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Composition, Structure, Dynamics, Productivity and Climate of Eocene Forests of the Canadian High Arctic: Comparing Reconstructions from Field Measurements and Nearest Living Relatives

http://www.sas.upenn.edu/earth/arctic/appb.html

Project Summary

Remarkable preservation of at least 28 forty-five million year old forests on eastern Axel Heiberg Island (79°55'N, 89°02'W) allows the use of standard field measurements to determine forest composition, architecture, dynamics, and productivity. The taxonomy and systematics of this middle Eocene flora have been studied for a dozen years, but a clear understanding of the basic ecology of the >500 km^2 of forests awaits further detailed analyses. Stumps, boles, litter, roots, seeds and soils are preserved as intact, *in situ*, mummified remains affording a unique opportunity to reconstruct many aspects of this ancient ecosystem from field measurements. We propose studies to determine species composition, diversity, basal area, density, fire history, histories of stand development, stand biomass, wood production and wood anatomy. Additionally, the intact preservation of belowground tissues, rhizoliths and soil organic matter affords the possibility for isotope studies of paleoclimate. At a minimum, mean annual temperature, atmospheric $\delta^{13}C$ and the incidence of moisture stress can be determined, and under favorable conditions, pCO_2 estimates can be obtained for the Eocene atmosphere. There are three different areas of investigation within this proposal that could be carried out as separate, stand-alone projects. These are: 1) reconstruction of the forests and determination of their ecological attributes; 2) determining the wood production rates of these forests; and 3) determining the physical and chemical nature of the Eocene climate at this locale from isotopic and anatomical/morphological studies. Each of the studies has obvious relevance to one or more specific disciplines. In addition we integrate all of the component studies under one umbrella idea which is to test the often-used premise that "nearest living relatives" (NLR's) provide a means for accurately reconstructing paleoclimates and paleoecosystems. NLR's are determined on the basis of anatomical and morphological similarities and it is assumed that the physiological tolerances and ecological characteristics of NLR's are similar to those of their paleo-relatives. Investigating this idea using Eocene Arctic forests provides a very powerful test of it's applicability because the Eocene forests grew in a light regime that is very different than that which the NLR's experience at present. Because light conditions influence many physiological processes and anatomical characteristics, the persistence of key physiological and ecological traits for 45 Ma in spite of dramatic changes in light regime, would be impressive support for the use of NLR's in reconstructing paleoecosystems and paleoenvironmental conditions. Accordingly, we propose to define the niches occupied by the key species of these Eocene forests and determine selected anatomical, physiological and ecological characteristics of the NLR's to see if those characteristics are appropriate for the niches filled by their Eocene relatives. Paleotemperatures are often reconstructed according to the temperature requirements of NLR's and/or by using the leaf physiognomy-MAT relationships constructed from modern flora. We propose to compare our isotopically derived estimates with biologically derived estimates.

INTRODUCTION

The middle Eocene (ca. 45 My), floodplain and swamp forests of Axel Heiberg Island (79°55 N, 89°02 W) became a focus for research in 1986 (Basinger 1986). These large-biomass, *Metasequoia*-dominated forests grew in a warm-temperate climate at a paleolatitude of ca. 77°N. The forest-bearing sediments are extensive (>500 km^2) and the preservation of plant remains is remarkable. The extensive, *in situ* mummification of litter, stumps, boles, roots, seeds, soils etc. represents a unique opportunity to reconstruct a terrestrial ecosystem and several aspects of the climate it was subject to. There are no modern analogs of these forests which, judging from their biomass and individual tree diameter growth rates, were important terrestrial C sinks that grew in 24 hours of sunlight for 3 months, then had to use stored C during three months of darkness when it apparently was not particularly cold (Basinger 1991). Given the extent of tropical forests during the Eocene (e.g. Wolfe 1985; Christophel and Greenwood 1989; Romero 1986; Axelrod and Raven 1978), the Eocene forests of Axel Heiberg Island probably represent the maximum terrestrial ecosystem productivity achievable near the poles.

GEOLOGICAL SETTING

The flat-lying, poorly consolidated sediments which include the mummified forests are assigned to the Buchanan Lake Formation (Ricketts 1986). The proposed study site is east of the Geodetic Hills on Axel Heiberg Island (79°55'N, 89°02'W). The Buchanan Lake Formation, (Ricketts 1986, 1991, 1994), consists of four members composed of interbedded non-marine conglomerate, sandstone, siltstone, and lignitic beds. The Upper Coal member contains the forests we propose to study. At the fossil forest site, the Upper Coal member is represented by approximately 400 m of sandstone, siltstone and forest layers. Individual sandstone-forest sequences are 1.5-5.0 m thick, composed of basal sandstone beds that fine upward into silty-sands and finally into siltstones. The sequence is commonly capped by the organic remains of a forest. Figure 1 shows the section of this sequence which has the most potential for the studies we propose.

During the Eocene, foreland style folding and faulting associated with uplift of the Princess Margaret Arch to the west, resulted in formation of the Axel Heiberg Basin and deposition of the Buchanan Lake Formation (Ricketts 1987, 1991; Ricketts and McIntyre 1986). Erosion of Upper Paleozoic and Mesozoic bedrock along the Stoltz Thrust resulted in the syn- and post-orogenic deposition of gravels, sands, and silts by braided and meandering river systems and debris flows in the Axel Heiberg Basin (McIntyre 1991; Ricketts 1986, 1987, 1991; Ricketts and McIntyre 1986; Tozer 1960). Figure 2 shows the spatial relationships among the Stoltz Thrust, the Buchanan Lake Formation, and the associated paleoenvironments. The fossil forests we propose to study constituted the meanderplain flora.

Preservation and Age

The Axel Heiberg fossils are largely preserved as mummifications. Although usually compressed, the wood and other remains are relatively unaltered chemically and biologically (Obst *et al*. 1991). Preservation of the fossils is exquisite, including leaf litter, cones, twigs, branches, boles, roots etc. Where these are not compressed, they are virtually indistinguishable from equivalent tissues found in the forest floor of modern conifer forests (Figs. 3, 4). The reasons why preservation is exceptional and there is so little mineralization remain obscure. Analysis of the organic remains indicate that they were buried in a fresh-water environment (Goodarzi *et al*. 1991).

