

# Nitrogen dynamics of a boreal black spruce wildfire chronosequence

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**Abstract** This study examined the nitrogen (N) dynamics of a black spruce (*Picea mariana* (Mill.) BSP)-dominated chronosequence in Manitoba, Canada. The seven sites studied each contained separate well- and poorly drained stands, originated from stand-killing wildfires, and were between 3 and 151 years old. Our goals were to (i) measure total N concentration ([N]) of all biomass components and major soil horizons; (ii) compare N content and select vegetation N cycle processes among the stands; and (iii) examine relationships between ecosystem C and N cycling for these stands. Vegetation [N] varied significantly by tissue type, species, soil drainage, and

stand age; woody debris [N] increased with decay state and decreased with debris size. Soil [N] declined with horizon depth but did not vary with stand age. Total (live + dead) biomass N content ranged from 18.4 to 99.7 g N m<sup>-2</sup> in the well-drained stands and 37.8–154.6 g N m<sup>-2</sup> in the poorly drained stands. Mean soil N content (380.6 g N m<sup>-2</sup>) was unaffected by stand age. Annual vegetation N requirement (5.9 and 8.4 g N m<sup>-2</sup> yr<sup>-1</sup> in the middle-aged well- and poorly drained stands, respectively) was dominated by trees and fine roots in the well-drained stands, and bryophytes in the poorly drained stands. Fraction N retranslocated was significantly higher in deciduous than evergreen tree species, and in older than younger stands. Nitrogen use efficiency (NUE) was significantly lower in bryophytes than in trees, and in deciduous than in evergreen trees. Tree NUE increased with stand age, but overall stand NUE was roughly constant (~150 g g<sup>-1</sup> N) across the entire chronosequence.

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## Introduction

The large size, high soil carbon content, sensitivity to disturbance, and projected warming of the

circumpolar boreal forest emphasize the great need to study boreal carbon and nitrogen cycles (Apps et al. 1993; Gower et al. 2001; Hobbie et al. 2002). Wildfires strongly influence boreal forest structure and function (Viereck 1983; Goldammer and Furyaev 1996), but the links between fire, soil drainage and temperature, and carbon and nutrient cycling are poorly understood (Stocks et al. 1996; Wan et al. 2001; Harden et al. 2003). This is particularly important as recent increases in wildfire frequency suggest that fire dynamics of this region may not be in equilibrium with predicted climate change (Flannigan et al. 1998; Kasischke and Stocks 2000).

Nitrogen (N) availability limits net primary production (NPP) in many high-latitude ecosystems (Van Cleve et al. 1983; Linder et al. 1987; Vitousek and Howarth 1991; Gower et al. 1994; Schulze et al. 1995). Boreal forest N transformations and uptake vary with forest type and location (Gower et al. 2000), and strongly affect production, successional patterns, and ecosystem structure and function (Van Cleve et al. 1971; Binkley 1992; Mäkipää 1995). Decomposition and mineralization of detritus are highly important nutrient sources in boreal forests (Ruess et al. 1996), in spite of the slow rates of these processes due to cold temperatures and poor soil drainage.

The N cycling dynamics of major North America boreal forest types have been studied largely in mature forests (Foster and Morrison 1976; Flanagan and Van Cleve 1983; Van Cleve et al. 1983; Foster et al. 1995; Ruess et al. 1996; Gower et al. 2000). Nitrogen cycling dynamics change dramatically during stand development (Vitousek and Reiners 1975; Zackrisson et al. 2004); this has been studied in Scots pine (*Pinus sylvestris*) (Mäkipää 1995; DeLuca et al. 2002a; Helmisaari et al. 2002; Wirth et al. 2002) and Dahurian larch (*Larix gmelinii*) (Schulze et al. 1995) forests, but we are unaware of a similar study for black spruce (*Picea mariana* (Mill.) BSP), the dominant North American boreal forest type. In addition, most studies have focused on well-drained areas, but boreal bryophytes are important in C and N cycling (Turetsky 2003), and dominant in the widespread poorly drained areas. In such areas, bryophytes not only exhibit high production and poor-quality litter, but also

form facultative symbioses with N-fixing cyanobacteria (DeLuca et al. 2002b; Turetsky 2003 and references therein).

The goals of this study were to (i) measure N concentration of all live and dead biomass components and major soil horizons for a 151-year chronosequence comprising well- and poorly drained black spruce stands; (ii) compare N content and select vegetation N cycle processes among the different-aged stands; and (iii) examine relationships between ecosystem C and N cycling for these stands, using data from previous published studies in this chronosequence.

## Methods

### Site descriptions

The study was conducted in a black spruce-dominated chronosequence west of Thompson, Manitoba, Canada, near the BOREAS Northern Study Area tower site (Sellers et al. 1997). All chronosequence sites originated from stand-killing wildfire between 3 and 151 years previously, with forest ages determined by tree coring (Bond-Lamberty et al. 2004b). Poor- and well-drained stands were located in each different-aged site. The stands have been extensively studied (Table 1) and differed in their species composition and leaf area (Bond-Lamberty et al. 2002c), soil CO<sub>2</sub> fluxes (Wang et al. 2002; Bond-Lamberty et al. 2004a), C distribution (Wang et al. 2003), and net primary and ecosystem production (Litvak et al. 2002; Bond-Lamberty et al. 2004b). The stands were dominated by three tree species: trembling aspen (*Populus tremuloides* Michx), black spruce, and jack pine (*Pinus banksiana* Lamb.). Early-successional deciduous tree species are replaced by black spruce in the older stands. In the well-drained stands, the black spruce canopy closure, at 50–60 years, is associated with reduced understory and growth of thick feather mosses (usually *Ptilium*, *Pleurozium* or *Hylocomium* spp.); in the poorly drained stands, the canopy remains open, with black spruce, Labrador tea (*Ledum groenlandicum* Oeder), and *Sphagnum* spp. dominating production. In the well-drained stands, soil temperatures declined

**Table 1** Stand characteristics for the chronosequence sites, by soil drainage and stand age

Site characteristic	Years since fire						
	3	6	12	20	37	71	151
<i>Well-drained stands</i>							
Tree diameter (cm)	–	1.3 (2.3)	0.0 (–)	1.7 (0.2)	3.0 (0.9)	4.7 (0.9)	7.9 (1.2)
Basal area (m <sup>2</sup> ha <sup>-1</sup> )	0.0 (–)	0.5 (1.1)	0.0 (–)	4.1 (1.0)	11.6 (3.9)	36.7 (4.0)	42.2 (8.6)
Overstory LAI	0.0 (–)	0.1 (0.2)	0.0 (–)	0.9 (0.2)	1.8 (0.7)	6.8 (0.7)	5.3 (0.9)
Vegetation C content (kg C m <sup>-2</sup> )	0.2 (0.0)	0.1 (0.0)	0.5 (0.1)	0.9 (0.2)	2.1 (0.5)	6.5 (1.3)	8.3 (1.6)
Total NPP (g C m <sup>-2</sup> yr <sup>-1</sup> )	106 (47)	180 (43)	366 (95)	366 (35)	406 (49)	358 (64)	211 (50)
Total NEP (g C m <sup>-2</sup> yr <sup>-1</sup> )	–136 (74)	–134 (93)	–2 (206)	43 (73)	97 (98)	112 (107)	–19 (106)
<i>Poorly drained stands</i>							
Tree diameter (cm)	–	0.0 (–)	0.0 (–)	1.0 (0.3)	2.3 (0.4)	4.7 (1.3)	3.5 (0.5)
Basal area (m <sup>2</sup> ha <sup>-1</sup> )	0.0 (–)	0.0 (–)	0.0 (–)	0.2 (0.1)	2.2 (1.0)	20.3 (5.1)	16.6 (6.1)
Overstory LAI	0.0 (–)	0.0 (–)	0.0 (–)	0.1 (0.1)	0.3 (0.1)	3.0 (0.8)	1.1 (0.4)
Vegetation C content (kg C m <sup>-2</sup> )	0.1 (0.0)	0.4 (0.1)	0.6 (0.1)	0.6 (0.1)	2.0 (0.4)	3.7 (0.8)	3.4 (0.7)
Total NPP (g C m <sup>-2</sup> yr <sup>-1</sup> )	72 (21)	447 (146)	239 (69)	534 (115)	401 (105)	311 (54)	261 (49)
Total NEP (g C m <sup>-2</sup> yr <sup>-1</sup> )	–76 (34)	131 (204)	–30 (169)	310 (146)	174 (142)	94 (119)	11 (112)

Standard deviations, in parentheses, are based on the plot as experimental unit ( $N=4$  in well-drained stands and 5 in poorly drained stands). Carbon (C) content data are from Wang et al. (2003), and net primary production (NPP) and net ecosystem production (NEP, negative value is a flux to atmosphere) from Bond-Lamberty et al. (2004b). Other data, including leaf area index (LAI, hemisurface basis) were reported in Bond-Lamberty et al. (2002a; c)

with increasing leaf area (Bond-Lamberty et al. 2005).

