

INTERACTING EFFECTS OF SOIL NITROGEN SUPPLY AND LIGHT AVAILABILITY  
ON UNDERSTORY SAPLING GROWTH AND FOLIAR ATTRIBUTES

by

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## Abstract

Light availability in forest understories is a well recognized constraint on sapling growth, but limitations in soil nitrogen (N) availability, and the link to foliar photosynthetic capacity, typically receive less consideration in describing stand dynamics. My primary hypothesis is that light and soil N availability have species-specific effects on photosynthetic activity and growth, and that together these resources will better define understory development in complex forests. To test these relationships, I examined 1) soil N indices and the tradeoffs between soil fertility and light attenuation in old-growth forest understories; 2) the effects of light and N constraints on understory sapling foliar N concentration ( $N_{\%}$ ), N per unit area ( $N_a$ ), and natural abundance of  $^{13}\text{C}$ ; 3) the effects of light and soil N supply on species growth and photosynthetic activity in a factorial field experiment; and 4) the mechanisms responsible for the stagnation of understory saplings. Soil N indices incorporating dissolved inorganic N and organic N were useful in characterizing differences in N supply among contrasting sites. Understory light availability declined with increasing soil N supply, while understory *Abies lasiocarpa* had strong correlations between foliar  $N_{\%}$  and soil N availability, despite shading effects. In partial-cut forests, understory *Tsuga heterophylla* and *Picea glauca* x *sitchensis* had consistent foliar  $N_{\%}$  across gradients of light availability; in contrast, foliar  $N_{\%}$  of *Betula papyrifera* and *Thuja plicata* declined with increasing shade, which would distort assessments of soil fertility and perhaps contribute to increased mortality of these species in deep shade. Strong correlations between foliar  $N_a$  and  $^{13}\text{C}$  or growth increment suggest foliar N per unit area is the simplest integration of light availability and N nutrition on leaf photosynthetic activity. Ontogenic interactions that occur among foliar attributes and tree size in forest understories, especially for saplings < 1 m in height, contribute to time effects on growth patterns and emphasize the need for long-term studies of species autecology and stand dynamics. My experimental manipulation of light and N supply on saplings was ineffective, and future research using natural gradients in site productivity may be more fruitful in defining species response to light and N interactions.

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## Co-authorship Statement

Chapter 2 was co-authored with Clive Dawson and Dave Dunn of the BC Ministry of Forests analytical lab. I designed and conducted the study, including plot selection, field sampling, soil preparation, data analysis and manuscript preparation. Clive Dawson and Dave Dunn undertook the chemical analysis of the soil and foliar samples. Will MacKenzie described the plant communities of the sites, Rick Trowbridge assisted me in soil classification and evaluation of nutrient/moisture regimes, and Peter Ott was consulted on statistical analysis. Marcel Lavigne and Bill Borrett assisted in the field work and sample preparation.

Chapter 3 was co-authored with Suzanne Simard. I designed and conducted the study, including light measurements, foliar and soil moisture sampling, data analysis and manuscript preparation. Marcel Lavigne and Bill Borrett assisted me in field work and sample preparation, while Clive Dawson and Dave Dunn undertook the foliar N analysis. Suzanne Simard assisted in the manuscript preparation and revisions.

Chapter 4 was co-authored with Suzanne Simard, Dave Coates and Rob Guy. I designed and conducted the study, including light measurements, foliar and soil nitrogen sampling, data analysis and manuscript preparation. Marcel Lavigne assisted me in field work and sample preparation, Clive Dawson and Dave Dunn undertook the foliar and soil analysis, Kathy Gordon undertook the  $^{13}\text{C}$  analysis, and Peter Ott was consulted on statistical analysis. Suzanne Simard, Dave Coates and Rob Guy assisted in experimental design and manuscript revisions. Dave Coates and colleagues from the Ministry of Forests in Smithers were responsible for establishing the Date Creek Research Forest.

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Chapter 6 was co-authored with Suzanne Simard, Dave Coates and Rob Guy. I designed and conducted the study, including light measurements, foliar and biomass sampling, data analysis and manuscript preparation. Marcel Lavigne and Bill Borrett assisted me in field work and sample preparation, Clive Dawson and Dave Dunn undertook the foliar analysis, Kathy Gordon undertook the  $^{13}\text{C}$  analysis, and Peter Ott was consulted on statistical analysis. Suzanne Simard, Dave Coates and Rob Guy assisted in experimental design and manuscript revisions.

# 1 Introduction

## Context

Forest managers in British Columbia are under pressure to adapt more complex silvicultural regimes that retain live trees and add structural diversity to managed stands (Coates and Burton 1997, Franklin et al. 2000). Commercial forests also undergo natural gap formation through disease, insects and blowdown that create multi-cohort stand conditions and structural complexity. Managing stands with overstory retention is challenging as the forest canopy reduces light levels by varying degrees, which affects growth responses and species interactions of the regenerating stand (Messier et al. 1999). The resulting uncertainty in stand performance has prompted scientists to examine tree growth and light conditions that can occur under partial-cutting systems. These relationships have been incorporated into models, such as SORTIE (spatially-explicit, mixed-species forest dynamics simulator), that predict juvenile tree growth (Coates et al. 2003). Currently these simulation models are based on species-specific growth relationships to light conditions, and do not yet allow for differences in tree productivity due to soils (or, more specifically, the effects of soils on tree nitrogen [N] status). This simplification may be adequate for modelling juvenile tree growth across constant site conditions, but is less appropriate where tree N status varies temporally or spatially.

Nitrogen is generally recognized as the largest nutritional limit to tree growth in northern temperate or boreal forests, and together with light, is one of the key growth-limiting resources acting on understory trees (Chapin et al. 1987). The relative ability of plant species to capture and compete for light and N resources simultaneously is one of the most fundamental attributes of species autecology, and is fundamental to plant succession theory in the ecological literature (i.e., resource-ratio hypothesis; Tilman 1985). For this reason, development of realistic models of forest regeneration and stand dynamics requires development of species-specific response curves along interacting resource gradients of light and N supply. Most of this research originated with greenhouse studies, which are instructive but require careful extrapolation from preliminary growth responses to the long life-spans of natural forests. In some cases, the results from seedling experiments have contradicted the evidence from natural history, leading to the suspicion of ontogenic effects that complicate interpretations of, for

example, shade tolerance (Niinemets 2006). Detailed studies of natural gradients in soil and light resources, or experimental manipulations of light and N status in field settings, could provide additional information to formulate a better understanding of species autecology.