Figure 1. The fossil forest site on northeastern Axel Heiberg Island, Arctic Canada showing *in situ* tree stumps and the black organic-rich forest layers.
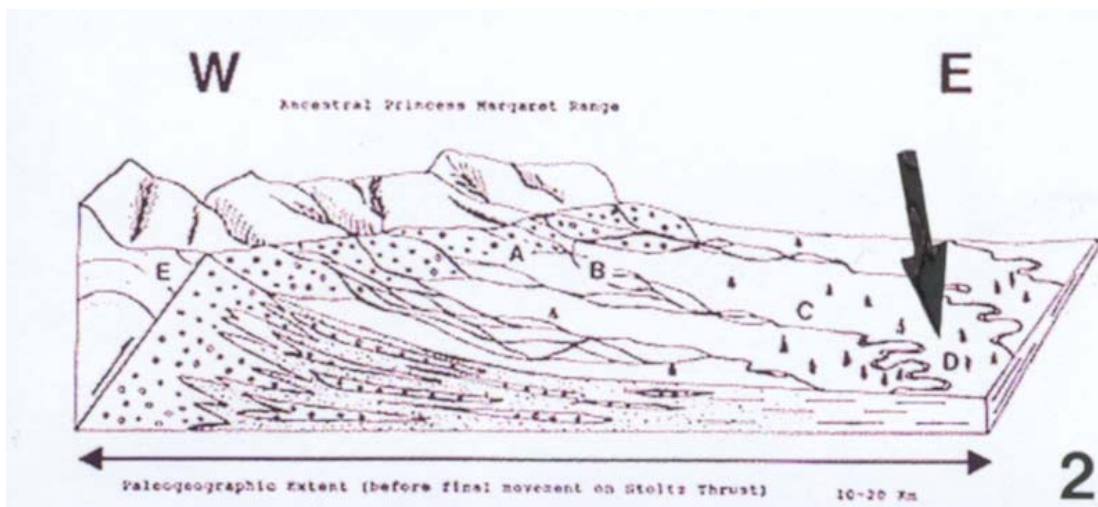

Figure 2. A cross-section of the Axel Heiberg Basin showing the members of the Buchanan Lake Formation and associated regional paleoenvironments. A) Mid-outer alluvial fan -   Conglomerate

member, B) Proximal to distal braidplain - Conglomerate-sandstone member, C) Transitional facies - Conglomerate-sandstone member, D) Meanderplain - Fossil forests, and E) Stoltz Thrust. Note that arrow points to the location of the fossil forest site.

Figure 3. Cleaned mummified leaf litter of *Metasequoia* sp. Scale bar = 1 cm.

Figure 4. Cleaned mummified seeds cones of *Pinus* sp. (A), *Picea* sp. (B), *Metasequoia* sp. (C), seed cones, a twig and leaves of *Larix altoborealis* (D), and fruits of *Juglans* sp. (E). Scale bar = 1 cm.

Figure 5. A log which has been permineralized with $CaCO_3$ with some of the original organic carbon (black rind) still preserved.

Figure 6. A well-preserved piece of wood showing the annual growth rings. Scale bar = 1 cm.

Figure 7. Cross section of wood from the stump shown in Figure 6. Note the lack of well-   defined growth rings and "late or summer" wood. The bar scale indicates the amount of wood produced in one growing season.

Figure 8. A *Metasequoia* log that measures 70 cm diameter and has 5 m of the trunk exposed.

