

# Carbon distribution and aboveground net primary production in aspen, jack pine, and black spruce stands in Saskatchewan and Manitoba, Canada

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**Abstract.** The objectives of this study are to (1) characterize the carbon (C) content, leaf area index, and aboveground net primary production (ANPP) for mature aspen, black spruce, and young and mature jack pine stands at the southern and northern Boreal Ecosystem-Atmosphere Study (BOREAS) areas and (2) compare net primary production and carbon allocation coefficients for the major boreal forest types of the world. Direct estimates of leaf area index, defined as one half of the total leaf surface area, range from a minimum of 1.8 for jack pine forests to a maximum of 5.6 for black spruce forests; stems comprise 5 to 15% of the total overstory plant area. In the BOREAS study, total ecosystem (vegetation plus detritus plus soil) carbon content is greatest in the black spruce forests (445,760–479,380 kg C ha<sup>-1</sup>), with 87 to 88% of the C in the soil, and is lowest in the jack pine stands (68,370–68,980 kg C ha<sup>-1</sup>) with a similar distribution of carbon in the vegetation and soil. Forest floor carbon content and mean residence time (MRT) also vary more among forest types in a study area than between study areas for a forest type; forest floor MRT range from 16 to 19 years for aspen stands to 28 to 39 years for jack pine stands. ANPP differs significantly among the mature forests at each of the BOREAS study areas, ranging from a maximum of 3490 to 3520 kg C ha<sup>-1</sup> yr<sup>-1</sup> for aspen stands to 1170 to 1220 kg C ha<sup>-1</sup> yr<sup>-1</sup> for jack pine stands. Both net primary production (NPP) and carbon allocation differ between boreal evergreen and deciduous forests in the world, suggesting global primary production models should distinguish between these two forest types. On average, 56% of NPP for boreal forests occurs as detritus and illustrates the need to better understand factors controlling aboveground and below-ground detritus production in boreal forests.

## Introduction

Boreal forests are of great interest to Earth system scientists because they are important in the global carbon cycle. Boreal forests contain the second largest percentage of the total world soil carbon of any biome and contain 31% of all forest soil carbon (calculated from Schlesinger, 1991). North temperate and boreal forests are believed to be a net C sink (i.e., net storage of carbon in terrestrial ecosystems), thus helping to offset rising atmospheric CO<sub>2</sub> concentration [Tans *et al.*, 1990; Cias *et al.*, 1995; Keeling *et al.*, 1996]. Other scientists, however, have questioned these conclusions and suggest that boreal forests may not be a large carbon sink [Quay *et al.*, 1992; Siegenthaler and Sarmiento, 1993].

The role of boreal forests in the global carbon cycle is determined by the net exchange of CO<sub>2</sub> between the terrestrial ecosystem and the atmosphere, commonly referred to as net ecosystem exchange (NEE). Net ecosystem exchange is the balance between net primary production, both above ground and below ground, and heterotrophic respiration. Wang and

Polglase [1995] coupled a soil and vegetation carbon model and examined the effects of climate on carbon budgets of tundra, boreal, and tropical forests; their analyses suggest that boreal forests oscillate from being a carbon sink to a carbon source.

A major focus of BOREAS is to examine the exchange of CO<sub>2</sub> between terrestrial ecosystems and the atmosphere [Sellers *et al.*, 1995]. A better understanding of the influence of environmental and ecological factors on the major components of NEE (net primary production (NPP) and heterotrophic respiration) is required to determine the causes for temporal and spatial variation in NEE. Despite the importance of boreal forests in the global carbon budget there are few complete net primary production budgets for boreal forests and no synthesis of the data is currently available. This paper focuses primarily on NPP.

Species/soil interrelationships, climate, and stand age influence NPP of forests. Species composition of the boreal forest is simple relative to other forest biomes [Landsberg and Gower, 1997] and is strongly influenced by soil type. Aspen occurs on fine textured upland soils, while jack pine occurs on excessively drained, sandy upland soils. Black spruce commonly occurs on poorly drained, organic lowland soils, but it can also occur on upland mineral soils. Water and nutrient availability differ among these contrasting soils and influences both NPP and carbon allocation [Gower *et al.*, 1995]. Large differences in carbon allocation may affect the soil carbon cycle because the different plant tissues decompose at very different rates. Car-

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**Table 1.** Select Climate Characteristics for the Southern Study Area (SSA) and Northern Study Area (NSA)

Climate Characteristic	SSA <sup>a</sup>	NSA <sup>b</sup>
Mean January air temperature, °C	-19.8	-25.0
Mean July air temperature, °C	+17.6	+15.7
Mean annual precipitation, mm	405	536

<sup>a</sup>Data based on a 48 year average from Prince Albert, Saskatchewan.

<sup>b</sup>Data based on a 23 year average from Thompson, Manitoba.

bon allocation patterns change as a stand ages, and these changes may directly or indirectly cause forest productivity to decline in older stands [Gower *et al.*, 1996; Ryan *et al.*, 1996]. Climate influences canopy architecture and leaf physiology which determine radiation interception and utilization efficiency, important determinants of canopy photosynthesis [McMurtrie *et al.*, 1994; Landsberg *et al.*, 1997].

The primary objective of this study is to characterize the distribution of carbon and aboveground net primary production (ANPP) for three dominant forest types at the southern and northern Boreal Ecosystem-Atmosphere Study (BOREAS) areas. A second objective is to compare NPP data for BOREAS and other boreal forests to determine if general NPP or carbon allocation "principles" exist for major functional types of boreal forests.

## Methods

### Study Areas

The study was conducted at two major study areas: Prince Albert National Park (PANP), Nipawin Provincial Forest region in central Saskatchewan, and Thompson, Manitoba, Canada. For brevity we refer to the two study areas as the southern

study area (SSA) and the northern study area (NSA). The SSA is near the southern boundary of the boreal forest in Saskatchewan, Canada. Permafrost does not occur in the top 2 m of soil in any of the stands. The NSA is located ~40–60 km west of Thompson, Manitoba, Canada. The soils are derived from parent material deposited by Glacial Lake Agassiz. Permafrost occurs in poorly drained forests and fens in the NSA. Winters are less harsh and summers are hotter and drier in the SSA than NSA (Table 1).

At each study area, we established four replicate plots in mature aspen and black spruce and young and mature jack pine stands. One objective of the BOREAS study is to estimate NEE for the different terrestrial ecosystems and understand the processes controlling the exchange of CO<sub>2</sub> between the BOREAS tower sites and the atmosphere. To achieve this objective we located four replicate plots immediately outside the footprint of the eddy flux towers, in forest representative of that inside the footprint. The size of the plots in each stand vary depending on the tree density. The number of trees per plot range from 60 to 140 (Table 2). The large number of trees and the random location of the four replicate plots are sufficient to adequately characterize the forest. Species, crown class [Daniel *et al.*, 1979], and diameter at breast height (dbh) (1.37 m) were tallied for all trees in each plot. Table 2 summarizes select stand characteristics for the eight stands.

The young (25–27 years) and old (60–65 years) jack pine (*Pinus banksiana* Lamb.) stands are even-aged and originated from wildfires. Bearberry (*Arctostaphylos uva-ursi* [L.] Spreng.) and reindeer lichen (*Cladonia mitis* [Sandst.] Hale & Culb) are the dominant ground cover in the young stands and reindeer lichen forms nearly a complete ground cover in the mature stands at both the SSA and the NSA. Isolated clumps of green alder (*Alnus crispa* [Ait.] Pursh) with a feathermoss

**Table 2.** Select Stand Characteristics for Forest Tower Flux Sites at NSA and SSA

Forest Type	Plot Size, m	Dominant Vegetation <sup>a</sup>	Age <sup>b</sup> years	Mean Tree Height, m <sup>c</sup>	Trees, ha <sup>-1</sup>	Basal Area, m <sup>2</sup> ha <sup>-1</sup>	DBH, cm		
							Mean	Range	
NSA									
Aspen (NA)	25 × 25	TA <sup>d</sup>	53	13.8	1,960	26.7 (96) <sup>f</sup>	12.5	(4.5–23.2)	
		W					5.2	(3.0–13.7)	
		JP, GA <sup>e</sup> , PB <sup>e</sup>					23.5	(—)	
Old black spruce (NBS)	15 × 15	BS	155	9.1	5,450	35.6 (98)	8.5	(2.5–18.6)	
		TA, W <sup>e</sup>					20.2	(15.4–25.0)	
Young jack pine (NYJP)	7.5 × 7.5	JP		2.9	15,160	7.2 (100)	2.1	(0.5–6.1)	
Old jack pine (NOJP)	25 × 25	JP	63	10.3	1,280	13.3 (97)	11.1	(3.0–18.7)	
		PB					12.3	(7.1–18.0)	
SSA									
Old aspen (SA)	30 × 30	TA <sup>d</sup>	67	20.1	980	33.5 (100)	20.5	(9.9–31.5)	
Black spruce (SBS)	15 × 15	BS,	115	7.2	5,900	27.2 (87)	7.1	(2.1–21.1)	
		JP					18.3	(14.1–22.7)	
		ET, W <sup>e</sup>					11.3	(5.1–16.1)	
Young jack pine (SYJP)	7.5 × 7.5	JP, GA <sup>e</sup>	25	3.7	10,670	11.9 (100)	3.2	(0.8–10.9)	
Old jack pine (SOJP)	25 × 25	JP	65	12.7	1,190	16.9 (100)	12.9	(3.0–23.2)	

<sup>a</sup>TA, trembling aspen; W, willow; JP, jack pine; GA, green alder; PB, paper birch; BS, black spruce; ET, eastern tamarack.