Study sites were selected to minimize differences in soil type. Soils generally derived from sedimentary materials deposited by glacial Lake Agassiz. Moderately well and imperfectly drained montmorillonite clays classified as Orthic Gray Luvisols (Typic Haplocryalfs) and Gleyed Gray Luvisols (Aquic Haplocryalfs) were the most common soils in the uplands; these clays were dominated by illite (average >50%), and contained 0–20% smectite, kaolinite and vermiculite (Veldhuis, unpublished data). The poorly drained areas were dominated by shallow organic soils, but included peaty, poorly drained mineral soils. These soils were classified as Terric Fibrisols (Terric Cryofibrists), Terric Humisols (Terric Cryosapristis), Terric Fibric Organic Cryosols (Terric Fibristels) and Terric Humic Organic Cryosols (Terric Sapristels). The associated mineral soils were predominantly Orthic and Humic Luvic Gleysols (Typic Cryoaqualfs). Permafrost was discontinuous, and when present occurred at 60–80 cm and deeper. These soil descriptions were based on pits dug at the well-drained stands (see below); further soil information for some of

these stands was given by Veldhuis (1995) and Halliwell and Apps (1997).

#### Biomass and net primary production

Above- and belowground biomass of tree components (stem, new and old branch, new and old foliage, and coarse root) was determined from site-specific allometric equations (Bond-Lamberty et al. 2002a; Wang et al. 2003). Net primary production (NPP, mean of 1999–2001) was calculated based on these allometric relationships and cores or disks taken from 15 to 20 trees per plot, as described by Bond-Lamberty et al. (2004b). Detritus production (litterfall) was measured using 8 and 6 litter baskets per plot in the well- and poorly drained stands, respectively, from 1999 to 2001. Detritus was sorted by species and type (foliage versus woody tissue).

Fine root production was measured using the maximum–minimum soil core method (Vogt et al. 1998), using ten soil cores (50 cm depth) taken from each replicate plot. The midsummer sample was assumed to represent maximum fine root biomass (Wang et al. 2003), based on previous minirhizotron studies in mature black spruce

stands (Steele et al. 1997; O'Connell et al. 2003). Annual fine root NPP was calculated as the difference between midsummer and autumnal biomass; the source of fine roots (trees versus understory) was not distinguished.

Understory biomass and growth were measured for three consecutive years using five randomly located subplots in, or immediately outside of, each replicate plot. All understory plants inside each subplot were clipped, separated into current-year and older growth, dried to a constant mass at 70°C, and weighed. Bryophyte growth was measured from May 2000 to October 2001. Crank wires were employed to measure *Sphagnum* NPP (Clymo 1970; O'Connell et al. 2003), while feather moss production was measured by clipping moss growth above pre-set mesh squares (Gower et al. 1997; Bond-Lamberty et al. 2004b). Growth and biomass estimates were scaled to the stand level based on moss coverage surveys (Wang et al. 2003). Woody debris biomass was estimated using transects at each replicate plot; woody debris samples were taken on a size- and decay-specific basis (Bond-Lamberty et al. 2002b).

Two to four soils were selected at each of the well-drained sites based on the information obtained from a grid survey of the sites carried out previously. Pits were dug to a depth of 100 cm to describe the soils in detail and to obtain samples for physical and chemical analysis, although the mineral soil was deeper than this. Composite samples were collected from each of the soil horizons, and separate samples for bulk density determination were collected from most horizons. Soils were classified according the Canadian System of Soil Classification (Soil Classification Working Group 1998).

#### Nitrogen concentration and content

A subset of the tissue and soil samples was used for nitrogen analysis. Approximately 4–6 subsamples were randomly selected from each tissue type (tree new foliage, understory old wood, etc). Tree foliage samples were randomly taken from throughout the canopy (Bond-Lamberty et al. 2002a); stem and branch samples were similarly randomized. Understory and bryophyte samples were not species-specific and thus

represented a spatially random mixture of all species present at each stand. Samples were ground to pass through a 2 mm screen and analyzed for total N concentration ( $[N]$ , equal to organic N +  $NH_4^+$  - N +  $NO_3^-$  - N +  $NO_2^-$  - N) on a biomass basis. Analysis was performed by the University of Wisconsin Soil and Plant Analysis Laboratory using sulfuric acid digestion with a Cu catalyst (Bremner 1965). No above-ground tree tissue samples were taken at the 151- or 71-year-old stands; the  $[N]$  values reported by Gower et al. (2000) for the 151-year-old stand (the BOREAS OBS site) were used instead.

The tissue samples used previously to calculate fine root biomass and NPP in these stands were not available for N analysis. Instead new foliage  $[N]$ , on a stand-specific basis, was used as a proxy for fine root  $[N]$ . This resulted in values consistent with values reported by Ruess et al. (2003) for Alaskan boreal black spruce.

Vegetation N content was calculated as the product of  $[N]$  and dry biomass, and soil N content as the product of each horizon's  $[N]$ , bulk density, and thickness. Annual N requirement was calculated as the sum of the product of new biomass produced (stem, branch, foliage, coarse root, fine root, understory, and bryophyte) and the respective tissue  $[N]$ . Mean residence time for canopy N was calculated as foliage N content divided by litterfall foliage N content. Percent foliage N retranslocation was estimated on a species-specific basis as (new foliage  $[N]$  minus foliage litterfall  $[N]$ ) divided by new foliage  $[N]$ . Uptake was then considered to be N requirement times (1–N retranslocation). Nitrogen use efficiency was computed as the amount of organic matter produced (i.e., NPP) per unit N uptake on a tissue-, species-, and stand-specific basis.

#### Statistical analysis

Statistical analyses were conducted using SAS version 8.1 software (SAS Institute Inc. 2001). It is important to note that the chronosequence design used here provided no true replication of stand age, although the stands are consistent with

a larger group of stands studied in the region (Bond-Lamberty et al. 2004b). For this reason we generally do not discuss effects of stand age below. A mixed effects procedure (PROC MIXED) was used to test [N] and other variables for the main effects of soil drainage and stand age by treating the former as nested within the latter, and assigning replicate plots within a (stand age  $\times$  soil drainage) combination as a random effect. Data were checked for normality or, when the sample size was very small, assumed to be adequate for parametric statistics; no transformations were performed. The PROC TTEST procedure was employed for one-sample or paired  $T$  tests. Unless otherwise noted, all

calculations and statistical analyses used the plot as the experimental unit and a significance level of  $\alpha = 0.05$ .

## Results

### Nitrogen concentration

Nitrogen concentration ([N]) differed significantly among tissue types ( $F_{5,670} = 109.11$ ;  $P < 0.0001$ ). Foliage had higher [N] than wood, and new tissues higher [N] than older tissues (Table 2). Tree species had a highly significant ( $F_{5,670} = 11.25$ ;  $P < 0.0001$ ) effect on tissue [N] which decreased as follows: paper birch > aspen,

**Table 2** Tree tissue nitrogen concentrations ([N], percent dry mass basis) for chronosequence stands, by species, biomass component, soil drainage and stand age; the [N]

values reported by Gower et al. (2000) were used for the 71- and 151-year-old stands

Years since fire	Species	Tissue type					
		S	NB	NF	OB	OF	CR
<i>Well-drained stands</i>							
6	<i>P. tremuloides</i>	1.20 (0.12)	1.22 (0.46)	0.99 (0.20)	0.91 (0.18)		
	<i>P. mariana</i>	0.88 (0.29)	0.95 (0.17)	0.98 (0.16)	0.87 (0.16)	1.02 (0.32)	
	<i>P. banksiana</i>	0.55 (0.48)		0.76 (–)	0.80 (–)	0.20 (–)	0.75 (0.06)
	<i>Salix</i> spp.	0.37 (0.04)	0.67 (0.08)	1.53 (0.13)	0.36 (0.14)		
12	<i>P. tremuloides</i>	1.39 (0.49)	0.76 (0.28)	0.84 (0.42)	0.83 (0.24)		0.32 (0.10)
	<i>B. papyrifera</i>	0.86 (0.43)	0.92 (0.25)	0.73 (0.36)	0.96 (0.40)		0.65 (0.18)
	<i>P. mariana</i>	0.64 (0.25)	0.79 (0.17)	0.88 (0.11)	0.78 (0.28)	0.85 (0.22)	0.38 (0.09)
	<i>Salix</i> spp.	0.34 (0.13)	0.72 (0.08)	1.68 (0.20)	0.44 (0.09)		0.58 (0.47)
20	<i>P. tremuloides</i>	0.38 (0.14)	0.74 (0.40)	1.62 (0.48)	0.38 (0.07)		
	<i>P. mariana</i>	0.35 (0.04)	0.60 (0.11)	0.73 (0.07)	0.38 (0.03)	0.51 (0.03)	0.25 (0.06)
	<i>P. banksiana</i>	0.41 (0.05)	0.64 (0.14)	1.09 (0.08)	0.40 (0.06)	0.84 (0.06)	
37	<i>P. tremuloides</i>	0.26 (0.05)	0.51 (0.31)	2.05 (0.19)	0.37 (0.10)		
	<i>P. mariana</i>	0.42 (0.04)	0.77 (0.14)	0.77 (0.36)	0.36 (0.07)	0.62 (0.06)	0.27 (–)
71	<i>P. mariana</i>						0.35 (0.05)
<i>Poorly drained stands</i>							
12	<i>P. tremuloides</i>	0.25 (0.03)	0.55 (0.04)	1.33 (0.14)	0.31 (0.05)		0.27 (0.04)
	<i>B. papyrifera</i>	0.28 (0.03)	0.71 (0.19)	1.43 (0.14)	0.36 (0.03)		0.32 (0.07)
	<i>P. mariana</i>	0.31 (0.07)	0.63 (0.10)	0.55 (0.25)	0.28 (0.07)	0.53 (0.09)	0.33 (0.05)
	<i>Salix</i> spp.	0.34 (0.03)	0.61 (0.29)	1.51 (0.09)	0.45 (0.06)		0.42 (0.10)
20	<i>P. tremuloides</i>	0.22 (0.03)	0.66 (0.12)	1.33 (0.18)	0.33 (0.02)		
	<i>B. papyrifera</i>	0.36 (0.05)	1.04 (0.14)	1.48 (0.23)	0.44 (0.12)		
	<i>P. mariana</i>	0.25 (0.05)	0.52 (0.03)	0.48 (0.06)	0.30 (0.04)	0.36 (0.05)	0.23 (0.06)
	<i>P. banksiana</i>	0.29 (0.02)	0.67 (0.03)	0.55 (0.40)	0.39 (0.08)	0.92 (0.06)	
	<i>L. laricina</i>	0.27 (0.08)	0.57 (0.10)	1.12 (0.15)	0.40 (0.05)		0.23 (0.09)
37	<i>Salix</i> spp.	0.27 (0.06)	0.82 (0.13)	1.63 (0.27)	0.37 (0.04)		
	<i>P. mariana</i>	0.25 (0.05)	0.64 (0.21)	0.66 (0.11)	0.28 (0.05)	0.37 (0.08)	0.23 (0.06)
	<i>P. banksiana</i>	0.13 (0.05)	0.46 (0.16)	0.62 (0.28)	0.23 (0.05)	0.36 (0.16)	0.23 (0.06)
71	<i>P. mariana</i>						0.36 (0.08)
151	<i>L. laricina</i>						0.30 (0.02)