Figure 9. Part of the trunk taken from the specimen illustrated in Figure 8 showing a branch along the length of the stem which is a good indication of self-pruned.
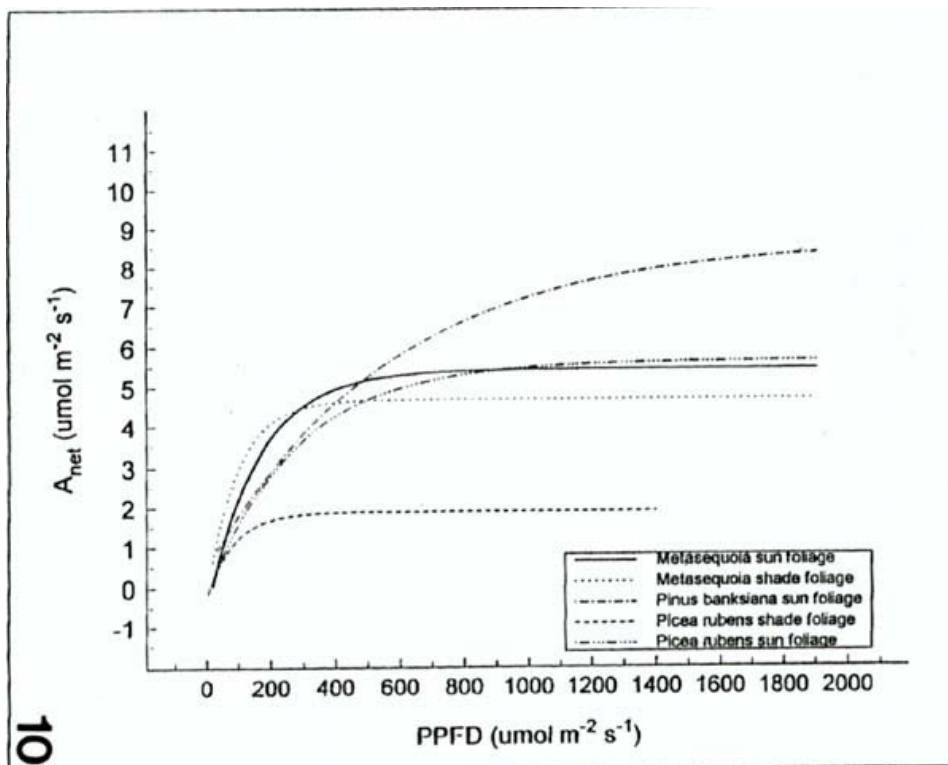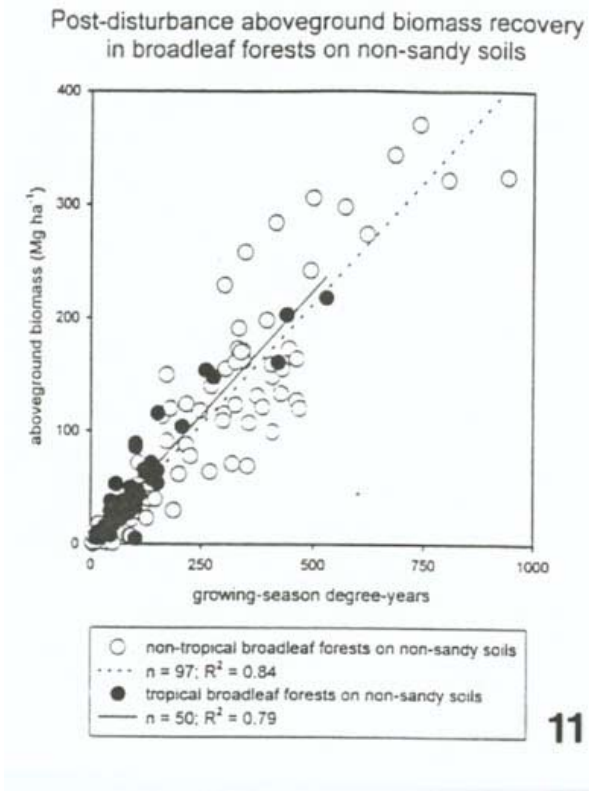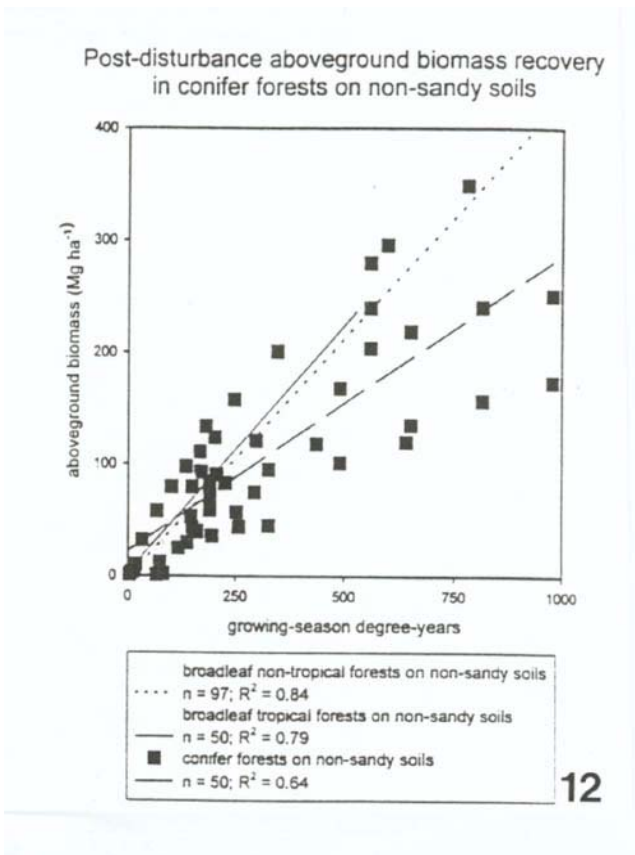

Figure 10. Light saturation curves for modern *Metasequoia glyptostroboides*, *Picea rubens*, and *Pinus banksiana*. The data show that *M. glyptostroboides* saturates at very low light levels.

Figure 11. Global-scale analysis of forest biomass accumulation rates for broadleaf forests on non-sandy soils.

Figure 12. Global-scale analysis of forest biomass accumulation rates for conifer forests on non-sandy soils.

The majority of the fossils are compressed by a factor of ca. 4:1, but morphological detail is well preserved. Preliminary wood analysis indicates carbohydrate degradation with removal of the hemicelluloses, but crystalline cellulose and lignin are present. Microscopy indicates an absence of fungi and bacteria and the degradation features commonly associated with those agents (Obst *et al*. 1991).

From structural, petrographic, stratigraphic, and palynological features, the fossil forests are middle, or possibly late Eocene (ca. 45 My., Ricketts 1986, 1987; McIntyre 1991; Ricketts and McIntyre 1986). *Pistillipollenites mcgregorii* occurs only in the middle and rarely late Eocene (Elsik and Dilcher 1974; Rouse 1977), and provides a minimum age for this formation (McIntyre 1991).

Characteristics of the Eocene Forests

Research at this site has been primarily of a taxonomic and systematic nature. Monographs of the evolutionary and biogeographic history of *Larix*, *Picea*, and *Pseudolarix* have been the focus thusfar (LePage and Basinger 1991a, 1991b, 1995a, 1995b; LePage 1993). The abundant undescribed taxa continue to be a focus of further research. Stand characteristics such as tree height, density, basal area, and spatial relationships have been addressed in preliminary fashion (Basinger 1991; Francis 1991; Greenwood and Basinger 1993, 1994; Basinger *et al*. 1994; Kumagai *et al*. 1995; Nobori *et al*. 1997).

Francis (1991) estimated the density of trees to be 484 and 325 trees/ha, with organic matter productivity estimated to be ca. 1200/gm/m^2/yr, roughly comparable to the productivity of living temperate, deciduous forests. In a later study Basinger *et al*. (1994) excavated buried stumps and estimated the tree density to be more than twice as high (1,100 trees/ha) and a stem volume of 946.1 m^3/ha. This is comparable to that of temperate old-growth forests.

Floristic Composition

Allochthonous fossil-plant assemblages occur in sands of the Upper Coal member in channel-lag and point-bar deposits. Fossils recovered from the sands include abrasion-resistant seed cones of *Larix*, *Picea*, *Pinus*, and *Metasequoia*, and rarely, angiosperm fruits (e.g., *Juglans*) (Basinger 1991). In forested horizons, autochthonous leaf litter mats represent the ancient forest floors of poorly drained floodplains and associated swamps (Ricketts 1986, 1991; Basinger 1991). Megafloral remains in forest floor mats include fertile and vegetative remains of the dominant conifers *Metasequoia* and *Glyptostrobus*, and minor occurrences of *Picea*, *Pseudolarix*, *Pinus*, *Betula*, *Alnus*, *Juglans*, *Chamaecyparis*, *Tsuga*, *Osmunda*, as well as a few unidentified angiosperm taxa (Ricketts and McIntyre 1986; Basinger 1991; LePage and Basinger 1991a; McIntyre 1991).

