

# Annual patterns within tree rings of the Arctic middle Eocene (ca. 45 Ma): Isotopic signatures of precipitation, relative humidity, and deciduousness

A. Hope Jahren\*

Department of Earth and Planetary Sciences, Johns Hopkins University, Baltimore, Maryland 21218, USA

Leonel S.L. Sternberg

Department of Biology, University of Miami, Coral Gables, Florida 33124, USA

## ABSTRACT

The spectacular preservation of middle Eocene (ca. 45 Ma) wood allows for intraseason sampling of stable carbon, oxygen, and hydrogen in order to reconstruct the paleoseasonal environment of this Arctic forest (paleolatitude  $78.6^\circ \pm 1.6^\circ$  N; present latitude  $80^\circ$  N). Carbon isotopes in bulk organics and cellulose reveal striking annual patterns interpreted as the seasonal switchover from stored to actively acquired carbon associated with deciduous growth in these unusual conifers. Oxygen and hydrogen stable isotopes of cellulose and cellulose nitrate allow for the calculation of changes in relative humidity and in the isotopic value of plant-available water. Clear annual patterns of increasing relative humidity resulting from tissue growth and concomitant transpiration are apparent, as is the systematic increase in the reconstructed oxygen isotope value of environmental water, reflecting progressively increasing temperatures during the growing season.

**Keywords:** Eocene, Arctic, *Metasequoia*, relative humidity, deciduousness, tree ring.

## INTRODUCTION

The Eocene (ca. 56 to ca. 34 Ma) commenced with extreme warming (Nicolo et al., 2007) followed by a period of uniquely warm polar environments (Moran et al., 2006). During this epoch, much of Earth's terrestrial landmasses north of the Arctic Circle supported lush conifer forests (Wolfe, 1985), including what is now the far north of Canada (Fig. DR1 in the GSA Data Repository<sup>1</sup>). Axel Heiberg Island (located at  $\sim 79^\circ$  N during the middle Eocene) contains more than 30 distinct fossiliferous sedimentary layers, abundant with nonlithified plant material (described within Jahren, 2007). Using the exceptionally well-preserved plant fossils excavated from the Fossil Forest (ca. 45 Ma), we have quantified the mesic mean annual temperature and high growing season average relative humidity (Jahren and Sternberg, 2003), as well as the high level of soil methanogenesis (Jahren et al., 2004). However, the annual patterns of environmental parameters remain elusive, though of importance, given the extreme fluctuations in sunlight (i.e., none in winter, continuous in summer; see Fig. DR2) imparted to these photosynthetic organisms. In this study, we subsampled a suite of particularly thick-ringed Arctic Eocene tree fossils for carbon, oxygen, and hydrogen stable isotope analysis, and interpreted the results in terms of annual changes in environmental and organismal element cycling.

## SAMPLES AND METHODS

Three particularly thick-ringed samples were selected from fossil wood excavated from the Fossil Forest site: "AH1," "AH2," and "AH3" (Fig. DR3 in the GSA Data Repository). The wood was identified in thin

section as *Metasequoia/Glyptostrobus* type (Jagels et al., 2003), representative of the most abundant trees within the Fossil Forest. Subsampling of the three samples was performed across transects spanning 10 (AH1), 11 (AH2), and 5 (AH3) consecutive rings. Each ring was divided tangentially into five to ten subsamples of equal thickness using a razor blade and Dremel tool; the number of subsamples was determined by the minimum amount of sample necessary for a suite of four isotopic analyses:  $\delta^{13}\text{C}$  on bulk carbon,  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  on  $\alpha$ -cellulose, and  $\delta\text{D}$  on cellulose nitrate ( $\sim 150$  mg; see the GSA Data Repository for details regarding sample preparation and isotopic analyses).