<sup>b</sup>Determined from stem disks taken at the soil surface for three dominant and codominant trees in each stand.

<sup>c</sup>Estimated from dbh/height relationship applied to stand inventory data.

<sup>d</sup>Aspen and balsam poplar not differentiated in stand inventory.

<sup>e</sup>Less than 1% of total basal area.

<sup>f</sup>Percent of total stand basal area.

(*Pleurozium* spp.) ground cover occur in the mature stands at both study areas [Vogel, 1997]. Paper birch (*Betula papyrifera* Marsh.) occurs in green alder clumps in the NSA. The soil in both jack pine stands is an excessively drained coarse sand. Coarse fragments occupy 20–30% of the soil volume in the NSA but are absent in the SSA. The soil in the NSA is a Dystrocrept and the soil in the SSA is a Eutrocrept.

The aspen stands are even-aged and consist largely of trembling aspen (*Populus tremuloides* Michx.), although a few balsam poplar (*Populus balsamifera* L.) are present. Hazel (*Corylus cornuta* Marsh) forms a continuous understory, reaching a height of 1.5–2.0 m, at both study areas. Willow (*Salix* spp.) also occurs in the understory at the NSA. The soils at both the SSA and the NSA are moderately drained loam to clay loam and are classified as Boralfs.

The black spruce stand at the SSA is dominated by black spruce (*Picea mariana* [Mill.] BSP), but tamarack (*Larix laricina* [Du Roi] K. Koch) and jack pine occur in the better drained areas. Black spruce is the only overstory species in the NSA. Several different black spruce forest communities are present at both the SSA and the NSA, but we restricted our analyses to the black spruce-feathermoss community. Dominant shrub species include Labrador tea (*Ledum groenlandicum* Oeder) and wild rose (*Rosa* spp.). Feathermoss (*Pleurozium* spp.) is the dominant ground cover at both study areas. The soil at the SSA is a 20–30 cm deep peat layer over a coarse-textured mineral soil, and the soil at the NSA black spruce stand is a 30–50 cm peat layer over a clay mineral soil.

#### Allometric Equations

Site specific allometric equations were developed for the dominant overstory species in each stand. In August 1994, two dominant, three codominant, three intermediate, and two suppressed trees were destructively sampled immediately outside the replicate plots. Trees with severe defects were avoided. All trees were harvested from late July to early August. Trees were cut at the soil surface, and total tree height and length of the live crown were measured. The live crown was marked into thirds (top, middle, and bottom), and all live and dead branches from each position were cut and weighed separately. One live branch from each canopy position was randomly selected for detailed analysis in the field immediately after the tree was felled.

Aspen branch samples were divided into foliated twig and nonfoliage-bearing branches. Jack pine branches were divided into current, 1, 2, 3, and  $\geq 4$  year old shoots (needles plus twig) and nonfoliage bearing branches. Black spruce branches were divided into current, 1–2, 3–4, and  $>5$  year old shoots and nonfoliage-bearing branches. Approximately 30 to 50 foliage-bearing shoots were selected from each shoot age class and canopy position for detailed measurements. The fresh mass of each component was determined by using an electronic balance and the sample was placed in a labeled bag and stored in a cold room (4°C) until transported to Wisconsin. Five to ten shoots from each subsample were used for specific leaf area measurement and moisture content determination of the leaf and wood tissue for each subsample, and the remaining shoots were dried at 70°C to a constant mass. Specific leaf area was measured using a volume displacement method [Chen *et al.*, this issue]. The needle surface area (one-half the total leaf area or hemisurface area) of each individual tree was calculated as the product of foliage mass and specific leaf area for each needle age class and canopy position [Fassnacht *et al.*, 1994].

The stems of young jack pine trees were cut into 1 m sections and weighed on an electronic balance, while the stems of large trees (all other stands) were cut into 2 m sections and weighed. A 2 cm thick disk was cut from the base of each stem section and weighed on an electronic balance. Stem disks also were cut from the base of the tree, breast height (1.37 m), and base of live crown to determine sapwood cross-sectional area. The dry biomass of each stem section was calculated by multiplying the wet mass of each stem section by the dry–wet ratio of each stem disk. The total dry biomass of each stem was calculated by summing the dry biomass of all stem sections. Stem area was calculated for each tree by assuming that the stem from dbh to base of live crown was a paraboloid and from dbh to the soil surface was a cylinder. Equations for each stem shape were obtained from Husch *et al.* [1982].

All fresh samples were stored at 4°–6°C in walk-in coolers at the end of each day. Samples were transported from Canada to Madison, Wisconsin, in an insulated, ice-cooled truck. In Madison, all samples were immediately placed in a walk-in, forced air drying oven and dried at 70°C to a constant mass. Sapwood area disks were stored at 2°C until processed. The sapwood-heartwood boundary was determined by placing a Q-beam 2001 (Quantum Devices Inc, Barneveld, Wisconsin) light source behind each sapwood disk and marking the boundary with a permanent pen; this technique provided a more reliable and rapid estimate of sapwood area than stains. The sapwood image was photocopied on clear acetate sheets and measured by using a Li-Cor 3100 area meter (Li-Cor Inc., Lincoln, Nebraska). Sapwood volume was calculated following procedures described by Gower *et al.* [1993]. A disk of known area was copied periodically with the sapwood disks and measured to ensure that copying did not introduce a bias in sapwood area estimates.

#### Aboveground Vegetation Biomass and Net Primary Production

Aboveground biomass of tree components (stem, new and old branch, and new and old foliage), sapwood volume, and stem and leaf area were determined from allometric equations that were developed for the major overstory species in each stand. Standing dead biomass (stem plus branch) was estimated from the stem and branch allometric equations. The allometric equations for aspen were used for balsam poplar, willow, and paper birch, while the allometric equations for tamarack in northern Wisconsin [Kloeppe, 1997] were used to estimate biomass and leaf area for tamarack in the SSA. The use of nonsite specific allometric equations introduced only a small error because the minor species together comprised less than 3% of the total stand basal area in each stand, except for the SSA black spruce stand where tamarack and jack pine comprised 13% of the total stand basal area. Vegetation wood and foliage biomass were multiplied by 0.50 and 0.45, respectively, to estimate C content [Atjay *et al.*, 1977].

Aboveground NPP was calculated as the sum of annual biomass increment ( $\Delta B$ ) and detritus production ( $D$ ). Overstory biomass increment was measured in variable radius plots using a 10 basal area factor prism. One to two variable radius plots, depending upon tree density, were established inside each of the four fixed area replicate plots. Variable radius plots were used to estimate NPP because they provide an unbiased subsample of trees. We did not core all the trees in each plot because we wanted to maintain a portion of the fixed area plot free from tree coring for long-term measurements. Two incre-

ment cores were removed at 1.37 m from each tree in the variable radius plots in October 1994. Annual stemwood radial increment for each year between 1986 and 1994 was measured using a dual axis optical micrometer (M-2001-D series) coupled to a Spalding B5 digital position display system (7109-C225, Gaertner Scientific Corp., Chicago, Illinois). Aboveground wood (stem plus branch) and foliage biomass were calculated for each year using allometric equations and the recreated tree dbh for the past 10 years. Aboveground detritus was measured using ten 40 × 60 cm litter screens that were placed in random locations in each of the four replicate plots. Litter screens were deployed in August 1993 and litter was collected in May, July, August, and October 1994 and May, July, August 1995.

### Understory Aboveground Biomass and NPP

Understory aboveground biomass and net primary productivity were measured in small plots that were randomly located inside or immediately outside each of the four replicate plots in each stand. The area of the understory plots ranged in size from 2 × 2 m for black spruce and jack pine stands to 1 × 1 m for aspen stands. All aboveground understory vegetation tissue was removed from each small plot and stored in a cold room (2°–4°C) until the tissue was processed. Vegetation was separated into annual herbs, new twig, and new foliage and old foliage and old twig. Samples were dried at 70°C and weighed to the nearest 0.1 g. Total biomass was calculated as the sum of the dry biomass of all components and ANPP was calculated as the sum of the dry biomass of herbs, new twig, and new foliage components. Except in the aspen stands, stem growth of understory vegetation was ignored because it was so small that it was difficult to obtain reliable estimates of stemwood radial increment.

Ten hazel shrubs, encompassing a wide range in stem diameters, were destructively sampled in each aspen stand. A disk was removed from the base of each stem and its diameter measured. A regression equation for stem mass was developed (stem mass (g) =  $1.73 + 2.58 \log_{10}(\text{basal diameter, cm})$ ,  $r^2 = 0.90$ ,  $p < 0.001$ , mean square error = 0.008,  $n = 20$ ). Equations for alder (*Alnus rubra*) were developed from an allometry harvest in August 1995 [Vogel, 1997]. The difference in biomass between years was calculated from the increment data and the regression equation. Foliage litterfall was measured in the litterbaskets.