The scarcity of pinaceous representatives (*Larix*, *Picea*, and *Pseudolarix*) relative to those of the Taxodiaceae (*Metasequoia* and *Glyptostrobus*) indicates the Pinaceae were uncommon constituents within Taxodiaceae-dominated depositional realm. Angiosperms are poorly represented in the swamp forests but, judging from fossils in the sandstones and siltstones, were apparently a significant component of the regional vegetation. The dominant taxa occurring in the flood plains include representatives of the Betulaceae, Platanaceae, Juglandaceae, Fagaceae, *Ginkgo*, and *Metasequoia*. A list of the taxa so far identified is provided in Table 1.

Nearest Living Relatives (NLR's)

Fossil floras are used to infer paleoclimate. One approach is based on climatic needs of the living forms, often called the "nearest living relatives" (NLR's). Another is based on an analysis of climate-related features, particularly leaf morphology.

TABLE 1

Ginkgoaceae

Ginkgo

Cupressaceae

Chamaecyparis

Pinaceae

Pinus

Picea sp. 1

Picea sp. 2

Picea sp. 3

Larix altoborealis LePage et Basinger

Pseudolarix wehrii Gooch

Pseudolarix amabilis (Nelson) Rehder

Keteleeria

Abies

Tsuga

Betulaceae

Betula

Alnus

Corylus

Ulmaceae

Fraxinus

Tiliaceae

Taxodiaceae

Metasequoia

Glyptostrobus

Taiwania

Platanaceae

Platanus

Aceraceae

Acer

Sparganiaceae

Sparganium

Fabaceae

unidentified

Cecidiphyllaceae

Cercidiphyllum

Juglandaceae

Carya

Nyssaceae

Nyssa

Menispermaceae

Cissampelos

Fagaceae

Fagus

Tilia	Ferns
Equisitaceae	*Osmunda*
Equisetum	* Nearest living relative determined

NLR's have been applied widely to interpret Tertiary environments. (e.g., MacGinitie 1941; Hickey 1977). In using this approach, we assume that the physiological requirements and climatic tolerances of the fossil representatives did not change appreciably through geologic time, though there is little theoretical or empirical support for this. Reliability of NLR use is increased when a) there is a close relationship between a fossil species and its NLR; b) there are a large number of NLR's representing members of a fossil flora which have similar climatic affinities; c) the living representatives belong to widespread and diverse groups; and d) the plant groups used possess anatomical and morphological features linked to their climatic tolerances (Wing and Greenwood 1993).

The presence of taxa such as *Ginkgo*, *Metasequoia*, or *Glyptostrobus* in the Axel Heiberg fossil floras are taken to indicate temperate to warm-temperate climates with cold month means (CMMs) of > 0-2°C (e.g., Schweitzer 1980; McIver and Basinger 1993; Basinger *et al*. 1994). However, while the distribution of these taxa presently coincides with the temperate and warm temperate regions of southeast China, their present ranges are very restricted and may not accurately reflect their actual range of physiological tolerances (Wolfe 1971, 1985; Hickey 1977). For example, *Metasequoia* grows (but probably does not reproduce) in arboreta in cities as far north as Montreal, and grows and reproduces in St. Louis where the mean minimum winter temperatures range from -4 to -8°C, with extreme cold temperatures reaching -25°C (temperature data from Ruffner and Bair 1984).

The presence of *Picea*, *Tsuga*, *Abies*, and *Larix* in the Axel Heiberg fossil floras is problematic for inferring relatively warm winters. First, living species of these genera tend to occur primarily in the boreal and montane regions where climate is cool to cryic. Second, *Tsuga, Picea*, and *Abies* are evergreen and elicit the question of the effect of respiration demands on survival given dark, but relatively warm high latitude winters. It is important in this regard, to determine if the remains of the evergreen conifers are in place, or if they were growing in the cooler climate of higher elevations and transported to the meanderplains by flooding.

Alligator sp. are used as an indicator for warm temperate climates with a CMM of ca. 4°C in the fossil record (e.g., Estes and Hutchison 1980; McKenna 1980; Hutchison 1982; Wing and Greenwood 1993; Basinger *et al*. 1994). The present northern limit of *Alligator* reportedly corresponds to a CMM of 4.4°C (Hutchison 1982). However, the historical northern limit of *Alligator* extends to regions where CMM temperatures range from ca. -3° to 1°C, and extreme cold temperatures -25°C have been recorded (Ruffner and Bair 1984).

Paleotemperature estimates based on foliar physiognomy provide another perspective (Wolfe 1993; Wilf 1997). While NLR analyses of the Axel Heiberg flora provide an estimate of mean annual temperature (MAT) of 12-15°C, warm month mean (WMM) of > 25°C, and a CMM of 0-4°C (Basinger *et al*. 1994). This is based on the assumption that frost sensitive species such as *Metasequoia* and *Glyptostrobus*, and the presence of crocodillians (*Alligator*) can be taken to imply frost-free conditions with a minimum CMM of 5-7°C. However, the foliar physiognomic signatures of two Arctic sites indicate a much cooler MAT of 8.2-9.3°C, a mean annual range of temperature (MART) of 13.8-14°C, and a CMM of -0.8 to -2°C (Greenwood and Wing 1995). Basinger *et al*. (1994) suggested that the temperature discrepancies between the two methods were a result of deciduousness induced by low winter light which produced physiognomy-based estimates that were too low compared to the NLR

estimates. In sum, there is enough uncertainty in temperature estimates that new, independent paleotemperature estimators will be valuable.

RESEARCH PROPOSED

Objective 1. Produce new calculations of mean annual temperature from the existing leaf collections and improved regression models that use leaf physiognomy.

