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Nutrient dynamics of the southern and northern BOREAS boreal forests[1]

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Abstract: The objective of this study was to compare nutrient concentration, distribution, and select components of nutrient budgets for aspen (*Populus tremuloides*), jack pine (*Pinus banksiana*), and black spruce (*Picea mariana*) forest ecosystems at the BOReal Ecosystem Atmosphere Study (BOREAS), southern and northern study areas near Candle Lake, Saskatchewan and Thompson, Manitoba, Canada, respectively. The vegetation (excluding fine roots and understory) in the aspen, black spruce, and jack pine stands contained 70-79%, 53-54%, and 58-67% of total ecosystem carbon content, respectively. Soil (forest floor and mineral soil) nitrogen (N), calcium (Ca), and magnesium (Mg) content comprised over 90% of the total ecosystem nutrient content, except for Ca and Mg content of the southern black spruce stand and Ca content of the southern aspen stand which were less than 90%. Annual litterfall N content was significantly greater ($p < 0.05$) for trembling aspen (30-41 kg N ha^{-1} yr^{-1}) than for jack pine (5-10 kg N ha^{-1} yr^{-1}) or black spruce (6-7 kg N ha^{-1} yr^{-1}), and was generally greater, but not significantly, for the southern than for the northern study area. Aboveground net primary production was positively correlated ($R^2 = 0.91$) to annual litterfall N content for the BOREAS forests, and for all boreal forests ($R^2 = 0.57$). Annual aboveground nutrient (N, Ca, Mg, and K) requirements (sum of the annual increment of nutrient in foliage, branches, and stems) were significantly greater ($p < 0.05$) for trembling aspen than for jack pine or black spruce forests. Annual aboveground N requirements ranged from 37-53, 6-14, and 6-7 kg N ha^{-1} yr^{-1} for trembling aspen, jack pine, and black spruce forests, respectively. The greater nutrient requirements of deciduous than evergreen boreal forests was explained by a greater annual production of biomass and lower use efficiency of nutrients. Nutrient cycling characteristics of boreal forests were influenced by climate and forest type, with the latter having a greater influence on litterfall N, annual nutrient requirements, nutrient mean residence time, and nutrient distribution.
Keywords: nutrient distribution, boreal forests, nutrient requirement, litterfall N, retranslocation.

Résumé : L'objectif de cette étude était de comparer les concentrations en éléments nutritifs, leurs distribution et certains aspects du budget de ces éléments chez des écosystèmes forestiers de peupliers faux-tremble (*Populus tremuloides*), de pins gris (*Pinus banksiana*) et d'épinettes noires (*Picea mariana*) des sites d'étude du sud et du nord du projet BOREAS (BOReal Ecosystem Atmosphere Study) près de Candle Lake, Saskatchewan, et de Thompson, Manitoba, Canada. La végétation (excluant les radicelles et la végétation de sous-bois) des peuplements de peupliers, d'épinettes noires et de pin gris contenait respectivement 70-79 %, 53-54 %, et 58-67 % du carbone total de l'écosystème. Les contenus en azote (N), calcium (Ca) et magnésium (Mg) du sol (humus et sol minéral) représentaient plus de 90 % du contenu total de ces éléments dans l'écosystème avec l'exception des contenus en Ca et Mg du peuplement d'épinettes noires du sud et du contenu en Ca du peuplement de peupliers du sud pour lesquels cette valeur était inférieure à 90 %. Le contenu en N de la litière était significativement plus grand ($p < 0,05$) chez le peuplier faux-tremble (30-41 kg N ha^{-1} an^{-1}) que chez le pin gris (5-10 kg N ha^{-1} an^{-1}) ou l'épinette noire (6-7 kg N ha^{-1} an^{-1}). Il était généralement plus grand chez les peuplements du sud que chez ceux du nord de la région étudiée, mais cette différence n'était pas significative. La production primaire nette aérienne était positivement corrélée au contenu annuel en N de la litière chez les forêts de BOREAS ($R^2 = 0,91$), ainsi que pour toutes les forêts boréales ($R^2 = 0,57$). Les besoins nutritifs (N, K, Ca et Mg) annuels aériens (somme de l'accumulation nette d'éléments nutritifs dans le feuillage, les branches et les tiges) étaient significativement plus grands ($p < 0,05$) chez les forêts de peupliers faux-tremble que chez celles de pins gris ou d'épinettes noires. Les besoins annuels aériens en N variaient respectivement de 37-53, 6-14 et de 6 à 7 kg N ha^{-1} an^{-1}, chez les forêts de peupliers faux-tremble, de pins gris et d'épinettes noires. Les plus grands besoins des forêts décidues comparativement aux forêts boréales de conifères sont expliqués par une plus grande production annuelle de biomasse et une meilleure efficacité d'utilisation des éléments nutritifs. Les caractéristiques du cycle des éléments nutritifs des forêts boréales étaient influencées par le climat et le type de forêt ; le second facteur avait une plus grande influence sur le contenu en N de la litière, les besoins annuels en éléments nutritifs, le temps de résidence des éléments nutritifs et la distribution de ceux-ci.
Mots-clés : distribution des éléments nutritifs, forêts boréales, besoin nutritif, chute de litière en N, retranslocation.

Introduction

Numerous environmental factors constrain net primary production of boreal forests. Environmental factors such as vapor pressure deficit, air and soil temperature, and photosynthetically active radiation directly affect canopy photosynthesis (Dang *et al.*, 1997, Goulden *et al.*, 1997, Jarvis *et al.*, 1997, Bergh & Linder, 1999). A short growing season, cold soils, and permafrost all slow decomposition and mineralization rates in boreal forests (Van Cleve *et al.*, 1983; 1991, Flanagan & Van Cleve, 1983). Decomposition and mineralization of surface detritus is the dominant source of nutrients for boreal forests (Ruess *et al.*, 1996); therefore, environmental factors can indirectly affect net primary production via nutrient availability (Landsberg & Gower, 1997). Precipitation and relative humidity are commonly lower in the summer for boreal forests than for temperate forests (Landsberg & Gower, 1997). The dry summer environment also contributes to slow decomposition and mineralization rates.