## RESULTS AND DISCUSSION

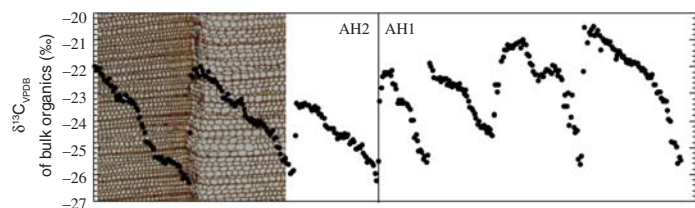
In order to assess within-ring variability of  $\delta^{13}\text{C}$ ,  $\delta^{18}\text{O}$ , and  $\delta\text{D}$  values, three overlapping transects were performed across four rings of AH2; variation due to different position was small compared to systematic variability across rings. As an example, average change in  $\delta^{13}\text{C}$  value of bulk carbon was about  $-3.5\text{‰}$  across the growing season, while maximum difference in  $\delta^{13}\text{C}$  value of bulk carbon at the same point on different transects approached  $1.0\text{‰}$ . Similarly low variability was observed in  $\delta^{18}\text{O}$  and  $\delta\text{D}$  values; however, these two variables were not correlated ( $R \approx 0.22$ ). Carbon isotope values ranged from  $-26\text{‰}$  to  $-20\text{‰}$  in the case of bulk carbon, and from  $-23\text{‰}$  to  $-18\text{‰}$  in the case of carbon in  $\alpha$ -cellulose. Ranges of  $15\text{‰}$ – $23\text{‰}$  in the  $\delta^{18}\text{O}$  of  $\alpha$ -cellulose, and  $-220\text{‰}$  to  $-165\text{‰}$  in the  $\delta\text{D}$  of cellulose nitrate, were observed. These values were within the ranges determined for bulk wood samples in our previous studies (Jahren et al., 2004; Jahren and Sternberg, 2003). Statistical analysis of periodicity demonstrated significant annual patterns for carbon, oxygen, and hydrogen stable isotope composition within fossil tree rings (detailed within the GSA Data Repository).

The carbon isotope composition of both bulk organics and  $\alpha$ -cellulose revealed clear, decreasing trends through the growing season. Ring anatomy was used to establish orientation (Fig. 1), and a concentric fossil (AH1; Fig. DR3B) was analyzed in order to confirm the direction

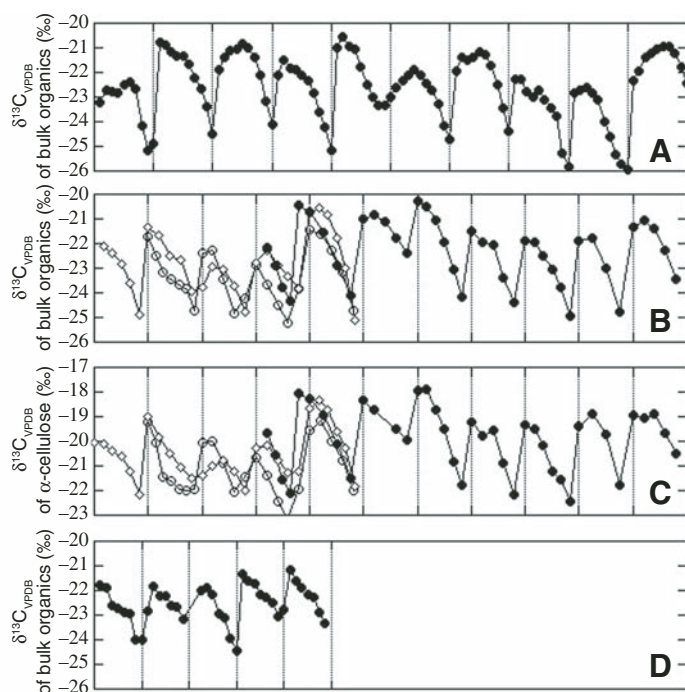
<sup>1</sup>GSA Data Repository item 2008030, a description of the site, the fossils, and the isotopic methods used, is available online at [www.geosociety.org/pubs/ft2008.htm](http://www.geosociety.org/pubs/ft2008.htm), or on request from [editing@geosociety.org](mailto:editing@geosociety.org) or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.

