Reconstruction of Tertiary *Metasequoia* forests. II. Structure, biomass, and productivity of Eocene floodplain forests in the Canadian Arctic

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Abstract.—Abundant fossil plant remains are preserved in the high-latitude middle Eocene deposits of the Buchanan Lake Formation on Axel Heiberg Island, Nunavut Territory, Canada. Intact leaf litter, logs, and stumps preserved in situ as mummified remains offer an opportunity to determine the structure, biomass, and productivity of two Taxodiaceae-dominated forests that grew north of the Arctic Circle (paleolatitude 75-80°N). We excavated fossil tree trunks and treetops to develop equations that describe the height, structure, and mass of the aboveground components of Eoceneage Metasequoia trees. We combined those data with surveys of in situ stumps to determine the structure, biomass, and productivity of two fossil forests, "N" and "HR." We calculated a canopy height of 40 \pm 3 m for the N forest and 25 m \pm 2 m for the HR forest. Buried knots in dissected logs and abundant branch-free bole wood indicate that these were tall, closed-canopy forests. Stem tapers indicate that the overstory was of uniform height. Stem volume equaled 2095 m³ ha⁻¹ and stem biomass was 628 Mg ha-1 in the N forest. Volume and biomass in the HR forest were much smaller, 211 m³ ha⁻¹ and 63.3 Mg ha⁻¹, respectively. We estimated understory tree biomass to be 40 Mg ha⁻¹ in the N forest and 3.5 Mg ha⁻¹ in the HR forest. Recovery of seven fossil treetops with exposed branch stubs enabled us to make estimates of branchwood and foliar biomass using allometric equations derived from modern, plantation-grown Metasequoia glyptostroboides. Estimated stand-level branch biomass was 13 and 6.7 Mg ha-1 in the N and HR forests, respectively. Standing foliar biomass was estimated to be 3.2 and 2.1 Mg ha⁻¹ in the N and HR forests, respectively. Using annual ring widths, the reconstructed parabolic stems, and wood density of modern Metasequoia, we calculated annual wood production to be 2.3 Mg ha-1 yr-1 for the N forest and 0.55 Mg ha-1 yr⁻¹ for the HR forest Assuming that the ancient Metasequoia were deciduous like their living relatives, annual aboveground net primary productivity was 5.5 Mg ha⁻¹ yr⁻¹ for the N forest and 2.8 Mg ha⁻¹ yr⁻¹ for the HR forest. Our estimated biomass and productivity values for N are similar to those of modern old-growth forests of the Pacific Northwest of the United States and old-growth coastal Cordillera forests of southern Chile.

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Introduction

Proxy records of paleoclimate indicate that during the Paleocene and Eocene, the Arctic regions of North America were about 25–30°C warmer on an average annual basis than at present (Wolfe 1985; Parrish 1998). Leaf-margin and nearest-living-relative analyses indicate mean annual temperatures of 7.9° and 9.3°C for terrestrial environments at 75–80°N during the Paleocene and Eocene (Basinger et al. 1994; Greenwood and Wing 1995). The composition and abundance of these early Tertiary high-latitude fossil terrestrial floras indicate that the climate could support moderately productive, high-biomass forests (e.g.,

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Schei 1903; Nathorst 1915; Francis 1991; Basinger 1991; McIver and Basinger 1999; Liu and Basinger 2000).

Some of the best-preserved Tertiary fossil forests are contained within sediments of the Buchanan Lake Formation of the Eureka Sound Group on Axel Heiberg Island at Napartulik (Inuk for "place of trees"). Logs, stumps, and intact treetops are preserved as mummifications (Fig. 1), although the relationship between individual logs and stumps is often obscured. Each forested horizon contains beautifully preserved autochthonous leaf litter mats that represent the ancient forest floors of these floodplain and associated swamp forests (Ricketts 1986, 1991; Basinger 1991). Foliage of the taxodiaceous conifer *Metasequoia* dominates most leaf litter mats.

The exquisite preservation has made these forests a focal point for systematic and biogeographic work on *Larix*, *Picea*, and *Pseudolarix* (LePage and Basinger 1991a,b, 1995a,b; LePage 2001), and preliminary investigations of the paleoecology of the forests have also been published. For example, Francis (1991), Basinger et al. (1994), and Greenwood and Basinger (1994) focused on the analysis of in situ stumps and leaf litter to understand basic stand characteristics such as floristic composition and the spatial distribution of the trees.

Fossil stumps offer little information about stand architecture, aboveground forest dynamics, and productivity (Chapman 1994). In contrast, the combination of in situ stumps and tree boles (the main stem or trunk) contain substantial information about stand structure, forest dynamics, biomass, and productivity (e.g., Larson 1963, 1965; Leblanc 1990). We designed this study to extract the information present in the diameter, taper, internal structure, growth rings, and branch stubs of fossilized tree trunks. We combined these data with the in situ stump data to determine several ecological attributes of two of the Napartulik forests. Our primary objectives were to

- use field measurements of fossil stem tapers to determine tree heights and evaluate these estimates by using the allometric relationships derived from modern *Metasequoia*;
- determine stand biomass from the dimensions and distribution of in situ stumps combined with estimates of tree height, branch weight, and foliar biomass obtained from allometric relationships derived from a combination of fossil and modern *Metasequoia* trees;
- determine whether stand density and biomass suggest that the stumps represent a

single forest or multiple generations of forests; and

4. estimate annual aboveground net primary productivity at the stand level.

Site Characteristics and Methods

Geological Context.—The study site is east of the Geodetic Hills on Axel Heiberg Island (79°55'N, 89°02'W). The Upper Coal Member of the Buchanan Lake Formation (Ricketts 1986, 1991, 1994) contains the fossil forests described in this study. At Napartulik, this member is represented by approximately 400 m of sandstone, siltstone, and fossil 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 organic remains of forests commonly cap the sequence.