Parent material and soil type also influence nutrient distribution and cycling. Common upland landform–soil associations in central Canada include moderately well-drained, fine-textured soils and excessively drained coarse sandy soils. Pure stands of aspen or mixed stands of aspen and white spruce occupy the fine-textured upland soils, and jack pine is the dominant tree species on the excessively drained sandy soils. Poorly drained lowland soils typically have deep surface (0.3-2 m) peat accumulations over a mineral soil. Black spruce dominates these sites, except in the most poorly drained areas where low stature fens and bogs are present.

The nutrient cycling patterns of boreal forests reflect the combined effect of edaphic conditions and species litter quality. Separating the influence of the numerous abiotic and biotic factors on nutrient distribution and cycling patterns of terrestrial ecosystems is difficult. Special circumstances are required where all but one of the soil-forming factors remains constant (Jenny, 1980; Son and Gower, 1991). More commonly, scientists examine the combined influence of all the factors on nutrient cycles, and obtain valuable information about general patterns of ecosystem function (Pastor *et al.*, 1984; Van Cleve *et al.*, 1983; Ruess *et al.*, 1996). Early studies by Van Cleve *et al.* (1983) and later by Ruess *et al.* (1996) in Alaska provide the main basis for the current understanding of nutrient budgets for boreal black spruce forests in North America. Biogeochemcial cycling research on jack pine forest ecosystems has been largely restricted to the southern boreal and cold temperate regions (Foster & Morrison, 1976; Foster *et al.*, 1994; Fassnacht & Gower, 1999). It is unclear, however, if nutrient cycling patterns differ among boreal forests of contrasting climate.

The BOReal Ecosystem Atmosphere Study (BOREAS) was designed to examine the exchange of energy, water, and carbon between boreal ecosystems and the atmosphere. Despite the important influence of nutrients on carbon budgets of boreal forests, very little nutrient cycling research was conducted during BOREAS (Sellers *et al.*, 1997). The primary objective of this study was to quantify and compare the nutrient distribution, annual requirements, and litterfall content for black spruce (*Picea mariana* [Mill.] BSP.), jack pine

(*Pinus banksiana* Lamb.), and trembling aspen (*Populus tremuloides* Michx.) forests at the southern study and northern study flux tower sites. The three selected forest ecosystems are important ecosystems in each of the study areas, and in the boreal forests in north-central Canada. A secondary objective was to compare the nutrient budgets for the BOREAS forests to other boreal forests of contrasting climate. Specific questions of interest were: (*i*) Do nutrient distribution and cycling rates differ among the three forest ecosystems for a similar climate? (*ii*) Do nutrient distribution and cycling patterns differ between the two study areas for a similar forest type? (*iii*) What is the relationship between litterfall N content, a proxy for N availability, and aboveground net primary production? (*iv*) Do annual nutrient requirements differ among forest types and between study areas?

Material and methods

STUDY SITES

The BOREAS southern study area (SSA) and northern study area (NSA) are located at Prince Albert National Park (PANP), Nipawin Provincial Forest complex in central Saskatchewan, Canada, and on Cree First Nation land near Thompson, Manitoba, Canada, respectively. The SSA has warmer, drier summers and milder winters than the NSA. The growing seasons at the NSA and SSA are 120 and 150 days, respectively (Steele *et al.*, 1997). A detailed description of each of the study areas is provided in Gower *et al.* (1997) and Steele *et al.* (1997).

The experimental design consisted of four replicate plots in mature aspen, jack pine and black spruce stands at the southern and northern study areas. The four plots were located in representative forests immediately outside the footprint of the eddy flux towers. The close proximity of the replicate plots of each forest type limits the inference that can be made from the results of this study. The size of the replicate plots in each forest type varied inversely to tree density, with the number of trees per plot ranging from 60 to 140. Species, crown class (Daniels, Helms & Baker, 1979) and diameter at breast height (1.37 m, dbh) were tallied for all trees in each plot. Table I summarizes select stand characteristics for the six stands.

The mature (60 to 65-year-old) jack pine stands were even-aged and originated from wild fire. Reindeer lichen (*Cladina mitis* [Sandst.] Hale & Culb) formed a near complete ground cover at both study areas. Bearberry (*Arctostaphylos uva-ursi* [L.] Sprenge.) and blueberry (*Vaccinium* spp.) were common understory plants. Isolated clumps of green alder (*Alnus crispa* [Ait.] Pursh) with a feathermoss (*Pleurozium schreberi*) ground cover occurred in the mature stands at both study areas (Vogel & Gower, 1998), but this study focused on the pure jack pine stands. Paper birch (*Betula papyrifera* Marsh.) occurred in green alder clumps in the NSA. The soil was an excessively-drained coarse sand. Coarse fragments occupied 20-30% of the soil volume in the NSA, but were absent in the SSA. The soils in the northern and southern study areas were classified as a Dystrocrept and Eutrocrept, respectively.

The aspen stands were even-aged and composed of trembling aspen and a few balsam poplar (*Populus balsamifera* L.). Hazel (*Corylus cornuta* Marsh.) formed a

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TABLE I. Stand characteristics for the aspen, jack pine, and black spruce study sites in the northern and southern study areas. Unless noted, values are given as the mean of four plots ± SE.

Site Characteristic	Southern Study Area			Northern Study Area		
	Aspen	Pine	Spruce	Aspen	Pine	Spruce
Location (latitude N & longitude W)	53.63° 106.2°	53.92° 104.69°	53.99° 105.12°	55.85° 98.04°	55.93° 98.62°	55.88° 98.48°
Stand age (year)	67	65	115	53	63	155
Average tree diameter [a]	20.5	12.9	7.1	12.5	11.1	8.5
(cm at breast height)	(10-30)	(3-23)	(2-21)	(5-23)	(3-19)	(3-19)
Basal area (m^{-2} ha^{-1})	33.5 ± 100	16.9 ± 100	27.2 ± 87	26.7 ± 96	13.3 ± 97	35.6 ± 98
Aboveground net primary	3 520	1 170	1 660	3 490	1 220	1 360
production [b] (kg C ha^{-1} yr^{-1})	±280	±80	±160	±380	±100	±60

[a] range given in parentheses; breast height = 1.37 m
[b] from Gower et al., (1997)

continuous understory, reaching a height of 1.5-2.0 m at both study areas. Willow (*Salix* spp.) occurred in the understory at the northern study area. The soils at both study areas were moderately drained loam to clay loam, and were classified as Boralfs.