Moss net primary production was measured in the black spruce stands using screen ingrowth plots. In late May, five 30 × 30 cm wire mesh screens (0.5 × 0.5 cm mesh) were carefully placed on the moss surface and bent to conform to the surface of the moss. The screens were secured to the ground with 25 cm long aluminum wire pegs placed in each corner of the screen. At the end of the growing season (mid-October) all the moss fronds sticking through the screen were clipped, collected in paper bags, dried at 70°C to a constant mass and weighed. Aboveground NPP was calculated as dry matter increment times 0.5 to convert dry biomass to carbon content.

### Soil Carbon Distribution

Three forest floor samples (25.2 cm diameter) were collected from random locations in each replicate plot in the aspen and jack pine stands. Live vegetation and coarse roots were removed and the forest floor tissue was dried at 70°C to a constant mass and weighed to the nearest 0.1 g. The dried

tissue was ground to pass through a 40 mm wire mesh and a 10 g subsample was dry ashed at 450°C for 24 hours to estimate percent mineral soil content in each forest floor sample; this value was used to correct each forest floor biomass value for mineral soil contamination. Forest floor organic matter was assumed to be 50% carbon [Atjay et al., 1977].

Mineral soil carbon data were obtained from BOREAS investigators. Soil carbon content was calculated for each soil horizon from horizon depth, bulk density, and percent organic carbon data and summed for all horizons to estimate total soil carbon content. If more than one soil pit was established in a stand, we computed an average for the pits. Soil carbon content was standardized to 70 cm because this was the minimum soil depth used by all BOREAS scientists. For most sites the 70 cm depth included the A and B horizons and occasionally the C horizon. We did not differentiate between forest floor and mineral soil carbon in the black spruce stands because of the difficulties in developing a satisfactory protocol for distinguishing surface detritus from dead feathermoss.

### Statistical Analysis

The equation,  $\log_{10} Y = a + b(\log_{10} X)$ , was used to correlate the dependent variable ( $Y$ , component biomass, sapwood volume, or leaf and stem area) to stem diameter ( $X$ ). A  $\log_{10}$ - $\log_{10}$  transformation was used to correct for nonhomogeneous variance of the independent variable. Equations of the form  $Y = a + bX$  and  $Y = a + b(\log_{10} X)$  were also examined, but a plot of the residuals suggested that these models provided an inadequate fit and/or did not correct for nonhomogeneous variance.

Levene's test was used to test for equal variance between species within a study area or within a species between study areas. We did not detect any evidence of unequal variance. An analysis of covariance [Zar, 1983] was used to determine if the allometric coefficients differed within a species between sites.

All stand values reported in the paper are the averages for the four replicate plots. We used an analysis of variance to determine the effect of forest type, study area, and their interaction on ecosystem characteristics. If an ecosystem characteristic differed among the forest types, a Fisher's least square difference (LSD) test ( $\alpha = 0.05$ ) was used to separate forest types.

## Results

### Allometry

Stem, branch, and foliage biomass, stem and leaf area, and sapwood volume are all highly correlated to dbh for each species at each site (Table 3). Allometric equations for stem and branch biomass do not differ between SSA and NSA for each species, but foliage biomass and leaf area allometric equations for black spruce and jack pine differ ( $p < 0.05$ ) between study areas. All allometric equations relating tissue mass and area to stem dbh differ ( $p < 0.01$ ) between young and old jack pine trees at both the SSA and NSA. Because allometric coefficients differ between the SSA and the NSA we used site specific allometric equations to estimate aboveground biomass and NPP.

### Stand Structure

The LAI (one-half total leaf surface area) of the BOREAS forests range from 1.8 for young jack pine at the NSA to 5.6 for black spruce at the SSA (Table 4). At both the SSA and the

**Table 3.** Regression Coefficients, Sample Size ( $n$ ), Adjusted  $r^2$  (Coefficient of Determination), Mean Square Error (MSE), and Correction Factor (CF) for Boreal Tree Species

Region Site	Species	DBH <sup>a</sup> Range	Tissue	<i>n</i>	<i>a</i>	<i>b</i>	<i>r</i> <sup>2</sup>	MSE	CF
NSA									
NA (T2Q6A) <sup>d</sup>	aspen	5.8–23.7	S <sup>b</sup>	12	−2.312	4.184	0.993	0.002	1.005
			SAP <sup>c</sup>	10	−5.211	4.345	0.996	0.001	1.004
			TF	8	−4.742	4.018	0.761	0.204	...
			TBR	8	−3.002	3.265	0.964	0.017	1.046
NBS (T3R8T)	black spruce	2.8–17.0	TLA	8	−3.349	3.798	0.752	0.191	...
			S	10	−1.294	2.584	0.996	0.001	1.003
			SAP	10	−4.309	2.514	0.982	0.006	1.016
			NF	9	−3.051	2.219	0.599	0.057	...
			OF	9	−2.478	2.706	0.990	0.001	1.003
			TF	9	−2.400	2.668	0.988	0.002	1.005
			NT	9	−4.232	2.742	0.543	0.108	...
			BR	9	−2.384	2.642	0.843	0.024	1.066
			TBR	9	−2.379	2.646	0.842	0.024	1.066
			NLA	9	−1.861	1.875	0.545	0.050	1.142
			OLA	9	−1.676	2.631	0.974	0.003	1.008
			TLA	9	−1.542	2.549	0.974	0.003	1.008
NYJP (T8S9T)	jack pine	0.9–6.7	S	10	−0.956	1.956	0.989	0.002	1.005
			SAP	10	−3.940	2.205	0.991	0.002	1.005
			NF	10	−2.185	1.843	0.931	0.014	1.038
			OF	10	−1.448	1.675	0.903	0.017	1.046
			TF	10	−1.374	1.705	0.921	0.014	1.038
			NT	10	−2.782	1.597	0.856	0.024	1.066
			BR	10	−1.566	2.028	0.948	0.013	1.035
			TBR	10	−1.541	2.012	0.948	0.013	1.035
			NLA	10	−1.271	1.768	0.908	0.018	1.049
			OLA	10	−0.629	1.610	0.916	0.014	1.037
			TLA	10	−0.538	1.642	0.932	0.011	1.030
			NOJP (T7Q8T)	jack pine	4.5–16.8	S	10	−1.148	2.440
SAP	10	−4.208				2.626	0.968	0.007	1.019
NF	10	−3.654				3.021	0.966	0.010	1.027
OF	10	−2.332				2.560	0.970	0.006	1.016
TF	10	−2.327				2.613	0.974	0.005	1.013
NT	10	−4.134				2.816	0.944	0.014	1.038
BR	10	−2.440				2.799	0.951	0.012	1.032
TBR	10	−2.430				2.798	0.952	0.011	1.030
NLA	10	−2.742				2.890	0.956	0.011	1.030
OLA	10	−1.535				2.519	0.972	0.005	1.013
TLA	10	−1.523				2.568	0.977	0.005	1.013
SSA									
SA (C3B7T)	aspen	11.3–29.8	S <sup>4</sup>	10	−2.505	4.212	0.988	0.002	1.004
			SAP	10	−4.127	2.739	0.874	0.021	1.057
			TF	10	−3.621	2.971	0.933	0.012	1.032
			TBR	10	−3.668	3.679	0.890	0.032	1.089
SBS (G8I4T)	black spruce	1.9–17.6	TLA	10	−2.011	2.611	0.905	0.014	1.038
			S	10	−1.177	2.418	0.991	0.005	1.013
			SAP	9	−4.081	2.226	0.979	0.011	1.030
			NF	9	−2.566	1.956	0.755	0.121	...
			OF	9	−1.364	1.800	0.866	0.050	1.142
			TF	9	−1.336	1.811	0.859	0.053	...
			NT	9	−3.506	2.264	0.671	0.239	...
			BR	9	−1.583	2.068	0.819	0.093	...
			TBR	9	−1.575	2.070	0.818	0.094	...
			NLA	9	−1.843	1.937	0.772	0.108	...
			OLA	9	−0.675	1.796	0.867	0.049	1.139
			TLA	9	−0.645	1.806	0.861	0.052	...
SYJP (F8L6T)	jack pine	0.8–6.4	S	10	−0.921	1.888	0.994	0.002	1.005
			SAP	10	−3.695	1.879	0.965	0.011	1.030
			NF	10	−1.879	1.621	0.917	0.021	1.057
			OF	10	−1.354	1.592	0.941	0.014	1.038
			TF	10	−1.239	1.606	0.957	0.010	1.027
			NT	10	−2.395	1.495	0.884	0.026	1.071
			BR	10	−1.743	2.277	0.959	0.020	1.054
			TBR	10	−1.662	2.204	0.961	0.018	1.049
			NLA	10	−1.041	1.545	0.901	0.023	1.063
			OLA	10	−0.597	1.575	0.944	0.013	1.035
			TLA	10	−0.462	1.575	0.959	0.010	1.027