During the Eocene, foreland-style folding and faulting associated with uplift of the Princess Margaret Arch to the west resulted in 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). The Napartulik fossils are mummified (compressed and desiccated) plant remains (Blanchette et al. 1991; Basinger et al. 1994) that were buried in a freshwater, low-oxygen environment that limited decay (Goodarzi et al. 1991). Structural, petrographic, stratigraphic, palynological, and paleontological features indicate that the fossil forests are middle Eocene in age (41.3-47.5 Ma [Ricketts 1986, 1987; Ricketts and McIntyre 1986; Mc-Intyre 1991; Eberle and Storer 1999]). The Eocene latitude of Napartulik is believed to be within $\sim 2^{\circ}$ of its present-day position (Irving and Wynne 1991; Basinger et al. 1994).

Methods.—Two in situ stump fields were used in this study. One, designated "level N" by Francis (1991) was remapped by T. Sweda (Ehime University) as reported by Basinger et

FIGURE 1. Fossil wood from the Napartulik fossil forests. A, Remains of large log (field no. 0933). B, Typical log excavated for dimensional analysis (field no. LEP9701). C, Internal anatomy of a dissected log (field no. 0926) showing the internal arrangement of buried branches.



al. (1994). We used Sweda's original stump measurements for this study. This data set includes Cartesian coordinates of 284 tree stumps exposed on level N. Diameters were measured on two-thirds of the stumps. One third of the mapped stumps have estimated diameters because crushing or distortion resulted in poor preservation. The sediment type in which each stump was rooted (e.g., sand, mud, organic matter) was recorded.

A second stand, designated "level HR" by Francis (1991), is located ~800 m to the northeast of, and stratigraphically higher than, level N. The original field measurements of stump size and location as published by Francis (1991) are not of sufficient detail to analyze, so we resurveyed the HR forest using a differentially corrected GPS mapping system (Trimble, ProXr) and determined stump diameters at ground level as the average of major and minor axes.

For both stump fields we used the nearest neighbor index (NNI) (Clark and Evans 1954) to evaluate stump spatial distribution. Nearest neighbor index compares the distances between nearest samples to distances that would be expected by chance. Values of NNI <1 indicate clustering, whereas values >1 indicate dispersal of individuals. An NNI close to 1 indicates an approximately uniform spatial distribution.

Fossil stems (i.e., tree trunks) were excavated from several strata including N, HR, and the layers in between. We preferentially sampled stems that were buried at shallow depths above the permafrost layer or were oriented in a direction parallel to the slope, an orientation that generally permitted greater lengths of stems to be exposed.

We measured the lengths of the excavated logs. Logs were typically found fractured into several segments; consequently, the gaps between the segments were measured to obtain a true length. Diameter measurements were made with calipers at 50-cm intervals along the stems. We avoided measurements where there was obvious damage and at swellings near exposed branches. The width of logs was assumed to approximate the original diameter even though the logs were compressed vertically during burial. We based this assumption on the work of others who used model systems to demonstrate that cylindrical objects (e.g., logs) are likely to retain their original horizontal dimensions when compressed during burial (Walton 1936; Rex and Chaloner 1983). Most of the buried logs we measured are flat and plank-like indicating that they primarily underwent vertical collapse with no lateral expansion (Niklas and Banks 1992). Thus, we believe that the measured width closely approximates the original diameter.

We mapped the location of exposed branch stubs and branch scars on each stem. On each branch stub, major and minor axes were measured to the nearest millimeter. Diameters were estimated for missing branch stubs from the dimensions of the scar on the trunk. We determined if a callus of wood had formed around the stub, and we used the presence of a pronounced callus as an indication that the branch was dead at the time the tree was buried in the sediment (Mattheck 1991).

We dissected a subset of fossil stems (n = 6) to study the internal branch architecture and branching history of each stem (see Fig. 1C). Stems were split longitudinally along the major axis using a chisel and hammer. The diameter of embedded knots (i.e., pruned branches) was measured, as was the distance of each knot from the center axis of the stem.

We sampled one or two small cross-sections from each stem to determine annual ring widths. The cross-sections were wrapped in wet newspaper, taped around the circumference, and stored in plastic bags to prevent desiccation and distortion. Each log was tagged and reburied in its original configuration. The location of each excavated area was determined by differential GPS.

We made standard petrographic thin-sections from each cross-section to observe the growth rings. Using standard light microscopy, and image analysis software (Leica, QWIN), we measured ten of the outermost annual growth rings. We found that most samples exhibited little or no compaction or distortion from pith to bark along the major axis. We made our measurements along this axis, avoiding areas with that indicated shearing or distortion of the growth rings.

Numerical Methods and Biomass Calculations

In a companion paper to this work, Williams et al. (2003a [this volume]) describe fully a method of reconstructing forest structure and biomass by using a limited set of stump, stem fragment, and treetop measurements. We used their method to reconstruct the Napartulik fossil forests and here we briefly describe the steps involved in this method. To generate biomass and productivity estimates comparable with modern forests, we reported values for tree diameter at breast height (DBH) measured at 1.4 m above the ground. All fossil stumps at Napartulik are less than 1.4 m and many were within 35 cm of the ground, so we transformed stump diameters by using regression equations relating measured stump diameter at 35 cm (D_{GL} in cm) to DBH developed on Metasequoia glyptostroboides in Japan $(DBH = 0.779*D_{GL}^{1.04} R^2 = 0.992; n = 410$ [Williams et al. 2003a]).

A second step involves the estimation of dominant tree height from parabolic curves simulating the shape of the main stem. We calculated fossil tree height using the taper of excavated fossil stems (Williams et al. 2003a). We compared the field-derived estimates heights calculated from the allometry of modern Metasequoia (see Fig. 4A,B). We used the relationship between crown diameter and the ratio of tree height to bole diameter of modern M. glyptostroboides to calculate how tall the fossil trees would have been given their diameters and spacing (Fig. 4A). We also modeled tree height as a function of stem DBH. Kuser et al. (1997) summarized the measurements of 52 M. glyptostroboides growing in different stands within its current, natural range in Hubei, China. Using the original data set, we developed the following allometric regression equation expressing the relationship between tree height (m) and DBH (m): Tree Ht = $42.26\text{DBH}^{0.678}$, (R² = 0.63; Fig. 4B).