The black spruce stand at the SSA was dominated by black spruce, but tamarack (*Larix laricina* [Du Roi] K. Koch) and jack pine occurred in the better-drained areas. Black spruce was the only overstory species in the NSA. Several different black spruce forest communities occurred at both the SSA and NSA, but we restricted our analyses to the black spruce-feathermoss community. Dominant shrubs species included Labrador tea (*Ledum groenlandicum* Oeder), *Vaccinium* spp. and wild rose (*Rosa* spp.). Feathermoss (*Pleurozium schreberi*) was the dominant ground cover at both study areas. The soil at the SSA was a 20-30 cm deep peat layer over sand and the soil at the NSA black spruce stand was a 30-50 cm peat layer over clay.

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 (Gower et al., 1997). The allometric equations were based on ten trees that spanned the entire diameter range of trees in the stand. Coefficients of determination (R^2) for the biomass equations were generally greater than 0.80, except for new twig biomass equations which ranged from 0.54 to 0.88. The allometric equations for aspen were used for balsam poplar, willow and paper birch, whereas allometric equations for tamarack in northern Wisconsin (Kloeppel, 1998) were used to estimate biomass for tamarack in the black spruce stand at the SSA. The use of non-site specific allometric equations introduced only a small error because the minor species 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.

Aboveground net primary production (ANPP) was calculated as the sum of annual wood (stem + branches) and foliage biomass production. One to two variable radius plots, depending on tree density, were established inside each of the four replicate plots. Variable radius plots were used to estimate NPP because they provide an unbiased subsample of trees (Husch, Miller & Beers, 1971). Two increment cores were removed at 1.37 m from each tree in the variable radius plots in October 1994. Foliage production was estimated from new foliage biomass allometric equations (Gower et al., 1997). Litterfall detritus production was measured using ten, 40 cm × 60 cm litterscreens that were placed at random locations in each of the four replicate plots. A detailed description of the procedures used to estimate NPP are provided by Gower et al. (1997).

SOIL CARBON AND NUTRIENT CONTENT AND DISTRIBUTION

Forest floor organic matter content was estimated from three samples (25.2 cm diameter circular ring) in each replicate plot in the aspen and jack pine stands. Live vegetation and coarse roots were removed and the sample was dried at 70°C to a constant mass, weighed to the nearest 0.1 g, and ground to pass through a 40 mm wire mesh. 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.

Nutrient data for the mineral soil at all stands and for the organic layer of black spruce at the NSA and SSA stands were provided by Veldius (1998) and Anderson (1998), respectively. Soil carbon content was calculated for each soil horizon from horizon depth, bulk density, and percent organic carbon data. Soil carbon content for each horizon was summed to estimate total soil carbon content. If more than one soil pit was established in a stand, we computed an average for the stand. Soil carbon and nutrient content were standardized to 100 cm because this was the minimum soil depth used by all BOREAS scientists. For most sites the 100-cm depth included the A and B horizons and occasionally the C horizon. Carbon concentration was determined using a LECO CR10 Carbon Determinator. Exchangeable cations were displaced from the exchange site using a BaCl solution (McKeague, 1978) and cation concentrations were measured using a Perkin-Elmer 3100 atomic absorption spectrophotometer.

NUTRIENT ANALYSIS

New foliage, old foliage, branch, stem wood, annual composites of leaf and woody litterfall subsamples, and forest floor samples from jack pine and aspen stands were ground and dried for 48 hours at 60°C. Approximately 200 mg of tissue was digested in a sulfuric acid-lithium sulfate mixture (Parkinson & Allen, 1975). Nitrogen was determined colori-

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metrically using a continuous flow ion analyzer (Lachat, 1988) and Ca, K, and Mg concentrations were determined using an ICP at the UW Soil and Plant Analysis Laboratory (Page, 1982).

Nutrient content of the vegetation was calculated as the product of nutrient concentration × dry biomass. Annual aboveground nutrient requirements were calculated as the sum of the product of new biomass produced (stem, branch, and foliage) × the nutrient concentration of the respective tissue for the overstory vegetation (Vogel & Gower, 1998). Nutrient concentration of current stem wood was determined for the last five years of sapwood for each of the stem disks collected every 2 m up the stem. All nutrient concentration data are expressed on a dry mass basis. Mean residence time for N in the canopy was calculated as foliage N content/litterfall foliage N content. Percent foliage N retranslocation was estimated as follows: (average N concentration of new foliage from the three canopy positions – N concentration of the foliage litterfall)/average N concentration of new foliage from the three canopy positions. The average canopy N concentration for each canopy position was estimated from new foliage from lower, middle, and upper canopy composite samples collected from ten trees that were destructively sampled in August 1994 (Gower *et al.*, 1997).

STATISTICAL ANALYSES

The four plots from each forest type were treated as replicates in the statistical analyses. The replicate plots of each forest type were always within 1.5 km of each other, thus limiting the inferences that can be made from the results of this study. Nutrient concentration, content, and nutrient cycling characteristics were compared among species in each study area (*e.g.*, aspen, jack pine, and black spruce at the SSA) and between study areas for a given species (*e.g.*, SSA *versus* NSA for jack pine). A two-way ANOVA test was used to determine if species and site differences were significant. A Fisher's least square difference (LSD) test ($p = 0.05$) was used to distinguish species and site mean values if the ANOVA test was significantly different. Total nutrient content and distribution data were not subjected to statistical analyses because the soil pits did not always occur in vegetation plots.

We also used regression analysis to determine if the observed patterns for the BOREAS NSA and SSA were consistent with other nutrient cycling data reported for boreal forests. The regression analysis (*e.g.*, litterfall N and ANPP) that we performed provided another statistical tool for examining general patterns in all boreal forests.