\*E-mail: [jahren@jhu.edu](mailto:jahren@jhu.edu)

of growth relative to isotopic signature; carbon isotope results from this fossil are shown in Figure 2A. Both AH2 and AH3 (Fig. DR3C) constituted fragments of wood; therefore the decreasing  $\delta^{13}\text{C}$  trend seen in the concentric fossil was used to confirm the direction of growth within the other fossils, given their  $\delta^{13}\text{C}$  patterns (Figs. 2B, 2C, and 2D). On average, the  $\delta^{13}\text{C}$  values of fossil rings decreased by  $\sim 3.5\%$  during the growing season; this decreasing trend was apparent for every fossil ring analyzed. A close look at the fossil transects, including transects through AH2 and AH1 made at high resolution (Fig. 1), reveals a steady decrease in  $\delta^{13}\text{C}$  value from the early growing season to the late growing season. The strong agreement between the  $\delta^{13}\text{C}$  value of bulk organics and the  $\delta^{13}\text{C}$  value of extracted  $\alpha$ -cellulose argues against the changing  $\delta^{13}\text{C}$  value being caused by differing relative amounts of lignin, lipids, or other specific compounds (Harlow et al., 2006).



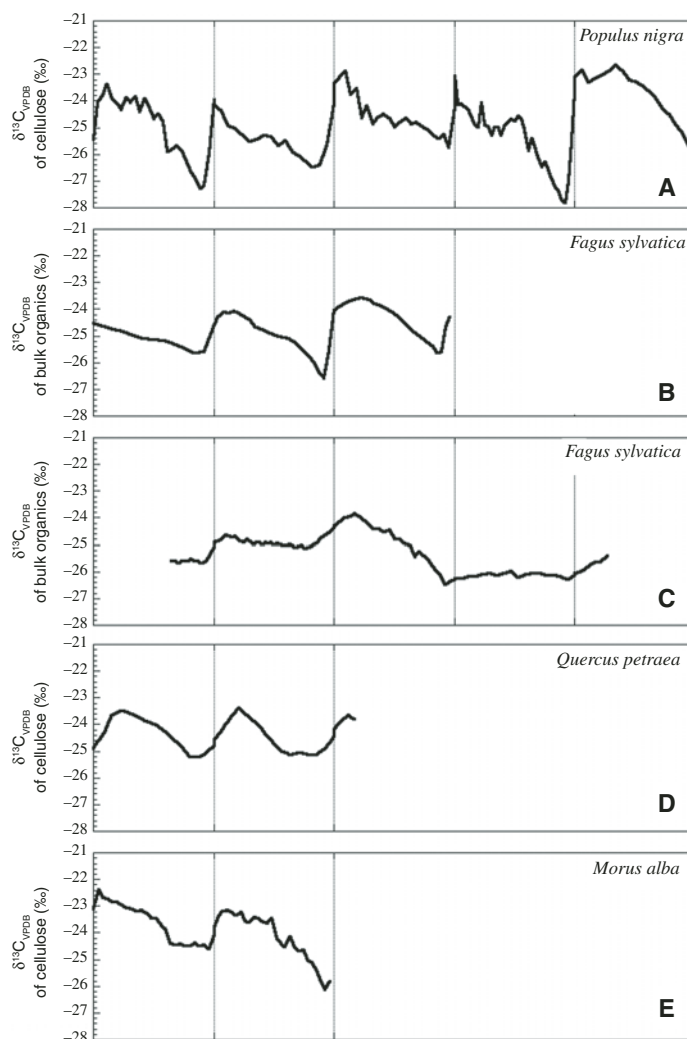
**Figure 1.** High-resolution microsampling of  $\delta^{13}\text{C}$  in bulk organics from seven fossil rings of AH2 ( $n = 54, 65,$  and  $79,$  respectively) and AH1 ( $n = 33, 46, 55,$  and  $65,$  respectively). Data are superimposed upon a  $17\ \mu\text{m}$  thin section (magnification =  $100\times$ ).