In this thesis, I explored relationships among soil N supply, light availability and physiology of selected tree species of northwestern British Columbia. The first specific objective was to refine indices of soil N availability, and to determine whether traditional measures of N mineralization were adequate for forest ecosystems with substantial rates of organic N uptake (Schimel and Bennett 2004). The second objective was to quantify the interacting effects of understory light attenuation and soil N supply on understory saplings in mature forests, and provide a more thorough framework for understanding growth-constraining resources in complex landscapes. The third objective was to link tree response to these limiting resources, not only through height and diameter growth responses, but also through foliar attributes that govern the photosynthetic capacity of the plant (Reich et al. 1998). In particular, the foliar concentration of N, leaf N per unit area, and natural abundance of  $^{13}\text{C}$  isotope were utilized to integrate and quantify light and N constraints to growth and photosynthesis. The fourth objective was to experimentally manipulate N supply around light availability gradients to fully test species response to these resource interactions. The final objective was to examine whether sapling growth response in forest understories was a constant and predictable function of light and N availability, or dependent in part on the current size of the tree.

## **Literature review**

### **Light and N as constraints on photosynthesis and growth**

Solar energy is absorbed by leaves and used in photosynthesis, and consequently there are strong causal relationships established between light availability and plant growth. For most plants, photosynthetic response to light intensity at the leaf level is roughly hyperbolic, with 90% of maximum net photosynthesis occurring between one-third and two-thirds of full sunlight (Kozlowski et al. 1991). These light response curves are characterized by a light compensation point ( $I_c$ ) where photosynthetic  $\text{CO}_2$  uptake and respiratory  $\text{CO}_2$  release are in equilibrium. When  $I_c$  is exceeded, there is at first a linear

increase in CO<sub>2</sub> uptake. The steepness of this slope indicates the efficiency of the light reactions, and can be expressed as a quantum yield. At higher light levels, the yield of photosynthesis increases only slightly until becoming light saturated (I<sub>s</sub>). At this point the rate of CO<sub>2</sub> uptake is limited by enzymatic processes and by the supply of CO<sub>2</sub>. The positions of I<sub>c</sub> and I<sub>s</sub> can vary between tree species due to differences in photosynthetic efficiencies, and often reflect adaptations to specific habitats or successional pathways (Larcher 2003).

Whole-plant growth response to light availability is difficult to predict from leaf-level studies because of the variable effects of leaf density and age, within crown differences in leaf structure and orientation, and self-shading within the crown. A number of field trials have therefore been used to quantify the relationship between juvenile tree growth and light availability for many tree species in northern temperate forests, including western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*), hybrid spruce (*Picea glauca* x *sitchensis*), subalpine fir (*Abies lasiocarpa*), paper birch (*Betula papyrifera*), and lodgepole pine (*Pinus contorta*) (Klinka et al. 1992, Wang et al. 1994, Kayahara et al. 1996, Chen 1997, Mailly and Kimmins 1997, Chen 1998, Wright et al. 1998, Coates and Burton 1999, Claveau et al. 2002).

Some differences in tree species response to light are apparent from these field studies, where shade-tolerant species respond better to an increase in light at low-light levels, while shade-intolerant species have greater growth rates at high light levels (Klinka et al. 1992, Walters et al. 1993, Pacala et al. 1994, Wright et al. 1998, Coates and Burton 1999). In general, however, there is a fairly large degree of overlap in light response curves for most tree species in northern temperate British Columbia. In contrast to leaf-level studies, diameter and height growth generally increase steadily with increasing irradiance, especially for the most shade-intolerant species, with no clear whole-plant light saturation point (Coates and Burton 1999, Drever and Lertzman 2001). This light requirement can be met in relatively small gaps, as opening sizes of 0.1 to 0.2 ha have produced similar growth rates to those found in the open conditions of clearcuts for most tree species (Coates 2000).

Nitrogen is required by plants for the construction of proteins that determine photosynthetic potential (Evans 1996). This includes the thylakoid and pigment-protein

complexes (chlorophyll) involved with light capture, photosynthetic electron transport and photophosphorylation. In the dark reactions of photosynthesis, N is needed primarily for rubisco (ribulose 1,5-bisphosphate carboxylase oxygenase) and other enzymes in the Calvin and photorespiratory cycles. As a consequence, photosynthetic capacity has been shown to increase linearly (or sometimes curvilinearly) with leaf N content for a number of plant species (Field and Mooney 1986, Evans 1989a). There is, however, significant variation in N-use efficiency (Berendse and Aerts 1987) between species and ecologically distinct plant groups (Reich et al. 1995, Evans 1996). The relationship between photosynthetic capacity and leaf N concentration is thought to be affected by the specific leaf area and leaf life-span, the specific activity of rubisco, and the N allocation within photosynthetic tissues (the amount of rubisco per unit soluble protein and the fraction of leaf N actively involved with photosynthesis) (Wullschleger 1993, Hikosaka and Hirose 2000).

A significant, positive relationship between foliar N and site index has been reported for juvenile trees under full light for many conifer species (Radwan and DeBell 1980, Radwan and Harrington 1986, Kayahara et al. 1995, Wang and Klinka 1997, Kranabetter et al. 2003). In addition, soil N availability is usually well correlated with tree productivity in temperate and boreal forests (Powers 1980, Adams and Attiwill 1986, Kraske and Fernandez 1990, Klinka et al. 1994, Reich et al. 1997, Wang 1997, Chen et al. 1998, Carlyle and Nambiar 2001), and N fertilization typically causes large increases in juvenile tree growth in many forests of the Pacific Northwest (Brockley et al. 1992). Improvements in soil N availability typically lead to higher foliar N concentration, increased leaf area, enhanced photosynthesis and a greater allocation of new growth to aboveground rather than belowground components (Brix 1971, 1981, 1983, MacDonald and Lieffers 1990, Mitchell and Hinckley 1993, Chandler and Dale 1995, Brown et al. 1996a, Canham et al. 1996, Pacquin et al. 2000).