**Table 3.** (continued)

Region Site	Species	DBH <sup>a</sup> Range	Tissue	<i>n</i>	<i>a</i>	<i>b</i>	<i>r</i> <sup>2</sup>	MSE	CF
SSA									
SOJP (G2L3T)	jack pine	6.6–18.8	S	10	–1.292	2.570	0.991	0.002	1.005
			SAP	10	–4.648	2.904	0.979	0.005	1.013
			NF	9	–3.200	2.404	0.925	0.013	1.035
			OF	9	–2.799	2.621	0.963	0.007	1.019
			TF	9	–2.661	2.578	0.966	0.006	1.016
			NT	9	–4.308	2.671	0.752	0.062	...
			BR	9	–3.460	3.697	0.951	0.019	1.052
			TBR	9	–3.443	3.688	0.951	0.019	1.052
			NLA	9	–2.444	2.412	0.924	0.013	1.035
			OLA	9	–2.054	2.609	0.961	0.007	1.019
			TLA	9	–1.911	2.568	0.964	0.007	1.019

All equations (except where noted) follow the form  $\log_{10} Y = a + b(\log_{10} X)$  where  $X$  is stem diameter<sup>1</sup> (cm) at breast height (1.37 m) and  $Y$  is mass (kg), stem sapwood volume (m<sup>3</sup>) or leaf area (m<sup>2</sup>). Tissue symbols are as follows: S, stem (wood + bark); SAP, stem sapwood volume; NF, new foliage; OF, old foliage; TF, total foliage; NT, new twig; BR, branch; TBR, branch + new twig; NLA, new leaf area (current year); OLA, old leaf area (>1 year); TLA, total leaf area.

<sup>a</sup>BOREAS site code.

<sup>b</sup>Regression form is  $\log_{10} Y = a + b(\log_{10} X) + cX$  where the  $C$  coefficient is  $-0.052$ .

<sup>c</sup>Regression form is  $\log_{10} Y = a + b(\log_{10} X) + cX$  where the  $C$  coefficient is  $-0.051$ .

<sup>d</sup>Regression form is  $\log_{10} Y = a + b(\log_{10} X) + cX$  where the  $C$  coefficient is  $-0.039$ .

NSA, LAI is significantly greater ( $p < 0.01$ ) in the black spruce than aspen or jack pine stands. LAI did not differ consistently between young and old jack pine stands at the two study areas. Stem surface area (one-half total stem surface area) range from 0.1 m<sup>2</sup> m<sup>-2</sup> for the young jack pine at the NSA to 0.6 for black spruce at the NSA and comprise 5–15% of one-half total tree area (excluding branches) for the eight stands. Stem sapwood volumes range from 13.3 m<sup>3</sup> for the young jack pine at the NSA to 327 m<sup>3</sup> for the aspen stand at the SSA (Table 4). Stem sapwood volume is 2–4 times greater for the old than for the young jack pine stands. At both the SSA and the NSA the leaf area:sapwood volume (LA:SA<sub>v</sub>) ratio is significantly greater ( $p < 0.01$ ) for young versus old jack pine stands. The lower ratio for the mature stand in the NSA is because of an increase in sapwood volume in the mature stand, but in the SSA, the lower ratio for the mature stand is because of an increase in sapwood volume and a decrease in LAI.

Carbon content and its relative distribution differ among the eight stands (Table 5). For the SSA and NSA, total ecosystem carbon content (vegetation plus detritus plus soil) is 2.8 to 2.9 times greater for black spruce than for aspen stands, and both are greater than the mature jack pine ecosystem. Soil contains the greatest percentage of the total ecosystem carbon content in black spruce forests (87–88%) but vegetation and soil contain a similar percentage of total ecosystem carbon content in the mature jack pine and aspen stands. Forest floor carbon content estimates for some stands vary greatly among BOREAS scientists (Table 5); potential explanations are examined in the discussion.

#### Aboveground Net Primary Production (ANPP)

ANPP varies by less than 20% between 1993 and 1994 for all the mature stands, except for the NSA aspen stand which varies by 29% (Table 6). The lower ANPP in 1993 is, in part, because understory NPP was not measured in 1993. Interannual variation (annual maximum – annual minimum/10 year average from 1985 to 1994) in woody biomass increment ranges from 21% for aspen at the SSA to 83% for mature jack pine at the NSA (Figure 1). Average (1985–1994) woody biomass increment for aspen, black spruce, and mature jack pine at the SSA are 1860, 720, 600 kg C m<sup>-2</sup> yr<sup>-1</sup> and at the NSA

are 1900, 600, and 450 kg C m<sup>-2</sup> yr<sup>-1</sup>, respectively. Woody biomass increment during the 1993–1994 BOREAS field campaigns is below the 10 year average for aspen and jack pine stands in the SSA and is above the 10 year average for black spruce in the SSA for all the forests in the NSA.

ANPP and carbon allocation differ more among forest types in a similar climate than for a similar forest type in the two contrasting climates. For example, at both study areas, woody biomass increment is 2 to 3 times greater for aspen than black spruce or jack pine stands. Leaf and total aboveground detritus production (i.e., litterfall) are significantly greater ( $p < 0.01$ ) for aspen than jack pine or black spruce stands at both the SSA and the NSA (Tables 6 and 7). On a relative basis, however, detritus production comprises a similar or greater fraction of ANPP in the conifer than deciduous aspen forests. Averaged

**Table 4.** Sapwood Volume, Leaf and Stem Area Index, Stem:Total Tree Area Index Ratio for Aspen, Black Spruce, and Jack Pine Stands at SSA and NSA

Study Area Forest Type	Sapwood Volume (m <sup>3</sup> ha <sup>-1</sup> )	Leaf Area Index (ha ha <sup>-1</sup> )	Stem Area Index (ha ha <sup>-1</sup> )	Stem:Total Tree Surface Area Ratio
SSA				
aspen	327.2 (72.5)	3.3 (0.7)	0.4 (<0.1)	11
black spruce	60.8 (9.8)	5.6 (1.7)	0.4 (0.1)	7
jack pine (young)	26.0 (8.4)	2.8 (0.8)	0.2 (<0.1)	5
jack pine (old)	56.9 (16.0)	2.4 (0.3)	0.2 (<0.1)	13
NSA				
aspen	196.0 (13.3)	2.2 (0.2)	0.4 (<0.1)	15
black spruce	82.5 (9.3)	4.2 (0.3)	0.6 (<0.1)	12
jack pine (young)	13.3 (5.7)	1.8 (0.6)	0.1 (<0.1)	5
jack pine (old)	54.7 (5.6)	2.2 (0.3)	0.2 (<0.1)	8

Values in parentheses are 1 standard deviation of the mean ( $n = 4$ ).

**Table 5.** Aboveground Carbon Distribution ( $\text{kg C ha}^{-1}$ ) by Ecosystem Component for Aspen, Black Spruce, and Young and Old Jack Pine Stands at SSA and NSA

Ecosystem Component	Aspen		Black Spruce		Jack Pine (Young)		Jack Pine (Old)	
	C	%	C	%	C	%	C	%
<i>Southern Study Area (SSA)</i>								
Vegetation								
stem	82,710	(52)	36,330	(8)	7,650	(15)	25,760	(37)
branch	8,970	(6)	6,750	(2)	2,430	(5)	4,130	(6)
new foliage	940	(<1)	450	(<1)	530	(1)	190	(<1)
old foliage	0	(0)	4,600	(1)	1,660	(3)	840	(1)
understory	720	(<1)	510	(<1)	na	(...)	160	(<1)
bryophyte	0	(0)	600	(<1)	na	(...)	3,470	(5)
total living	93,340	(59)	49,240	(11)	12,260	(24)	34,550	(51)
Detritus								
standing dead	9,680	(6)	6,160	(1)	0	(0)	5,670	(8)
forest floor	19,430	(12)	...		18,100	(36)	14,560	(21)
	90,290 <sup>a</sup>						16,780 <sup>a</sup>	
mineral soil	35,990	(23)	390,360	(88)	20,160	(40)	14,200	(20)
Total ecosystem	158,440		445,760		50,530		68,980	
<i>Northern Study Area (NSA)</i>								
Vegetation								
stem	49,780	(28)	47,370	(10)	4,820	(6)	19,060	(28)
branch	5,720	(3)	4,910	(1)	1,370	(2)	2,520	(4)
new foliage	720	(<1)	350	(<1)	230	(<1)	240	(<1)
old foliage	40	(0)	3,610	(1)	1,070	(2)	1,490	(2)
understory	690	(<1)	0	(0)	310	(<1)	580	(1)
bryophyte/lichen	0	(0)	970	(<1)	na	(...)	5,100	(7)
total living	56,950	(32)	57,210	(12)	7,800	(10)	28,990	(42)
Detritus								
standing dead	6,390	(4)	3,810	(1)	0	(0)	2,120	(3)
forest floor	15,880	(9)	...		40,260 <sup>c</sup>	(53)	11,480	(...)
	70,510 <sup>b</sup>				128,010 <sup>b</sup>		223,400 <sup>b</sup>	
mineral soil	97,170	(55)	418,360	(87)	28,430	(37)	25,780	(38)
Total ecosystem	176,390		479,380		76,490		68,370	

Values in parentheses are the contribution of each component to the total ecosystem carbon content.

<sup>a</sup>T. Nerbus and D. Anderson (unpublished data, University of Saskatchewan, 1996).

<sup>b</sup>H. Veldius (unpublished data, University of Manitoba, 1996).

