Humidity estimate for the middle Eocene Arctic rain forest

A. Hope Jahren* Department of Earth and Planetary Sciences, Johns Hopkins University, Baltimore, Maryland 21218, USA
Leonel Silveira Lobo Sternberg Department of Biology, University of Miami, Coral Gables, Florida 33124, USA

ABSTRACT

The exquisite preservation of fossilized *Metasequoia* trees that grew near 80°N latitude during the middle Eocene (ca. 45 Ma) in Nunavut, Canada, allowed for δD and $\delta^{18}O$ analyses of cellulose, techniques previously restricted to wood <30,000 yr old. From the isotopic results, we determined that the middle Eocene Arctic atmosphere contained ~2× the water found in the region's atmosphere today. This water vapor contributed to a middle Eocene greenhouse effect that insulated the polar region during dark polar winters.

Keywords: Arctic, Eocene, *Metasequoia*, cellulose, stable isotope, humidity.

INTRODUCTION

The Eocene (57.8–36.6 Ma) has been conceived by many as the zenith of Cenozoic global tropical climate; the beginning of this epoch coincided with a massive release of methane hydrates (Dickens et al., 1995) followed by extreme changes in global climate (e.g., Wing et al., 2000). The fossil record in Arctic regions is particularly striking during the Eocene, containing remarkable examples of deciduous conifer forests (Greenwood and Basinger, 1994) and large reptiles (Eberle and Storer, 1999) living at ~80°N latitude. Stable isotope analyses of Arctic molluscs revealed seasonally warm (up to 15 °C) temperatures during the late Paleocene (58–57 Ma; Tripati et al., 2001). Middle Eocene (52.0–43.6 Ma) Arctic terrestrial paleoclimate has been characterized using morphological features of plant fossils (Table 1); our study represents the first geochemical approach toward quantifying the terrestrial paleoclimate of the middle Eocene Arctic. The preservation of *Metasequoia* wood in fossils excavated on Axel Heiberg Island in the high Arctic of Nunavut, Canada, suggests little alteration beyond drying and slight compression. The site is usually interpreted to be middle Eocene in age (ca. 45 Ma; Eberle and Storer, 1999); younger ages, up to Oligocene, have also been suggested (discussed in Jahren and Sternberg, 2002). The exquisite preservation of these Paleogene fossils allowed us to implement stable isotope techniques that had been restricted to Quaternary applications due to a lack of suitable fossils.

SAMPLES, METHODS, AND RESULTS

Thirteen *Metasequoia* individuals excavated from Fossil Forest lignite layer F on Axel Heiberg Island were analyzed in duplicate for δD values of cellulose nitrate and $\delta^{18}O$ values of α-cellulose. Diagenesis of fossil wood in samples was determined to be minimal by comparing C/N, % C, and Fourier Transform Infrared spectra with that of modern wood. Lipids, lignin, and hemicellulose were removed from bulk wood to obtain pure α-cellulose (Sternberg, 1989); cellulose content of extracted samples was verified using classical biochemical assay techniques. Carbon in cellulose was combusted to CO_2 at 895 °C; oxygen in cellulose was converted into CO_2 for $\delta^{18}O$ analysis via reaction with $HgCl_2$ (Sauer and Sternberg, 1994). A 200 mg portion of α-cellulose was subjected to standard nitration procedure; water produced by the combustion of cellulose nitrate was recovered as H_2 (Sternberg, 1989). Pure CO_2 gas was analyzed for $^{18}O/^{16}O$ on a VG Isogas Prism dual-inlet isotope ratio mass spectrometer (IRMS) at the University of Miami; pure CO_2 and H_2 gases were analyzed for $^{13}C/^{12}C$ and D/H on an Isoprime dual-inlet IRMS at the Johns Hopkins University. All stable isotope values are reported in standard δ notation; measured $\delta^{18}O$ and δD values are reported relative to standard mean ocean water (SMOW); measured $\delta^{13}C$ are reported relative to Peedee belemnite (PBD). Total uncertainty in value of each sample, conservatively calculated as the total of field variability and analytical uncertainty, was found to be ±0.2‰ for $\delta^{18}O$; ±4‰ for δD; and ±0.1‰ for $\delta^{13}C$ values.