We used the estimated tree heights and stem diameters to calculate individual tree stem volume and biomass from a parabolic stem volume equation and an assumed wood density of fossil *Metasequoia* (300 kg/m³ [Williams et al. 2003a]). To refine our aboveground biomass estimates we used branch diameter measurements from fossil tree tops and branch diameter versus dry-weight regressions for foliage and branchwood developed for living *M. glyptostroboides* trees (Williams et al. 2003a) to estimate fossil foliage and branch biomass.

Annual aboveground net primary productivity (ANPP) is the sum of wood and foliar biomass produced. Average annual diameter increment determined from the outer ten years of the sample cross-sections was used with the parabolic volume equation to compute the annual volume of wood produced by each fossil tree represented by a stump. The annual volume increment was multiplied by average bole wood density to estimate annual wood biomass production. We assumed that the ancient Metasequoia were deciduous like their modern relatives, so annual foliar production is equal to the standing summer foliar biomass as calculated from branch allometry (Williams et al. 2003b).

We treated the boundaries of the exposed fossil-bearing areas as the boundaries of a sample plot. We present two estimates of biomass and productivity and for each stand: total and overstory. Overstory estimates are calculated by using a uniform canopy height for all trees over 30-cm DBH. The 30-cm DBH cutoff was based on the theoretical critical buckling length (L) of a self-supported column (Niklas 1992). We used published values of wood mechanical properties (Polman et al. 1999) to calculate the minimum diameter for a tree capable of reaching canopy height from the equation $L = 0.792(E/w)^{1/3}d^{2/3}$, where E =Young's modulus, w = specific density, and d= stem basal diameter (Niklas 1992). Trees under 30 cm are assumed to have been in the understory. Total biomass estimates are the sum of the overstory biomass and an estimate for understory biomass. We derived understory biomass for all trees less than 30 cm by using a variable height calculated from published regressions of height vs. diameter relationships for young M. glyptostroboides (Nakai and Nakane 1994).

Three-dimensional reconstruction of fossil forest structure was completed with the Stand Visualization Software System developed by the United States Forest Service (McGaughey 1997). This software is available via internet (http://forsys.cfr.washington.edu/svs.html).

Results

Fossil Stem Diameter and Density.-On level N, 284 tree bases were mapped within an area of 2227 m². Reconstructed DBH of the sampled stumps ranged from <5 cm to >137 cm, with a concentration of stems between 5 and 15 cm (Fig. 2A). The level N forest was heterogeneous with regard to tree diameters and spacing. Stumps rooted on mineral soil (mean 35.0 cm; SE \pm 2.48; n = 81) were significantly larger (*t*-test: t = 5.55; p < 0.0001) than stumps found rooted in organic matter (mean 18.7 cm; SE \pm 1.62; *n* = 189). Overall stem density was 1275 stems per ha⁻¹. This included 400 stems per ha⁻¹ on mineral soil and 835 stems ha⁻¹ on organic soil. The spatial distribution of stumps on N was not random according to nearest neighbor analysis (NNI = 1.21, mean nearest neighbor distance = 1.7 m). When analyzed according to sediment type, stumps rooted in mineral sediment were dispersed and farther apart (NNI = 1.41, mean nearest neighbor distance = 3.8 m) than stumps rooted in organic matter (NNI = 0.85, mean nearest neighbor distance = 1.6 m).

We mapped 111 tree stumps within the 2800 m² HR forest plot. This stand was smaller and less complex than the stand on level N. The reconstructed DBH distribution of HR trees ranged from <6 cm to >85 cm, with a concentration of stumps between 15and 25 cm (Fig. 2B). Mean DBH was 22.8 cm (SE \pm 1.47, range 5.5 to 87.8 cm). Stem density was 396 stems ha⁻¹. The HR stumps were not randomly distributed spatially according to nearest neighbor analysis. Nearest neighbor index was 1.20, and the mean nearest neighbor distance was 3.1 m. A notable pattern in HR is a band of stumps oriented in a southwest-tonortheast direction along the southeast edge of the exposure. This row of stumps included six of the largest stumps on HR (average DBH 75 cm, range 54 to 88 cm). Several were hollow, and Francis (1991) suggested that they were dead at the time the forest was buried. These individuals were excluded from subsequent height and biomass calculations.

Dimensions of Fossil Logs.—We measured 44 fossil logs (Table 1, Fig. 1B). The longest specimen we recovered from sediments was 14.8 m long. It averaged 45.1 cm in diameter, showed little taper and was mostly free of branches or knots along its length. The largest-diameter specimen we recovered was what appeared to be the basal part of a tree stem. It was 3.5 m in length and tapered rapidly from a diameter of 2.8 m at the proximal end to 1.97 m at 1.0 m from the base (Fig. 1A). None of the stems we excavated represented forked or multiple stemmed trees. Logs were compressed in the vertical dimension by an average ratio of 4.6:1.

Fossil Tree Height.—We used the average reconstructed DBH (105 cm) of the five largest well-preserved stumps found on level N to calculate tree height for that stand. Using the parabolic equations developed from taper measurements on fossil logs (Fig. 3) and the jackknifed regression for the maximum boundary relationship (dh/dt = -0.027r), we determined fossil tree height to be 37 ± 3 m. Individual log tapers plotted on Figure 3 were scattered as is typical of stands with even canopy height, and the upper boundary was easily identifiable.

Using the regression equation relating crown spread to the height: diameter ratio of Metasequoia in a range of modern forests, we determined the fossil tree height for an average canopy spread of 3.8 m (from nearest neighbor analysis) to be 42 m (Fig. 4A). The relationship between tree height and stem diameter would thus yield a height of 44 m for the average canopy-dominant tree with a DBH of 105 cm (Fig. 4B). Given that parabolic equations tend to underestimate conifer height in general, and particularly the heights of modern M. glyptostroboides growing in closed-canopy stands (Williams et al. 2003a), we estimate that tree heights in the level N forest were probably 40-42 m. Reconstructed tree height of the HR forest was lower than for the level N forest. Calculations based on the largest HR stumps indicated that the largest trees were 27 m tall. Using the spacing of stumps, we estimated a crown spread of 3.1 m, which, in conjunction with the regression for crown spread versus tree height to diameter, results in a



FIGURE 2. A, Reconstructed stem diameter distribution for the level N fossil forest at Napartulik. Solid bars represent tree stumps associated with an organic horizon. Hollow bars represent tree stumps associated with a mineral substrate. Inset shows diameter distribution of all stumps from level N. B, Reconstructed stem diameter distribution for the level HR fossil forest at Napartulik.

canopy height of 23 m for a 55 cm DBH tree (the largest stump without heart rot). Heightto-diameter relationships indicated that the height of a 55 cm DBH tree would be 27 m.