<sup>c</sup>Data from *Trumbore et al.* [this issue].

for the two years, fine woody detritus comprises 23–37% of the total aboveground detritus. In both 1993 and 1994, leaf and total detritus production are significantly greater ( $p < 0.01$ ) in the SSA than in the NSA for all three forest types.

## Discussion

### Canopy Architecture

Canopy architecture influences light interception and therefore effects  $\text{CO}_2$  exchange between terrestrial ecosystems and the atmosphere. The canopy architecture of boreal forests differs from most temperate forests in two important ways, both of which effect radiation absorption and canopy photosynthesis. On average, LAI is lower in boreal than in temperate forests [Landsberg and Gower, 1997]. The LAI for the dominant forest types in the two BOREAS study areas ranges from 1.8 to 5.6 and averages 3.1 (Table 4). In contrast, the LAI of the six major forest types forming the transition from cold temperate to boreal forests in northern Wisconsin ranges from 1.9 to 8.4 and averages 4.9 [Fassnacht and Gower, 1997]. Comparative and experimental studies have shown that nutrient availability limits the LAI of boreal forests. For example, the LAI of jack pine forests containing green alder, a nitrogen-fixing shrub, is 29 to 34% greater than for adjacent jack pine stands where green alder is absent [Vogel, 1997]. The maximum

or near-maximum LAI of control, irrigated and fertilized Scots pine (*Pinus sylvestris*) were 1.0, 1.3, and 3.6, respectively [Waring and Schlesinger, 1985]. Low nutrient availability of most boreal forests is caused by cold soils and poor litter quality which adversely affect litter decomposition and nutrient mineralization [Flanagan and Van Cleve, 1983]. Severe winter environmental conditions also restrict LAI [Gholz, 1982].

A second important canopy architecture characteristic of the boreal forests is foliage clumping—the nonrandom distribution of foliage in the canopy. The distribution of foliage elements in the canopy influences the fraction of the canopy that is sunlit versus shaded and total radiation interception, especially in forests that have low LAIs. Less radiation is absorbed if foliage is clumped versus randomly distributed. Direct estimates of LAI (see Table 4) agree with optical estimates only when the indirect estimates of LAI are corrected for foliage clumping at the shoot, branch, and tree level [Chen *et al.*, this issue; Kucharik *et al.*, this issue]. Ecosystem process models that ignore the large foliage clumping in forests with low LAIs (e.g., boreal forests) will overestimate canopy photosynthesis [Kucharik *et al.*, this issue]. Future global terrestrial carbon models should account for the nonrandom distribution of foliage in boreal forests to accurately simulate  $\text{CO}_2$  exchange between terrestrial ecosystems and the atmosphere.

**Table 6.** Aboveground Net Primary Production (ANPP) ( $\text{kg C ha}^{-1} \text{ yr}^{-1}$ ) for 1993 and 1994 by Component for Aspen (A), Black Spruce (BS), and Old (OJP) and Young (YJP) Jack Pine Stands at NSA and SSA

Vegetation Component	A		BS		OJP		YJP, 1994
	1993	1994	1993	1994	1993	1994	
Southern Study Area							
Biomass increment							
wood	1,640 (190)	1,760 (250)	780 (170)	800 (130)	570 (70)	590 (60)	380 <sup>d</sup> (20)
foliage	0	0	70 (20)	80 (20)	20 ( $<10$ )	20 ( $<10$ )	10 ( $<10$ )
understory	240 (40)	530 (50)	na <sup>b</sup>	130 (60)	na	50 ( $<10$ )	na
bryophytes	0	0	na	120 (60)	na	$<10$ ( $<10$ )	na
Detritus	1240 (150)	1230 (60)	590 (100)	530 (100)	520 (50)	510 (50)	530 <sup>c</sup> (20)
ANPP	3120 (210)	3520 (280)	1440 (190)	1660 (160)	1110 (80)	1170 (80)	920 (80)
Northern Study Area							
Biomass increment							
wood	1,750 (230)	2,140 (320)	660 (10)	730 (20)	690 (80)	650 (70)	170 <sup>d</sup> (10)
foliage	0	0	50 ( $<10$ )	50 ( $<10$ )	50 ( $<10$ )	50 ( $<10$ )	40 ( $<10$ )
understory	na	330 (60)	na	$<10$ ( $<10$ )	na	160 (40)	70 (10)
bryophytes	0	0	na	120 (60)	na	$<10$ ( $<10$ )	na
Detritus	740 (60)	1020 (60)	400 (20)	460 (40)	240 (30)	360 (20)	230 <sup>c</sup> (20)
ANPP	2490 (280)	3490 (380)	1110 (40)	1360 (60)	980 (100)	1220 (100)	510 (50)

Values in parentheses are  $\pm 1$  standard error.

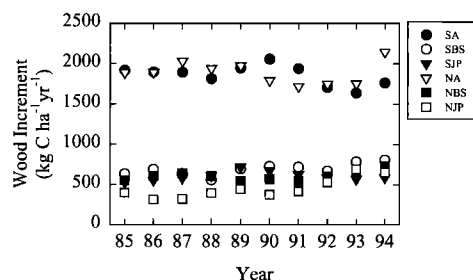
<sup>a</sup>Calculated as standing biomass/stand age.

<sup>b</sup>na, not available.

<sup>c</sup>Estimated from new foliage production.

### Forest Floor C Dynamics

Estimates of forest floor carbon content for some stands differ greatly among BOREAS investigators. Forest floor carbon content in aspen stands at the SSA ( $19,430 \text{ kg C ha}^{-1}$ ) and NSA ( $15,880 \text{ kg C ha}^{-1}$ ) are roughly one-fifth the values of  $90,290 \text{ kg C ha}^{-1}$  reported for the SSA aspen stand (D. Anderson and T. Nerbas, personal communication, 1996) and  $70,510 \text{ kg C ha}^{-1}$  reported for the NSA aspen stand (H. Veldhuis, personal communication, 1996). Forest floor carbon content estimates for the NSA old jack pine stand differ even more among BOREAS scientists, ranging from  $11,480 \text{ kg C ha}^{-1}$



**Figure 1.** Interannual variation (annual maximum – annual minimum/10 year average) in wood biomass increment for the aspen, black spruce, and jack pine stands at the southern study area (SSA) and northern study area (NSA).

(this study) to  $223,400 \text{ kg C ha}^{-1}$  (H. Veldhuis, unpublished data, 1996). The large differences in forest floor carbon content are disturbing because soil carbon cycling process models that simulate heterotrophic respiration, a major component of NEE, require forest floor carbon content as an input variable. We cannot explain the large discrepancies, but note that our estimates are comparable to values reported for similar forest types in Canada and Alaska. For example, our estimates for forest floor carbon content for the aspen stands are similar to  $23,750 \text{ kg C ha}^{-1}$  (assuming organic matter is 50% C) for trembling aspen stands in Alaska [Van Cleve *et al.*, 1983], and our estimates of forest floor carbon content for mature jack pine stands are similar to  $10,150 \text{ kg C ha}^{-1}$  (assuming organic matter is 50% C) for jack pine forests in northern Ontario [Foster and Morrison, 1976].

Forest floor carbon content is the long-term integrated difference between detritus inputs (e.g., litterfall and fine root turnover) and litter decomposition. Mean residence times (MRT) for carbon in the forest floor, calculated as the ratio of forest floor carbon content and aboveground litterfall carbon, provides a simple index of the balance of these two processes. The calculation assumes that forest floor and litterfall carbon are in steady state; this assumption appears to be valid for these stands because leaf litterfall does not greatly differ between years (Table 7) and is similar to new foliage production (Tables 6 and 7). Forest floor carbon MRT varies more among



**Table 7.** Aboveground Detritus Production ( $\text{kg C ha}^{-1} \text{ yr}^{-1}$ ) by Tissue Component for Aspen, Jack Pine and Black Spruce Stands at SSA and NSA

Litter Component	Southern Study Area			Northern Study Area		
	Aspen	Jack Pine	Black Spruce	Aspen	Jack Pine	Black Spruce
<i>1993</i>						
Foliage						
dominant overstory	660 (60)	380 (40)	260 (20)	450 (10)	160 (20)	240 (20)
other overstory	0	10 (10)	90 <sup>a</sup> (40)	10 <sup>b</sup> (<10)	10 <sup>c</sup> (<10)	0
understory	260 (60)	10 (<10)	<10 (<10)	130 (10)	10 (<10)	<10 (<10)
total	920	400	350	590	180	240
Woody	320 (100)	120 (20)	240 (100)	150 (60)	60 (20)	160 (10)
Total	1240 (150)	520 (50)	590 (100)	740 (60)	240 (30)	400 (20)
<i>1994</i>						
Foliage						
dominant overstory	730 (80)	380 (30)	330 (60)	620 (10)	260 (10)	300 (10)
other overstory	<10 (<10)	<10 (<10)	90 (40)	10 (<10)	20 <sup>c</sup> (10)	<10 (<10)
understory	260 (30)	<10 (10)	0 (0)	130 (20)	0	0
total	990	390	420	760	280	300
Woody	240 (20)	130 (20)	110 (10)	260 (70)	80 (10)	160 (30)
Total	1230 (60)	510 (50)	530 (100)	1020 (60)	360 (20)	460 (40)
<i>Average</i>						
Foliage	955	395	385	675	230	270
Woody	280	125	175	205	70	160
Total	1235	515	560	880	300	430

Values in parentheses are  $\pm 1$  standard error. All values are rounded to the nearest  $10 \text{ kg C ha}^{-1} \text{ yr}^{-1}$ .