Nitrogen response curves are not as well developed as light response curves for juvenile trees because of the difficulty in creating or locating a wide gradient of N availability in the field. In one example, Kranabetter et al. (2003) reported strong linear correlations between height growth of saplings and foliar N concentrations. On these sites, the difference in leader growth between contrasting sites was comparable in



magnitude to the productivity differences between deeply shaded and unshaded saplings (e.g. 5 to 70 cm height increment), which reaffirms the contribution of soil fertility to stand dynamics. Similar to light saturation points, conifers can achieve levels of adequate nutrition where growth, and presumably photosynthesis, no longer respond to increased N supply. Adequate concentrations of foliar N have been determined through fertilizer trials for many conifer species of the Pacific Northwest, and usually fall between 14 and 16 g N kg<sup>-1</sup> (van den Driessche 1974, Ballard and Carter 1986, Walker and Gessel 1991, Carter 1992, Brockley 2001).

### **The interaction of light and N constraints on photosynthesis and growth**

Phenotypic plasticity allows for plants to optimize response curves and carbon gain across varying irradiance and N supplies. At high light levels, N is invested in carboxylation to maximize electron transport, while at low light levels N is partitioned into chlorophyll to maximize light absorption (Field and Mooney 1986, Evans 1989b, Evans 1996). Shade-tolerant plants tend to partition more N into the thylakoids than shade-intolerant plants (Evans 1989b). Grassi and Bagnaresi (2001), for example, found that shade-tolerant *Abies alba* responded to high light only through changes in leaf morphology, while more intolerant *Picea abies* was also able to allocate more N to rubisco and increase photosynthetic activity under high light. Plants can also respond to light gradients within a canopy by allocating a higher proportion of N to the upper leaves (which are exposed to higher irradiances) to maximize photosynthesis (Field 1983).

The ability at the leaf and whole-plant level to react to both light and N availability is therefore a key attribute for maintaining productivity under shade (Niinemets 1997). Niinemets et al. (1998) further concluded that the response of leaf N to irradiance at low light levels is a strong determinant of species shade tolerance. For example, trees are at an advantage if they can compensate for photosynthesis loss under low light with ample foliar N (Mitchell and Hinckley 1993). In a greenhouse study of *Tsuga heterophylla* and *Abies amabilis*, Mitchell and Arnott (1995) suggested that the N nutrition (~ 1.8% foliar N) was high enough to allow sufficient production of chlorophyll to prevent limitations to photosynthesis imposed by shade. Canham et al. (1996) demonstrated a similar tradeoff between light and N availability, where seedlings (*Acer*

*rubrum*, *Pinus strobus*, *Quercus rubra* and *Acer saccharum*) at 20% light and high N availability (with no water stress) achieved greater biomass than seedlings at full light with limited N availability. In contrast, shaded seedlings in field settings have experienced increased mortality with N fertilizer application (Catovsky and Bazzaz 2002), suggesting an imbalance between above- and belowground resources. Moisture limitations can also reduce N compensation; Jose et al. (2003), for example, reported that high N status increased net photosynthesis for shaded *Pinus palustris* seedlings only if soil moisture was not limiting.

There have been some investigations into the significance of interactions between light availability and tree N status (or relative site quality) on sapling growth within natural ecosystems. Carter and Klinka (1992) reported that shade-tolerance of western redcedar, western hemlock and Douglas-fir varied to some degree with site quality. For example, western hemlock was classified as shade tolerant on slightly dry sites and moderately tolerant on fresh and moist sites. Walters and Reich (1997) found that *Acer saccharum* seedling growth in low light understories varied three-fold with regional variation in soil N and water availability. There were also strong relationships between leaf N and growth for low-light seedlings, which likely indicated greater photosynthetic activity through light capture. Finzi and Canham (2000) examined sapling growth in response to light and N availability for six species in the northeastern US. Variation in light availability explained most of the variation in sapling growth, with only small effects from N availability detected for red maple and sugar maple. It was likely that the selection of sites did not encompass a wide range in N availability, which probably minimized the apparent significance of nitrogen effects on tree growth. Drever and Lertzman (2001) found little effect of site quality (both nutrient and moisture availability) on growth of Douglas-fir at light levels below approximately 40% full sun. There was substantial variation in height growth at a given light level in this retrospective study, which may have resulted from microsite variation in N supply. Kobe (2006), in one of the most thorough studies to date, reported interspecific differences in sapling growth in response to soil resources and light, and concluded that N effects were strongest in high-light early successional communities. Foliar N concentrations were used as a predictor of growth response, but these concentrations were not linked to site resources. The

relationships derived by Kobe (2006) would have been more useful in understanding stand dynamics across landscapes (i.e., where sites vary in quality or light exposure) if foliar N concentrations had been linked to variability in soil fertility and light availability.

## **Overview of thesis**

The primary objective of my thesis was to relate soil N supply and light availability to leaf photosynthetic capacity for each species of interest, and through these relationships, develop tools (indices of soil N supply, light availability and foliar attributes) for facilitating further research into soil-tree interactions driving stand dynamics in complex landscapes. In Chapter 2, I investigate indices of soil N availability, especially organic N, for improving characterization of soil fertility in cool, moderately-productive forest ecosystems. In Chapter 3, I compare soil N supply, along with light availability, across soil productivity gradients in undisturbed old-growth forests to better understand the tradeoffs in resource constraints acting on understory saplings. Foliar N concentrations ( $N_{\%}$ ) and N per unit area ( $N_a$ ) were investigated for both subalpine fir and lodgepole pine to verify interpretation of these parameters. In Chapter 4, I examine foliar attributes of understory saplings across partial-cutting gradients to develop species-specific relationships between foliar  $N_{\%}$  or  $N_a$  and light availability under a stable soil N supply. In this same experimental setting, I attempted to manipulate N supply across these light gradients to fully test the response of tree species to combinations of these resources (Chapter 5). Lastly, in Chapter 6, I investigate the possible reasons for growth stagnation of understory saplings in partially-cut forests, and whether the loss in productivity for these saplings was related to declining photosynthetic capacity. I end the thesis with general conclusions on light-N interactions, and suggest further avenues of inquiry and recommendations for improving methods for exploring these relationships.