TABLE II. Nutrient concentrations (percent dry mass basis) for aspen, jack pine, and black spruce tree components for the southern and northern study areas. Values are means of four plots ± 1 SE. Standard errors were not available for forest floor and mineral soil.

Biomass Component	Southern Study Area			Northern Study Area		
	Aspen	Jack Pine	Black Spruce	Aspen	Jack Pine	Black Spruce
SAPWOOD						
N (%)	0.05 ± 0.01	0.06 ± 0.02	0.08 ± 0.01	0.13 ± 0.00	0.04 ± 0.01	0.08± 0.01
Ca (%)	0.18 ± 0.05	0.09 ± 0.02	0.18 ± 0.03	0.34 ± 0.33	0.09 ± 0.02	0.17 ± 0.04
K (%)	0.24 ± 0.01	0.20 ± 0.01	0.22 ± 0.01	0.29 ± 0.07	0.21 ± 0.01	0.22 ± 0.01
Mg (%)	0.03 ± 0.01	0.02 ± < 0.01	0.02 ± < 0.01	0.04 ± 0.02	0.02 ± 0.01	0.02 ± < 0.00
HEARTWOOD						
N (%)	0.07 ± 0.00	0.05 ± 0.02	0.07 ± 0.01	0.08 ± 0.01	0.03 ± < 0.01	0.07 ± 0.01
Ca (%)	0.17 ± 0.01	0.11 ± 0.01	0.12 ± 0.01	0.14 ± 0.01	0.10 ± 0.01	0.12 ± 0.01
K (%)	0.22 ± 0.00	0.19 ± 0.00	0.20 ± < 0.01	0.22 ± 0.01	0.19 ± < 0.01	0.21 ± < 0.01
Mg (%)	0.02 ± 0.00	0.02 ± < 0.01	0.01 ± < 0.01	0.02 ± < 0.01	0.02 ± < 0.01	0.01 ± < 0.01
BRANCH						
N (%)	0.60 ± 0.10	0.37 ± 0.10	0.27 ± 0.05	0.54 ± 0.15	0.29 ± 0.03	0.33 ± 0.04
Ca (%)	1.48 ± 0.30	0.39 ± 0.08	0.67 ± 0.12	1.75 ± 0.34	0.32 ± 0.06	0.52 ± 0.10
K (%)	0.57 ± 0.08	0.31 ± 0.03	0.30 ± 0.03	0.55 ± 0.08	0.30 ± 0.02	0.36 ± 0.05
Mg (%)	0.15 ± 0.02	0.06 ± 0.01	0.06 ± 0.01	0.12 ± 0.03	0.06 ± 0.01	0.07± 0.01
NEW FOLIAGE						
N (%)	2.50 ± 0.35	1.48 ± 0.034	0.72 ± 0.08	2.27 ± 0.10	1.16 ± 0.31	0.85 ± 0.07
Ca (%)	1.68 ± 0.29	0.54 ± 0.08	0.54 ± 0.16	1.51 ± 0.22	0.05 ± 0.02	0.38 ± 0.09
K (%)	1.48 ± 0.30	0.63 ± 0.22	0.79 ± 0.11	1.37 ± 0.11	0.58 ± 0.06	0.86 ± 0.02
Mg (%)	0.25 ± 0.05	0.12 ± 0.02	0.11 ± 0.02	0.18 ± 0.02	0.10 ± 0.02	0.11± 0.02
OLD FOLIAGE						
N (%)		1.02 ± 0.14	0.60 ± 0.06		0.76 ± 0.17	0.66 ± 0.09
Ca (%)		0.55 ± 0.08	1.67± 0.55		0.54 ± 0.08	1.34± 0.32
K (%)		0.47± 0.05	0.41± 0.04		0.38 ± 0.04	0.51± 0.07
Mg (%)		0.09 ± 0.01	0.10 ± 0.01		0.08 ± < 0.01	0.07 ± 0.01
FOREST FLOOR						
N (%)	0.021	0.005	0.007	0.018	0.011	0.006
Ca (%)	0.012	0.001	0.004	0.011	0.001	0.005
Mg (%)	0.001	< 0.001	0.001	0.001	0.001	0.002

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Results

Nutrient concentrations (expressed on a dry mass basis) of foliage, branches, and stems were generally significantly greater for aspen than the two evergreen conifers (Table II). Nitrogen concentrations were greater for jack pine than black spruce, and Ca and Mg concentrations were greater for black spruce than jack pine (Table II). Forest floor and mineral soil nutrient concentrations were variable and no inter-species patterns were evident.

Organic matter and nutrient content were not evenly distributed between the vegetation and soil. The vegetation (excluding fine roots and understory) in the aspen, black spruce and jack pine stands contained 70-79%, 53-54%, and 58-67% of total ecosystem carbon content, respectively (Figure 1). Conversely, the soil (forest floor + mineral soil to 1 m depth) contained greater than 90% of the total ecosystem nutrient content, except for the Ca and Mg content of the southern black spruce stand, and the Ca content of the southern aspen stand (Figure 2). Our estimates for nutrient content are slightly conservative because fine roots and understory were excluded in the calculations. The exclusion does not greatly affect the nutrient content budgets because fine roots and understory comprised < 2% of the total organic matter in each forest ecosystem (Gower et al., 1997).

Aspen stands had roughly the same N content in their new foliage as the coniferous stands had in their total foliage. Nitrogen content of branch and stem wood components in aspen stands were approximately two to four times greater in the SSA and one to six times greater in the NSA than black spruce or jack pine stands (Figure 2). Coarse roots contained < 1% of total ecosystem organic matter, N, Ca, and Mg for all stands, except for the SSA black spruce stand for which roots comprised < 2% of the total ecosystem Ca content (not shown).

Leaf litterfall biomass and N content were more than two times greater for trembling aspen than jack pine or black spruce (Table III). Total litterfall (leaf + wood) biomass and N content were also significantly greater ($p < 0.05$) for trembling aspen than the two evergreen conifers. For a given forest type, leaf litterfall N content was significantly greater ($p < 0.05$) for the southern than for the northern study area.