We observed strikingly low hydrogen and oxygen stable isotope values in the Axel Heiberg fossil cellulose compared to all published values of modern tree cellulose (Epstein et al., 1977): the range of measured δD and $\delta^{18}O$ ($n = 13$) was −197 to −140‰ and 15.8 to 21.0‰, respectively. In addition, the relationship we observed between $\delta^{18}O$ and δD values in the fossil cellulose differed dramatically from all reported studies of plant cellulose, as well as environmental water. Cellulose δD and $\delta^{18}O$ values revealed a highly significant ($p < 0.001$) linear relationship (Fig. 1). The slope (m) describing this linear relationship ($m = 9.5$) is very high compared to the slope of the global meteoric water line (GMWL, $m = 8$; Craig, 1961) and to all reported evaporating water bodies (Martinelli et al., 1996). In addition, the slope described by our fossil data is much higher than all reported slopes describing measured δD and $\delta^{18}O$ values in plant cellulose (Table 2), leading us to believe that the isotopic composition of Axel Heiberg fossil cellulose may reflect the local meteoric water line of Axel Heiberg Island during the Eocene.

We believe that the *Metasequoia* of Axel Heiberg Island did not experience extreme individual-to-individual levels of water stress due to the limited range of $\delta^{13}C$ values found in α-cellulose (mean ± total variability = −19.3 ± 1.5‰; $n = 21$), suggesting low variability in soil moisture levels and/or relatively high levels of humidity in these Eocene forests. For this reason, we conclude that the total range of oxygen and hydrogen isotopic values seen in Axel Heiberg fossil cellulose (range = 57‰ for δD and 5.2‰ for $\delta^{18}O$) resulted from local-scale below-ground heterogeneity in the isotopic composition of soil water, as controlled by seasonal patterns of input and infiltration.

DISCUSSION

The ultimate oxygen and hydrogen isotopic composition of cellulose in tree rings is controlled by processes internal and external to the tree. Processes external to the tree govern the isotopic composition of environmental water in the ecosystem and contribute to the isotopic labeling of cellulose contained in nonphotosynthetic tissues such as tree trunks and roots, resulting in the heterotrophic component of the

TABLE 1. PALEOTEMPERATURE ESTIMATES FOR THE ARCTIC MIDDLE EOCENE

Study	MAT (°C)	CMM (°C)	Method of determination
(Greenwood and Wing, 1995)	8.2–9.3	−2.0 to −0.8	Multiple regression model described by Wing and Greenwood (1993)
(Basinger et al., 1994)	12–15	0–4	NLR
(Wolfe, 1994)	13.7–17.2	3.3–8.6	CLAMP
This study	13.2 ± 2.0	—	Isotopic equilibrium between terrestrial carbonate and environmental water

Note: MAT—mean annual temperature; CMM—cold month mean temperature; NLR—nearest living relative analogy; CLAMP—climate–leaf analysis multivariate program.

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*E-mail: jahren@jhu.edu.

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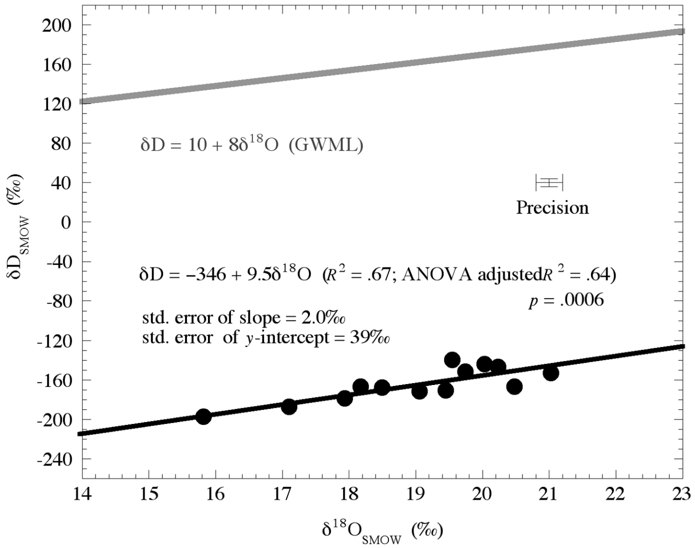