Bailey and Sinnott (1915, 1916) recognized a strong relationship between temperature and the percentage of dicot species within a flora that have leaves with entire margins. Wolfe (1979) established a linear regression of MAT vs. the percentage of dicot species with entire margins for Asian forests and generalized and improved the model by using a multivariate approach called Climate-Leaf Analysis Multivariate Program (CLAMP; Wolfe 1993). Wilf (1997) recently demonstrated that the temperature signal is dominated by the leaf-margin character in the multivariate approach and suggested using a univariate rather than a multivariate approach. We propose to use the Wilf (1997) model, and the leaves of the Eocene taxa to calculate MAT as one estimate of paleotemperature.

Stable Isotopes

We propose to use stable isotope techniques to estimate $\delta^{13}C$ value of the Eocene atmosphere, the $\delta^{18}O$ and δD values of paleoprecipitation at the site, site mean annual temperature (MAT), site growing season temperatures, and pCO_2 of the Eocene atmosphere. In addition we propose to use isotopes to inform us about the following paleoecological parameters: water-stress differences between age classes of *Metasequoia* at each site, water-stress differences between different taxa on each site, and variation within a taxon between sites, and taxonomic contributions to ecosystem productivity via paleosol isotopic composition. Since *Metasequoia* (and to a lesser extent *Glyptostrobus*) was planted widely in arboreta during the first half of this century, **we have the opportunity to make isotopic measurements on the mummified wood and on extant, mature individuals growing in a variety of temperature and soil moisture regimes**. This is expected to provide useful calibration for interpreting the isotope data obtained from the Eocene samples.

Objective 2. Reconstruct $\delta^{13}C$ and possibly pCO_2 of the Eocene atmosphere.

Organic carbon in fossil wood, leaf and reproductive tissues, paleosol organic matter, and fossil roots will be prepared for stable isotope analysis via combustion in sealed tubes containing Cu, CuO, and Ag (Minagawa *et al.* 1984). Released CO_2 will be purified cryogenically, and collected for $^{13}C/^{12}C$ measurement on the mass spectrometer. We will infer the $\delta^{13}C$ value of the mid Eocene atmosphere from the mean $d^{13}C$ value of organic carbon from all site taxa using an empirical relationship between $d^{13}C$ plant and $d^{13}C$ atmosphere developed from 671 published $\delta^{13}C$ plant measurements on 288 C3 plant species across a wide variety of environmental conditions (Arens *et al.*, in review). This work shows that $\delta^{13}C$ atmosphere = ($\delta^{13}C$ plant + 18.92)/1.05 for the C3 vascular land plant tissue averaged over the contribution of several species. This relationship has shown dramatic changes in global carbon cycling in the Early Cretaceous when used to interpret $\delta^{13}C$ measurements made on a terrestrial carbon sequence in Colombia (Jahren *et al.*, in review); our results will identify the important carbon sources and sinks to the middle Eocene atmosphere, which can be recognized based on differences in the isotope composition of each carbon pool.

For individual plants, isotopic fractionation during carbon assimilation via the C3 photosynthetic pathway can be described by (Farquhar *et al.* 1982):

$$\delta^{13}C \text{ plant} = \delta^{13}C \text{ atmosphere} - a - (b - a)C_i /C_a \qquad [1]$$

Where $\delta^{13}C$ plant is the isotopic composition of individual plant tissue derived from C3-photosynthetic carbon assimilation, $\delta^{13}C$ atmosphere is the composition of the atmospheric CO_2; "a" is the isotopic discrimination dominated by a simple diffusivity comparison of $\delta^{13}CO_2$ vs. $\delta^{12}CO_2$ in air (Craig 1953) and does not depend on stomatal density or conductivity; "b" is the isotopic discrimination imparted during carboxylation, mainly through the initial carbon-fixation enzyme in C3 plants, RuBisCO; and C_i/C_a is the ratio of intercellular to atmospheric pCO_2 expressed in parts per million. The influence of C_i/C_a on $\delta^{13}C$ values of plant tissue has been central to the application of [1] to carbon assimilation and water-use efficiency (WUE) studies. Theory predicts that when stomatal conductance is low relative to CO_2-fixation capacity, C_i is small and $\delta^{13}C$ plant tends toward larger values. Both $\delta^{13}C$ plant and C_i/C_a have been measured under a variety of controlled conditions; Farquhar and colleagues (1982) reported C_i/C_a in several species subjected to water-stress and reported a range in C_i/C_a value of 0.30-0.85. Therefore, if $\delta^{13}C$ atmosphere is known (or can be determined via the above means), individual $\delta^{13}C$ plant values can be inserted into [1] to solve for C_i/C_a in individual plants, thus giving an indication of individual water stress status. $\delta^{13}C$ plant values have been used to indicate water-stress status in modern trees (Dupouey *et al.* 1993; Marshall and Zhang 1994) and other plants (Toft *et al.* 1989). We can determine if there are differences in modern *Metasequoia* growing in seasonally dry vs. continuously moist climates, and on dry vs. poorly drained sites as a means of verifying this approach. The exceptional preservation of Eocene wood from Axel Heiberg Island allows us to extend this technique to the fossil record.

Comparisons of $\delta^{13}C$ values of paleosol organic matter and tissues of different taxa at the site will allow for estimation of relative contribution of different taxa to the overall productivity of the site, as averaged by soil forming processes. These results will be compared to independent estimates of taxa productivity gained from field measurements of annual wood production (see below).

Another opportunity is the potential for atmospheric pCO_2 determination from co-existing organic carbon and pedogenic carbonate. Some nearby fossils from the Buchanan Lake Formation contain extensive calcium carbonate rhizoliths (Fig. 5): the pedogenic carbonate $\delta^{13}C$ value, taken in conjunction with estimates of $\delta^{13}C$ atmosphere (determined above) and the $\delta^{13}C$ value of the source of respired CO_2 ($\delta^{13}C$ of paleosol organic matter), can be used to determine pCO_2 level in the Eocene atmosphere (Cerling 1992). This approach has been used to determine pCO_2 levels in the Middle to Late Paleozoic atmosphere (Mora *et al.* 1996). An assessment of the age and environment of the rhizoliths, diagenesis (via $\delta^{18}O$ vs $\delta^{13}C$ comparisons in samples, trace element concentrations, and petrographic microscopy) and an examination of the likelihood of co-formation of carbonate and organic substrates may allow for similar determination at this site.

Objective 3: Reconstruct Eocene Temperatures From $^{18}O/^{16}O$ and D/H Analyses.