<sup>a</sup>Tamarack.

<sup>b</sup>Jack pine.

<sup>c</sup>Paper birch.

<sup>d</sup>Willow spp.

forest types in a similar climate (i.e., study area) than for a similar species in the two contrasting climates. The forest floor carbon MRT for the jack pine stands (28–39 years) are greater than the calculated values of 5 years reported for jack pine forests in Minnesota [Perala and Alban, 1982] and Ontario [Foster and Morrison, 1976] and 7 years for jack pine stands in northern Wisconsin [Fassnacht and Gower, 1997]. The forest floor carbon MRT for the aspen stands (16–19 years) in this study are less than the calculated values of 30 years for aspen stands in Alaska [Van Cleve *et al.*, 1983] but are greater than 8 years for aspen stands in northern Wisconsin [Ruark and Bockheim, 1988] and 6 years for aspen stands in Minnesota [Perala and Alban, 1982].

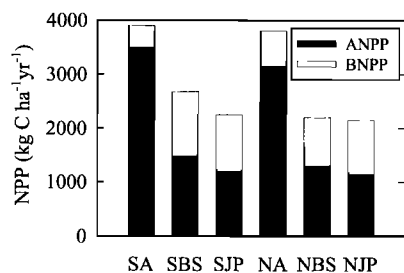
#### Net Primary Production

ANPP for the mature forest stands ranges from 1170 to 3520  $\text{kg C ha}^{-1} \text{ yr}^{-1}$  in 1994. The average ANPP for the black spruce stands is about twofold greater than the 565  $\text{kg C ha}^{-1} \text{ yr}^{-1}$  reported for black spruce forests in Alaska [Van Cleve *et al.*, 1983]. The average ANPP for the aspen stands is lower than the 5548  $\text{kg C ha}^{-1} \text{ yr}^{-1}$  (assuming organic matter is 50% C) for an upland birch-aspen forest in Alaska [Ruess *et al.*, 1996] but is similar to 2825  $\text{kg C ha}^{-1} \text{ yr}^{-1}$  (assuming organic matter is 50% C) for a trembling aspen stand in Alaska [Van

Cleve *et al.*, 1983]. ANPP does not differ between the mature jack pine stands in the SSA and NSA and the average in 1994 is smaller than the average ANPP of 2050  $\text{kg C ha}^{-1} \text{ yr}^{-1}$  (assuming organic matter is 50% C) for eight jack pine stands in northern Wisconsin [Fassnacht and Gower, 1997].

ANPP is the most commonly measured component of forest production budgets, but belowground net primary production (BNPP) can equal or exceed ANPP in forests [Landsberg and Gower, 1997]. Moreover, fine root turnover is a large C input to the soil. Ruess *et al.* [1996] reported that fine root production, measured using soil cores, accounted for 49 and 32% of total NPP in coniferous and deciduous boreal forests in Alaska, respectively. Using the below-ground NPP data for these stands [Steele *et al.*, 1997], we estimate that BNPP comprises 41–46% of total NPP in the conifer stands and 10–19% in the aspen stands (Figure 2). The data from Ruess *et al.* and this study suggest that a greater percentage of total NPP is allocated to roots in boreal coniferous than deciduous forests. Clearly, fine root production must be included to construct complete carbon budgets for boreal forests.

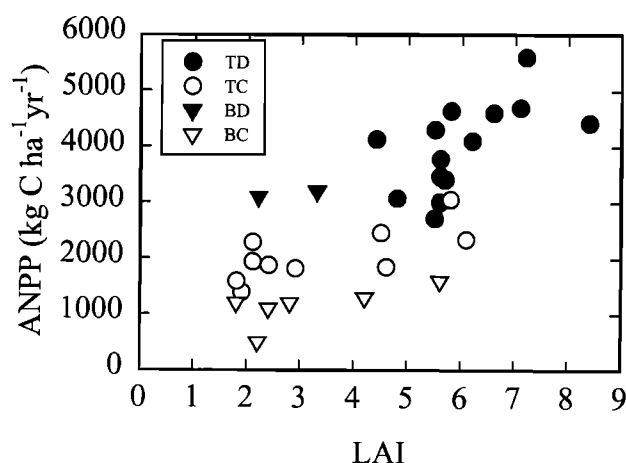
One consistent pattern at both study areas in ANPP is greater for the deciduous than coniferous forests. Other scientists have also reported that ANPP is greater for deciduous than evergreen boreal forests [Van Cleve *et al.*, 1983; Ruess *et*



**Figure 2.** Net primary production budgets for the mature aspen (A), black spruce (BS), and jack pine (JP) stands in the SSA (S) and NSA (N). The young jack pine stands are not included because fine root NPP was not measured in these stands. Root NPP data are from *Steele et al.* [1997] and ANPP data are for 1994.

*al.*, 1996]. Possible causes for the greater ANPP of deciduous than evergreen conifer boreal forests include greater capacity to absorb light (i.e., LAI), greater intrinsic physiological capacity of the canopy to convert solar radiation to dry matter, fewer environmental constraints on leaf photosynthesis and less allocation of C to roots and mycorrhizae. Aboveground NPP is positively correlated to LAI in many temperate forests [Gholz, 1982; Gower *et al.*, 1992; Runyon *et al.*, 1994; Fassnacht and Gower, 1997]. LAI differs by more than twofold among the BOREAS forests (Table 4), but ANPP is not significantly correlated to LAI except when only conifer stands are considered ( $r^2 = 0.70$ ,  $n = 6$ ) (Figure 3). Production efficiency (ANPP/LAI) is significantly greater ( $p < 0.01$ ) for aspen than for conifer forests in both the SSA and the NSA (Figure 4). Fassnacht and Gower [1997] observed greater production efficiency for deciduous than evergreen conifer temperate forests in northern Wisconsin.

It is unclear why production efficiency is greater for deciduous than for evergreen conifer forests in boreal and cold temperate regions. One possible explanation for the "apparent" higher production efficiency of deciduous forests is that



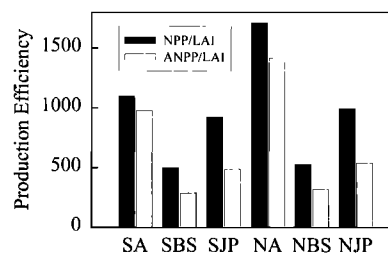
**Figure 3.** Relationship between aboveground net primary production (ANPP) and leaf area index (LAI) for aspen, black spruce, and jack pine stands at the SSA and NSA. Solid and open triangles depict boreal deciduous (BD) and boreal evergreen conifer (BC), respectively. For comparison, data for temperate deciduous (TD) and temperate evergreen conifer (TC) from northern Wisconsin [Fassnacht and Gower, 1997] are included.

deciduous and evergreen coniferous forests allocate different amounts of carbon to root production. Including BNPP in the production efficiency calculations does not diminish the difference in production efficiency between deciduous and evergreen forests (Figure 4). The fraction of total NPP allocated to root production, however, is smaller for deciduous (0.14) than for coniferous stands (0.44) in this study (Figure 2 and Table 8). We speculate that production efficiency and NPP differ between deciduous and evergreen forests because deciduous forests have a greater light use efficiency [Hunt and Running, 1993] and experience less environmental constraints on photosynthesis (see below).

The slope of the regression line describing the relationship between ANPP and LAI is similar for the conifer stands in this study and conifer forests (largely jack pine) in northern Wisconsin. However, the  $Y$  intercept is greater for temperate than for boreal coniferous forests, suggesting the production efficiency is greater for temperate than for boreal forests. The most likely explanation for the lower production efficiency of boreal than temperate forests is that environmental constraints on canopy photosynthesis are greater in boreal environments. McMurtie *et al.* [1994] used a forest ecosystem process model BIOMASS to elucidate the relative importance of various environmental controls on pine forest productivity and found that incomplete light interception and short growing season were the major constraints on leaf photosynthesis for boreal Scots pine forests in Sweden. Low LAI and large foliage clumping are common characteristics of boreal forests and contribute to incomplete light interception in these forests. Long, harsh winters restrict the growing season in the SSA and NSA to 150 and 120 days, respectively [Steele *et al.*, 1997]. In addition, frozen soil is an important constraint on the carbon balance of evergreen conifers, especially in black spruce forests, in the spring because solar radiation and air temperatures are often sufficient for photosynthesis by evergreen conifers at this time [Frolking *et al.*, 1996]. Canopy photosynthesis for all three tree species in the NSA is adversely affected by atmospheric vapor pressure deficit during the growing season [Dang *et al.*, this issue].

