$ and D isotopes “rain-out” during Rayleigh distillation. Furthermore, traveling clouds are replenished with moisture evaporated from continental lakes and with moisture transpired through vegetation (Moreira et al., 1997). Therefore, the isotopic composition of moisture arriving at a given latitude is dependent upon dominant storm paths of moisture transport. Recycling of water to the atmosphere via transpiration in forested regions must have been an important meteorologic influence during the Eocene, as highly productive vegetation extended from the low to high latitudes (Ziegler et al., 1983).

We suggest that the absence of polar ice during the early Tertiary was an important factor in determining meteoric transport patterns during the Eocene. At present, high latitudes are consistently cold due to the stable configuration of the Polar Front, the abrupt separation between the low-temperature arctic atmosphere and the higher-temperature mid-latitude atmosphere that encourages west-east circumpolar

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**TABLE 1. ISOTOPIC FRACTIONATION BETWEEN ENVIRONMENTAL WATER AND METASEQUOIA CELLULOSE AS MEASURED IN MODERN SYSTEMS**

<table>
<thead>
<tr>
<th>Site of Collection</th>
<th>$\delta^{18}O_{\text{plant water}}$ [‰]</th>
<th>$\delta^{18}O_{\text{cellulose}}$ [‰]</th>
<th>$\Delta = \delta^{18}O_{\text{cellulose}} - \delta^{18}O_{\text{plant water}}$ [‰]</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kyoto, Japan</td>
<td>-8.4</td>
<td>25.3</td>
<td>33.7</td>
</tr>
<tr>
<td>Tanashi, Japan (40-year stand)</td>
<td>-9.3</td>
<td>25.9</td>
<td>35.2</td>
</tr>
<tr>
<td>Tanashi, Japan (70-year stand)</td>
<td>-9.3</td>
<td>26.8</td>
<td>36.1</td>
</tr>
</tbody>
</table>

**Note:** Mean value = 35.0
transport. The steep atmospheric-temperature gradient across the Polar Front results from low radiation absorption by the high-albedo ice cap, relative to the ice-free lower latitudes. Today’s \(3 \times 10^{13} \text{ m}^2\) of arctic ice cover (annual average) has albedo of \(~60\%\), and absorbs \(~1 \times 10^{15} \text{ W}\) of energy annually. By comparison, the same area forested, or covered by water during the Eocene would have meant albedo of \(~10\%\), resulting in the absorption of \(~2.3 \times 10^{15} \text{ W}\) each year in the region—more than doubling the amount of heat energy impacting the Arctic, relative to today. A weak net temperature gradient from equator to pole would exist during the Eocene, due to the 2\(\times\) annual difference in incoming solar radiation between 90° and 0° N lat. This would give rise to meridional weather patterns as warm air swept north across North America to the Arctic and continued in a transpolar pattern across the north pole and into Siberia.

Evidence of meridional weather patterns during the Eocene is apparent in the δ\(^{18}\)O value of fossil cellulose from the Fossil Forest site of Axel Heiberg Island: Figure 6 illustrates how source water with δ\(^{18}\)O (VSMOW) = −1.0‰ (Bice et al., 2000b) originating off the coast of Mexico in the Pacific Ocean is fractionated during transport across arid and forested regions of North America. Field experiments measuring precipitation across a Rayleigh-distillation dominated inland transect of Central Africa revealed a δ\(^{18}\)O (VSMOW) gradient of −1.58‰ per 100 km (Njitchoua et al., 1999). Combining these observations with the fact that western Mexico was persistently arid during the Cenozoic (Parrish et al., 1982), we calculated that a traverse across the ~500 km region would result in a change in δ\(^{18}\)O (VSMOW) value, \(\Delta = -7.9\%\) (Fig. 6). Measurements made of precipitation across large transects in the forested Amazon basin revealed a δ\(^{18}\)O (VSMOW) gradient of −0.08‰ per 100 km (Gat and Matsui, 1991), and allowed us to calculate a final δ\(^{18}\)O (VSMOW) value = −15‰ of Eocene precipitation arriving at the Axel Heiberg site after traversing the vegetated ~7000 km expanse of Canada (Fig. 6).

**SUMMARY**

We present a meridional-transport model that explains the low-δ\(^{18}\)O value of meteoric water arriving at the Fossil Forest site during the Eocene. This value agrees with the δ\(^{18}\)O value of Eocene meteoric water calculated using the oxygen isotope composition of Axel Heiberg fossil wood. We suggest that meridional weather patterns were responsible for the simultaneous delivery of warm air and moisture to high latitudes during the Eocene. In addition, the extensive Eocene conifer communities of Siberia (LePage and Basinger, 1995) may have been maintained by transpolar weather patterns as this warm, wet air continued across the North Pole.

The extremely bioproductive Eocene *Metasequoia* forests of Axel Heiberg Island were deciduous ecosystems restricted to a short, intense growing season. These trees endured four months of total darkness during winter months and gained most of the light required for growth during four months of continuous summer daylight. The temperature gradient between the equator and the North Pole was at an annual minimum during Eocene summer months as high latitudes received maximum solar radiation, facilitating meridional transport. Thus, moisture transported from equatorial latitudes supplied water to Axel Heiberg Island during summer episodes of explosive vegetative growth, as was recorded in the isotopic composition of fossil cellulose. Our results suggest that a meridional weather pattern was the dominant path of water transport to the high latitudes during the Eocene, but do not preclude coexisting north-to-south or other weather patterns, particularly during the drier seasons. During the winter months, the equator-to-pole temperature gradient was highest, opening the possibility of east-west moisture transport, or transport from the adjacent ice-free Arctic Ocean. Both of these possibilities would deliver a small amount of meteoric water with relatively high-δ\(^{18}\)O value (perhaps −2‰ to −5‰) prior to the start of each growing season. We plan to look for this heavy isotopic signal in the cellulose of early-season wood preserved in Fossil Forest *Metasequoia* fossils by performing a series of oxygen isotope analyses within single growth rings (Fig. 4).

Our work presents isotopic evidence that weather patterns are subject to change on a global scale during the evolution of Earth’s surface and features. During the Eocene, tree cellulose was synthesized in the Arctic using water transported from the equatorial Pacific Ocean. Such weather patterns are radically different than those thought to be in place during the Mesozoic (White et al., 2001) and may partially account for the abundance of vegetation at high latitudes during the
Eocene relative to the Cretaceous or any other period. The Eocene fossil forests of Axel Heiberg demanded environmental resources (e.g., nitrogen, phosphorous, water) at rates meeting or exceeding those displayed in modern conifer forests. We suggest that the vital resources of warm air and summer moisture were delivered via meridional transport, and supported this unusual and dramatic annual growth at high latitudes.

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