Tissue types include stem (S), new branch (NB), new foliage (NF), old branch (OB), old foliage (OF), and coarse root (CR). Tree-to-tree standard deviations ( $N = 4-7$ ) are in parentheses

tamarack, willow > black spruce, jack pine. Trees from well-drained stands had significantly ( $F_{1,670} = 42.97$ ;  $P < 0.0001$ ) higher [N] than trees from poorly drained stands, while trees from the middle-aged stands (37-, 20-, and 12-year-old stands) had significantly lower [N] than trees from the youngest or oldest stands ( $F_{5,670} = 5.79$ ,  $P < 0.0001$ ; Table 2). Tree diameter and tissue [N] were negative correlated, even after the effects of species, tissue type, soil drainage, and stand age were accounted for (data not shown). This effect was greatest in the youngest stands, with tissue

[N] decreasing about 0.1% for every additional cm of dbh.

Understory [N] (Table 3) differed significantly among stands and tissue types (new foliage > new wood, old foliage > old wood) but not between soil drainage classes ( $F_{1,185} = 1.43$ ;  $P = 0.233$ ). Live bryophyte tissue (Table 3) had higher [N] than dead bryophyte tissue across the chronosequence ( $F_{5,67} = 3.21$ ;  $P = 0.012$ ), and the interaction between stand age and soil drainage class had a significant effect on bryophyte [N] ( $F_{6,67} = 2.92$ ;  $P = 0.014$ ).

**Table 3** Nitrogen concentrations (percent dry mass basis) for understory and bryophyte samples, by soil drainage and stand age

Biomass component		Years since fire						
		3	6	12	20	37	71	151
<i>Well-drained stands</i>								
Understory	Wood	0.58 (0.12)	0.49 (0.12)	0.80 (0.11)	0.62 (0.14)		1.15 (0.76)	0.67 (0.17)
	New wood	0.84 (0.12)	0.92 (0.05)	1.63 (0.47)	1.05 (0.25)		1.97 (0.43)	0.93 (0.05)
	Foliage	1.12 (0.24)	0.90 (0.07)	1.11 (0.17)	1.09 (0.15)		1.20 (0.67)	1.09 (0.20)
Bryophytes	New foliage	1.56 (0.21)	1.36 (0.22)	1.95 (0.12)	1.40 (0.16)		2.49 (0.06)	1.64 (0.62)
	Living	–	1.06 (0.07)	0.91 (0.15)	1.40 (0.54)	1.10 (0.24)	0.79 (0.04)	0.83 (0.10)
	Dead/forest floor	1.05 (0.17)	0.94 (0.16)	0.88 (0.11)	1.15 (0.20)	1.16 (0.28)	1.10 (0.05)	0.72 (0.01)
<i>Poorly drained stands</i>								
Understory	Wood	0.68 (0.12)	0.66 (0.12)	0.43 (0.21)	0.59 (0.22)		0.45 (0.08)	0.45 (0.07)
	New wood	1.02 (0.07)	1.05 (0.20)	1.19 (0.20)	1.36 (0.22)		1.24 (0.35)	1.03 (0.16)
	Foliage	1.19 (0.08)	1.08 (0.31)	0.97 (0.21)	1.38 (0.16)		1.18 (0.06)	1.00 (0.04)
Bryophytes	New foliage	1.89 (0.12)	1.56 (0.07)	1.64 (0.26)	1.47 (0.15)		1.82 (0.27)	1.50 (0.24)
	Living	–	1.34 (0.09)	1.13 (0.32)	1.06 (0.20)	1.00 (0.14)	0.74 (0.16)	0.73 (0.11)
	Dead/forest floor	1.00 (0.04)	0.97 (0.14)	1.00 (0.17)	0.86 (0.23)	0.88 (0.05)	0.95 (0.23)	0.93 (0.19)

Understory and bryophyte samples were not separated by species. Plot-to-plot standard deviations ( $N = 4$  in well-drained stands and 5 in poorly drained stands) are in parentheses

**Table 4** Nitrogen concentrations (percent dry mass basis) for litterfall, by soil drainage and stand age

Litterfall component	Years since fire						
	3	6	12	20	37	71	151
<i>Well-drained stands</i>							
Coniferous foliage	–	0.56 (0.15)	0.61 (0.02)	0.37 (0.03)	0.31 (0.05)	0.32 (0.05)	0.50 (0.10)
Coniferous non-foliage	–	0.56 (0.09)	0.39 (0.01)	0.36 (0.07)	0.45 (0.11)	0.37 (0.02)	0.70 (0.20)
Broadleaf foliage	–	0.43 (0.03)	0.56 (0.03)	0.91 (0.21)	0.76 (0.29)	0.81 (0.11)	1.30 (0.10)
Broadleaf non-foliage	–	0.92 (0.62)	0.30 (0.06)	0.56 (0.17)	0.39 (0.08)	0.27 (0.09)	1.30 (0.60)
<i>Poorly drained stands</i>							
Coniferous foliage	–	0.61 (0.10)	0.52 (0.09)	0.44 (0.06)	0.26 (0.03)	0.24 (0.05)	0.50 (0.10)
Coniferous non-foliage	–	1.11 (0.55)	0.40 (0.17)	0.50 (0.03)	0.44 (0.11)	0.52 (0.07)	0.70 (0.20)
Broadleaf foliage	–	0.65 (0.14)	0.66 (0.03)	0.75 (0.14)	0.60 (0.10)	0.63 (0.14)	1.30 (0.10)
Broadleaf non-foliage	–	0.73 (0.48)	0.45 (0.11)	0.54 (0.18)	0.54 (0.07)	0.78 (0.02)	1.30 (0.60)

Plot-to-plot standard deviations ( $N = 4$  in well-drained stands and 5 in poorly drained stands) are in parentheses. Values for the 151-year-old stands are from Gower et al. (2000)

Soil drainage had no consistent effect on litter-fall [N] (Table 4). No consistent difference was seen between woody and leaf litter [N] ( $F_{2,183} = 1.85$ ;  $P = 0.160$ ), although some individual sites showed significant differences. The difference between deciduous and coniferous litter [N] (0.3%) was significant ( $F_{1,183} = 20.88$ ;  $P < 0.0001$ ). Woody debris [N] (Table 5) was significantly affected by site, debris size, and decay state ( $P < 0.0001$  for all) but not by soil drainage ( $P = 0.051$ ). Larger and less-decayed woody debris had lower [N].

Soil [N] (measured only in the well-drained stands) ranged from 0.03% to 0.21% (Table 6), and did not differ significantly between stands ( $F_{7,38} = 1.69$ ;  $P = 0.141$ ). Concentrations declined significantly with soil horizon depth ( $F_{2,38} = 21.28$ ;  $P < 0.0001$ ) at all sites, with mean values ranging from ~0.2% in the A horizon to 0.05% in the C.

#### Nitrogen content and requirement

Nitrogen content of vegetation plus detritus ranged from 18.4 to 99.7 g N m<sup>-2</sup> in the well-drained stands and 37.8–154.6 g N m<sup>-2</sup> in the poorly drained stands (Fig. 1). Dead moss and forest floor tissue dominated non-soil N storage, with trees (in the well-drained stands) and live moss (in the poorly drained stands) secondarily

important. Vegetation + detritus N content generally was significantly higher in older stands. Drainage had a significant effect ( $F_{1,49} = 4.86$ ;  $P = 0.032$ ) on vegetation + detritus N content, with lower values in the well-drained stands, primarily because of the large amount of N stored in dead moss (on average 62% of non-soil N in the well-drained stands and 75% in the poorly drained stands; Fig. 1). Trees (21%) and live moss (14%) were also important in the well- and poorly drained stands, respectively.