Canopy Structure.—The remains of fossil branches were common only on smaller-diameter logs (Fig. 5B,C). More than 75% of the branches occurred on logs less than 20 cm in diameter (Fig. 6). The larger logs (>30 cm) had very few or no external branch remains. We recovered four nearly intact upper stem segments (i.e., canopy), and three partial upper stem segments (Table 2). Branch diameter did not vary consistently along the length of each top (Fig. 7). Branch diameters measured on exposed branch stubs from recovered up-

Field	Length of	Lower	Upper	Ave.	Taper
ID no.	segment (m)	diameter (cm)	diameter (cm)	radius (cm)	(m/cm)
3002	3.0	13.7	6.2	5.0	-0.79
3009	8.0	16.0	7.7	5.9	-1.93
3014	3.4	39.7	27.4	16.8	-0.54
3018	2.1	62.5	60.6	30.8	-2.21
3019	1.4	20.6	19.6	10.1	-2.78
901	4.2	18.9	17.7	9.2	-6.92
902	8.1	21.1	8.5	7.4	-1.26
904	1.2	13.0	11.1	6.0	-1.24
905	2.2	23.4	22.3	11.4	-3.93
906	1.9	23.1	22.0	11.3	-3.45
907	2.1	35.0	26.4	15.4	-0.49
908	3.1	17.5	8.3	6.5	-0.67
909	2.3	30.2	21.8	13.0	-0.55
910	2.8	31.0	21.7	13.2	-0.59
911	2.4	7.4	4.5	3.0	-1.63
913	3.6	44.2	40.5	21.2	-1.93
914	0.6	14.3	13.4	6.9	-1.24
915	0.5	7.9	7.5	3.9	-2.35
3021	7.1	54.7	40.5	23.8	-1.00
916	2.1	22.2	17.3	9.9	-0.87
917	1.4	49.6	46.0	23.9	-0.75
918	6.3	18.1	8.5	5.5	-1.31
920	2.6	54.6	53.0	26.9	-3.23
921	1.6	47.9	46.7	23.7	-2.70
923	4.0	78.8	70.2	37.3	-0.93
925	1.7	21.2	18.4	9.9	-1.21
926	3.2	58.6	56.7	28.8	-3.37
929	3.6	20.4	12.6	8.3	-0.93
930	4.5	49.2	39.3	22.1	-0.90
931	1.1	21.2	17.5	9.7	-0.59
934	2.8	47.8	46.7	23.6	-5.05
935	2.1	55.1	54.3	27.4	-5.12
936	0.7	23.9	22.5	11.6	-1.00
3024	1.5	48.0	46.4	23.6	-1.81
3025	3.9	38.0	36.0	18.5	-3.90
LEP9701	2.8	71.5	64.8	34.1	-0.84
3027	1.4	15.0	14.5	7.4	-5.44
938	0.8	24.9	24.2	12.3	-2.14
939	3.7	18.3	14.4	8.2	-1.87
940	1.3	20.9	14.9	9.0	-0.43
943	2.0	20.7	16.1	9.2	-0.86
942	0.9	75.7	74.0	37.4	-1.00
944	3.5	54.7	44.2	24.7	-0.67
3054	6.0	15.8	7.2	5.7	-1.40

TABLE 1. Physical dimensions of logs used to calculate stem taper of fossil logs from Napartulik fossil forest.

per stem segments averaged 2.5 cm (range <0.5–7.6, n = 565). The average distance between branches (13.5 cm) varied significantly between samples ($F_{3,228} = 14.03$; p < 0.001), with one sample having significantly lower interbranch distances than the other three tops. From branch characteristics and calluses on the longest fossil treetop we recovered, we estimated the height of the live canopy of the fossil *Metasequoia* trees to be 9 m.

Dissected Stems.—We found numerous "buried" branch stubs inside the logs (Figs. 1C, 5A). Our measurements indicate that larger logs devoid of branch stubs on the surface had branches when they were younger. The majority of buried branches terminated ~5 cm from the center (average distance 5.3 cm), though we did find buried branches up to 25 cm from the center in some instances (Fig. 8A). The size of a buried branch was positively correlated with distance from the center of the log (Fig. 8B; Spearman's rho = 0.738; p < 0.0001, n = 88). The average diameter of the buried branches was 1.8 cm (range 0.3–4.6 cm). The



FIGURE 3. Relationship between log taper and segment radius of fossil logs recovered from the Napartulik fossil forest deposit.

average inter-branch spacing was 13.3 cm, ranging from 2 to 31 cm.

We dissected an upper stem segment (field ID no. 0918) to determine the pattern of branching. In the top three meters, all branches were expressed on the surface and were traceable to the center of the log (Fig. 5D). Below 3 m from the sample apex we found only eight buried branches, seven of which were <1 cm in diameter. These buried branches were spaced an average of 47 cm apart.

Biomass and Productivity.--We estimated annual stemwood volume increment by combining reconstructed stem diameters with the average of our estimated canopy heights for each forest. Table 3 presents estimates of stemwood volume and stemwood biomass for the average height estimates generated for both forests. Reconstructed overstory stemwood volume for the N forest was substantially larger than for the HR forest (2095 versus 211 m³ ha⁻¹). Adding the understory increased the total stand volume estimates to 2228 and 223 m³ ha⁻¹ respectively. Overstory stemwood biomass was estimated at 628 and 63.3 Mg ha⁻¹, and adding in the understory trees increased those estimates to 668 and 66.8 Mg ha⁻¹. Foliar biomass, based on the branches on fossil treetops, was estimated to average 6.6 kg per treetop. When applied to each stand, standing foliar biomass for the overstory trees in the N forest equaled 3.2 Mg ha⁻¹. Standing foliar biomass for the HR forest equaled 2.1 Mg ha⁻¹. The average treetop was estimated to have 27.1 kg of branchwood. When applied to each stand, branch biomass for the overstory trees in the N forest equaled 13 Mg ha⁻¹. Standing branch biomass for the HR forest equaled 6.7 Mg ha⁻¹. Thus, total aboveground biomass for the N stand equaled 684 Mg ha⁻¹, whereas the HR forest had a standing above ground biomass of 75.6 Mg ha⁻¹.