Figure 1. δD and δ^{18}O of fossil *Metasequoia* cellulose from Axel Heiberg Island in comparison to global meteoric water line (GWML). SMOW is standard mean ocean water; ANOVA is analysis of variance.

plant's isotopic signature. In addition, the plant's internal response to environmental humidity governs the isotopic composition of leaf water and contributes to the isotopic labeling of carbohydrates at the site of photosynthesis, resulting in the autotrophic component of the plant's isotopic signature. Both types of processes are recorded as a component of the isotopic composition of tree-ring cellulose via isotopic exchange during cellulose synthesis. The final isotopic value (δ = either δD or δ^{18}O) of tree-ring cellulose can therefore be described by

$$\delta_{\text{cellulose}} = f(\delta_{\text{heterotrophic}}) + (1 - f)(\delta_{\text{autotrophic}}) \tag{1}$$

(Roden and Ehleringer, 1999), which separates the heterotrophic and autotrophic contribution of ecosystem processes into fractional (*f*) contributions to the ultimate cellulose composition. Previous measurements on three species of trees indicated that 32% of H and 42% of O atoms in cellulose have undergone exchange with stem water during cellulose synthesis; the remainder retained the isotopic signal acquired during isotopic exchange with leaf water (Roden and Ehleringer, 1999; Roden et al., 2000). The net biochemical fractionation between cellulose and water during heterotrophic synthesis of cellulose was observed to be 158‰ for δD and 27‰ for δ^{18}O (Luo and Sternberg, 1992; Sternberg et al., 1986; Yakir and DeNiro, 1990). Experiments with *Lemna gibba* have indicated that the total change in isotopic composition due to autotrophic processes between leaf water and carbohydrate intermediates during cellulose synthesis is −171‰ for δD and 27‰ for δ^{18}O (Yakir and DeNiro, 1990). These findings lead to the relationship

$$\delta_{\text{cellulose}} = f(\delta_{\text{stem water}} + \varepsilon_{\text{heterotrophic}}) + (1 - f)(\delta_{\text{leaf water}} + \varepsilon_{\text{autotrophic}}), \tag{2}$$

which recasts the heterotrophic contribution as the composition of stem water modified by the net heterotrophic biochemical isotopic fractionation between stem water and carbohydrate intermediates during cellulose synthesis ($\varepsilon_{\text{heterotrophic}}$), and recasts the autotrophic contribution as the composition of leaf water modified by the net autotrophic biochemical isotopic fractionation between leaf water and carbohydrate intermediates during cellulose synthesis ($\varepsilon_{\text{autotrophic}}$).

TABLE 2. $\delta D = m\delta^{18}O + b$ FOR PLANT CELLULOSE FROM SINGLE-GENUS STUDIES

Plant sampled	*n*	*m*	*b*	R^2
*Linum usitatissimum**	29	5.8	−274	.86
*Zea mays**	15	5.4	−178	.59
Abies pindrow†	30	5.8	−231	.63
Celtis occidentalis‡	4	5.2	−206	.99
Pinus spp.§	6	5.1	−249	.80
Fossil *Metasequoia***	13	9.5	−346	.67

*As reported in DeNiro et al. (1998).
†As reported in Ramesh et al. (1985); calculated in DeNiro et al. (1998).
‡As reported in Jahren (1996).
§As reported in Epstein et al. (1977).
**Axel Heiberg Island (this study).

The isotopic composition of leaf water undergoing transpiration is described by

$$\delta_{\text{leaf water}} = \delta_{\text{stem water}} + E_{\text{eq}} + E_{\text{k}} + (\delta_{\text{vapor}} - \delta_{\text{stem water}} - E_{\text{k}})(e_{\text{a}}/e_{\text{l}}) \tag{3}$$