Soil N content ranged from 323 to 518 g N m<sup>-2</sup>. Pit-to-pit variability was high, and soil N content did not significantly differ between stands ( $F_{6,16} = 2.09$ ;  $P = 0.112$ ). The overall mean soil N was 380.6±93.4 g N m<sup>-2</sup>. Soil N was not measured in the poorly drained stands.

Annual vegetation N requirement ( $N_{REQ}$ ) varied with stand age (Fig. 2), and was significantly higher in poorly drained stands ( $F_{1,49} = 4.95$ ;  $P = 0.031$ ) because of extremely high bryophyte growth in a few of these stands. Trees comprised the greatest fraction of total stand  $N_{REQ}$  in most of the well-drained stands, while bryophytes dominated poorly drained stand  $N_{REQ}$  in the poorly drained stands. In both chronosequences, the fine roots  $N_{REQ}$  comprised a greater fraction of total  $N_{REQ}$  in the older stands.

**Table 5** Nitrogen concentrations (percent dry mass basis) for woody debris, by debris size and decay class

Decay class	Diameter (cm)					Mean
	1–2	2–5	5–10	10–20	20+	
I	0.15 (0.06)	0.06 (0.03)	0.04 (0.04)	0.02 (0.01)	0.04 (0.02)	0.07 (0.06)
II	0.14 (0.05)	0.13 (0.06)	0.08 (0.04)	0.05 (0.03)	0.05 (–)	0.11 (0.06)
III	0.30 (0.08)	0.15 (0.06)	0.20 (0.16)	0.28 (0.29)		0.24 (0.13)
Mean	0.20 (0.10)	0.11 (0.06)	0.10 (0.11)	0.06 (0.12)	0.04 (0.02)	0.13 (0.11)

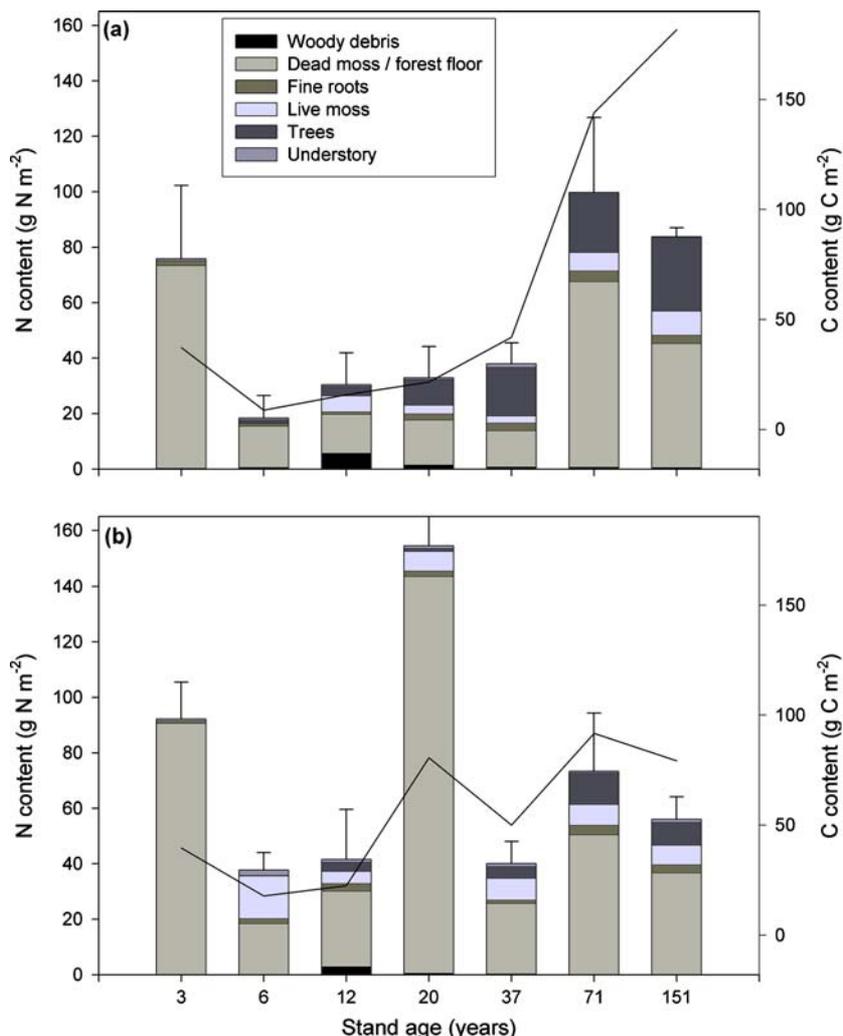
Decay classes (I = least decayed, III = most decayed) were defined by Bond-Lamberty et al. (2002b). Site-to-site standard deviations ( $N = 14$ ) are in parentheses

**Table 6** Soil nitrogen concentrations (percent dry mass basis), by major horizon

Horizon	Years since fire						
	3	6	12	20	37	71	151
<i>Well-drained stands</i>							
A	0.10 (0.04)	0.11 (0.06)	0.21 (0.03)	0.15 (0.04)	0.20 (0.03)	0.17 (0.06)	0.08 (–)
B	0.06 (0.02)	0.05 (0.01)	0.07 (0.02)	0.07 (0.04)	0.14 (0.04)	0.10 (0.01)	0.08 (0.01)
C	0.05 (0.02)	0.03 (0.01)	0.04 (0.01)	0.03 (0.02)	0.04 (0.01)	0.05 (0.02)	0.03 (0.01)

Pit-to-pit standard deviations ( $N = 3$  for most stands) are in parentheses

**Fig. 1** Nitrogen (N) content by tissue type for the (a) well- and (b) poorly drained chronosequences, excluding soil. Error bars show total nitrogen content standard error ( $N = 4$  in well-drained stands and 5 in poorly drained stands). For clarity, figures have been scaled to cut off large error bar (of  $91 \text{ g N m}^{-2}$ ) in 20-year-old poorly drained stand. Line graph (right-hand axis) shows stand carbon content (Wang et al. 2003)



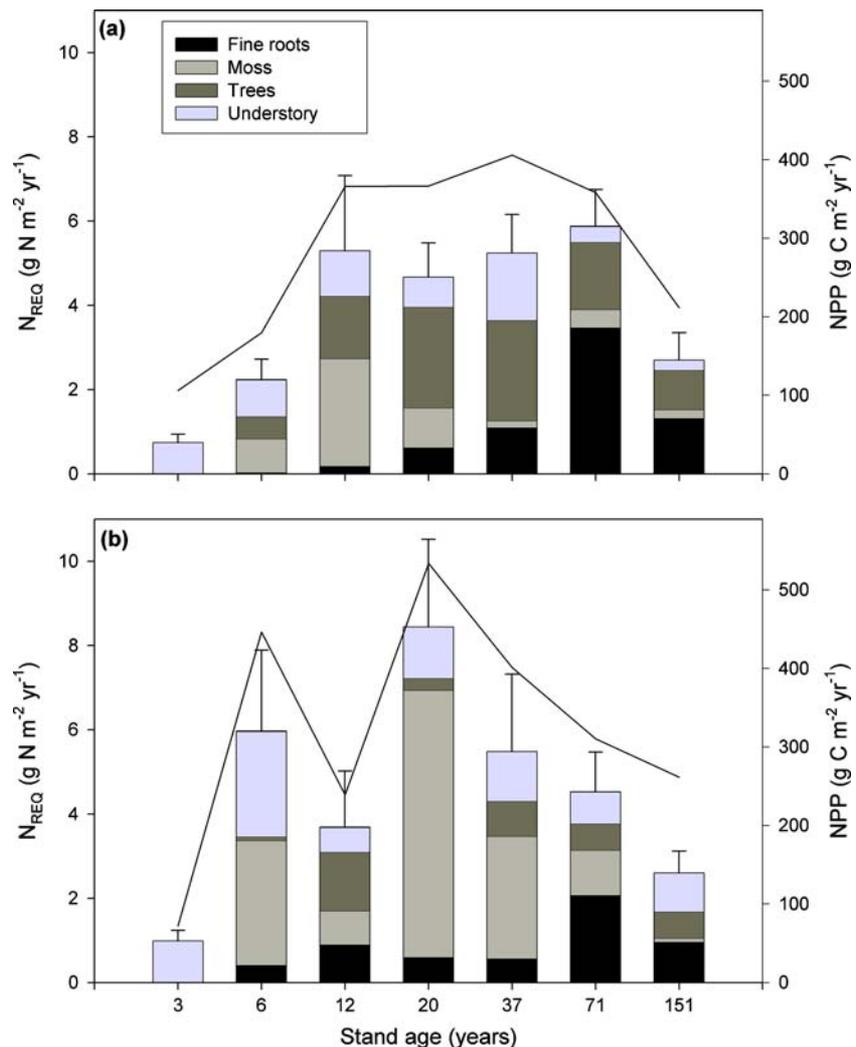
### Nitrogen use efficiency and retranslocation