From the average ten-year diameter increment determined from the outermost fossil tree rings (Table 4) and the reconstructed parabolic stems, we estimated annual stemwood production for the N forest to be 2.3 Mg ha⁻¹ yr⁻¹. Estimated annual stemwood production for the HR forest equaled 0.55 Mg ha⁻¹ yr⁻¹. We believe that this is an underestimate of the stemwood production for the HR stand. HR is probably younger than the level N stand and, in accordance with the trends in ring widths as conifers age, the ring widths may have been larger in HR than in N. We do not have a large enough sample of logs from HR to confirm this, and the ring widths on the stumps may be misleading.

We assumed that the Eocene Metasequoia



FIGURE 4. A, Plot of average canopy diameter against average ratio of tree height to stem diameter at DBH for *Metasequoia glyptostroboides* grown in open- and closed-canopy settings. Error bars are \pm one standard error. Regression equation: $H/D = -0.18837 C_d^2 + 1.2895C_d + 40.0025$; $R^2 = 0.96$, where C_d is canopy diameter in meters and H/D is height to diameter ratio in meters. Fossil tree height was estimated using the average distance between trees to estimate crown spread (C_d) in meters. We used a canopy diameter of 3.8 m and a diameter of the largest and best-preserved stumps (D) in meters and a stem diameter of 1.05 cm to calculate fossil tree height for level N forest. Data are from Kuser (1982, 1983), Kuser et al. (1997), Saito et al. (1970), and Williams et al. (2003b). B, Bivariate plot of natural-log-transformed height and diameter data for *Metasequoia glyptostroboides* grown in natural stands in Hubei Province, China. Regression equation: Tree Ht = 42.26DBH^{0.678}; R² = 0.63.

FIGURE 5. Detail of upper stem segments recovered from the Napartulik fossil forest deposits. A, View of \sim 2-cmdiameter buried branch exposed by longitudinally sectioning a fossil log (no. 926). B, Partial upper stem segment; note exposed branches on the exterior of the log (no. 3009). C, Detail of exposed branches near the apex of an upper stem segment (no. 3082). D, Internal anatomy exposed in a longitudinal section of an upper stem segment (no. 918) showing branch anatomy from pith to the exterior of log.



were deciduous like their modern relatives. Accordingly, foliar production is equal to the standing foliar biomass. Total aboveground net primary production (sum of wood and foliage) for the N forest was 5.5 Mg ha⁻¹ yr⁻¹, whereas aboveground net primary production for the HR forest was 2.85 Mg ha⁻¹ yr⁻¹.

Discussion

Forest Structure and Canopy Dynamics.—Forest structure is largely determined by the growth rates and shade tolerance of the species present. Therefore, the composition of the Napartulik forests is an important aspect to consider in the interpretation of forest structure. Analysis of fossil wood anatomy and the pattern of branching in all 46 of our stems indicate the wood is Taxodiaceous and almost certainly that of *Metasequoia*. In concert with the wood anatomy, the overwhelming abundance of *Metasequoia* foliage indicates that *Metasequoia* dominated the floodplain forests at Napartulik.

Interpretation of size structure data from the N forest is complicated by the differences between stumps rooted in organic soils and stumps rooted in mineral soil. Collectively, the reconstructed stem sizes of level N trees formed a reverse-J-shaped distribution (inset, Fig. 2A) considered characteristic of unevenaged stands. Accordingly, the level N forest was interpreted to be an uneven-aged stand by Basinger et al. (1994) and Nobori et al. (1997). In contrast, single-cohort stands of modern Metasequoia with similar canopy height have a wide range of stem diameters (19.8-50.3 cm in a 48-year-old plantation [Williams et al. 2003b]), indicating that size structure is not a good proxy for age structure in Metasequoia forests.

Furthermore, interpretation of stand age structure from size frequency distributions is confounded by the lack of a definitive taxonomic identification for each stump. This is problematic because it is possible for a mixedspecies even-aged stand to have the same reverse-J-shaped distribution (Smith et al. 1997), a result of different growth rates and shade tolerances among species. Often, in mixedspecies stands, shade-tolerant species are slower growing, occupy the lower canopy, and are of smaller diameter and will predominate on the left side of a reverse-J-shaped distribution. In contrast, shade-intolerant overstory trees often grow quickly, forming a closed canopy or uniform height, and occur as a bellshaped distribution characteristic of a maturing even-aged population of trees. A composite-diameter distribution therefore may appear to be uneven-aged when in fact the diameters are merely segregated by species.

We attempted to clarify the interpretation of the stem diameter distribution in stand N by separating the mapped stumps into those rooted in mineral sediment and those rooted in organic soil. The resulting diameter distributions indicate that they probably represent different populations (Fig. 2A). The diameter distribution pattern for stems rooted on mineral matter, though slightly right-skewed, is more typical of an aging population of an even-aged cohort (e.g., He and Duncan 2000). In contrast, the pattern for stems rooted in organic matter was strongly right-skewed and indicative of either a population of shade-tolerant species or, more likely, a population of more recently established individuals.

The reconstructed stem size distribution of the HR forest is easier to interpret and appears characteristic of a maturing even-aged population of trees (Fig. 2B). The line of several large trees present in the stand appears in the right tail of the distribution. These trees may indicate the remnants of a prior stand or, alternatively, individuals that may have grown along a stream bank or other opening where they had access to more resources e.g., water or sunlight.