$\delta^{18}O$ values will be determined for cellulose isolated from Eocene *Metasequoia* tree rings following pyrolysis with mercuric chloride and conversion of resulting O_2 gas to CO_2 for measurement on the mass spectrometer. δD values in the same samples will be determined in cellulose nitrate purified from cellulose and combusted in excess O_2 to produce water which is then reduced to H_2 gas for measurement on the mass spectrometer. Methods used for cellulose isolation and analysis will take advantage of new variants (Sheu and Chiu 1995) of the original method of Epstein *et al.* 1976, 1977). For example, recent

advances allow for cellulose-isolation batch processing of small wholewood samples (Leavitt and Danzer 1993, Loader *et al.* 1997) and high resolution isotopic analysis of single rings and single tissues (Loader *et al.* 1995).

Established relationships between $\delta^{18}O$ value of cellulose and $\delta^{18}O$ value of site precipitation (Burk and Stuiver 1981) and between dD value of cellulose-nitrate and δD value of site precipitation (Yapp and Epstein 1977) allow determination of paleoprecipitation isotopic composition. Furthermore, the documented relationship between the isotopic composition of precipitation and site temperature (Dansgaard 1964) provide a means for paleotemperature estimation. The above methodology has been used extensively to determine paleotemperatures in the Holocene (e.g., Yapp and Epstein 1977; Feng and Epstein 1994) but lack of well-preserved fossils has prevented application in deep time. For verification, we propose to run similar analyses on extant *Metasequoia* from a range of climates to determine if the isotopic signatures give reasonable estimates of present temperatures.

As indicated in Figure 6, some trees have large annual rings, and the cellular anatomy suggest differences in cell morphology in the spring and fall light/dark season compared to cells produced in the continuously light midsummer period (Fig. 7). $\delta^{18}O$ values may vary across each annual ring in a way that reflects temperature. Thus, we will attempt to determine seasonal temperatures by subsampling annual rings of modern and fossil trees to obtain isotopic data for different parts of the growing season. Again, the unusual preservation of wood, the presence of very wide annual rings, and modern *Metasequoia* growing in a variety of climates presents a unique opportunity to extract and verify paleoclimate information.

Stand-Level Measurements

Objective 4. Determine Forest Composition, Basal Area, Density, Wood Volume and Age.

We propose to excavate accessible areas to create plots useful for measuring several stand-level characteristics. In spite of permafrost, this is achievable by making use of the existing topography which allows considerable areas to be exposed by removal of < 1 m of overburden (see Fig. 1). Four areas are targeted. Two represent high-basal area conifer-dominated forests. One is underlain by deep peat (currently about 70 cm deep with an estimated 6:1 compression of roots), and the second has about 20 cm of litter underlain by oxidized (brown) mineral soil. A third stand, also on 70 cm of peat, has abundant Betulaceae litter, but not enough stumps are exposed to estimate the size of the trees. The fourth area is a dense, even-aged stand of young conifers 10-15 cm in diameter, growing in mineral soil with a minimal litter layer. We estimate that it will be possible to expose in the vicinity of 0.2 ha per field season. We plan to do this in a systematic fashion using rectangular plots that will facilitate restoration of the landscape at the conclusion of the study. We will defer a decision on plot dimensions until excavation, but five 5 X 30 m plots per each of the 4 sites are probably achievable with minimal interference from permafrost. Within the exposed areas, we will measure the diameter of each stump and determine its identity from wood anatomy.

Within the target areas are stems up to 0.8 m diameter. We propose to excavate and measure 25-30 stems across a variety of size classes which are unequivocally related to identifiable stumps. These stems will be excavated in addition to the 20 plots described above, using available opportunities. The dimensions and taper of the stems will be used to 1) create a regression relating diameter at breast height (dbh-the standard for reporting stand basal area) to stump diameter; 2) create regressions of stem height and volume on stump diameter. The latter is used to estimate stand stem volume from the measured

stumps, and is equivalent to the standard for determining stem volume from diameter at breast height (dbh) in modern forests (e.g. Vann *et al.* 1998). Example of the precision of these relationships for *Fitzroya cupressoides* and *Pilgerodendron uvifera* and some of their uses is included in the paper by Vann *et al.* (1998). These relationships are generally robust, and are expected to produce estimates of plot stem volume (Vann *et al.* 1998) acceptable by reasonable standards (e.g. ± 15-20%).

We note that the uppermost portions of the stems seldom remain intact which will lead to difficulty in reconstructing heights, but there are anatomical indicators of tree height (see objective 8 below) which will help constrain height reconstructions. Relatively little mass is contained in the top of the stems, so that the effect on calculated stand biomass is expected to be small.

Preservation of stumps is such that it is difficult to measure ring widths on most of them. However, the annual rings are readily identifiable in the longitudinal sections of the main stems. Through a combination of stump ring counts and ring counts in the longitudinal sections, we can age many of the individuals directly, and for others, age may have to be estimated from diameter/age relationships.

Objective 5. Determine the Evolution of Stand Architecture.

Longitudinal sections of tree stems contain important evidence about the growth, dynamics, architecture and history of injury (Duff and Nolan 1953, 1957; Farrar 1961; Myers 1963; Larson 1963, 1965; Fayle and Bentley 1989; Leblanc 1990). The stubs of pruned branches buried in newer wood (e.g. embedded knots) record the architecture and branching pattern of the tree as it grew, so the evolving architecture of a stand can be qualitatively determined. Using allometric equations developed from modern *Metasequoia*, branch length, branch weight and foliar weight per branch can be determined as a function of the diameter of the branch where it joins the stem (Vann *et al.* 1998), so it is possible to reconstruct how the sampled trees looked at different stages of their life history, and make interpretations of the nature of the stand at different times during its development.

One large *Metasequoia* log (70 cm diameter, 5 m of excavated length) was sectioned to determine how much information was preserved in the stem (Figs. 8, 9). It had branches along the length of the stem which were later self-pruned resulting in embedded knots (Fig. 9). This is characteristic of even-aged stand development, where the earliest cohort grows in a dense stand of bushy saplings, which thins through competition. As the canopy closes, lower branches are too shaded to have a positive carbon balance, and they are "pruned" by the tree. Smaller *Metasequoia* stems in the same level (<20 cm) do not have branches along their full length which suggests that *Metasequoia* was reproducing in the stand, and that it was shade tolerant.