Annual aboveground nutrient requirements were significantly greater ($p < 0.05$) for trembling aspen than for jack pine or black spruce (Figure 3) and were generally greater (but not always significant) for the southern than for the northern study area. Average canopy N residence time differed significantly among the three species, ranging from 1.3-1.6 years for trembling aspen, 5.9-9.8 years for jack pine, and 14.1-16.8 years for black spruce (Figure 4). Nitrogen retranslocation from senescing leaves did not consistently differ among the three species for a given study area, or between study areas for a given species (Figure 5). Jack pine retranslocated the highest percentage of its foliage N content, and black spruce retranslocated the lowest percentage of its foliage N (Figure 5).
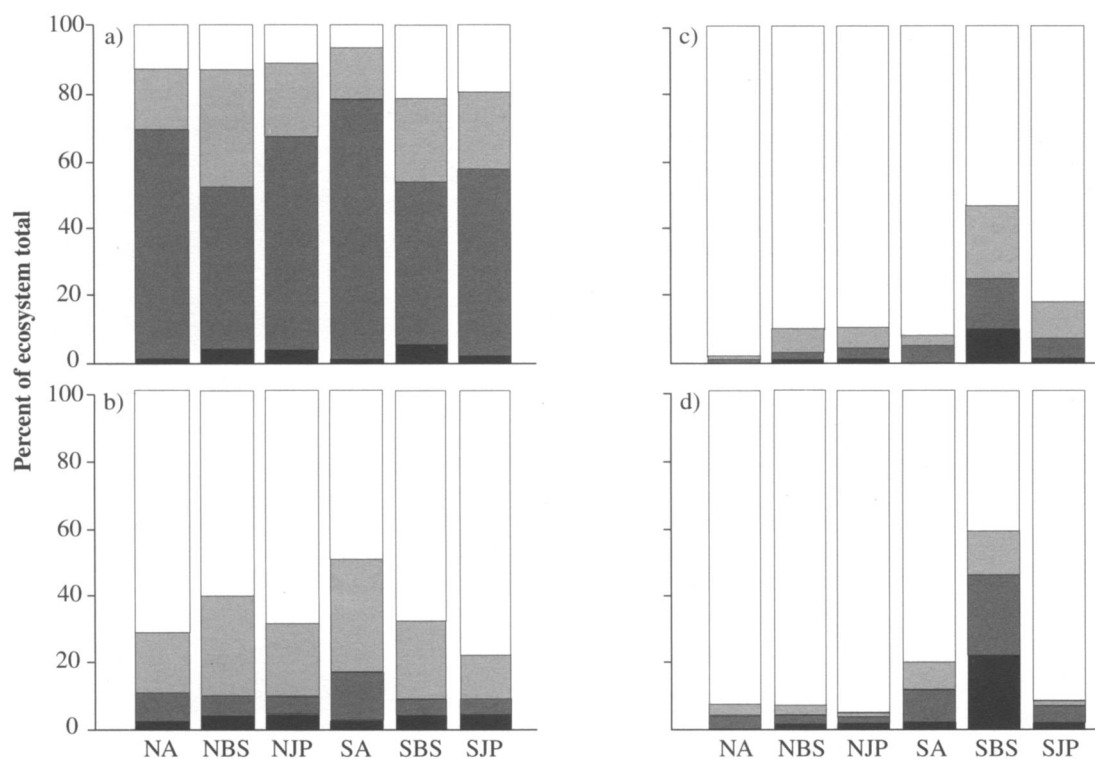

FIGURE 1. Percent nutrient distribution for trembling aspen, jack pine and black spruce forests at the BOREAS nothern study area (NA, NBS, NJP) and southern study area (SA, SBS, SJP). Figure a-d are for carbon, nitrogen, calcium, and magnesium, respectively. For all panels the four components from top to bottom are mineral soil, forest floor, wood (stem, branch, and coarse roots), and foliage. Fine roots and understory are excluded, but comprised < 2% of the total ecosystem organic matter budget.
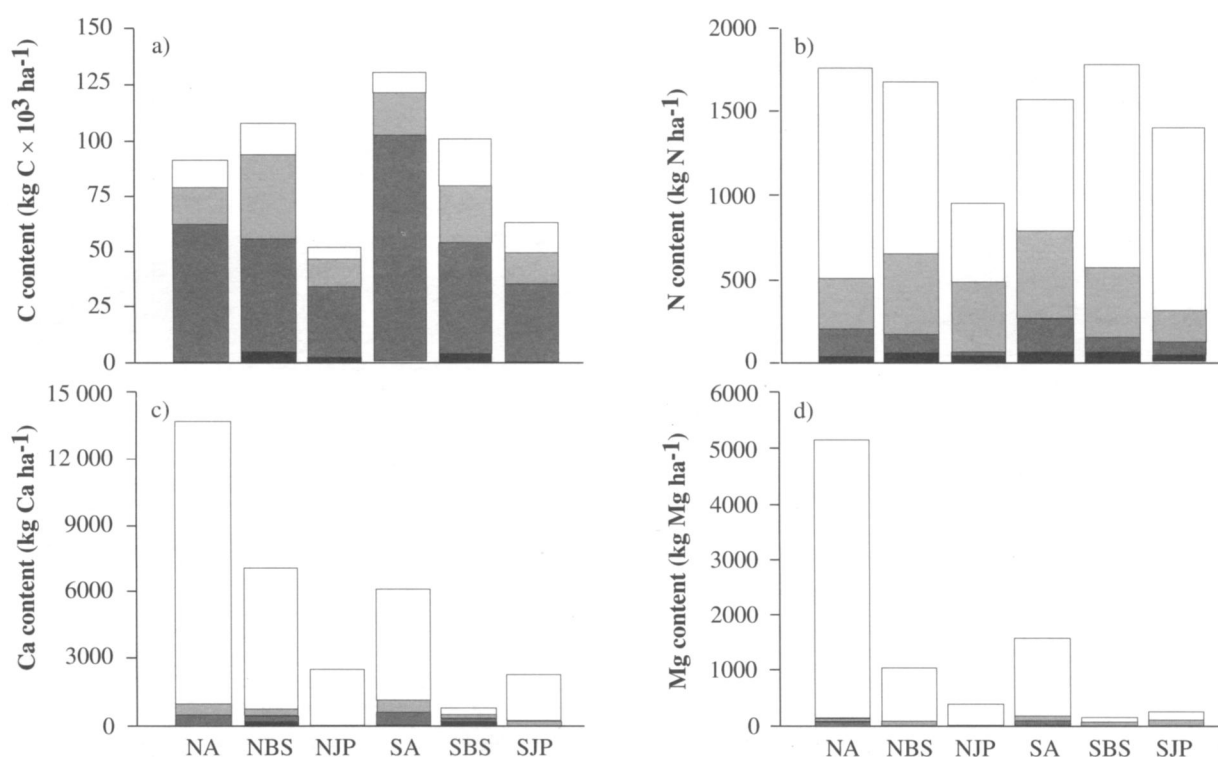
FIGURE 2. Nutrient content for trembling aspen, jack pine and black spruce forests at the BOREAS northern study area (NA, NBS, NJP) and southern study area (SA, SBS, SJP). Figure a-d are for carbon, nitrogen, calcium, and magnesium, respectively. For all panels the four components from top to bottom are mineral soil, forest floor, wood (stem, branch, and coarse roots), and foliage. Fine roots and understory are excluded, but comprised < 2% of the total ecosystem organic matter budget