Greenwood and Basinger (1993) proposed that there may be multiple forests superimposed on one another in the stump assemblage from level N. This has been a question raised in studies of other fossil forests as well (Mosbrugaer et al. 1994). To test for the possibility that there were multiple generations of forests in level N, we make use of constraints on the density and size of live stems common to virtually all modern monospecific or nearly monospecific stands. The relationship between average growing space (or trees per area) to tree size (expressed as either volume



FIGURE 6. Frequency distribution of exposed branch stubs on fossil logs of different diameters.

or mass) has been empirically demonstrated to have an upper limit with a slope of approximately -1.2 to -1.8 when both axes are log-transformed (Yoda et al. 1963; Westoby 1984; Weller 1987). Enquist et al. (1998) suggest that the relationship between average tree mass and stand density is -4/3 across a wide range of plant sizes and densities. Using these relationships allows us to determine the maximum population density that would be expected given the average plant mass in level N. As shown in Figure 9, the fossil forest plots slightly above the self-thinning line, but well within the 95% confidence interval for a predicted value and well within the spread of modern forests.

Enquist and Niklas (2001) also describe general scaling relationships whereby the number of individuals per unit area in a given size class scales as -2 power of stem diameter, and they suggest that this holds true for modern forests worldwide. Recent analyses by Enquist (2002) indicate that this holds true for the Napartulik fossil forest as well. Enquist (2002) reported a fitted scaling exponent of -2.195 for the Napartulik fossil forest data, which is statistically indistinguishable from that of modern forests worldwide. Thus, the metrics used by Enquist et al. (1998) and Enquist (2002) are not consistent with the interpretation that level N stumps represent multiple stands. This should not be taken to mean there

TABLE 2. Physical dimensions of four intact upper stem segments recovered from Napartulik fossil forest, Axel Heiberg Island, Nunavut, Canada. Means followed by the same letter are not significantly different from each other at alpha = 0.05 according to Tukey's HSD.

	Field ID no.			
	#0902	#0918	#3009	#3054
Total length (m)	9.6	6.3	8.0	6.6
Diameter at base (cm)	21	18.1	16	15.8
Diameter at apex (cm)	5	8.5	7.7	4
No. of branches	45	46	108	39
Mean branch diameter $(\pm SE)$ (cm)	3.5 (0.19)a	3.2 (0.12)a	1.4 (0.068)b	2.4 (0.12)c
Range (cm)	1.5, 7.9	1.7, 4.8	0.5, 3.6	0.9, 4.4
Average interbranch distance (cm)	18.6 (1.86)a	12.8 (1.84)a	6.1 (1.20)b	13.5 (2.02)a
Foliar biomass* (kg)	10.8	7.7	4.7	4.3
Branchwood biomass* (kg)	43.7	27.1	10.8	12.6

* Branchwood and foliar biomass calculated from allometric equations presented in Williams et al. 2003a: Table 2.



Branch Stub Diameter (cm)

FIGURE 7. Vertical distribution of exposed branch stubs of four nearly intact upper stem segments; A, No. 09020. B, No. 0918. C, No. 3009. D, No. 3054.

were no dead trees in the Napartulik forests; it is probable that some of the stumps do represent dead individuals as all modern forests have some standing dead trees. In modern forests, typically 15% of the stems are dead (Tritton and Siccama 1990).

The diameters and parabolic shape of the preserved Eocene tree trunks indicate that level N *Metasequoia* were ~37 m tall across a wide range of diameters. Considerable experience with conifers growing in closed stands suggests that using a purely parabolic model underestimates total height because the stem of the live crown can be conical (Gray 1956). Thus we suspect that the 37 m estimate is slightly low. The calculated heights would be greater if we considered the stem of the live crown to be conical, or something between conical and parabolic. We did not have enough intact fossil treetops to justify this refinement, however.

The allometric relationships we derived for modern *Metasequoia glyptostroboides* (Fig. 4A,B) allowed two independent predictions of height given the stand density and stump diameters of the Eocene forests. The height estimates of 42 and 44 m derived from the modern trees are reasonably consistent with results obtained from measurements of the Eocene trees given the way we reconstructed the fossil tree heights. The uncertainty in tree height has a very small effect on the biomass and productivity calculations because such a small fraction of the stem biomass is in the top few meters of the trees.

Our height estimates for the level N forest are greater than those made by Nobori et al. (1997); their predicted mean height of \sim 21 m was based on a regression approach developed on open-grown modern Metasequoia. The findings that there are very few branches on the larger stems and that nearly all branches were small diameter is inconsistent with the open-grown Metasequoia model used by Nobori et al. (1997). Our height estimates are consistent with observations of modern Metasequoia in plantations and with the heights measured in natural Metasequoia forests in China (Kuser et al. 1997), and the branch diameters of the fossil stems are very similar to those in modern Metasequoia glyptostroboides growing in closed plantation stands.

Canopy Structure.—Our measurements show that the canopy structure of fossil *Metasequoia* trees was consistent with that of modern *M. glyptostroboides* and other shade-intolerant conifers growing in closed stands. Our analysis of dissected stems and the outer anatomy of

Frequency distribution of pruned branches from Napartulik trees (n = 6 logs, 88 branches)



FIGURE 8. A, Frequency distribution of 88 buried branches terminating at different distances from the center axis of six dissected fossil logs. B, Bivariate plot of buried branch diameter versus distance from the center axis of six dissected fossil logs. Spearman's nonparametric correlation = 0.74.

fossil logs indicates that the Eocene *Metase-quoia* were strongly self-pruning. Open-grown or widely spaced trees have larger-diameter dead branches than trees grown at narrower spacing. The small size (<4.5 cm diameter) of the buried branches in the fossil tree stems argues for rapid stand development in a high-density forest. Observation of open-grown modern *Metasequoia* indicate that they typically have much larger branch diameters (>16 cm on 48-year-old trees) than forest-grown *Metasequoia* of a similar age (<8 cm on 48-year-old trees; [Vann et al. in press]), supporting the idea that the Napartulik *Metase*

quoia forests developed from dense thickets of saplings.