**Figure 2.** Carbon isotope analyses on fossil wood. Five to ten subsamples were taken from each ring; ring boundaries are indicated by the placement of dotted lines. Concentric fossil wood showed a distinct annual decrease in the  $\delta^{13}\text{C}$  value of bulk organics of AH1 (A); this pattern was reflected in all wood collected from the site (B [AH2] and D [AH3]). The  $\delta^{13}\text{C}$  value of bulk organics of AH2 (B) was highly correlated with the  $\delta^{13}\text{C}$  value of  $\alpha$ -cellulose (C) extracted from the same sample ( $R^2 = 0.95;$   $n = 88$ ), indicating excellent chemical preservation. Overlapping sampling transects revealed low isotopic variability compared to annual trend (B and C; different transects are represented by  $\diamond,$   $\circ,$  and  $\bullet$ ).

Several factors may control the  $\delta^{13}\text{C}$  values of tree rings, including carbon storage patterns, changes in environmental temperatures, water stress, and changes in concentrations of secondary metabolites (Leavitt and Long, 1991). Studies of carbon isotopes within modern mid- to high-latitude deciduous trees have demonstrated clear patterns of decreasing  $\delta^{13}\text{C}$  values during the growing season (Fig. 3), thought to reflect a switchover from the use of isotopically heavy, stored carbon to the use of isotopically light, actively photosynthesized carbon for the construction of new tissue (Helle and Schleser, 2004; Loader et al., 1995). In contrast, modern evergreen conifers exhibit highest  $\delta^{13}\text{C}$  values in the middle of the growing season, when environmental temperatures are highest (Fig. 4) (Barbour et al., 2002; Walcroft et al., 1997), and tropical trees have not been shown to produce clear intra-annual patterns of changing  $\delta^{13}\text{C}$  value (Poussart et al., 2004). Carbon isotope patterns found in Axel Heiberg fossil wood (Figs. 1 and 2) are clearly similar to those exhibited by deciduous trees (Fig. 3).

We used a combination of  $\delta^{18}\text{O}$  and  $\delta\text{D}$  values in each sample (Figs. 5A and 5B) to calculate the  $\delta^{18}\text{O}$  value of environmental water available to



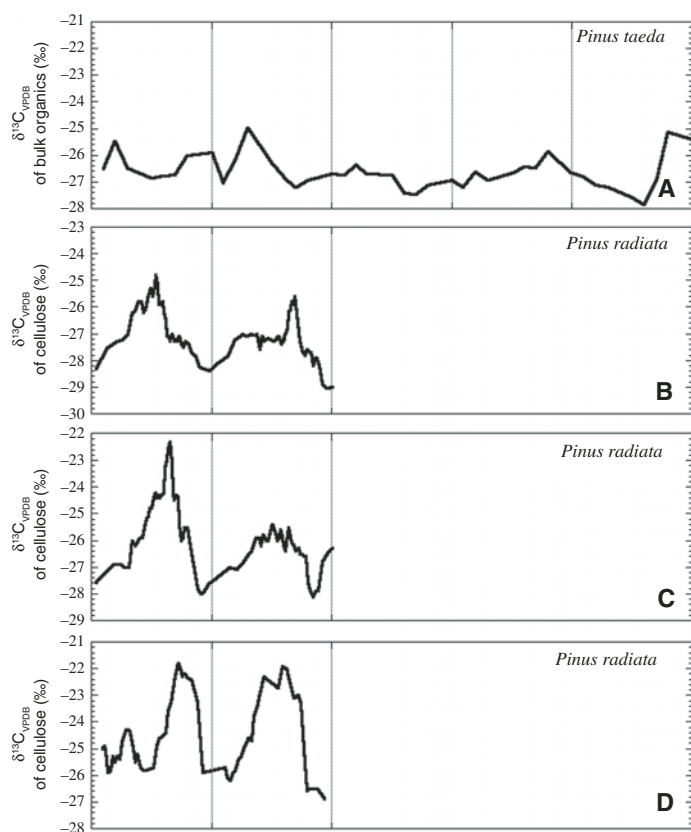
**Figure 3.** High-resolution microsampling of  $\delta^{13}\text{C}$  in modern deciduous tree rings. Data from five transects across four angiosperm species, as reported by Helle and Schleser (2004); lines represent data trends evidenced by  $>100$  measurements per ring. All trees were sampled at low-elevation, mid- to high-latitude ( $51^\circ$ – $55^\circ\text{N}$ ) sites in central Europe and represent measurements on both cellulose (A, D, and E) and bulk organics (B and C). Measurements encompass 2–5 yr periods between 1959 and 1995.