TABLE III. Annual litterfall organic matter and nitrogen content (N) from foliage and non-foliage tissues for aspen, jack pine, and black spruce in the northern and southern study areas. Values given are means of four plots ± 1 SE.

Biomass Component	Southern Study Area			Northern Study Area		
	Aspen	Pine	Spruce	Aspen	Pine	Spruce
FOLIAGE LITTERFALL						
organic matter (kg/ha)	2170 ± 167	860 ± 85	785 ± 121	1672 ± 42	619 ± 36	684 ± 20
N concentration (%)	0.015 ± 0.002	0.009 ± 0.002	0.006 ± 0.002	0.013 ± 0.001	0.005 ± 0.001	0.005 ± 0.001
N input (kg/ha)	32 ± 3	8 ± 1	5 ± 1	22 ± 1	3 ± < 1	3 ± < 1
NON-FOLIAGE LITTERFALL						
organic matter (kg/ha)	546 ± 59	266 ± 47	243 ± 26	594 ± 172	170 ± 26	354 ± 61
N concentration (%)	0.017 ± 0.004	0.009 ± 0.002	0.009 ± 0.002	0.013 ± 0.006	0.010 ± 0.002	0.007 ± 0.002
N input (kg/ha)	9.10 ± 2.12	2.33 ± 0.43	2.19 ± 0.29	7.68 ± 2.64	1.77 ± 0.30	2.47 ± 0.44
TOTAL LITTERFALL						
N input (kg/ha)	41 ± 3	10 ± 1	7 ± 1	30 ± 3	5 ± < 1	6 ± 1

Discussion

Net primary production of boreal forests is limited by nutrient availability (Linder & Axelsson, 1982; Tamm, 1991). Few studies have identified which nutrient(s) limit growth, but nitrogen is probably the most limiting (Tamm, 1991). Annual total litterfall N content is a good indicator of nutrient availability (Vitousek *et al.*, 1982; Reich *et al.*, 1997), and therefore ANPP should be correlated to litterfall N content. Annual litterfall N content averaged 36 kg (deciduous) and 7 kg (evergreen) N ha^{-1} yr^{-1} in the BOREAS forests in this study. The average litterfall N content for the two BOREAS aspen forests (35 kg N ha^{-1} yr^{-1}) is greater than the average of 21 kg N ha^{-1} yr^{-1} calculated for all boreal deciduous forests (Table IV). The average total litterfall N content of the four BOREAS evergreen conifer forests is very similar to the 9 kg N ha^{-1} yr^{-1} summarized for 19 boreal

evergreen conifer forests (Table IV). The litterfall N content for the four BOREAS jack pine stands is three times smaller than the litterfall N value reported for a jack pine stand in northern Ontario (Foster & Morrison, 1976), but is similar to the litterfall N content reported for a nutrient-poor jack pine stand (Foster *et al.*, 1995). Litterfall N content for the two BOREAS black spruce stands were within the range reported for black spruce stands in Alaska (Van Cleve *et al.*, 1983, Ruess *et al.*, 1996). The greater annual litterfall N content for deciduous than evergreen boreal forests (Table IV) is consistent with results reported for boreal forests in Alaska (Cole & Rapp, 1980; Van Cleve *et al.*, 1983, Ruess *et al.*, 1996) and Finland (Finer, 1989).