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## 2 Indices of dissolved organic nitrogen, ammonium and nitrate along productivity gradients of boreal forests<sup>1</sup>

### Introduction

The assessment of soil nitrogen (N) availability, one of the most fundamental properties of forest ecosystems, is being reconsidered in light of the evidence for plant uptake of organic N (Schimel and Bennett 2004). The significance of organic N availability versus inorganic N is felt to increase in less productive, N-poor soils (arctic, alpine and boreal ecosystems) where decomposition is limited and microbial N immobilization is high. A number of examples of organic N uptake by plants have been reported in field studies, and these findings suggest a need to improve upon the methodologies for assessing plant-available N (Lipson and Näsholm 2001, Read and Perez-Moreno 2003). As intriguing as these developments are, however, there are still uncertainties about the extent to which organic N contributes to plant nutrition (Jones et al. 2005), and more field-based evidence is needed before discrediting techniques and indices (e.g. *in situ* buried bags, ion exchange resins; Binkley and Hart 1989) that have often proven successful in characterizing forest soil fertility.

A useful exploration of soil N indices would be from natural gradients in soil fertility, as characterized by plant communities which develop in relation to site features (Pojar et al. 1987, Wang 2000). In upland boreal forests, plant communities and soils typically range from ericaceous shrubs, bryophytes and mor humus forms on poor, dry soils to lush forests with herbaceous understories and moder or mull humus forms (Moss 1953, Wali and Krajina 1973). Significant relationships among boreal plant communities and soil N availability have been demonstrated through broad indices such as total soil N, C:N ratios or mineralizable N (Lahti and Väisänen 1987, Klinka et al. 1994, Chen et al. 1998) and rates of N mineralization and nitrification (Giesler et al. 1998, Diekmann and Falkengren-Grerup 1998). More recently, Nordin et al. (2001) described how N availability on poor ericaceous sites in Fennoscandian boreal forests was dominated by amino acids, while soil  $\text{NH}_4^+$  and  $\text{NO}_3^-$  concentrations increased through the low-herb and tall-herb forests. Organic N sources may therefore be as important as inorganic N sources in sites of low plant productivity, and have key influences on plant community structure and species diversity (Kielland 1994, McKane et al. 2002).

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Developing more biologically-relevant indices of soil N availability through organic N measures could facilitate research into ecological relationships and forest management issues of boreal forests. Ideally such indices would reflect rates of organic N depolymerization or mineralization, rather than providing only static measures of N pools (Schimel and Bennett 2004). I tested a possible approach, using a simple variation of the buried bag technique (Binkley et al. 1990), where both dissolved organic N (DON) and dissolved inorganic N (DIN) were extracted after an *in situ* incubation. These indices, along with microbial N, mineralizable N and related soil properties, were compared across plant associations, similar to those described from Fennoscandian boreal forests (Giesler et al. 1998), which represent the widest range in soil fertility and corresponding site potential in southern boreal forests of British Columbia.

The objectives of this study were to 1) document the abundance and *in situ* production of DON and DIN in mineral soils and forest floors along natural boreal forest productivity gradients; 2) evaluate the utility of DON indices compared to inorganic, microbial and other related indices of N availability in correlations with site potential; and 3) discuss how N patterns from these localized boreal forests fit with the model hypothesized for N availability gradients across terrestrial ecosystems (Schimel and Bennett, 2004).

## **Materials and Methods**

### **Site descriptions**

The southern boreal forest of British Columbia is designated as the Sub-Boreal Spruce Zone (SBS), and is located in the montane landscape of the central interior, within the closed forest portion of the Cordilleran boreal region (Meidinger and Pojar 1991, Pojar 1996). The SBS has a continental climate characterized by severe, snowy winters and short, warm, moist summers. Upland coniferous forests are comprised of lodgepole pine (Pl) (*Pinus contorta* Dougl. ex Loud), hybrid white spruce (Sx) (*Picea glauca* x *Picea engelmannii* [Moench] Voss) and subalpine fir (Bl) (*Abies lasiocarpa* [Hook.] Nutt.). Soils are free of permafrost and formed on predominantly deep blankets of lacustrine sediments, glacialfluvial deposits or glacial tills with coarse fragments of mixed lithology (Valentine et al. 1978).

The study sites were located in the moist cold (mc) subzone of the SBS near Smithers, British Columbia, Canada (54°49' 127°10'; elevation 522 m). Smithers has a mean annual air temperature of 3.9°C and mean annual precipitation of 513 mm (354 mm as rainfall) (Environment Canada, 2006). Four site series (represented by climax plant communities corresponding to soil moisture and nutrient regime; Pojar et al. 1987) were sampled to provide a wide range in upland edaphic conditions: (02) xeric and poor P1 – *Cladonia*; (01) mesic and medium Sx – Huckleberry; (06) subhygric and rich Sx – Oak fern; and (09) subhygric and very rich Sx – Devil's club (Banner et al. 1993). Site series are hereafter referred to by their nutrient regime and plant association name.

Five transects, with one replicate of each site series, were located along a 25 km portion of the McDonnell Forest Service Road (54°40' to 47' and 127°16' to 36') at approximately 900 m elevation (Table 2.1). I was unable to find a suitable VR – Devil's club plot on the fourth transect, however, so the study was limited to 19 plots. Each plot was 50 m x 30 m (0.15 ha) in size. Plots were separate and generally < 200 m apart within a transect. All plots had coniferous forests (Table 2.1) and were mostly multicohort due to gap-phase disturbance caused by bark beetles, root pathogens and wind throw, as well as a small amount of partial harvesting (ranging from 0-10% of the basal area) that occurred through the valley in the 1950's.

The Poor - *Cladonia* plots were coarse-textured fluvial fans or eskers and very rapidly drained, with a typical rooting depth of 35 cm. Soils were described as Eluviated or Orthic Dystric Brunisols (Soil Classification Working Group 1998), with thin forest floors characterized as Hemimors (matted, tenacious Fm horizon; Green et al. 1993). Plant communities included *Cladonia* lichens, with scattered black huckleberry (*Vaccinium membranaceum*), kinnikinnick (*Arctostaphylos uva-ursi*) and soopolallie (*Shepherdia canadensis*).

The Medium – Huckleberry plots were well to moderately-well drained sites on slopes of approximately 20%, with a typical rooting depth of 35 cm. Soils developed on morainal blankets and were described as Orthic Dystric Brunisols or Eluviated Dystric Brunisols, with Hemimor humus forms. Feathermosses (*Pleurozium schreberi*, *Ptilium crista-castrensis*, and *Hylocomium splendens*) carpeted the forest floor, along with

scattered five-leaved bramble (*Rubus pedatus*), black huckleberry, heart-leaved arnica (*Arnica cordifolia*) and bunchberry (*Cornus canadensis*).