#### Global NPP and Carbon Allocation Patterns for Boreal Forests

Global terrestrial primary production models are useful tools to examine the role terrestrial ecosystems play in the global C budget; however, few NPP data are available for comparison. Information on carbon allocation is even more scarce, and as a result, many models use a constant allocation coefficient (i.e., aboveground and below-ground NPP) for all



**Figure 4.** Comparison of production efficiency based on net primary production (NPP/LAI) and aboveground net primary production (ANPP/LAI). NPP is expressed in  $\text{kg C ha}^{-1} \text{ yr}^{-1}$  and LAI is  $\text{m}^2 \text{ m}^{-2}$ .

**Table 8.** Net Primary Production Rates for Boreal Forests of the World

Species	Location	Latitude Longitude	Tree ANPP			Understory ANPP			BNPP	NPP	BNPP, NPP	D, ΔB	Reference
			ΔB	D	total	ΔB	D	total					
Evergreen													
<i>Picea abies</i>	Ilomantsi, Finland	62 51 N 30 53 E	1050	250	1300	...	...	...	1550	2850	0.54	1.71	1
<i>Picea glauca</i> , FP <sup>a</sup>	Alaska, United States	64 45 N 148 15 W	1850	750	2600	...	...	...	1100	3700	0.29	1.00	2
<i>Picea glauca</i> , UP <sup>b</sup>	Alaska, United States	64 45 N 148 15 W	2250	850	3100	...	...	500	700	4300	0.16	0.69	2, 3
<i>Picea mariana</i>	Alaska, United States	64 45 N 148 15 W	350	300	650	...	...	550	1050	2250	0.47	3.86	2, 3, 4
<i>Picea mariana</i> <sup>c</sup>	Saskatchewan, Canada	53 92 N 104 69 W	800	530	1330	0	130	130	1200	2660	0.45	2.32	5, 6
<i>Picea mariana</i> <sup>c</sup>	Manitoba, Canada	55 93 N 98 62 W	730	460	1190	0	100 <sup>h</sup>	100	900	2190	0.41	2.00	5, 6
<i>Picea mariana</i> , B <sup>d</sup>	Manitoba, Canada	49 53 N 95 54 W	900	550	1450	200	650	850	...	...	...	1.09	7
<i>Picea mariana</i> , M <sup>e</sup>	Manitoba, Canada	49 53 N 95 54 W	200	150	350	450	800	1250	...	...	...	1.46	7
<i>Picea mariana</i> , P <sup>f</sup>	Minnesota, United States	49 53 N 95 54 W	400	1050	1450	150	50	200	...	...	...	2.00	8, 9
<i>Picea mariana</i> (R <sup>g</sup> )	Minnesota, United States	49 53 N 95 54 W	200	250	450	650	1750	2400	...	...	0.27	...	8, 9
<i>Picea</i> (average)					1390 (280)			960 (230)	1080 (120)	2990 (260)	0.39 (0.04)	1.93 (0.46)	
<i>Pinus banksiana</i> <sup>c</sup>	Saskatchewan, Canada	53 92 N 104 69 W	650	510	1160	0	50	50	1050	2260	0.46	2.48	5, 6
<i>Pinus banksiana</i> <sup>c</sup>	Manitoba, Canada	55 93 N 98 62 W	700	360	1060	0	150	150	1000	2210	0.45	2.16	5, 6
<i>Pinus sylvestris</i>	Ilomantsi, Finland	62 51 N 30 53 E	850	600	1450	...	...	...	1150	2600	0.44	2.06	1
<i>Pinus sylvestris</i>	Ilomantsi, Finland	62 51 N 30 53 E	700	500	1200	...	...	...	550	1750	0.31	1.50	1
<i>Pinus sylvestris</i>	Jadraas, Sweden	60 49 N 16 30 E	1550	750	2300	...	...	...	1000	3300	0.30	1.13	10
<i>Pinus</i> (average)					1430 (220)			100 (50)	950 (80)	2420 (260)	0.39 (0.04)	1.87 (0.24)	
Deciduous													
<i>Alnus–Populus</i>	Alaska, United States	64 45 N 148 15 W	4800	1550	6350	...	...	...	1600	7950	0.20	0.66	2
<i>Betula papyrifera</i>	Alaska, United States	64 45 N 148 15 W	4050	1350	5400	...	...	<50	1250	6650	0.19	0.64	2, 3
<i>Betula pubescens</i>	Ilomantsi, Finland	62 51 N 30 53 E	750	350	1100	...	...	...	400	1500	0.27	1.00	1
<i>Larix gmelini</i>	Inner, Mongolia	62 51 N 30 53 E	2050	650	2700	...	800	800	...	...	...	...	1
<i>Populus balsamifera</i>	Alaska, United States	64 45 N 148 15 W	3250	900	4150	...	...	...	2000	6150	0.32	0.89	2
<i>Populus tremuloides</i> <sup>c</sup>	Saskatchewan, Canada	53 92 N 104 69 W	1760	970	2730	530	260	790	400	3920	0.10	0.71	5, 6
<i>Populus tremuloides</i> <sup>c</sup>	Manitoba, Canada	55 93 N 98 62 W	2140	890	3030	330	130	4600	650	3490	0.19	0.68	5, 6
Deciduous (average)					3640 (560)			525 (180)	1050 (270)	4740 (840)	0.21 (0.03)	0.76 (0.09)	
Evergreen (average)					1400 (200)			620 (230)	1020 (70)	2730 (230)	0.39 (0.03)	1.90 (0.26)	

All values have been converted to kg C m<sup>-2</sup> yr<sup>-1</sup> assuming wood is 50% C and foliage and fine roots are 45% C. All values are rounded to the nearest 10 kg C.

1, *Finer* [1989, 1991]; 2, *Ruess et al.* [1996]; 3, *Oechel and Van Cleve* [1986]; 4, *Van Cleve et al.* [1983]; 5, this study; 6, *Steele et al.* [1997]; 7, *Reader and Stewart* [1972]; 8, *Grigal et al.* [1985]; 9, *Grigal* [1985]; 10, *Linder and Axelsson* [1982].

<sup>a</sup>FP, flood plain.

<sup>b</sup>UP, upland.

<sup>c</sup>Data from 1994.

<sup>d</sup>B, bog.

<sup>e</sup>M, muskeg.

<sup>f</sup>P, perched.

<sup>g</sup>R, raised.

<sup>h</sup>Moss only.

forest biomes. A second objective of this paper is to relate the results of this study to other boreal forests to determine if general NPP or carbon allocation paradigms exist. Table 8 summarizes NPP by major component for boreal forests of the world. Average NPP is  $3510 \text{ kg C ha}^{-1} \text{ yr}^{-1}$  ( $n = 17$ ) and is very similar to  $3600 \text{ kg C ha}^{-1} \text{ yr}^{-1}$  calculated by *Whittaker and Likens* [1973], cited by *Schlesinger* [1991]. Few complete primary production budgets exist for boreal forests, but the available data suggest several interesting patterns that warrant further investigation. ANPP is greater for deciduous than evergreen boreal forests ( $3640$  versus  $1400 \text{ kg C m}^{-2} \text{ yr}^{-1}$ ), corroborating the results from this study and *Ruess et al.* [1996]. Carbon allocation patterns also differ between boreal deciduous and evergreen forests. Evergreen conifer forests allocate a greater fraction of carbon to root production (mean =  $0.39$ , standard error =  $0.03$ ,  $n = 15$ ) than deciduous forests (mean =  $0.21$ , standard error =  $0.03$ ,  $n = 6$ ). Detritus production (i.e., litterfall and fine root turnover) is a major component of NPP for boreal forests, and the fraction appears to differ among major forest types. The ratio of detritus production:biomass increment is greater for evergreen conifer ( $1.90$ ) than for deciduous forests ( $0.76$ ), especially for *Picea* (spruce) forests. Bryophytes can comprise a large percentage of the total detritus production in some spruce stands [*Oechel and Van Cleve*, 1986].

In summary, LAI, carbon content and distribution, and NPP and carbon allocation vary more among forest types in each study area than for a similar species in the two study areas. Many of the differences in NPP and carbon allocation between evergreen and deciduous forests in the BOREAS study appear to be general patterns for boreal forests. Because many of the components of carbon budgets differ between boreal evergreen and deciduous forests, we suggest that global terrestrial primary production models could be improved by distinguishing between deciduous and evergreen boreal forests and incorporating carbon allocation coefficients that reflect apparent differences between these two functional groups. Finally, a better understanding of the factors that control leaf litter production and fine root turnover in boreal forests is needed because detritus production constitutes a large fraction of NPP for boreal forests and is the major pathway for C input in boreal forest soil.