the plant during growth, as well as the value of ambient relative humidity at the time of growth. Equations describing the  $\delta D$  and  $\delta^{18}O$  values of wood cellulose in terms of environmental influences (Roden et al., 2000) were solved simultaneously for two unknowns: the  $\delta^{18}O$  value of ambient water and the relative humidity (described within Jahren and Sternberg, 2003). We used a biochemical fractionation factor for oxygen of 30‰ based on recent work suggesting the biochemical oxygen isotope fractionation can vary as a function of metabolism as well as of the oxygen isotope ratios of available water (Sauer et al., 2001; Sternberg et al., 2006).

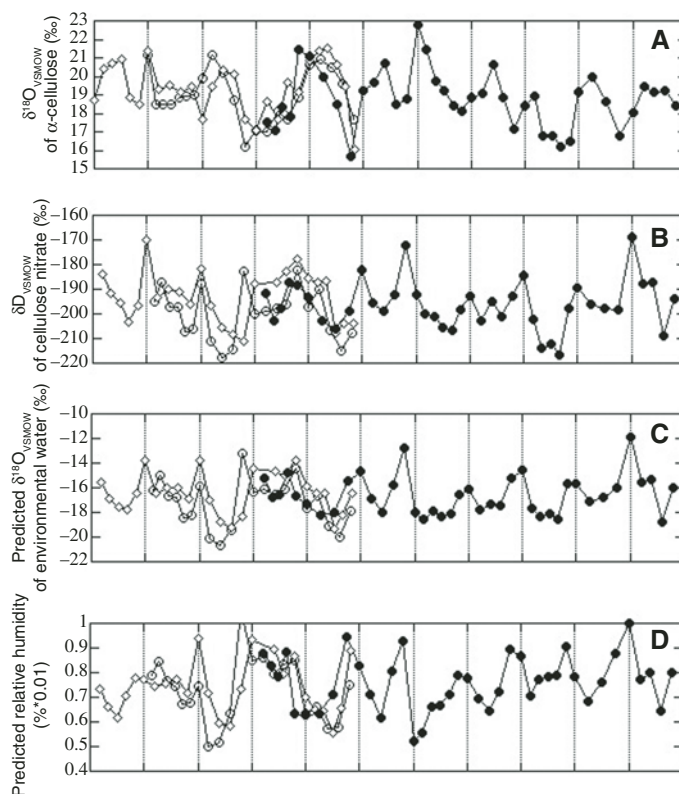
Eight of the 11 growing seasons sampled show a systematic increase during the growing season in the predicted  $\delta^{18}O$  of environmental water (average change  $\approx +3\%$ ) and show an increase in relative humidity (average change  $\approx +30\%$ ), indicating consistent seasonal environmental processes within the Eocene Arctic ecosystem (Figs. 5C and 5D). Spectral analysis confirms this pattern; spectral power for one cycle per growing season exceeded the 90% confidence interval for relative humidity and exceeded the 95% confidence interval for the predicted  $\delta^{18}O$  of environmental water. Our data indicate that environmental water available for plant uptake becomes enriched in  $^{18}O$  during the growing season as the result of increasing temperature at the site of atmospheric condensation during the growing season. This temperature increase could be caused by a combination of increasing day length, as well as increasing atmospheric insolation due to seasonal methane production (Jahren et al., 2004). Later in the growing season,  $\delta^{18}O$  of environmental water continues to increase

as high rates of transpiration add water vapor to the atmosphere (Moreira et al., 1997), further leading to enriched precipitation and subsequently isotopically enriched plant-available water; elsewhere we have explored the possibility of meridional atmospheric patterns that supplied the Arctic region with water transported overland from low latitudes (Jahren and Sternberg, 2002). We rule out increasing evaporation from the soil water as an explanation for increasing  $\delta^{18}O$  of source water because as the site humidity increases, we expect soil evaporation to decrease.