The Rich – Oak fern plots were located across lower slopes and were imperfectly drained, with mottles and seepage at 35 – 55 cm depths (in the spring) and rooting to 30 cm. Soils were described as Gleyed Dystric Brunisols or Orthic Dystric Brunisols, with relatively thick forest floors, usually characterized by aggregated, less matted humus forms (Fa horizons – Leptomoder or Lignomoder; Green et al. 1993). Feathermosses carpet the forest floor, but understory herbs and shrubs were also abundant, especially oak fern (*Gymnocarpium dryopteris*), foam flower (*Tiarella trifoliata*) and thimbleberry (*Rubus parviflorus*).

The Very Rich – Devil's club plots were located near ephemeral or permanent streams, but with no standing water table due to either deeper seepage (> 1 m depth) or more dynamic soil moisture regimes (pulses after rain events rather than constant seepage). Soils were described as Orthic Dystric Brunisols or Orthic Sombric Brunisols, with weakly aggregated, friable humus forms (Mormoder to Leptomoder; Green et al. 1993), intermittent Ah horizons and rooting to 35 cm. Plant cover was dominated by vigorous devil's club (*Oplopanax horridus*), oak fern, prickly gooseberry (*Ribes lacustre*) and highbush cranberry (*Viburnum edule*).

### **Soil sampling**

Soil samples were collected in late spring (June 5-9, 2006), at the onset of the active growing season, for N parameters, soil nutrients and microbial biomass. Three microsites were randomly selected per plot. From each of these microsites, I bulked three subsamples of forest floor and mineral soil taken within a 2.5 m radius. Forest floors were sampled with a 15 cm diameter template to the mineral soil interface (some microsites with thin forest floors were sampled across 20-30 cm to obtain enough material for analysis) and the depths of the F and H horizons were noted. Pure decayed wood was avoided when sampling forest floors. Mineral soils were sampled to a 20 cm depth using a stony soil auger (4 cm in diameter). The soil samples were run through a 5 mm sieve and a subsample taken for moisture content (105°C for 24 hours; these mineral subsamples were then ground and resieved to 2 mm to correct for remaining coarse fragment content). Samples were refrigerated and a portion immediately shipped on ice

for an analysis of microbial C + N, amino acids and DON. The remaining soil was used either for an aerobic laboratory incubation or air-dried for soil chemical analyses (both forest floors and mineral soils after air-drying were ground and sieved to 2 mm).

At this same time, forest floor and mineral soils were incubated *in situ* for 5 weeks using buried bags (Hart et al. 1994). Intact forest floor was sampled using a 15 cm template, avoiding pure decayed wood. Mineral soils were too rocky to extract as an intact core, so a stony auger was used to sample down to 20 cm. Mineral soils were gently poured back into a polyethylene bag lining the sample hole, and the bag was sealed with a twist tie. Forest floor cores were put into a separate polyethylene bag, which was placed on top of the mineral soil bag, and covered with moss or leaf litter. This was repeated at 5 random microsites per plot. After 5 weeks, the bags were retrieved and each sample gently run through a 5 mm sieve. One subsample was taken for moisture content (mineral subsamples were ground and resieved to 2 mm to correct for remaining coarse fragment content), while a second subsample was immediately shipped on ice to the Forest Service lab for the analysis of DIN and DON.

An aerobic long-term incubation of N potential ( $N_0$ ) was undertaken using the collected fresh bulk soils described above. An equivalent dry weight of 100 g mineral soil and 25 g forest floor was put into 1 L glass jars. A uniform gravimetric moisture content at approximately field capacity was used in the incubation, determined beforehand to be 300% for forest floors and 40% for mineral soils. Moisture content of the soils was adjusted with distilled water, and the jars were covered and incubated at 22°C in the dark, with the lids removed once a week to replenish the air. The weight of the jar plus moist soil was noted at the beginning of the experiment, and distilled water was added every two to three weeks to maintain this moisture content. After 12 weeks the samples were shipped to the Forest Service Lab for an analysis of inorganic N.

Gravimetric soil moisture contents of the forest floors and mineral soils (0-20 cm depth) were measured every 3 weeks from mid May to early September. Three random microsites were sampled and bulked together per plot. Moisture content was determined by drying soils at 105°C for 24 hours. Mineral soils were then ground and sieved to determine gravimetric moisture content of the fine fraction (< 2 mm).

### **Forest measures**

The oldgrowth forests (~ 180 years) on our sites had ceased height growth (i.e., reached an asymptote) decades earlier. The full extent of tree height closely reflects site index (Ryan and Yoder 1997), and I used the asymptotic or ‘maximum obtainable’ stand height of the oldgrowth forests as a measure of site potential. The height of three mature trees of each species were measured with a Forester Vertex (Haglöf, Sweden), for a total of nine trees per plot where possible (in some of the Poor - Cladonia stands only lodgepole pine occurred). From the upper canopy, I selected codominant trees with good form (no broken tops, forks, large sweeps, etc.) and no evidence of ongoing height growth. Where numerous candidate trees were available, I selected trees widely spaced across the plot to obtain a better stand average. Basal area was determined in two fixed-radius plots of 5.65 m by measuring diameter at 1.3 m (DBH) on every tree > 12 cm in diameter. Tree age was determined from increment cores taken from one codominant tree per species, and the leading age was reported for each plot (Table 2.1).

Foliage was sampled from five randomly selected co-dominant subalpine fir in September 18-21, 2006, except in Poor - Cladonia plots where subalpine fir was found in the subcanopy. Foliage in the upper 1/3 of mature trees was retrieved by removing small branches (using a 12-gauge shotgun), and the five sample trees were combined for one bulk sample per plot.

### **Laboratory analyses**

Analytical methods follow procedures described in Kalra and Maynard (1991) and Carter (1993). Total C, N and S were measured using combustion elemental analysis with a Fisons/Carlo-Erba NA-1500 NCS analyzer (Thermo Fisher Scientific, Waltham, MA), except for total S in the mineral soils which was measured by Leco S Analyzer (LECO Corp., St. Joseph, Mich.). Mineralizable N (min-N) was determined by a 2 week anaerobic incubation at 30°C, followed by a 1M KCl extraction and colorimetric analysis for ammonium N. Exchangeable cations and cation exchange capacity (CEC) were determined with 0.1 M barium chloride. Soil pH in H<sub>2</sub>O was determined with a 1:2 soil to solution ratio using an electronic pH meter and mineral soil texture was determined by the hydrometer technique. Foliar samples were oven-dried (70°C for 24 hours), ground



with a Wiley mill and analyzed for N by dry combustion with a Fisons/Carlo-Erba NA 1500 NCS analyzer.