(discussed in Yakir and Sternberg, 2000), where δ_{vapor} is the isotopic composition of water vapor in the atmosphere, E_{eq} and E_{k} are the respective equilibrium and kinetic isotopic fractionations between liquid water and the vapor generated during evaporation, and e_{a} and e_{l} represent atmospheric vapor pressure and the vapor pressure inside the leaf, respectively. Environmental water has been shown to enter the plant passively without isotopic fractionation (i.e., $\delta_{\text{stem water}} = \delta_{\text{environmental water}}$; White, 1988). Assuming that atmospheric water vapor is in isotopic equilibrium with environmental water allows us to express the isotopic composition of atmospheric water vapor as

$$\delta_{\text{vapor}} = \delta_{\text{stem water}} - E_{\text{eq}}. \tag{4}$$

In addition, assuming that the temperature of the leaf is nearly equal to that of the atmosphere allows for the vapor pressure ratio $e_{\text{a}}/e_{\text{l}}$ to be approximated by fractional humidity (*h*):

$$\delta_{\text{leaf water}} = \delta_{\text{stem water}} + (E_{\text{eq}} + E_{\text{k}})(1 - h). \tag{5}$$

Substitution of equation 5 into 2 results in

$$\delta_{\text{cellulose}} = f(\delta_{\text{stem water}} + \varepsilon_{\text{heterotrophic}}) + (1 - f) \times [\delta_{\text{stem water}} + (E_{\text{eq}} + E_{\text{k}})(1 - h) + \varepsilon_{\text{autotrophic}}]. \tag{6}$$

Widespread observation of the linear relationship $\delta D = m\delta^{18}O + b$ in environmental water (Craig, 1961) allows us to use equation 6 to solve for fractional humidity (*h*) during the Eocene using the isotopic composition of fossil cellulose. Specification of equation 6 for δ^{18}O and δD values yields

$$\delta D_{\text{cellulose}} = m\delta^{18}O_{\text{environmental water}} + b + f_{\text{H}}\varepsilon_{\text{heterotrophic-H}} + (1 - f_{\text{H}})[(E_{\text{eq-H}} + E_{\text{k-H}})(1 - h) + \varepsilon_{\text{autotrophic-H}}] \tag{7}$$

and

$$\delta^{18}O_{\text{cellulose}} = \delta^{18}O_{\text{environmental water}} + (f_{\text{O}}\varepsilon_{\text{heterotrophic-O}}) + (1 - f_{\text{O}})[(E_{\text{eq-O}} + E_{\text{k-O}})(1 - h) + \varepsilon_{\text{autotrophic-O}}], \tag{8}$$

where *m* is the slope and *b* is the *y*-intercept of the linear relationship between environmental δ^{18}O and δD values, and the subscripts H and