Tree nitrogen use efficiency (NUE) varied with soil drainage, tree species, and between stands (Fig. 3). The NUE of aspen (overall mean of  $93 \text{ g g}^{-1} \text{ N}$ ) and black spruce ( $149 \text{ g g}^{-1} \text{ N}$ ) were both significantly lower than that of jack pine ( $176 \text{ g g}^{-1} \text{ N}$ ;  $P < 0.01$  in both cases). Both aspen and jack pine NUE were significantly lower in dry stands than in wet ones ( $P < 0.001$  in both cases), but soil drainage had no effect on black spruce NUE ( $F_{1,53} = 0.24$ ;  $P = 0.62$ ). Total tree NUE was significantly higher in older stands than in younger ones ( $F_{5,53} = 33.88$ ;  $P < 0.001$ ), both because of shift from deciduous to evergreen leaf habit, and higher NUE in older stands for both black spruce and jack pine (data not

shown). On a tissue-specific level, wood and foliage were about equally “efficient” to construct, as measured using NUE, for both black spruce and jack pine (Fig. 4). Aspen wood was relatively low-efficiency, a function not of high new branch [N] (cf. Table 2) as much as its low NPP for this N investment (Bond-Lamberty et al. 2004b). Foliage N mean residence time (MRT) was 7.4 years for jack pine and 13.4 years for black spruce.

Bryophyte NUE was lower than tree NUE, ranging from  $< 100 \text{ g g}^{-1} \text{ N}$  in the youngest stands to 120–140 in the oldest (Fig. 3). Bryophyte NUE was unaffected by soil drainage but increased significantly ( $F_{5,52} = 13.07$ ;  $P < 0.0001$ ) with stand age (Fig. 3c). Total stand NUE (i.e., total NPP divided by total  $N_{\text{REQ}}$ ) was

**Fig. 2** Nitrogen requirement ( $N_{REQ}$ ) by tissue type for the (a) well- and (b) poorly drained chronosequences. Error bars show total nitrogen requirement standard error ( $N = 4$  in well-drained stands and 5 in poorly drained stands). Line graph (right-hand axis) shows net primary production (NPP) (Bond-Lamberty et al. 2004b)



~150  $g g^{-1} N$  for all stands except the very youngest (Fig. 3).

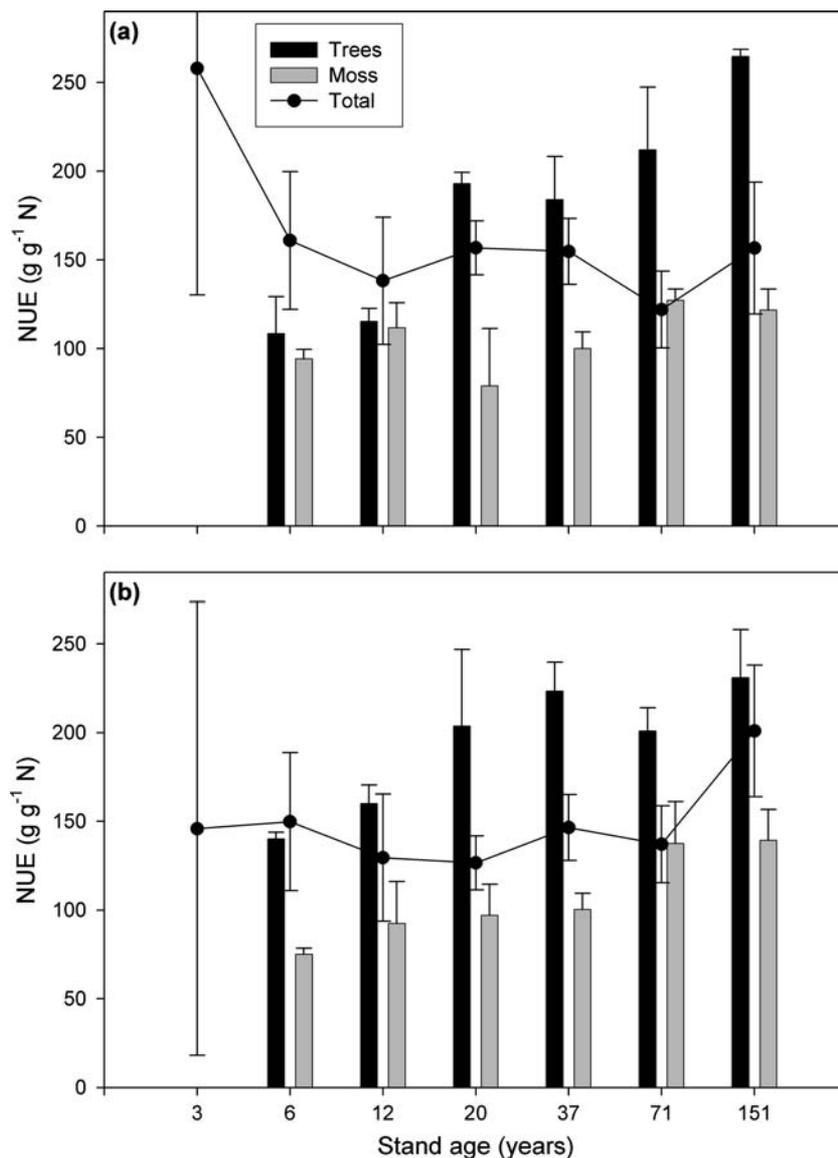
Stand age generally affected  $N_{RETRANS}$  more strongly than either species or soil drainage (Fig. 5). Black spruce had significantly lower  $N_{RETRANS}$  than aspen (42–48% vs. 49–65%, respectively,  $P = 0.021$ ) but not jack pine (47–56%,  $P = 0.156$ ). Soil drainage affected only the jack pine  $N_{RETRANS}$  ( $F_{1,25} = 37.47$ ;  $P < 0.001$ ), with much higher rates in well-drained stands.

## Discussion

The chronosequence design is useful for studying long-term changes in ecosystem structure and

function following disturbance, but problematic because distinguishing the effects of time and changes in treatment can be difficult, particularly concerning soil pools and fluxes, which are slow-acting and difficult to measure (Turvey and Smethurst 1989). The chronosequence discussed here was not formally replicated, but, the stand characteristics of this chronosequence were consistent with those from a broad range of extensive study plots across the BOREAS Northern Study Area (Bond-Lamberty et al. 2004b). In addition, our results generally corroborate results from similar studies in temperate forests. For these reasons, we assume the study sites comprise a true chronosequence in this discussion.

**Fig. 3** Nitrogen use efficiency (NUE) for major trees, moss, and total (including understory) in the (a) well-drained and (b) poorly drained stands. Error bars show plot-to-plot standard error ( $N = 4$  in well-drained stands and 5 in poorly drained ones)



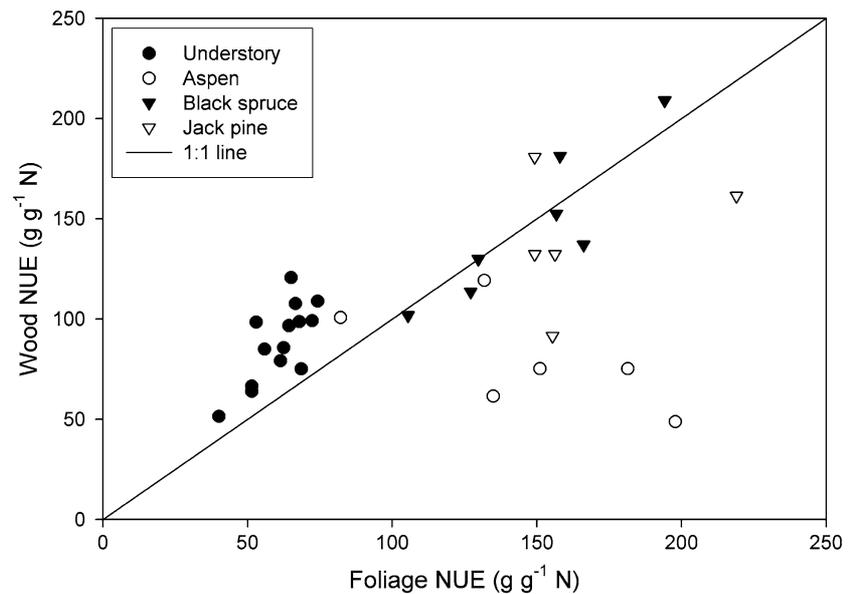
### Nitrogen concentration and content

The N concentration and N content values reported in this study are similar to those reported for other boreal stands (Cole and Rapp 1981; Van Cleve et al. 1983; Gower et al. 2000; Wirth et al. 2002). Schulze et al. (1995) and Wirth et al. (2002) found no correlation between stand age and ecosystem N content in Siberian boreal forests, but we observed positive correlations between total N content and stand age in both the well-drained and, less clearly, poorly drained