Dissolved organic nitrogen,  $\text{NH}_4\text{-N}$  and  $\text{NO}_3\text{-N}$  were determined from a 5-g and 2-g dry-soil equivalent of mineral soil and forest floor, respectively (Hart et al. 1994, Jones and Willett 2006). A 2 M KCl solution was added to the soils at a 1:5 w/v ratio, and samples were shaken for 1 hour at 20°C. Samples were clarified by centrifugation for 15 minutes at 850 g. The extract was pipetted from the clear supernatant into an auto-analyzer cup for analysis. The  $\text{NH}_4\text{-N}$  and  $\text{NO}_3\text{-N}$  in the extracts were measured colorimetrically using an Alpkem Flow System IV analyzer (OI Analytical, College Station, Tex.).

A modified persulphate solution (low-N potassium peroxydisulphate) was used to convert dissolved organic N of the extract to nitrate (Qualls 1989). A 1-mL aliquot of persulphate solution was added to 1 mL of soil extract in a glass vial, which was then sealed and autoclaved (121°C for 30 minutes). Nitrate concentrations in the persulphate digests were measured colorimetrically on an Alpkem Flow System IV analyzer, and DON was calculated by subtracting DIN concentrations from the total. Colour absorption by the digest reagents was corrected for using control N blanks. Amino acids in the extract were measured using a ninhydrin method (Jones et al. 2002). 100  $\mu\text{L}$  of extract was mixed and shaken with 50  $\mu\text{L}$  of ninhydrin color reagent. The samples were heated for 25 minutes at 100°C, then cooled and mixed with 0.95 ml ethanol (50% v/v). Absorbance at 570 nm was measured with a UV-Visible spectrophotometer and corrected for  $\text{NH}_4^+$  levels in the determination of amino acid concentrations.

Microbial biomass C and N were determined by the chloroform fumigation-extraction method (Voroney et al. 1993) using a 10-g and 2.5-g dry-soil equivalent of mineral soils and forest floors, respectively. Soil samples were brought to uniform moisture contents of 300% and 40% for forest floors and mineral soils, respectively, immediately prior to fumigation. The unfumigated and fumigated extracts (0.5 M  $\text{K}_2\text{SO}_4$ ) were analyzed for total organic C and N using with a Shimadzu TOC-5050 (Kyoto, Japan) coupled with an Antek 9000-N Nitrogen Analyzer (Töllsjö, Sweden).

All nutrient concentration data ( $\text{g kg}^{-1}$  or  $\text{mg kg}^{-1}$ ) were expressed per kg soil. Forest floor concentration data were converted to mass per area ( $\text{kg ha}^{-1}$ ) using the

average depth of the F + H layer at each plot and a bulk density of  $100 \text{ kg m}^{-3}$ . Mineral soil conversions were based on a 20 cm depth, corrected for average coarse fragment content obtained via moisture sampling. Bulk density of mineral soil was assumed to be  $1000 \text{ kg m}^{-3}$  for the fine fraction ( $< 2 \text{ mm}$ ), with a particle density of the coarse fragments of  $2650 \text{ kg m}^{-3}$ . Bulk density values of forest floors and mineral soils were based on extensive soil sampling in unharvested stands of the SBS (J.M. Kranabetter, P. Sanborn, B. Chapman; unpublished data).

### **Statistical analyses**

The study was organized in a randomized complete block design. Parameters were tested using Proc Mixed in SAS (SAS Inc. 1988) with block and block interactions set as random factors (soil moisture was tested with repeated measures under proc Mixed). Residuals from the analyses were examined, and natural log transformations of DON and DIN parameters (both bulk soils and buried bags) were required to meet the assumptions of equal variance. Most soil chemical properties met the assumptions of equal variance with the exception of mineral soil S, Ca and Mg, which were also transformed for analysis. Concentration data were tested with subsamples ( $n = 57$  for bulk soils and  $n = 95$  for buried bags) while N content of the profile was tested with plot means ( $n = 19$ ). Significant differences among least square means of each plant association were tested using pairwise  $t$  tests at a significance level of 0.05.

A number of measures for N availability were tested against site potential of the plots. I tested parameters as a single variable for the soil profile by adding forest floor and mineral soil amounts ( $\text{kg ha}^{-1}$ ) together; an exception was C:N ratios which were tested separately by substrate. The GLM procedure in SAS using Type 1 Sums of Squares was used to test linear and curvilinear regressions between plot means for soil, foliar and stand attributes. The  $r^2$  value of curvilinear correlations was calculated using the corrected sums of squares through Proc NLIN in SAS.

## **Results**

### **Site characteristics**

Site potential, as determined by asymptotic stand height, ranged from 17 to 38 m (Table 2.1), and differed significantly among plant associations (Table 2.2). Foliar N

concentrations of subalpine fir ranged from 9.0 to 14.2 g kg<sup>-1</sup>, and increased across plant associations as well (Table 2.2). Throughout the summer, mineral soils were significantly wetter on the subhygric sites (R-Oak fern and VR-Devil's club), with mesic sites intermediate to the dry, poor sites (Table 2.2). Humus depth (F and H horizons) increased with plant association to an average maximum of 7 cm on rich and very rich sites (Table 2.2).

There were large differences in N mineralization potential (N<sub>o</sub>) of both forest floors and mineral soils, with some overlap between plant associations; N<sub>o</sub> concentrations of medium and rich sites differed between mineral horizons but not forest floors, while poor and medium sites differed by forest floors rather than mineral horizons (Table 2.2). For this reason the fertility gradient was more clearly differentiated among plant associations when expressed as N<sub>o</sub> of the whole profile (Table 2.2). Significant differences in the N status of the sites were also reflected by increasing total N and mineralizable N concentrations of forest floors and mineral soils with declining C:N ratios (Table 2.3). Other soil nutritional differences among plant associations include total S, CEC and exchangeable Ca + Mg, with slight increases in pH across nutrient regimes (Table 2.3).