In the two mature *Metasequoia*-dominated stands, we propose to measure longitudinal sections of 8-10 individuals in each of three size classes to qualitatively interpret stand development. We will seek permission to non-destructively sample living *Metasequoia* and *Glyptostrobus* growing at the US National Arboretum (Washington, D.C.) and Morris Arboretum (Philadelphia) to determine the allometric relationships necessary to calculate branch geometry from branch diameter at the main stem. We developed and used this non-destructive method on protected *Fitzroya cupressoides* in Chile with satisfactory results (Vann *et al.* 1998).

If they are present, we will examine longitudinal sections of *Pinus*, *Larix* and *Picea* in the larger size classes to determine how they were affected by their neighbors in the developing stand.

We will examine cross-sections of the stumps and lower stems for fire scars, though the lack of charcoal in the litter layers we have excavated suggests that fire was not a frequent form of disturbance.

As already noted, the preservation of stems and branches of the upper crown may not be sufficient to gain a full understanding of the architecture of the upper canopy, but useful longitudinal sections of the stem should be obtainable to diameters of ca. 10 cm, which is likely to be >80% of the height of the larger trees.

For now, the specific hypotheses guiding our efforts need to be rather general, as we are in the initial stage of exploring a large and variable ecosystem. Based on our experience to date, we expect the stand reconstructions will show that:

Hypothesis 1. Swamps and floodplains were occupied by mature forests which are closed canopy, *Metasequoia*-dominated, >25 m in height, with basal areas (at breast height) >100 m^2 ha^{-1}. These will be high-biomass forests by modern standards. We expect that at least some of the mature forest studied will be even aged. That is, the oldest and largest trees will be the same age. Younger trees which did not have any portion of their crowns in the upper canopy will be the same species as the older trees, indicating shade tolerance.

Objective 6. Describe the Physical Characteristics and Megafloral Components of the Soils.

Organic horizons (or "litter layers") are remarkably well preserved. In swamp forests, the top 30 cm is little decomposed. Over brown (well-drained) mineral soil, there is up to 20-30 cm of well-preserved litter. Most of the foliage is identifiable to the genus level. There are abundant seeds, fruits and roots down to a diameter of 5 mm. Soil oxygen conditions in the mineral soils will be inferred from the presence or absence of mottling or gleying, and depending on microsite, both aerobic and anaerobic soils will be encountered. We assume that the deep accumulations of peat were the result of high water table, and that soils were saturated much of the year. Isotopic analyses (see above) may confirm these inferences of water availability.

Within each .015 ha excavated, we will randomly locate five $0.5m^2$ soil plots which will be excavated quantitatively (e.g., Johnson *et al*. 1991). A complete inventory of leaf litter mass, root mass and diameter distribution, seeds and cones will be done. Mineral soil will be excavated to at least the bottom of the root zone, deeper if practical. Soil texture will be determined using standard procedures and water holding capacity of the mineral soil will be inferred from texture.

Objective 7. Summarizing the "place niche" of a species--the climatic conditions and the range of light and soil conditions under which each taxon lived successfully.

The abundance of individuals of a species, their size, age and position in the canopy or understory, whether or not they produced cones and seeds, and the substrates on which they grew will be used to describe the "place-niche" occupied by the different taxa of the Eocene stands and in an assessment of their success in the forest. It is obvious that *Metasequoia* was extremely successful across the variety of sites that comprise this landscape because it occurs virtually everywhere we have looked. The site and competitive conditions in which the other species lived is unknown.

Objective 8. Determine from wood anatomy, additional constraints on tree, stand, and climate characteristics.

From the isotope studies and stand reconstructions, we can likely assemble a fairly detailed understanding of climate and the major characteristics of the stand. Better yet, the unusual preservation of the Eocene plant remains allows detailed measurements of anatomical characteristics which can further constrain some of our interpretations, and which may yield interesting insights when compared with the anatomy of NLR's. We suggest that the following are useful measurements:

8a. (1) Live crown:main stem ratio and (2) fibril angles.

These are indices of how much of the stem of the tree supports branches with live foliage. As such, they provide an independent check on the reconstructions made from field samples. Fibril angle (as an indicator of juvenile vs. mature wood) of longitudinal tracheids is a measure of the closeness of the live crown to cambial initials (Romberger *et al*. 1993, Panshin and de Zeeuw 1980). Large fibril angles for outer growth rings near the base of a tree indicate a long live crown and wide tree spacing, or moderate tree spacing and extreme shade tolerance. When combined with the morphology of dissected stems to determine the distribution of embedded knots, surface knots, and the spacing of stems in the plots, inferences about shade tolerance can be made. It seems possible that uninterrupted light might change this relationship (continuous light might stimulate greater auxin production leading to higher levels at the base of the tree), so comparison to modern *Metasequoia* would be useful in constraining interpretations of shade tolerance of the Eocene trees.

8b. Determine seasonal differences in moisture supply from tracheid morphology.

In modern temperate-region conifers, earlywood tracheid diameters reflect turgor pressure achieved and auxin availability in cambial initials. Typically, temperate region conifers show a rapid increase in earlywood tracheid diameter in spring, followed by a reduction in diameter by mid or late summer, coinciding with a reduction in soil moisture (Larson 1963, Jagels *et al*. 1994). Preliminary investigation of tracheid diameter along radial files indicates larger tracheid diameters in the middle of the growing season suggesting that the fossil *Metasequoia* may have had maximum moisture availability in mid summer. Alternatively, this may be a signal of light-controlled auxin transport. While the best way to distinguish between these possibilities is through controlled experiments, comparison of tracheid dimensions with the $\delta^{13}C$ isotopic signatures of early, middle and late wood would provide useful guidance in interpreting seasonal moisture availability and moisture stress (see objective 2, above).

8c. Determine if the Eocene trees were shorter or taller than their modern counterparts.