We observed a significant positive correlation between ANPP and litterfall N content for the BOREAS stands and for all boreal forests (Figure 6). The exact form of the relationship is unclear, so we used a simple linear relationship.
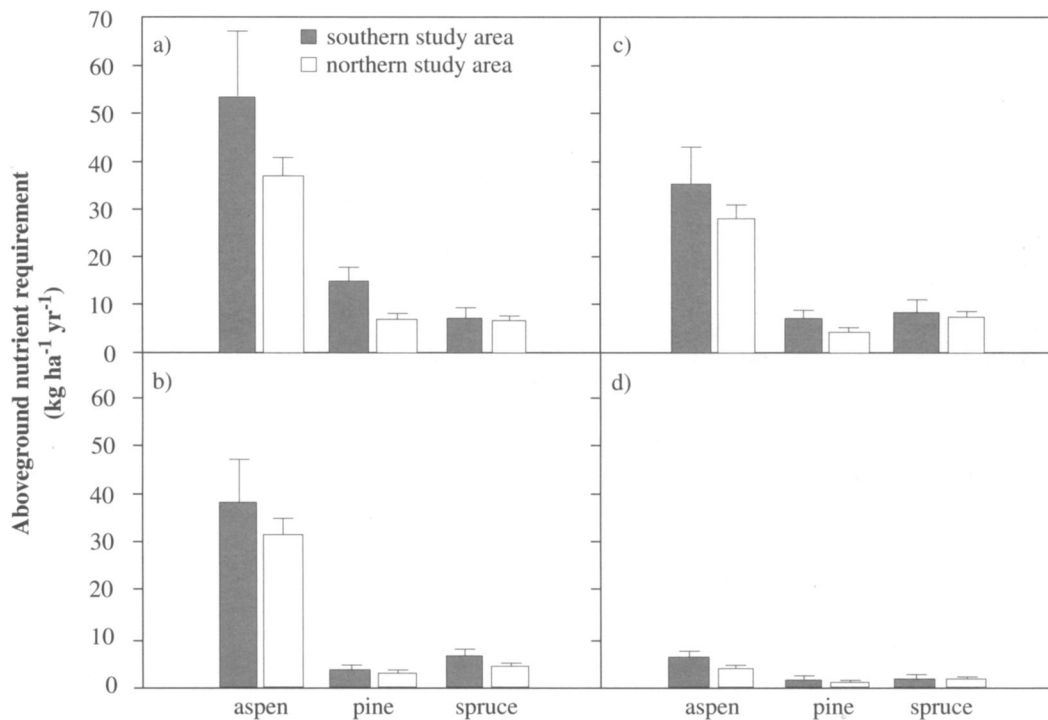
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FIGURE 3. Annual above-ground nutrient requirement for trembling aspen, jack pine, and black spruce forests at the BOREAS southern and northern study areas. All values are in kg ha^{-1} yr^{-1}. Bars are the means of four plots ± SE.

TABLE IV. Summary of aboveground net primary production (ANPP, kg ha^{-1} yr^{-1}), above-ground litterfall N content (kg N ha^{-1} yr^{-1}) and annual above-ground N requirement (kg N ha^{-1} yr^{-1}) for boreal forests. The SE of the mean is provided in parentheses.

Species	Location	ANPP	Litterfall N	N Requirement	Source
DECIDUOUS					
Alnus/Populus	Alaska, U.S.A.	9970	32	43	a
Betula papyrifera	Alaska, U.S.A.	4700	19	58	b
Betula/Populus	Alaska, U.S.A.	8100	14	24	a
Betula pubescens[10]	Ilomantsi, Finland	2760	10	30	c
Betula pubescens[1, 10]	Ilomantsi, Finland	2980	5	28	3
Populus balsamifera	Alaska, U.S.A.	6470	15	24	a
Populus balsamifera	Alaska, U.S.A.	5520	33	56	b
Populus tremuloides	Saskatchewan, Canada	7330	41	53	d
Populus tremuloides	Manitoba, Canada	7270	30	37	d
Populus tremuloides	Alaska, U.S.A.	5650	15	61	b
Average		6075	21	41	
SE		(710)	(4)	(5)	
EVERGREEN					
Picea abies	Ilomantsi, Finland	3430	3	17	c
Picea abies[1]	Ilomantsi, Finland	4580	3	22	c
Picea glauca[2]	Alaska, U.S.A.	3670	8	15	a
Picea glauca[3]	Alaska, U.S.A.	4530	10	19	a
Picea glauca	Alaska, U.S.A.	3660	9	16	b
Picea mariana	Saskatchewan, Canada	3460	7	8	d
Picea mariana	Manitoba, Canada	2830	6	7	d
Picea mariana	Alaska, U.S.A.	1130	3	5	b
Picea mariana	Alaska, U.S.A.	680	3	4	a
Pinus banksiana	Saskatchewan, Canada	2400	5	12	d
Pinus banksiana[4]	Saskatchewan, Canada	2920	12	17	e
Pinus banksiana	Manitoba, Canada	2460	3	6	d
Pinus banksiana[4]	Manitoba, Canada	4170	10	10	e
Pinus sylvestris[10]	North Karelia, Finland	3180	11	11	f
Pinus sylvestris[5, 10]	North Karelia, Finland	3070	13	13	f
Pinus sylvestris[6, 10]	Ilomantsi, Finland	3280	5	21	f
Pinus sylvestris[7, 10]	Ilomantsi, Finland	4080	6	21	f
Pinus sylvestris[8, 10]	Ilomantsi, Finland	2320	8	10	f
Pinus sylvestris[9, 10]	Ilomantsi, Finland	2420	9	10	f
Pinus sylvestris	Tammela, Finland	2445	3	13	g
Pinus sylvestris	Juuparjoki, Finland	4060	5	20	g
Pinus sylvestris	Tammela, Finland	5100	10	25	g
Average		3160	7	14	
SE		(230)	(1)	(1)	

Footnotes: [1] fertilized, [2] floodplain, [3] upland, [4] Alnus crispa understory, [5] NPK fertilization treatment, [6] VNRm forest type, [7] fertilized VNRmu forest type, [8] RhNRmu forest type, [9] fertilized RhNRmu forest type, [10] calculated as the product of average annual increment (Appendix 33) and tissue N concentration (Appendix 23-24) for stem wood, stem bark, branches, and foliage. 6 - 9 are Swedish and Finnish forest types.
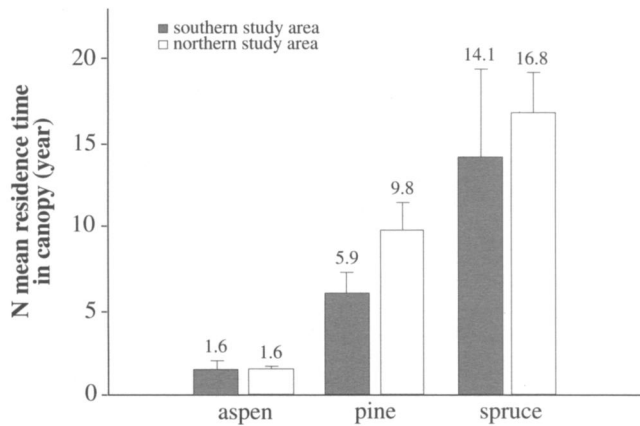
FIGURE 4. Average canopy N residence time (years) for trembling aspen, jack pine, and black spruce forests at the BOREAS southern and northern study areas. The bars are 1 SE and the value above the standard error bar is the actual mean value.
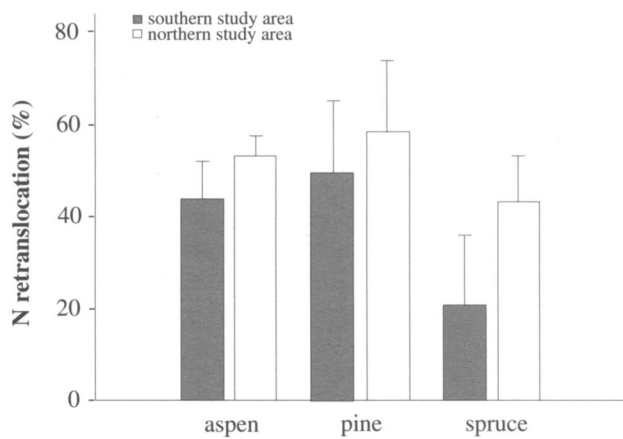