The lack of substantial branches on the outer surfaces of larger logs is also indicative of growth in a closed-canopy situation where branches are not retained on the lower portion of the tree stem. This is identical to the growth strategy of extant *M. glyptostroboides*. For example, in low-density (~800 trees/ha) stands of *M. glyptostroboides*, stand closure and selfpruning begin when trees are less than 17 years old (Satoo 1974) and the average live crown ratio (i.e., ratio of crown length to tree height) is 71%. At 48 years, the live crown ra-

Forest variable	Napartulik high-biomass forest (N level)	Napartulik low-biomass forest (HR level)
Total stem density	1275 trees ha ⁻¹ (400*/835†)	396 trees ha^{-1}
Total basal area	117 m ² ha ⁻¹	30 m ² ha ⁻¹
Canopy height	$40 \pm 3 \text{ m}$	$25 \pm 2 \text{ m}$
Length of live crown	>9 m	>9 m
Total stem volume	2228 m ³ ha ⁻¹	223 m ³ ha ⁻¹
Overstory stem volume	2095 m ³ ha ⁻¹	211 m ³ ha ⁻¹
Overstory stem biomass	628 Mg ha ⁻¹ dry weight	63.3 Mg ha ⁻¹ dry weight
Standing branch biomass	13 Mg ha ⁻¹ dry weight	6.7 Mg ha ⁻¹ dry weight
Foliar biomass in the top 9 m of canopy	3.2 Mg ha ⁻¹ dry weight	2.1 Mg ha ⁻¹ dry weight
Total aboveground biomass	684 Mg ha ⁻¹ dry weight	75.6 Mg ha ⁻¹ dry weight
Total overstory standing biomass	644 Mg ha ⁻¹ dry weight	72.1 Mg ha ⁻¹ dry weight
Annual primary productivity (wood plus foliage)	5.5 Mg ha ^{-1} yr ^{-1} dry weight	2.8 Mg ha ⁻¹ dry weight

TABLE 3. Forest structure, biomass, and productivity for two middle Eocene-age fossil forests at the Napartulik locality.

* Stem density on mineral soil. + Stem density on organic soil.

tio of the same stand had dropped to 32%, indicating that the base of the live canopy had retreated upward (Vann et al. in press). The live crown ratio of extant *M. glyptostroboides* 43–48 years old ranged from 25% to 32%. From the length of our excavated treetops, we estimate a live crown ratio of 22–25%, which is similar to large modern *Metasequoia* (Williams et al. 2003b).

TABLE 4. Ten-year average ring width of fossil logs from the Napartulik fossil forest.

Field	Mean ring		
ID no.	width (mm)	Max	Min
3014	0.34	0.60	0.12
3018	0.45	0.61	0.28
901	0.97	2.11	0.48
905	0.98	1.85	0.45
907	0.87	1.83	0.39
908	0.31	0.47	0.17
909	0.50	1.00	0.26
913	0.55	0.78	0.23
914	1.17	2.92	0.48
916	0.86	1.37	0.48
917	0.35	0.68	0.13
919	0.76	1.20	0.42
920	0.99	1.74	0.35
921	0.28	0.40	0.14
925	0.34	0.52	0.24
929	0.59	0.80	0.37
930	0.36	0.47	0.26
931	0.91	1.28	0.48
934	0.72	0.92	0.56
935	0.59	0.73	0.46
936	0.93	1.43	0.49
3024	0.28	0.32	0.15
3027	0.79	0.90	0.66
939	1.43	1.94	0.88
940	1.00	1.41	0.67
944	0.49	0.91	0.29

The vertical distribution of branch diameters for fossil Metasequoia displayed no consistent pattern along each top (Fig. 7). For modern conifers, the pattern of branch diameter with depth in crown has been shown to vary with the age of the tree. Increasing branch diameter down the crown has been documented in young coniferous trees (Colin and Houllier 1992; Maguire and Bennett 1996). However, measurements of older conifers have documented a high degree of variability in the vertical distribution of branch diameters (Massman 1981; Ishii et al. 2000). In some cases, the vertical distribution of branch diameters may also indicate the degree of stand openness. Lower-density stands have deeper light penetration and therefore may allow the survival of more foliage deeper in the crown (e.g., Kellomaki et al. 1980). Our measurements indicate that the depth of crown of fossil Metasequoia is similar to that of modern M. glyptostroboides growing at similar densities.

Biomass and Productivity.—The older sections of stems were approximately 250 years old, though the true ages of the N and HR forests are not known because it is not possible to age the stumps. The annual rings of the trees we sampled were narrower than those reported previously for this site (0.68 mm \pm 0.3 vs. 2.0 mm [e.g., Francis 1991]). This difference may be because previous investigators reported ring widths from samples of stump wood where root flare creates irregular and exaggerated growth rings (Chapman 1994).



FIGURE 9. Bivariate plot of log-transformed average plant mass (grams) versus stem density. Data are from Enquist et al. (1998). Data have been truncated to populations growing at densities common to forests although the regression line and confidence intervals are those determined on the entire data set. Diamonds represent modern plantation *Metasequoia glyptostroboides* from data presented by Saito et al. (1970), Satoo (1974), Nakane and Nakai (1994), and Williams et al. (2003b). Solid cross represents the N forest density of 1275 stems/ha and corresponding average plant mass of 491 kg. Broken lines show the 95% confidence interval for a single predicted independent variable.

Kumagai et al. (1995) analyzed stemwood and reported rings with measurements similar to ours (0.78 mm) from a nearby late Paleocene locality and larger ring widths from a nearby early Eocene locality (1.65 mm).

We were able to estimate the aboveground biomass of three plant components: stemwood, branchwood, and foliage. Our estimates of stemwood biomass are based on the assumption that wood density in modern Metasequoia is equivalent to that in fossil Metasequoia. At present, it is uncertain how well modern Metasequoia wood density represents fossil Metasequoia wood density. Modern Metasequoia has relatively low-density wood compared with other temperate conifer and hardwood species (Forest Products Laboratory 1999). This finding implies that estimates of fossil biomass and productivity in this paper are likely to be minimum estimates if fossil Metasequoia had higher wood density than its nearest living relative. To make estimates of branchwood and foliar biomass we relied on the allometric equations developed for modern M. glyptostroboides grown in closed-canopy plantations. This is a standard practice in forestry and forest ecology where allometric equations from other sites are used to calculate biomass (Whittaker and Woodwell 1968; Whittaker et al. 1974; Arthur et al. 2001). Comparisons between fossil and extant Metasequoia indicate that the genus has undergone little morphological change during the last 50 Myr (Liu et al. 1999; Stockey et al. 2001). Moreover, the constraints on tree growth in closed forest settings usually result in allometric equations being very similar among growth types and congeners (Hamburg et al. 1997). Thus, we expect that the allometric equations we developed on modern M. glyptostroboides should be applicable to fossil Metasequoia.