There appears to be many stems that are nearly intact which will be exposed by excavation, but precise heights may be difficult to determine from the excavated specimens since the uppermost portion of the trees often appear decayed, or broken and scattered. This will cause uncertainty in stem dimension reconstruction efforts. Tracheid length and maximum diameter are positively correlated with tree height across genera, and to some extent, within genera (Panshin and de Zeeuw 1980). We propose to measure these in the three outer rings of NLR's of varying heights to see if there are within-genus relationships that would be useful for reconstructing tree heights. Tracheid dimensions in Eocene trees of similar diameter growth rates (very slow growing trees have shorter tracheids) can then be used to estimate tree height for comparison with reconstructions of recovered specimens.

8d. Determine ray volumes of Eocene species and NLR's.

Ray volume is a measure of stored carbohydrate needed when trees begin growth in the spring. In northern temperate regions deciduous conifers have higher ray volume than co-occurring evergreen

conifers (e.g., *Larix* sp. 10-11%; var 2.1% vs. *Picea rubens* 4.9% var. 2-4%; *Pinus strobus* 5.4% var. 0.4%; *Thuja occidentalis* 3.4% var. 0.6%; Panshin and de Zeeuw 1980). In contrast, in warm temperate regions, deciduous and evergreen conifers do not differ in ray volume (e.g., *Taxodium distichum* 6.6% var. 2.6%; *Sequoia sempervirens* 7.9% var. 2.5%; *Pinus taeda* 7.6% var. 1.6%; Panshin and de Zeeuw 1980). It is worth exploring whether ray volumes in modern *Metasequoia* vary in response to temperature regime, and if this parameter can be used as another estimator of the Eocene climate of Axel Heiberg Island. Based on the relationship observed in modern conifers, we expect that ray volumes of the Eocene deciduous and evergreen conifers should be similar if they grew in a warm temperate climate.

Objective 9. Determining the physiological and ecological traits of the NLR's, and learning if the NLR's have characteristics appropriate to the place-niches determined in the field.

Table 1 shows the taxa present in the Buchanan Lake Formation. Nearest living relatives have been determined for a number of taxa, with most showing affinity to living representatives growing in the mixed mesophytic forests of southeast Asia. Although all of the taxa studied to date have been gymnosperms, most of the angiosperms from the Axel Heiberg forests appear to be most similar to their relatives growing in China. Some physiological characteristics have been measured for a few of the NLR's, and the ecological characteristics are known in a general way for some. To achieve Objective 9 we propose to use existing literature and selected field measurements to update and extend the list of NLR's for the key Eocene taxa and determine the following for as many NLR's as is practical:

 1) Shade tolerance/ light response curves for photosynthesis

 2) Limits of warm and cold season mean monthly temperatures in the natural range of each NLR.

 3) soil moisture and drainage requirements

 4) reproductive strategies including flowering, fertilization and seed set requirements, seed dispersal mechanisms, germination and seedling establishment requirements

 5) symbionts

 6) deciduous/evergreen

The fit between NLR physiological and ecological characteristics and the Eocene forest niches is difficult to predict for some of the species. For *Metasequoia*, the data we have suggests that the characteristics of the extant species are very appropriate for its Eocene niche. We have preliminary data on the photosynthesis light response curve for modern *Metasequoia* growing in Maine and in Washington, DC. Figure 10 shows that this species saturates at very low light levels. Modern *Metasequoia* could effectively fix appreciable carbon at the low light levels of Arctic latitude summers, and it is shade tolerant and capable of reproducing under a dense canopy (Chu and Cooper 1950). Compared to *Picea* and *Pinus*, modern *Metasequoia* would be a better competitor in low-light environments. It even surpasses red spruce (*Picea rubens*) which is one of the most shade tolerant species in the forests of the northeastern U.S. The fact that *Metasequoia* is deciduous gives it an even a greater advantage over the evergreen conifers that would have had to use more of their reserve carbon during the dark season for foliar maintenance. Thus the first evidence from NLR's is consistent with *Metasequoia* dominating mature forests at high latitudes.

Objective 10. Determining Biomass Accumulation Rate.

Figures 11 and 12 show the results of a global-scale analysis of forest biomass accumulation rates (Johnson *et al.*, in review). Across a wide range of conditions, accumulated temperature during the growing season is a good predictor of stand biomass. We are certain that at least one of the stands we propose to excavate is even-aged, and that its age can be accurately determined from ring counts. It appears to be about 20-25 y old. At least one of the other three stands appears to be "ageable"-- that is, the earliest cohort of trees have the same age, and the live biomass of the stand accumulated over the interval represented by the oldest cohort. This floodplain forest is nearly monospecific, with many large *Metasequoia* stems of similar diameter (ca. 70 cm) and age (ca. 90 y) which makes it reasonable to do the calculations shown in Figures 11 and 12. We will attempt to use the isotope-derived estimates for light- and light/dark-season temperatures (assuming they are reliable) and the age of the stands determined from longitudinal sections and stumps of the oldest cohort in even-aged stands to determine accumulated temperatures (growing season degree years, x-axis in Figures 11 and 12). Wood volume will be estimated from stump diameters and the allometric equations determined from trees on each of the four sites. Eocene wood density will be assumed to be the same as in the NLR's. Foliar and branch biomass (<10% the total forest biomass) will be estimated from allometric relationships derived from modern *Metasequoia*, *Glyptostrobus,* etc. Above ground biomass (wood + foliage) can then be compared with the data in Figures 11 and 12 to determine how quickly those polar forests accumulated biomass under light and CO_2 conditions that differ markedly from those experienced by any modern forests. The high density of large-diameter stems at this locale (ca. 1000 stems/ha) and their rapid radial growth leads us to speculate that the rate of biomass accumulation in this Eocene forest exceeds that of any of the forests in Figures 11-12.

One problem to be resolved is that it is difficult to determine how many of the existing stumps represented dead trees vs. live trees. Note that Figures 11 and 12 show measures of live aboveground biomass. There are constraints on the density of live stems and their size to which virtually all modern monospecific stands conform, and this can be used to constrain the percentage of live trees in the stands we sample. This is known as the "negative 3/2's power law" (*sensu* Perry 1994).

Reasonably well-constrained biomass accumulation rates from the High Arctic region of the CO_2-enriched Eocene would be a starting point for physiological investigations aimed at providing insights into how forests respond (or don't respond) to this light regime and an atmosphere enriched in CO_2.

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