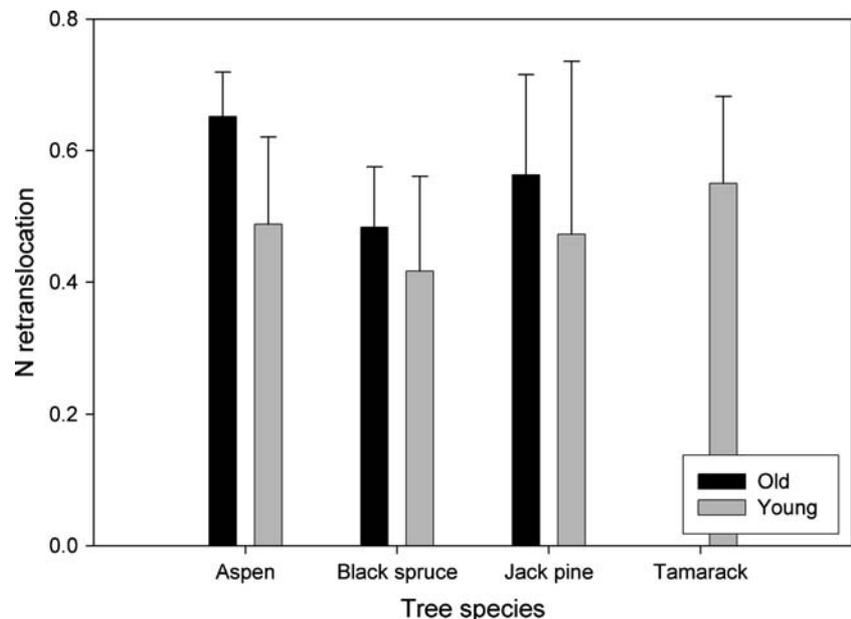
stands (Fig. 1). The inverse relationship between tree diameter and [N], a result of N moving out of cells as they senesce, has previously been noted for woody parts of both conifer and hardwood trees (Santantonio et al. 1977; Kozłowski and Pallardy 1997).

Trees contained the greatest fraction of total biomass (live + dead, excluding soil) in both the well- and poorly drained stands (Wang et al. 2003), but as noted above dead moss and forest floor dominated N storage in these stands. Woody debris had 0–19% of total non-soil N content,

**Fig. 4** Wood versus foliage nitrogen use efficiency (NUE), by species



**Fig. 5** Fraction nitrogen (N) retranslocation from senescing foliage for the dominant tree species in the chronosequence. “Old” refers to the 71- and 37-year-old stands; “young” stands are the 20-, 12-, and 6-year-old stands



with a mean of 3%, lower than previously reported values for northern coniferous forests (Laiho and Prescott 2004); the correlation between woody debris decay state and [N] results from long-term N immobilization by decomposer microbes (Lambert et al. 1980). Soil N comprised 76–96% of total system N, generally declining as a percentage with increasing stand age. Previous studies provided estimates of soil N for Manitoba black spruce forests that ranged from 300–

800  $\text{g N m}^{-2}$  (Trumbore and Harden 1997; Gower et al. 2000; Harden et al. 2003); the mean value reported here for the well-drained stands (381  $\text{g N m}^{-2}$ ) falls at the lower end of this range.

#### Nitrogen requirement and retranslocation

Nitrogen requirement values of 3–8  $\text{g N m}^{-2} \text{yr}^{-1}$  are commonly measured in boreal systems (Cole and Rapp 1981), a range consistent with the  $N_{\text{REQ}}$

**Table 7** Tree nitrogen requirement ( $N_{REQ}$ ,  $g\ N\ m^{-2}\ yr^{-1}$ ) and uptake for the well- and poorly drained chronosequences, by stand age, tissue type and soil drainage

	Years since fire						
	3	6	12	20	37	71	151
<i>Well-drained stands</i>							
Foliage $N_{REQ}$	0.0 (–)	0.41 (0.47)	0.97 (0.12)	0.93 (0.08)	0.99 (0.80)	1.23 (0.38)	0.73 (0.16)
Foliage uptake	0.0 (–)	0.24 (0.28)	0.27 (0.08)	0.46 (0.07)	0.34 (0.25)	0.43 (0.14)	0.33 (0.08)
Wood $N_{REQ}$	0.0 (–)	0.12 (0.19)	0.52 (0.06)	1.48 (0.21)	1.38 (0.30)	0.37 (0.10)	0.22 (0.06)
Total tree uptake	0.0 (–)	0.35 (0.46)	0.79 (0.09)	1.94 (0.27)	1.72 (0.53)	0.80 (0.23)	0.55 (0.14)
<i>Poorly-drained stands</i>							
Foliage $N_{REQ}$	0.0 (–)	0.04 (0.01)	0.83 (0.30)	0.20 (0.12)	0.51 (0.14)	0.54 (0.15)	0.50 (0.13)
Foliage uptake	0.0 (–)	0.04 (0.01)	0.38 (0.18)	0.21 (0.18)	0.27 (0.12)	0.19 (0.04)	0.23 (0.13)
Wood $N_{REQ}$	0.0 (–)	0.04 (0.02)	0.57 (0.15)	0.13 (0.10)	0.32 (0.09)	0.09 (0.02)	0.13 (0.04)
Total tree uptake	0.0 (–)	0.08 (0.02)	0.95 (0.30)	0.34 (0.27)	0.59 (0.20)	0.28 (0.06)	0.37 (0.16)

Plot-to-plot standard deviations ( $N = 4$  in well-drained stands and 5 in poorly drained stands) are in parentheses

values reported here (Fig. 2). In this study the middle-aged stands (20–71 years) had the highest  $N_{REQ}$  values, a pattern consistent with that observed by Cole and Rapp (1981) for a variety of boreal stands. The lowest  $N_{REQ}$  values were in the 3-year-old stands; the N requirements of such young stands with low N storage are met through a combination of fixation, atmospheric deposition, and a “fire fertilization” effect (Harden et al. 2003).

The interaction between N and fine roots is complex and poorly understood (Ruess et al. 1996; Nadelhoffer 2000). Fine root uptake comprised the greatest fraction of  $N_{REQ}$  in the older chronosequence stands (Fig. 2), although we emphasize that these results depend on fine root [N], which was not measured in this study. The foliar values used as proxies for fine root [N] correspond well, however, to Alaskan boreal black spruce fine root [N] (Ruess et al. 2003). In addition, the fine root NPP values also used in the  $N_{REQ}$  calculation have the largest errors, and are the most uncertain, of all NPP values measured in these stands (Bond-Lamberty et al. 2004b). Thus the fine root  $N_{REQ}$  and N content values reported here should be viewed as approximate.

Boreal evergreen needleleaf and deciduous broadleaf forests exhibit large differences in ecosystem structure and function, differences that have been extensively studied (Cole and Rapp 1981; Gower et al. 1995; Reich et al. 1997). Less attention has been paid to physiological changes within a species or functional group over time

(Zackrisson et al. 2004). For example, process models normally have a single parameterization for a species (Amthor et al. 2001), but our  $N_{RETRANS}$  results suggest that the differences between young and old members of a species may be just as significant as inter-specific differences. The data in Table 7 also imply that N derived from foliar retranslocation may supply 60–76% of N required by the trees in these stands. The only exceptions were the 37- and 20-year-old dry stands, both with relatively large deciduous (particularly aspen) tree populations, in which  $N_{RETRANS}$  was 36–38% of  $N_{REQ}$ .

The poorly drained stands in this study exhibited notably different patterns of N storage and requirements from their well-drained counterparts. Bryophytes form a critical part of C and N cycles in poorly drained boreal systems (O’Connell et al. 2003; Turetsky 2003). The bryophytes in these poorly drained stands had both moderate tissue [N] (Table 3) and high productivity (Bond-Lamberty et al. 2004b), and as a result comprised a large fraction of total stand  $N_{REQ}$  (Fig. 2). Bryophytes are generally less N-limited than vascular plants (Turetsky 2003 and references therein), and their production often declines as N availability increases (Mäkipää 1995; Hobbie et al. 2002).