### **DON and DIN indices**

DON concentrations in late spring from bulk soils showed weak differences among plant associations for both forest floors and mineral soils (Table 2.4). There were significant differences in DON mass per area, which was progressively greater with more productive soil nutrient regimes. Amino acid N averaged 20% of DON for both forest floors and mineral soils, and patterns across plant associations were similar to those for DON (Table 2.4). Microbial biomass N concentrations were not significantly different among plant associations for either forest floors or mineral soils, and only small increases were noted in microbial N mass per area (Table 2.4).

DON concentrations after the 5 week *in situ* incubation were slightly lower than those found earlier in the summer for bulk soils (10% and 2% lower on average for forest floors and mineral soils, respectively, across plant associations). DON concentrations of the forest floors were highest on medium sites, and lowest on very rich sites, with no differences detected in mineral soils (Table 2.5). Total DIN concentrations after the 5

week *in situ* incubation were weakly significant across forest floors, with larger differences detected in mineral soils (Table 2.5). The majority of inorganic N was  $\text{NH}_4^+$ , and only two very rich sites had notable amounts ( $> 2 \text{ mg kg}^{-1}$ ) of  $\text{NO}_3^-$  in forest floors and mineral soils.

On an area basis, DON contributed the largest proportion of extracted N in both substrates, and peaked in forest floors on rich sites and mineral soils on very rich sites (Fig. 2.1). Forest floors had greater amounts of DIN than mineral soils on all but the very rich sites (Fig. 2.1). The amount of DON in the combined profile was lowest on poor sites, with small increases through medium and richer sites (Table 2.5). DIN amounts in the profile were significantly different among plant associations, and were 2-3 times greater in magnitude with each progressive change in soil nutrient regime (Table 2.5). The proportion of DIN in the profile compared to DON nearly doubled with each plant association, from 6% on poor sites, on average, to 12%, 23% and 46% on medium, rich and very rich sites, respectively.

### **Correlations between nitrogen indices and site potential**

A number of standard soil properties were found to strongly correlate with asymptotic stand height, including total N, mineralizable N and C:N ratios (Table 2.6, Fig. 2.2). Microbial N mass was weakly significant ( $p < 0.10$ ) as a positive correlation to stand height, while microbial C:N of the forest floor was negatively correlated to stand height.

The amount of DON or amino acids in bulk soil was also significant in relation to stand height, but more weakly correlated than the other soil N indices (Table 2.6). The correlation for *in situ* DON was less precise than for *in situ* inorganic N (Table 2.6), but the DIN index fit best as a curvilinear regression with stand height (Fig. 2.3a). In contrast, the combined amount of *in situ* DON + DIN was linearly correlated to stand height, and was more significant than DON alone (Fig. 2.3b). Overall, I found that DON was the predominant form of extractable N in the soil profile, and was increasingly supplemented by  $\text{NH}_4^+$  on productive sites (Fig. 2.4). Small amounts of  $\text{NO}_3^-$  were found inconsistently along the productivity gradient, and only one very rich site had more inorganic N as  $\text{NO}_3^-$  than  $\text{NH}_4^+$ .

## Discussion

### Nitrogen status and forest productivity

Plant associations and site potential of these boreal forests were clearly related to inherent differences in N availability, and a number of N indices were very effective in evaluating the relative fertility of these soils. None of the more traditional parameters measured, such as *in situ* N mineralization, C:N ratio, or mineralizable N, could be considered inaccurate, and results were quite consistent with patterns of soils and fertility reported across many northern forest ecosystems (e.g., Van Cleve et al. 1983; Wang 1997). However, the assessment of DON, especially in relation to  $\text{NH}_4^+$  and  $\text{NO}_3^-$ , potentially provides more insights into N cycles and the nature of N uptake by plants than these other indices offer, and so could be an improved methodology for comparisons of functional differences in N availability.

The productivity gradient was fundamentally characterized by substrate availability (increasing N concentration and total N content of the profile) and quality (decreasing C:N ratios that reduce N immobilization), consistent with a variety of ecosystems (Booth et al. 2005). This enhanced N availability reflects the improved soil moisture regime and related geochemical effects (base cation supply, pH) down slopes or across landforms that influence key processes such as microbial activity, ion diffusion, disturbance severity, rates of N fixation and litter quality (Gosz 1981, Chapin 1991, Giesler et al. 1998, Högberg et al. 2006). Microbial C:N ratios were overall quite low, perhaps due to the season of sampling (Högberg et al. 2003), and the decline in this ratio suggested more humus forms on poor sites were fungal dominated, shifting to more bacterial biomass in moderate humus forms on richer sites (Högberg et al. 2003). Overall, the amount of plant-available N, as measured by *in situ* DIN + DON, averaged < 2% of total soil N, which demonstrates how little of the total N was actively cycled and potentially released for plant uptake.

### An evaluation of DON and DIN indices

The challenges to the paradigm of N mineralization as the sole source of plant-available N (Schimel and Bennett 2004) were supported by these results. First, the total amount of N mineralized and extracted after a substantial portion of the growing season was very low, perhaps too small to support forest needs. Estimates of annual N uptake

average  $14 \text{ kg ha}^{-1} \text{ year}^{-1}$  (range  $4 - 25 \text{ kg ha}^{-1} \text{ year}^{-1}$ ) for conifers and  $41 \text{ kg ha}^{-1} \text{ year}^{-1}$  ( $24 - 61 \text{ kg ha}^{-1} \text{ year}^{-1}$ ) for deciduous species across boreal forests (Gower et al. 2000), which is far more than the DIN supply across our sites, especially on poor to medium soils. In contrast, the supply of DIN + DON over this portion of the growing season, at  $10 - 55 \text{ kg ha}^{-1}$ , was more realistic given the likely magnitude of N uptake. Secondly, the relationship between DIN and site potential was curvilinear, suggesting N supply was increasingly underestimated on poorer sites. An alternative explanation for the curve would be luxury uptake of N on rich to very rich soils, but foliar N concentrations were not above levels considered adequate ( $\sim 14.5 \text{ g kg}^{-1}$ ; Carter 1992). In keeping with this, correlations between foliar N concentrations and asymptotic stand height were strongly linear across these sites, which would advocate for the combined DON + DIN index rather than DIN alone (Chapter 3). Despite these shortcomings, it should be noted that *in situ* N mineralization could still be a legitimate index of soil fertility since sites with increasing  $\text{NH}_4^+$  and  $\text{NO}_3^-$  concentrations were consistently more productive.