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## References

- Atjay, G. L., P. Ketner, and P. Duvigneaud, Terrestrial primary production and phytomass, in *The Global Carbon Cycle*, edited by B. E. Bolin, T. Degens, S. Kempe, and P. Ketner, scope vol. 13, pp. 129–181, John Wiley, New York, 1977.
- Chen, J., P. W. Rich, S. T. Gower, J. M. Norman, and S. Plummer, Leaf area index of boreal forests: Theory, techniques, and measurements, *J. Geophys. Res.*, this issue.
- Cias, P., P. P. Tans, M. Trolier, J. W. C. White, and R. J. Francey, A large northern hemisphere terrestrial  $\text{CO}_2$  sink indicated by the  $^{13}\text{C}/^{12}\text{C}$  ratio of atmospheric  $\text{CO}_2$ , *Science*, 269, 1098–1102, 1995.
- Dang, Q.-L., H. A. Margolis, M. Sy, M. R. Coyea, G. J. Collatz, and C. L. Walthall, Profiles of photosynthetically active radiation, nitrogen, and photosynthetic capacity in the boreal forest: Implications for scaling from leaf to canopy, *J. Geophys. Res.*, this issue.
- Daniel, T. W., J. A. Helms, and F. S. Baker, *Principles of Silviculture*, 2nd ed., McGraw-Hill, New York, 1979.
- Fassnacht, K. S., and S. T. Gower, Interrelationships among the edaphic and stand characteristics, leaf area index, and aboveground net primary production of upland forest ecosystems in north central Wisconsin, *Can. J. For. Res.*, 27, 1058–1067, 1997.
- Fassnacht, K. S., S. T. Gower, J. M. Norman, and R. E. McMurtrie, A comparison of optical and direct methods for estimating foliage surface area index in forests, *Agric. For. Meteorol.*, 71, 183–207, 1994.
- Finer, L., Biomass and nutrient cycle in fertilized and unfertilized pine, mixed birch and pine and spruce stands on a drained mire, *Acta For. Fenn.*, 208, 6–54, 1989.
- Finer, L., Effect of fertilization on dry mass accumulation and nutrient cycling in Scots pine on an ombrotrophic bog, *Acta For. Fenn.*, 223, 1–42, 1991.
- Flanagan, P. W., and K. Van Cleve, Nutrient cycling in relation to decomposition and organic matter quality in taiga ecosystems, *Can. J. For. Res.*, 13, 795–817, 1983.
- Foster, N. W., and I. Morrison, Distribution and cycling of nutrients in a natural *Pinus banksiana* ecosystem, *Ecology*, 57, 11–120, 1976.
- Frolking, S., et al., Modelling temporal variability in the carbon balance of a spruce/moss boreal forest, *Global Change Biol.*, 2, 343–366, 1996.
- Gholz, H. L., Environmental limits on aboveground net primary production, leaf area, and biomass in vegetation zones of the Pacific Northwest, *Ecology*, 63, 469–481, 1982.
- Gower, S. T., K. A. Vogt, and C. C. Grier, Carbon dynamics of Rocky Mountain Douglas-fir: Influence of water and nutrient availability, *Ecol. Monogr.*, 62, 43–65, 1992.
- Gower, S. T., B. E. Haynes, K. S. Fassnacht, S. W. Running, and E. R. Hunt Jr., Influence of fertilization on the allometric relations for two pines in contrasting environments, *Can. J. For. Res.*, 23, 1704–1711, 1993.
- Gower, S. T., J. G. Isebrands, and D. W. Sheriff, Carbon allocation and accumulation in conifers, in *Resource Physiology of Conifers*, edited by W. Smith and T. M. Hinckley, Academic, San Diego, Calif., 217–254, 1995.
- Gower, S. T., R. E. McMurtrie, and D. Murty, Aboveground net primary production decline with stand age: Potential causes, *Trends Ecol. Evol.*, 11, 378–382, 1996.
- Grigal, D. F., Sphagnum production in forested bogs of northern Minnesota, *Can. J. Bot.*, 63, 1204–1207, 1985.
- Grigal, D. F., C. G. Buttlerman, and L. K. Kernik, Biomass and productivity of the woody strata of forested bogs in northern Minnesota, *Can. J. Bot.*, 63, 2416–2424, 1985.
- Hunt, E. R., Jr., and S. W. Running, Simulated dry matter yields for aspen and spruce stands in the North American boreal forests, *Can. J. Remote Sens.*, 18, 126–133, 1992.
- Husch, B., C. I. Miller, and T. W. Beers, *Forest Mensuration*, 3rd ed., 402 pp., John Wiley, New York, 1982.
- Keeling, C. D., J. F. S. Chin, and T. P. Whorf, Increased activity of northern vegetation inferred from atmospheric  $\text{CO}_2$  measurements, *Nature*, 382, 146–149, 1996.
- Kloppel, B. D., Aboveground net primary production and resource use of larch and sympatric evergreen conifers in contrasting climates, Ph.D. dissertation, Univ. of Wisconsin, Madison, 1997.
- Kucharik, C. J., J. M. Norman, L. M. Murdock, and S. T. Gower, Characterizing canopy nonrandomness with a multiband vegetation imager (MVI), *J. Geophys. Res.*, this issue.
- Landsberg, J. J., and S. T. Gower, *Applications of Physiological Ecology to Forest Management*, Academic, San Diego, Calif., 1997.
- Landsberg, J. J., S. D. Prince, P. G. Jarvis, R. E. McMurtrie, R. Luxmoore, and B. E. Medlyn, Energy conversion and use in forests: The analysis of forest production in terms of radiation utilization efficiency ( $\epsilon$ ), in *The Use of Remote Sensing in the Modeling of Forest Productivity at Scales From Stands to Globe*, edited by H. L.

- Gholz, K. Nakane, and H. Shirada, Kluwer Acad., Norwell, Mass., 1997.
- McMurtrie, R. E., H. L. Gholz, S. Linder, and S. T. Gower, Climatic factors controlling the productivity of pine stands: A model-based analysis, *Ecol. Bull.*, 43, 173–188, 1994.
- Oechel, W. C., and K. Van Cleve, The role of bryophytes in nutrient cycling in the taiga, in *Forest Ecosystems in the Alaskan Taiga*, edited by K. Van Cleve, F. S. Chapin III, P. W. Flanagan, L. A. Viereck, and C. T. Dyrness, Springer-Verlag, pp. 121–137, New York, 1986.
- Perala, D. A., and D. H. Alban, Biomass, nutrient distribution, and litterfall in *Populus*, *Pinus* and *Picea* stands on two different soils in Minnesota, *Plant Soil*, 64, 177–192, 1982.
- Quay, P. D., B. Tilbrook, and C. S. Wong, Oceanic uptake of fossil fuel CO<sub>2</sub>: Carbon-13 evidence, *Science*, 256, 74–79, 1992.
- Reader, R. J., and J. M. Stewart, The relationship between net primary production and accumulation for a peatland in southeastern Manitoba, *Ecology*, 53, 1024–1037, 1972.
- Ruark, G. A., and J. G. Bockheim, Biomass, net primary production, and nutrient distribution for an age sequence of *Populus tremuloides* ecosystems, *Can. J. For. Res.*, 18, 435–443, 1988.
- Ruess, R. W., K. Van Cleve, J. Yarie, and L. A. Viereck, Contributions of fine root production and turnover to the carbon and nitrogen cycling in taiga forests of the Alaskan interior, *Can. J. For. Res.*, 26, 1326–1336, 1996.
- Runyon, J., R. H. Waring, S. N. Goward, and J. M. Welles, Environmental limit on net primary production and light use efficiency across the Oregon transect, *Ecol. Applic.*, 4, 226–237, 1994.
- Ryan, M. G., D. Binkley, and J. H. Fownes, Age-related decline in forest productivity: Pattern and process, *Adv. Ecol. Res.*, 27, 213–262, 1996.
- Schlesinger, W. H., *Biogeochemistry: An Analysis of Global Change*, Academic Press, 1991.
- Sellers, P., et al., The Boreal Ecosystem-Atmosphere study (BOREAS): An overview and early results from the 1994 field year, *Bull. Am. Meteorol. Soc.*, 76, 1549–1577, 1995.
- Siegenthaler, U., and J. L. Sarmiento, Atmospheric carbon dioxide and the ocean, *Nature*, 365, 119–125, 1993.
- Steele, S. J., S. T. Gower, J. G. Vogel, and J. M. Norman, Root biomass, net primary production and turnover of aspen, jack pine and black spruce stands in Saskatchewan and Manitoba, Canada, *Tree Physiol.*, 17, 577–587, 1997.
- Tans, P. P., I. Y. Fung, and T. Takahashi, Observational constraints on the global atmospheric CO<sub>2</sub> budget, *Science*, 247, 1431–1438, 1990.
- Van Cleve, K., L. K. Oliver, P. Schlentner, L. A. Viereck, and C. T. Dyrness, Productivity and nutrient cycling in taiga forest ecosystems, *Can. J. For. Res.*, 13, 747–766, 1983.
- Vogel, J. G., Carbon and nitrogen dynamics of boreal jack pine stands with different understory vegetation, M.S. thesis, Univ. of Wisconsin, Madison, 1997.
- Wang, Y. P., and P. J. Polglase, Carbon balance in the tundra, boreal forest and humid tropical forest during climate change: Scaling up from leaf physiology and soil carbon dynamics, *Plant Cell Environ.*, 18, 1226–1244, 1995.
- Waring, R. H., and W. H. Schlesinger, *Forest Ecosystems: Concepts and Management*, Academic, San Diego, Calif., 1985.
- Whittaker, R. H., and G. E. Likens, Carbon in the biota, in *Carbon and the Biosphere*, edited by G. M. Woodwell and E. V. Pecan, *Conf. 720510*, pp. 281–302, Natl. Tech. Inf. Serv., Springfield, Va., 1973.
- Zar, J. H., *Biostatistical Analysis*, Prentice Hall, Englewood, Cliffs, N. J., 1983.
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