#### Nitrogen-carbon dynamics

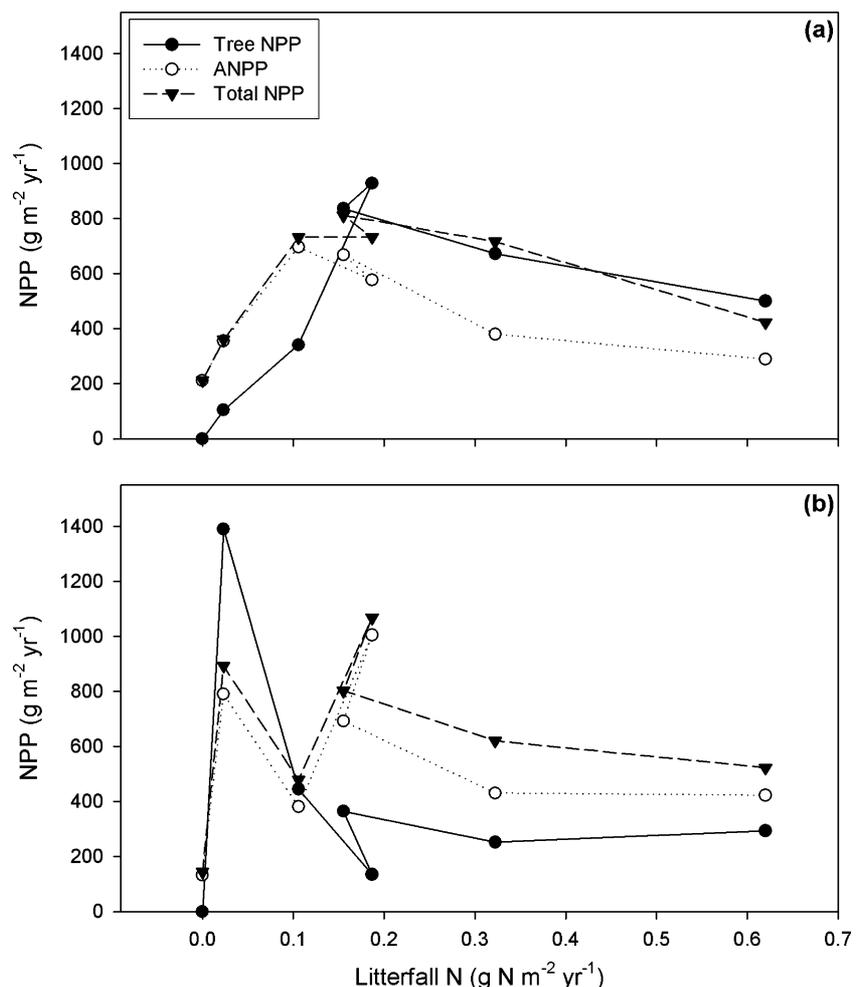
The NUE values reported here were at the low end of reported boreal NUE (Gower et al. 2000 and

references therein), but were similar to values reported for boreal *Picea mariana* and *Picea abies* stands (Van Cleve et al. 1983; Helmisaari et al. 2002; Finér et al. 2003). NUE at the stand level is influenced by a number of physiological factors, including the NUE of photosynthetic tissue, retranslocation efficiency, leaf turnover, leaching losses, and nutrient absorption rates per unit of root or mycorrhizae tissue (Landsberg and Gower 1997; Schlesinger 1997). A strong inverse relationship exists between NUE and litterfall N content in world forests (Vitousek 1982); however Vitousek (1982) explicitly excluded young and poorly drained stands from his study. The pattern observed in this study, encompassing stands of varying drainages and seven ages, was quite different: tree NUE was positively correlated to litterfall N and stand age (Fig. 3). This may be

related to the exhaustion of post-fire N from the forest floor and soil (Dyrness and Norum 1983; Dyrness et al. 1989; Harden et al. 2003). The fact that total stand NUE was constant with stand age implies overall conservative patterns of N use, however, consistent with the paradigm that black spruce forests are N-limited (Van Cleve et al. 1983).

Linear relationships between litterfall N and aboveground net primary production (ANPP) have been shown for temperate and boreal stands forests (Reich et al. 1997; Gower et al. 2000). The stands studied by these authors, however, were generally mature and comprised of a single dominant species. A simple relationship between litterfall N and tree NPP was not observed for the chronosequence stands in this study. Some broad patterns were evident, however. In the well-drained stands, low NPP was coincident with low and high litterfall N values (Fig. 6a),

**Fig. 6** Litterfall nitrogen (N) versus tree net primary production (NPP), aboveground net primary production (ANPP), and total NPP, for the (a) well-drained and (b) poorly drained stands. Lines connect successive stands in the chronosequence



corresponding respectively to very young postfire stands and the mature, closed-canopy black spruce stands. At moderate litterfall N—the mixed, high-productivity stands in the middle of the chronosequence—NPP was high. In the poorly drained stands, low tree litterfall conditions and high bryophyte productivity were common (Wang et al. 2003; Bond-Lamberty et al. 2004b), resulting in a fundamentally different relationship between NPP and litterfall N (Fig. 6b). This emphasizes the difference in N dynamics between aggrading successional stands and better-studied mature forests.

## Conclusion

Boreal forests are generally considered to be N-limited, but relatively little work has been done to elucidate how N dynamics change with stand age in the North American *Picea mariana* forest. The results of this study show that variables such as N concentration, requirement, and retranslocation change significantly with stand age. In addition, the N dynamics of poorly drained black spruce stands differ considerably from the better-studied, well-drained stands. Further work elucidating the links between fire, soil drainage, and nutrients will improve our understanding of this important system, and our ability to model future changes in biogeochemical cycles.

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## References

- Amthor JS, Chen JM, Clein JS, Frolking SE, Goulden ML, Grant RF, Kimball JS, King AW, McGuire AD, Nikolov NT, Potter CS, Wang S, Ofsy SC (2001) Boreal forest CO<sub>2</sub> exchange and evapotranspiration predicted by nine ecosystem process models: intermodal comparisons and relationships to field measurements. *J Geophys Res-Atmos* 106(D24):33623–33648
- Apps MJ, Kurz WA, Luxmoore RJ, Nilsson LO, Sedjo RA, Schmidt R, Simpson LG, Vinson TS (1993) The changing role of circumpolar boreal forests and tundra in the global carbon cycle. *Water Air Soil Poll* 70:39–53
- Binkley D (1992) Mixtures of N<sub>2</sub>-fixing and non-N<sub>2</sub>-fixing tree species. In: Cannell MGR, Malcolm DC, Robertson P (eds) *The ecology of mixed species stands of trees*. Blackwell, Oxford, pp 99–123
- Bond-Lamberty B, Wang C, Gower ST (2002a) Above- and belowground biomass and sapwood area allometric equations for six boreal tree species of northern Manitoba. *Can J For Res* 32(8):1441–1450
- Bond-Lamberty B, Wang C, Gower ST (2002b) Annual carbon flux from woody debris for a boreal black spruce fire chronosequence. *J Geophys Res-Atmos* 108(D3): art. no. 8220 (WFX 1-1 to 1–10)
- Bond-Lamberty B, Wang C, Gower ST (2002c) Leaf area dynamics of a boreal black spruce fire chronosequence. *Tree Physiol* 22(14):993–1001
- Bond-Lamberty B, Wang C, Gower ST (2004a) The contribution of root respiration to soil surface CO<sub>2</sub> flux in a boreal black spruce fire chronosequence. *Tree Physiol* 24(12):1387–1395
- Bond-Lamberty B, Wang C, Gower ST (2004b) Net primary production and net ecosystem production of a boreal black spruce fire chronosequence. *Global Change Biol* 10(4):473–487
- Bond-Lamberty B, Wang C, Gower ST (2005) Spatio-temporal measurement and modeling of boreal forest soil temperatures. *Agric For Meteorol* 131(1–2):27–40
- Bremner JM (1965) Total nitrogen. *Methods of Soil Analysis, Part 2*. C. A. Black, Madison, WI. *Am Soc Agron* 9:1149–1178
- Clymo RS (1970) The growth of *Sphagnum*: methods of measurement. *J Ecol* 58(1):13–49
- Cole DW, Rapp M (1981) Element cycling in forest ecosystems. In: Reichle DE (ed) *Dynamic properties of forest ecosystems*. Cambridge University Press, London, pp 341–409
- DeLuca TH, Nilsson M-C, Zackrisson O (2002a) Nitrogen mineralization and phenol accumulation along a fire chronosequence in northern Sweden. *Oecologia* 133:206–214
- DeLuca TH, Zackrisson O, Nilsson M-C, Sellstedt A (2002b) Quantifying nitrogen-fixation in feather moss carpets of boreal forests. *Nature* 419:917–920
- Dyrness CT, Norum RA (1983) The effects of experimental fires on black spruce forest floors in interior Alaska. *Can J For Res* 13:879–893
- Dyrness CT, Van Cleve K, Levison JD (1989) The effect of wildfire on soil chemistry in four forest types in interior Alaska. *Can J For Res* 19:1389–1396
- Finér L, Mannerkoski H, Piirainen S, Starr M (2003) Carbon and nitrogen pools in an old-growth, Norway spruce mixed forest in eastern Finland and changes associated with clear-cutting. *For Ecol Manage* 174:51–63
- Flanagan LB, Van Cleve K (1983) Nutrient cycling in relation to decomposition and organic-matter quality in taiga ecosystems. *Can J For Res* 13:795–817
- Flannigan MD, Bergeron Y, Engelmark O (1998) Future wildfire in circumboreal forests in relation to global warming. *J Veg Sci* 9(4):469–476
- Foster NW, Morrison IK (1976) Distribution and cycling of nutrients in a natural *Pinus banksiana* ecosystem. *Ecology* 57:110–120