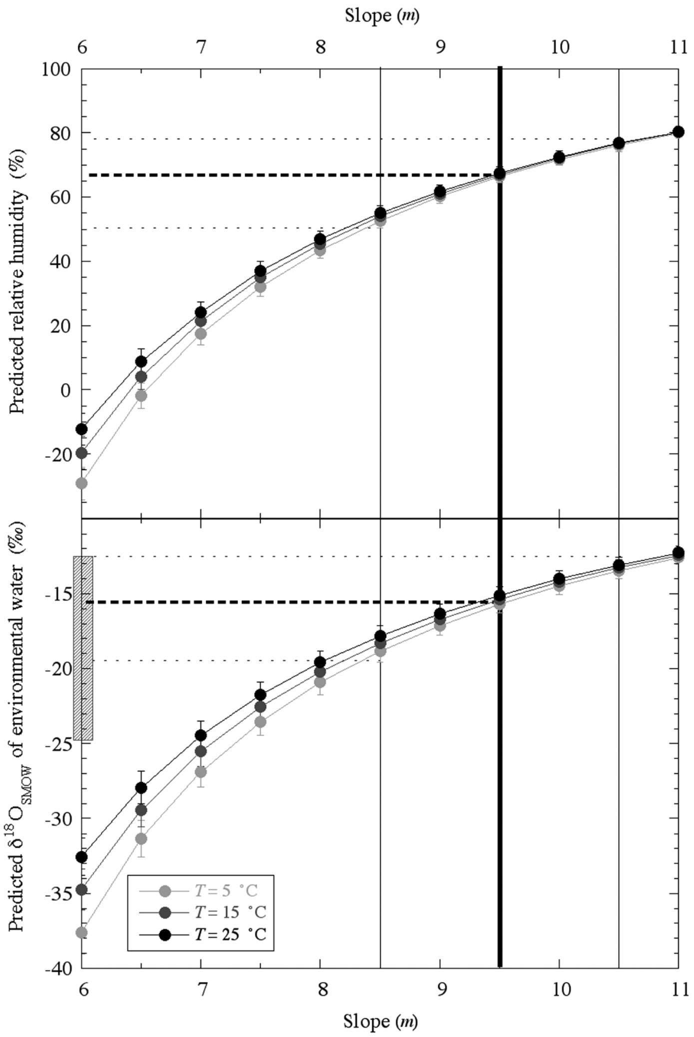

Figure 2. Predictions of relative humidity and δ^{18}O of environmental water across a range of slopes describing δD vs. δ^{18}O values. Relative humidity (RH) is related to fractional humidity (*h*) according to: RH = *h* × 100 (%). Solid lines highlight slope given by δD and δ^{18}O of fossil *Metasequoia* cellulose (*m* = 9.5; standard error = 2.0; Table 2; Fig. 1); dashed lines highlight relative humidity and δ^{18}O of environmental water predictions for Arctic middle Eocene using this slope. Shaded box encompasses range of environmental water δ^{18}O values determined for middle Eocene Axel Heiberg Island using observed fractionation between tree cellulose and environmental water (Table 3). SMOW is standard mean ocean water.

O specify the relevant isotope. Given the known and fixed terms describing the isotopic linear relationship of environmental water, and the biochemical and kinetic fractionations for both isotopes, we solved equations 7 and 8 simultaneously for humidity and $\delta^{18}O_{\text{environmental water}}$ on Axel Heiberg Island during the middle Eocene. Because the solution to the above equations is not sensitive to the value of the *y*-intercept (0.67% change in *h* for every 1‰ change in *b*), we have fixed on a value of $b = 10$ in keeping with the GMWL (Craig, 1961). These equations are particularly insensitive to temperature, which only slightly affects E_{eq} over large ranges (Fig. 2; Majoube, 1971). Because the solution to equations 7 and 8 is highly sensitive to the value of the slope (*m*) used to characterize the relationship between environmental δ^{18}O and δD values, and because fossil cellulose from Axel Heiberg Island exhibited a strikingly high slope value ($m = 9.5$; Fig. 1 and Table 2), we have included a large range of *m* in our calculation of Eocene humidity. This range encompasses observed slopes in the relationship between δ^{18}O and δD in cellulose of modern plants ($m =$ 5.1–5.8; Table 2), in terrestrial standing water ($m = 6.7$; Sternberg, 1988), in the GMWL ($m = 8$; Craig, 1961), and in the fossil cellulose of Axel Heiberg Island ($m = 9.5$; Fig. 1).

TABLE 3. OXYGEN ISOTOPE FRACTIONATION BETWEEN TREE CELLULOSE AND ENVIRONMENTAL WATER IN MODERN ECOSYSTEMS

Site of collection	Species	Δ*
Axel Heiberg Island (site 1)	*Salix arctica* (Arctic Willow)	41.4
Axel Heiberg Island (site 2)	*Salix arctica*	42.7
Kyoto, Japan	*Metasequoia glyptostroboides* (Dawn Redwood)	33.7
Tanashi, Japan (site 1)	*Metasequoia glyptostroboides*	35.2
Tanashi, Japan (site 2)	*Metasequoia glyptostroboides*	36.1
		Mean value = 37.2

*$\Delta = \delta^{18}O_{\text{cellulose}} - \delta^{18}O_{\text{plant water}}$ (‰).