FIGURE 5. Average percent retranslocation of N from senescing foliage for trembling aspen, jack pine, and black spruce forests at the BOREAS southern and northern study areas. The bars are 1 SE.

Aboveground NPP appeared not to increase when litterfall N content exceeded 30 kg N ha^{-1} yr^{-1}, suggesting that other nutrients or environmental factors limited net primary production on the most fertile boreal forest soils.

Annual nutrient requirements reported for the BOREAS forests are similar to values reported for similar boreal forests. Van Cleve et al., (1983) reported annual N, Ca, and Mg requirements of 5, 3, and < 1 kg ha^{-1} yr^{-1} for black spruce and 58, 38, and 10 kg ha^{-1} yr^{-1} for all deciduous forests, respectively (Van Cleve et al., 1983; Table IV). On average, the annual aboveground N requirement is four times greater for deciduous than evergreen conifer forests (41 kg versus 14 kg N ha^{-1} yr^{-1}) a pattern that is consistent with results for nutrient cycling studies for boreal forests in Alaska (Van Cleve et al., 1983) and Finland (Finer, 1989).

The greater annual N requirement of deciduous than evergreen conifer boreal forests is partly explained by the greater ANPP or nutrient demand of deciduous trees (Table IV). However, ANPP was two times greater for the deciduous than for the evergreen conifer forests, whereas nutrient requirements were four times greater. Nutrient use efficiency, defined as the amount of organic matter produced (*i.e.*, ANPP) per unit nutrient uptake, also influences nutrient
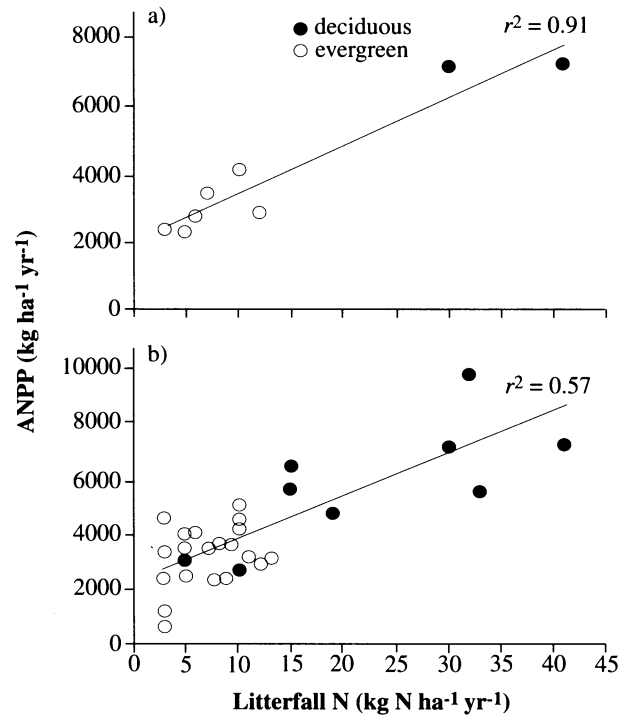

FIGURE 6. Relationship between aboveground net primary production (ANPP, kg ha^{-1} yr^{-1}) and annual litterfall N content (kg ha^{-1} yr^{-1}) for (a) boreal forests in the BOREAS study ($r^2 = 0.91$, $p < 0.01$) and (b) for all boreal forests ($r^2 = 0.57$, $p < 0.05$).

demand. Nutrient use efficiency was almost two times greater for evergreen conifers (433 kg ANPP/kg N required) than deciduous forests (245 kg ANPP/kg N required). The greater N use efficiency was not explained by greater retranslocation of N from senescing leaves (Figure 5). In fact, the percent N retranslocation was relatively low compared to previously reported values for boreal tree species (Chapin & Kedrowski, 1981). The smaller nutrient requirements of the evergreen than the deciduous forest was explained by the longer canopy N residence time of the evergreen trees (Figure 4). For example, black spruce retained N in the canopy 10 times longer than aspen, and was greater for a similar conifer species located in the NSA than the SSA. We speculate that the greater canopy N mean residence time for conifers in the NSA than in the SSA is related to the greater leaf longevity of conifers in colder climates (Reich *et al.*, 1995).

Nutrient distribution and cycling characteristics varied more between evergreen and deciduous forests in a similar climate than between similar forest types in the two contrasting climates in the BOREAS study. A similar pattern was observed for all boreal forests surveyed in this study. Net primary production and carbon allocation patterns also differed consistently between evergreen and deciduous boreal forests (Steele *et al.*, 1997; Gower *et al.*, 1997; Gower *et al.*, 2000). For example, approximately two times more total net primary production is allocated to root production in boreal evergreen forests than in deciduous forests. The large differences in ecosystem function between evergreen and deciduous boreal forests suggest that global biogeochemical models should use distinct boreal evergreen and deciduous forest cover types, and use appropriate carbon allocation

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and nutrient cycling parameters (nutrient requirement, litterfall N content, etc.). The data from this study did not provide sufficient evidence to support using different percent retranslocation coefficients for evergreen and deciduous forests.

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