- Foster NW, Morrison IK, Hazlett PW, Hogan GD, Salerno MI (1995) Changes in nutrient procurement with age and site productivity in jack pine forests. *New Zeal J For Ecol* 24:169–182
- Goldammer JG, Furyaev VV (1996) Fire in ecosystems of boreal Eurasia: ecological impacts and links to the global system. In: Goldammer JG, Furyaev VV (eds) *Fire in ecosystems of boreal Eurasia*, vol 48. Kluwer Academic Publishers, Dordrecht, pp 1–20
- Gower ST, Gholz HL, Nakane K, Baldwin VC (1994) Production and carbon allocation patterns of pine forests. *Ecol Bull (Copenhagen)* 43:115–135
- Gower ST, Hunter A, Campbell JS, Vogel JG, Veldhuis H, Harden JW, Trumbore SE, Norman JM, Kucharik CJ (2000) Nutrient dynamics of the southern and northern BOREAS boreal forests. *Écoscience* 7(4):481–490
- Gower ST, Isebrands JG, Sheriff DW (1995) Carbon allocation and accumulation in conifers. In: Smith WK, Hinckley TM (eds) *Resource physiology of conifers*. Academic Press, San Diego, pp 217–254
- Gower ST, Krankina ON, Olson RJ, Apps MJ, Linder S, Wang C (2001) Net primary production and carbon allocation patterns of boreal forest ecosystems. *Ecol Appl* 11(5):1395–1411
- Gower ST, Vogel JG, Norman JM, Kucharik CJ, Steele S, Stow TK (1997) Carbon distribution and aboveground net primary production in aspen, jack pine, and black spruce stands in Saskatchewan and Manitoba, Canada. *J Geophys Res* 102(D24):29029–29041
- Halliwell DH, Apps MJ (1997) Boreal ecosystem-atmosphere study (BOREAS) biometry and auxiliary sites: soils and detritus data. AB, Forestry Canada, Northern Forestry Centre, Edmonton
- Harden JW, Mack M, Veldhuis H, Gower ST (2003) Fire dynamics and implications for nitrogen cycling in boreal forests. *J Geophys Res-Atmos* 108(D3):art. no. 8223
- Helmisaari H-S, Makkonen K, Kellomäki S, Valtonen E, Mälkönen E (2002) Below- and above-ground biomass, production and nitrogen use in Scots pine stands of eastern Finland. *For Ecol Manage* 165:317–326
- Hobbie SE, Nadelhoffer KJ, Högberg P (2002) A synthesis: the role of nutrients as constraints on carbon balances in boreal and arctic regions. *Plant Soil* 242(1):163–170
- Kasischke ES, Stocks BJ (eds) (2000) *Fire, climate change, and carbon cycling in the boreal forest*. Springer-Verlag, New York
- Kozlowski TT, Pallardy SG (1997) *The physiological ecology of woody plants*. Academic Press, San Diego
- Laiho R, Prescott CE (2004) Decay and nutrient dynamics of coarse woody debris in northern coniferous forests: a synthesis. *Can J For Res* 34(4):763–777
- Lambert RL, Lang GE, Reiners WA (1980) Loss of mass and chemical change in decaying boles of a subalpine balsam fir forest. *Ecology* 61(6):1460–1473
- Landsberg JJ, Gower ST (1997) Applications of physiological ecology to forest management. Academic Press, San Diego
- Linder S, Benson ML, Myers BJ, Raison RJ (1987) Canopy dynamics and growth of *Pinus radiata*. 1 Effects of irrigation and fertilization during a drought. *Can J For Res* 17(10):1157–1165
- Litvak M, Miller S, Wofsy SC, Goulden ML (2002) Effect of stand age on whole ecosystem CO<sub>2</sub> exchange in the Canadian boreal forest. *J Geophys Res-Atmos* 108(D3):art. no. 8225 (WFX 6–1 to 6–11)
- Mäkipää R (1995) Effect of nitrogen input on carbon accumulation of boreal forest soils and ground vegetation. *For Ecol Manage* 79:217–226
- Nadelhoffer KJ (2000) The potential effects of nitrogen deposition on fine-root production in forest ecosystems. *New Phytol* 147:131–139
- O’Connell KEB, Gower ST, Norman JM (2003) Net ecosystem production of two contrasting boreal black spruce forest communities. *Ecosystems* 6(3):248–260
- Reich PB, Grigal DF, Aber JD, Gower ST (1997) Nitrogen mineralization and productivity in 50 hardwood and conifer stands of diverse soils. *Ecology* 78(2):335–347
- Ruess RW, Hendrick RL, Burton AJ, Pregitzer KS, Sveinbjornsson B, Allen MF, Maurer GE (2003) Coupling fine root dynamics with ecosystem carbon cycling in black spruce forests of interior Alaska. *Ecol Monogr* 73(4):643–662
- Ruess RW, Van Cleve K, Yarie J, Viereck LA (1996) 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(8):1326–1336
- Santantonio D, Hermann RK, Overton WS (1977) Root biomass studies in forest ecosystems. *Pedobiologia* 17:1–31
- SAS Institute Inc (2001) SAS OnlineDoc® Version 8. Cary, NC
- Schlesinger WH (1997) *Biogeochemistry: an analysis of global change*. Harcourt Brace & Company, San Diego
- Schulze E-D, Schulze W, Kelliher FM, Vygodskaya NN, Ziegler W, Kobak KI, Koch H, Arneth A, Kusnetsova WA, Sogatchev A, Issajev A, Bauer GA, Hollinger DY (1995) Aboveground biomass and nitrogen nutrition in a chronosequence of pristine Dahurian *Larix* stands in eastern Siberia. *Can J For Res* 25(6):943–960
- Sellers J, Hall FG, Kelly D, Black TA, Baldocchi DD, Berry JA, Ryan MG, Ranson KJ, Crill PM, Lettenmaier DP, Margolis H, Cihlar J, Newcomer J, Fitzjarrald DR, Jarvis PG, Gower ST, Halliwell DH, Williams D, Goodison B, Wickland DE, Guertin FE (1997) BOREAS in 1997: experiment overview, scientific results, and future directions. *J Geophys Res* 102:28731–28769
- Soil Classification Working Group (1998) *The Canadian system of soil classification*. NRC Research Press, Ottawa, Canada
- Steele S, Gower ST, Vogel JG, Norman JM (1997) Root mass, net primary production and turnover in aspen, jack pine and black spruce forests in Saskatchewan and Manitoba, Canada. *Tree Physiol* 17:577–587

- Stocks BJ, Lee BS, Martell DL (1996) Some potential carbon budget implications of fire management in the boreal forest. In: Apps MJ, Price DT (eds) Forest ecosystems, forest management and the global carbon cycle vol 40. Springer, Berlin, p 451
- Trumbore SE, Harden JW (1997) Accumulation and turnover of carbon in organic and mineral soils of the BOREAS northern study area. *J Geophys Res-Atmos* 102(D24):28817–30
- Turetsky MR (2003) The role of bryophytes in carbon and nitrogen cycling. *The Bryologist* 106(3):395–409
- Turvey ND, Smethurst PJ (1989) Apparent accumulation of nitrogen in soil under radiata pine: misleading results from a chronosequence. Research Strategies for Long-term Site Productivity, Proceedings, IEA/BE A3 Workshop, Seattle, WA, August 1988. IEA/BE Report No. 8, Forest Research Institute, New Zealand
- Van Cleve K, Oliver L, Schlentner RE, Viereck LA, Dyrness CT (1983) Productivity and nutrient cycling in taiga forest ecosystems. *Can J For Res* 13:747–767
- Van Cleve K, Viereck LA, Schlentner RE (1971) Accumulation of nitrogen in alder (*Alnus*) ecosystems near Fairbanks, Alaska. *Arctic Alpine Res* 3:101–1141
- Veldhuis H (1995) Soils of the Tower Sites and Super Site, Northern Study Area (BOREAS), Thompson, Manitoba, Canada. Winnipeg, MB, Agriculture and Agri-Food Canada, Res. Branch, Centre for Land and Biological Resources Research, Manitoba Land Resource Unit, p 61
- Viereck LA (1983) The effects of fire in black spruce ecosystems of Alaska and northern Canada. In: Wein RW, MacLean DA (eds) The role of fire in northern circumpolar ecosystems. John Wiley & Sons, New York, pp 201–220
- Vitousek PM (1982) Nutrient cycling and nutrient use efficiency. *Am Nat* 119(4):553–572
- Vitousek PM, Howarth RW (1991) Nitrogen limitation on land and in the sea: how can it occur? *Biogeochemistry* 13:87–115
- Vitousek PM, Reiners WA (1975) Ecosystem succession and nutrient retention: a hypothesis. *BioScience* 25(6):376–81
- Vogt KA, Vogt DJ, Bloomfield J (1998) Analysis of some direct and indirect methods for estimating root biomass and production of forests at an ecosystem level. *Plant Soil* 200:71–89
- Wan S, Hui D, Luo Y (2001) Fire effects on nitrogen pools and dynamics in terrestrial ecosystems: a meta-analysis. *Ecol Appl* 11(5):1349–1365
- Wang C, Bond-Lamberty B, Gower ST (2002) Soil surface CO<sub>2</sub> flux in a boreal black spruce fire chronosequence. *J Geophys Res* 108(D3):art. no. 8224 (WFX 5-1 to 5–8)
- Wang C, Bond-Lamberty B, Gower ST (2003) Carbon distribution of a well- and poorly-drained black spruce fire chronosequence. *Global Change Biol* 9(6):1–14
- Wirth C, Schulze E-D, Lühker B, Grigoriev S, Siry M, Harges G, Ziegler W, Backor M, Bauer GA, Vygodskaya NN (2002) Fire and site type effects on the long-term carbon and nitrogen balance in pristine Siberian Scots pine forests. *Plant Soil* 242(1):41–63
- Zackrisson O, DeLuca TH, Nilsson M-C, Sellstedt A, Berglund LM (2004) Nitrogen fixation increases with successional age in boreal forests. *Ecology* 85(12):3327–3334