Our intra-annual records show large increases in relative humidity, often reflecting an end-of-season humidity regime of between 90% and 100% (Fig. 5D). Such massive increases in relative humidity would also be expected from an ecosystem that experienced a large amount of evapotranspiration associated with deciduous growth (Mora and Jahren, 2003). This geobiological contribution of water to the atmosphere would serve to further insolate the ecosystem, and trap heat derived from radiation within the lower atmosphere (Jahren and Sternberg, 2003). We note that high values of relative humidity are often correlated with low values of  $\delta^{13}C$  (i.e., Fig. 5D versus Figs. 2B and 2C), and acknowledge the long-standing observation of stomatal response to relative humidity and resultant tissue  $\delta^{13}C$  value (Farquhar et al., 1989). However, the magnitude of change in  $\delta^{13}C$  values across the growing season is much larger than what can be attributed to changes in water use efficiency due to changing relative humidity (Winter et al., 1982).



**Figure 4.** High-resolution microsampling of  $\delta^{13}C$  in modern conifer tree rings. Data from four transects across two *Pinus* species, as reported by Barbour et al. (2002); lines represent data trends evidenced by >100 measurements per ring. All trees were sampled at low-elevation, mid- to high-latitude sites in New Zealand (B–D; 39°–41° S) and the United States (A; 32° N) and represent measurements on both cellulose (B–D) and bulk organics (A). Measurements encompass 2–5 yr periods between 1987 and 1998.



**Figure 5.**  $\delta^{18}O$  analyses of  $\alpha$ -cellulose (A) and  $\delta D$  analyses of cellulose nitrate (B) from overlapping transects within fossil wood rings of AH2. Five to ten subsamples were taken from each ring; rings are indicated by the placement of dotted lines; different transects are represented by  $\diamond$ ,  $\circ$ , and  $\bullet$ ; overlapping sampling transects revealed low isotopic variability compared to annual trend. Predictions of annual variation in the  $\delta^{18}O$  of environmental water (C) and relative humidity (D) were made by solving two simultaneous equations (Jahren and Sternberg, 2003) and showed systematic increases in both values during 8 of the 11 growing seasons sampled.

## CONCLUSIONS

Paleobotanists have assumed that the middle Eocene Arctic forests were deciduous based on analogy with modern *Metasequoia* (Liu et al., 2007); our carbon isotope work confirms deciduousness in the dominant conifers of the site. Because the amount of carbon saved via the elimination of dark respiration is not enough to offset that lost during senescence (Royer et al., 2003), deciduousness is not of benefit in Arctic regions. Instead, these plants merely retained the deciduous strategies they acquired at lower latitudes. The dominance of *Metasequoia* in the Arctic forests comes from its ability to compete effectively within poorly drained, acidic soils and high-humidity environments.

Intra-annual isotopic records provide invaluable insight into ancient seasonal processes (e.g., Ivany et al., 2004; Buick and Ivany, 2004), yet are rarely obtainable from ancient substrates. Despite the widespread application of stable isotope analyses of tree rings to reconstructions of paleoenvironment, this study represents the first intra-annual isotope analyses of pre-Quaternary wood. This unique temporal resolution yields a seasonal picture of changing seasonal climate consistent with a highly productive deciduous ecosystem. As the days become longer and approach continuous light regime, temperatures increase, reliance turns to active photosynthate, and plant water cycling reaches its maximum.

## ACKNOWLEDGMENTS

We thank W.M. Hagopian and T.L. Greaver for laboratory assistance, G.E. Visscher and R. Jagels for their wood anatomy expertise, and N.C. Arens for advice. Supported by the Mellon Foundation and by the National Science Foundation Office of Polar Programs grants 0323877 and 0322364. This paper was improved thanks to criticism by L.C. Ivany and two anonymous reviewers.

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Manuscript received 8 April 2007

Revised manuscript received 29 August 2007

Manuscript accepted 6 September 2007

Printed in USA