The values for aboveground biomass (684

Mg ha⁻¹) and productivity (5.5 Mg ha⁻¹ yr⁻¹) that we derived for the level N forest overlap with the range of values for old, modern temperate forests. The larger Napartulik fossil forest biomass is similar to the biomass of modern old-growth forests of the Pacific Northwest (United States) (Grier and Logan 1977; Gholz 1982) and the old-growth coastal Cordillera conifer forests of southern Chile (Johnson et al. 2000; Battles et al. 2002). For example, for ~200-year-old Pseudotsuga menziesii-dominated forests in western Oregon, Gholz (1982) reported values of 407-749 Mg ha⁻¹ stemwood biomass and 6.2–10.5 Mg ha⁻¹ yr⁻¹ annual net primary productivity. Tsuga heterophylla-dominated forests were even higher, at 960-1316 Mg ha⁻¹ stemwood biomass and 13–15 Mg ha⁻¹ yr⁻¹ ANPP. Vann et al. (2002) and Joshi (2001) found ANPP values of 4.6 and 8.2 Mg ha⁻¹ yr⁻¹, respectively, for Fitzroya cupressoides- and Pilgerodendron uvifera-dominated forests in the coastal Cordillera of southern Chile.

A major difference between the Napartulik fossil forest and the modern old-growth forests noted above is that the ancient Arctic deciduous coniferous forests had less standing foliar biomass than the modern Pacific maritime forests, where the trees are evergreen and retain foliage for several years.

Our estimates also overlap in both total aboveground biomass and annual productivity with modern Taxodiaceous forests such as *Taxodium disticum* (Brown 1981; Duever et al. 1984). Our estimates of foliar production are similar to annual foliage production in modern cool-temperate deciduous forests (e.g., Whittaker et al. 1974; Johnson and Lindberg 1992), though somewhat lower than in modern *M. glyptostroboides* plantations (4.3–13.5 Mg ha⁻¹ [Ando et al. 1991; Nakai and Nakane 1994; Williams et al. 2003b]).

Conceptual Model of Forest Development.— Stand initiation requires a lethal disturbance to create vacant growing space for new plants to colonize. The sedimentology suggests that the Napartulik fossil forests were situated in a dynamic floodplain environment. A repeating sequence of fining-upward sediments commonly capped by coaly layers is indicative of fluvial sediments. In particular, the prominence of sandstone-coal and siltstone-coal associations is evidence for extensive overbank floodplain and crevasse-splay deposition (Ricketts 1991, 1994). Thus there is ample evidence for the creation of new resource space for *Metasequoia* to colonize. Forest fire, a major disturbance agent in some modern forests, does not appear to be a major factor given the rarity of fusain (i.e., fossil charcoal) in the Buchanan Lake Formation deposits (Goodarzi et al. 1991; Hawke and Stasiuk 2000).

The regeneration characteristics of Metasequoia seem ideally suited for single-cohort recruitment capable of exploiting recently deposited barren fluvial sediments. Extant and fossil Metasequoia seeds are small, winged, and ideal for wind dispersal (Liu et al. 1999). Fossil evidence from other locations indicates that Metasequoia was capable of germinating on fresh floodplain sediments alongside Equisetum and Onoclea sensibilis (Falder et al. 1999). Extant Metasequoia is also a colonizer of mineral sediments within its native range in China (Chu and Cooper 1950). Our germination trials also indicate that extant Metasequoia germinates more successfully on mineral compared to organic soils (Vann et al. in press). Hence, both the autecology of extant Metasequoia and evidence from in situ fossil material indicate that stand initiation on fresh floodplain deposits by a single cohort is the most reasonable inference for the origin of the Napartulik stands we studied.

Following the stand initiation stage, the above and below-ground growing space fills quickly with plants. Our analysis of dissected stems and the outer anatomy of fossil logs indicated that stand thinning and self-pruning occurred in the fossil *Metasequoia* as the stands developed from dense stands of pole-size trees. The lack of substantial branches on the outer surfaces of larger logs is indicative of growth in a closed-canopy situation where branches are not retained on the lower portion of the tree stem. This is identical to the growth strategy of extant *M. glyptostroboides*.

A third stage of development, the understory reinitiation phase (Oliver and Larson 1990), is entered gradually and represents a period of forest growth when mortality claims scattered canopy-dominant trees. One result of



FIGURE 10. Three-dimensional reconstruction of the Napartulik level N and HR fossil forests with vertical profiles shown as insets.

the freeing of resources is the establishment of new trees beneath the old stands if they are more tolerant of shade. If the fossil forests had entered the understory reinitiation phase, it would indicate that there had been some mortality of the canopy trees and an understory of smaller trees had become established in the stands. This is reasonably consistent with the size distribution of remnant stumps of the level N forest and the diversity of taxa so far recovered and identified from this layer (LePage personal observation).

Our estimates of vertical structure paired with the spatial distribution of fossil stumps make it possible to reconstruct the fossil forests in three dimensions. Figure 10 illustrates our interpretation of the structure of the level N and HR forests based on elements from the conceptual model presented above and physical dimensions acquired directly from the fossil trees and visualized using the Stand Visualization System (McGaughey 1997).

Conclusions

The middle Eocene floodplain forests of Napartulik were dominated by Metasequoia, which probably colonized fresh fluvial sediments. In the polar light regime, the trees of these forests grew to heights of about 40 m, and the stands were capable of accumulating biomass equal to that of present-day oldgrowth coastal forests of the northwestern United States and Chile within a few centuries. The net primary productivity values we determined are consistent with the productivity of modern cool-temperate coniferous forests. The internal and external anatomy of the fossil logs, and the nature, size, and distribution of branches are consistent with those features in the modern representative of this genus growing in plantations where the trees have achieved densities and spacing similar to those of the Napartulik stands. We found no evidence that the stump fields represented multiple forests, nor any strong evidence that the Eocene Metasequoia had characteristics or ecological strategies substantially different from those of its nearest living relative.

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