Figure 2 presents calculated values of relative humidity and $\delta^{18}O_{\text{environmental water}}$ for Axel Heiberg Island during the middle Eocene. At all values of *m*, variation of temperature across 20 °C did not affect the relative humidity prediction by >4%, nor did it affect the prediction of $\delta^{18}O_{\text{environmental water}}$ by >2.7‰. We reject the predictions made using slopes ($m = 5.1$–5.8; Table 2) observed in modern plant systems: in all cases these low values of *m* yielded impossible predictions of relative humidity (i.e., relative humidity < 0%). The value of $\delta^{18}O_{\text{environmental water}}$ predicted for the middle Eocene using $m = 9.5$ agreed within 1.0‰ with the value of middle Eocene $\delta^{18}O_{\text{environmental water}}$ previously determined using empirical observations of fractionation between $\delta^{18}O_{\text{environmental water}}$ and $\delta^{18}O_{\text{cellulose}}$ in living *Metasequoia* trees (Jahren and Sternberg, 2002). This $\delta^{18}O_{\text{environmental water}}$ prediction also falls within the range of values determined using empirical observations of fractionation between $\delta^{18}O_{\text{environmental water}}$ and $\delta^{18}O_{\text{cellulose}}$ in cellulose forming under the Arctic light regime (Fig. 2; Table 3). These converging results led us to conclude that the Arctic Eocene enjoyed a growing season with relative humidity of ~67%. Today, conifer forests exist at growing season relative humidities ranging from 32 to 98%; our prediction for the middle Eocene falls near to the mid-point of this range.

The total amount of water existing as vapor in the atmosphere is strongly controlled by temperature. We determined a middle Eocene mean annual temperature (MAT) for Axel Heiberg Island using the temperature-dependent isotopic equilibrium between calcite and water described by Friedman and O'Neil (1977). For this calculation, $\delta^{18}O_{\text{environmental water}}$ was estimated by applying the isotopic fractionation observed during cellulose synthesis under an Arctic light regime (Table 3) to $\delta^{18}O_{\text{cellulose}}$ from Axel Heiberg fossil cellulose (Fig. 1; Fig. 2). X-ray diffraction identified calcite as the secondary mineral replacing wood in *Metasequoia* fossils from Stang Bay, Axel Heiberg Island; permineralization occurred rapidly in a subsoil or shallow aqueous environment prior to deformation associated with burial. Twenty carbonate samples yielded a narrow range of $\delta^{18}O_{\text{SMOW}}$ values ($\delta^{18}O_{\text{calcite}} = 7.0$–$8.3$‰, mean = 7.8‰); assuming that this calcite formed in equilibrium with environmental water during the middle Eocene yielded a MAT prediction of 13.2 ± 2.0 °C, which agrees well with other paleotemperature predictions for the middle Eocene Arctic (Table 1).

Application of the Clausius-Clapeyron equation in conjunction with the ideal gas law allowed us to calculate the actual vapor pressure of water in the atmosphere as well as its total mass in a given volume. Present-day high Arctic ecosystems have actual vapor pressure = 4.1 mm Hg during the growing season (4.3 g H_2O per m^3 of atmosphere). Using MAT = 13.2 ± 2.0 °C for the Arctic middle Eocene, as specified above, we calculated an actual paleo–vapor pressure of ~8.2 ± 0.9 mm Hg on Axel Heiberg Island (8.3 ± 0.9 g H_2O per m^3 of atmosphere). This value indicated an ~2× increase in Arctic atmospheric water content during the middle Eocene, relative to today. Overall, the paleotemperature and relative humidity conditions predicted for Axel Heiberg during the middle Eocene resemble the spring climate of the ''seasonal rainforest'' (Vézina et al., 1997, p. 71) of the Pacific Northwest.

A number of studies have suggested that most of the land area that exists as tundra today was home to forests similar to those fossilized at Axel Heiberg Island during the middle Eocene (Wolfe, 1977, 1985). If we consider 1000 m of height above the canopy to comprise the convective boundary layer (Lloyd et al., 1996) over this land area ($\approx 8 \times 10^{12}$ m^2; Schlesinger, 1977), we predict the total mass of canopy atmospheric water to be $\sim 66 \pm 7$ Gt (1 Gt = 1×10^{15} g) during the middle Eocene, compared to ~ 35 Gt of water contained in the same volume of atmosphere today. This increased atmospheric water content would have contributed to a greenhouse effect during the middle Eocene, particularly if this increase was also represented at higher levels of the atmosphere (i.e., the middle troposphere and above; Held and Soden, 2000). The warm MAT (= 13.2 °C) indicated by this study implies mild winter temperatures, which may have increased winter convection, thus increasing atmospheric mixing and delivering water vapor to higher levels of the Arctic atmosphere. Although such a water-vapor feedback would not have caused middle Eocene warm temperatures, it would have helped to maintain the warmth, particularly through the dark polar winters.

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