Nordin et al. (2001) and Yu et al. (2003) suggested DON is proportionally more important on infertile soils, and a similar argument could be made here given the pattern in DON concentrations of forest floors. However, I would emphasize the complete profile in evaluating N cycles, rather than solely humus layers, since rooting was abundant in both forest floors and upper mineral soil horizons. When converted to mass per area, DON of the profile did not decline with site potential, nor the proportion of amino acids, so logically this supply of N for plant uptake would be significant across the entire range of sites (Wallenda and Read 1999, Persson and Näsholm 2001, Kielland et al. 2006), unless amino acid N uptake becomes inhibited (Persson and Näsholm 2002). Actual rates of organic N uptake remain hypothetical, but conceptually at least, DON was the predominant form of extractable N in the soil profile, and was increasingly supplemented, rather than replaced, by  $\text{NH}_4^+$  and  $\text{NO}_3^-$  on productive sites (Fig. 2.4). As a consequence, the proportions of DIN:DON rarely surpassed 50%, which would suggest the most productive boreal ecosystems still occupy the comparatively limited stages of soil N availability and flux (i.e. Case A-B; Schimel and Bennett 2004). The nutritional contribution of DON in absolute amounts ( $\text{kg ha}^{-1}$ ) might therefore decline only in more productive temperate or deciduous forests.

### Comments on DON supply and assessment

Some consideration as to the source of the DON pool in boreal soils is warranted given its likely importance. All of the N forms measured *in situ* are typically in a state of rapid flux, often with a mean residence time of less than one day due to microbial uptake (McFarland et al. 2002, Nordin et al. 2004, Högberg et al. 2006). The small decline in DON concentrations after 5 weeks compared to initial bulk soils could indicate fairly continuous cycling of the more accessible soil organic N pools. Perhaps an ongoing supply of DON and DIN would reflect in part the grazing activity of soil fauna on the microbial community (Huhta et al. 1998, Heneghan and Bolger 1998). Forest floors and mineral soils in the SBS have remarkable numbers of fungal- and bacterial-feeding mites and collembola (approx. 250,000 m<sup>-2</sup>; Battigelli et al. 2004), which could produce N-compounds through feeding (cell lysis) and excretion that undergo depolymerization by extracellular enzymes (often supplied by ectomycorrhizal fungi; Read and Perez-Moreno 2003) for direct plant uptake. Some portion of DON is also of high molecular weight, and slow to breakdown (Johnsson et al. 1999, Jones and Kielland 2002, Jones et al. 2004), but the comparatively large pool of amino acids found here, at 20% of DON on average, clearly indicates a significant, more dynamic proportion (Yu et al. 2002, Berthrong and Finzi 2006). There are also likely to be seasonal pulses of DON through leaching of decomposing leaf and root litter in the spring, along with the die-off of winter microbial communities (Schmidt and Lipson 2004). The spring sampling was timed to coincide with this potential pulse of N, at the onset of root uptake, and subsequently DON might decline through other seasons (Yu et al. 2003, Weintraub and Schimel 2005).

There are undoubtedly potential artefacts in any assessment of organic N when physically disrupting soils, severing roots and processing samples (Jones et al. 2005, Jones and Willett 2006). Consequently it is difficult, if not impossible, to determine an absolutely accurate rate of N supply over time, and further refinement of DON and amino acid dynamics, especially in the rhizosphere, remains a challenge. Although not a direct measure of N-species uptake by trees, an assay of DON and DIN production, such as a 5 wk *in situ* incubation, could provide at least an indication of differences in N cycles and availability among sites or experimental treatments. The buried bag technique usually includes a preincubation measure for an estimate of net N production (Hart et al. 1994),

but with DON this net value may be less relevant. A peak flush of DON in the spring, or a more continuous flux via soil fauna, could lead to minor net gains or even losses over an incubation (Hannam and Prescott 2003) and reveal little of the true N supply to plants. In addition, soils have a high inherent variation in N across microsites, so the range in pre- and postincubation N concentrations could potentially overwhelm small differences in depolymerization or mineralization rates. My suggestion is to consider total extractable N, rather than net changes, as a simpler and more precise assay that can capture both substrate quantity (soil N concentration) and quality (immobilization via C:N ratios) effects on N availability. Nitrogen indices of forest floors or mineral soils alone, either as  $N_o$  potential or field measures of DON and DIN, did not reveal the full extent of fertility differences among sites, and combined estimates of N supply are recommended to incorporate the influence of forest floor depth and density of mineral soil.

## **Conclusions**

The relative shift in N forms, from a predominance of DON to a progressively greater ratio of DIN:DON, was consistent with the proposed N forms along gradients of N availability (Schimel and Bennett 2004), although the actual amount of DON increased, rather than decreased, with site potential. Based on this, I suggest organic N uptake has the potential to contribute to plant nutrition along the entire productivity gradient of soils in southern boreal forests. A more traditional analysis of inorganic N production could be an effective index of soil productivity as well, but it is important to recognize the potential curvilinear relationship between this index and site potential. The predominance of DON in these boreal stands contrasts strongly to the extent of  $NO_3^-$  in an N-rich tropical forest (Schwendenmann and Veldkamp 2005), and demonstrates the possible value of more detailed investigations into functional differences in plant-available N forms across ecosystems.



Table 2.1: Site, soil and stand characteristics of the 19 plots comprising the productivity gradient.

Plant association	Elev.	F+H depth	Soil texture	C.F.	Age	Stand ht.	Basal area	Pl	Bl	Sx
	(m)	(cm)	(20 cm)	(%)	(yrs)	(m)	(m <sup>2</sup> ha <sup>-1</sup> )	(%)	(%)	(%)
P – Cladonia	972	1.5	SL	65	180	20.2	37	80	20	0
P – Cladonia	895	1.3	SL	40	193	21.0	34	67	25	7
P – Cladonia	900	1.1	SL	50	190	16.8	36	83	17	0
P – Cladonia	885	1.2	LS	10	115	23.1	29	79	11	11
P – Cladonia	855	1.3	L	45	165	24.9	44	88	3	9
M - Huckleberry	955	3.3	SL	25	185	27.3	46	57	34	9
M - Huckleberry	940	3.7	SL	30	180	26.5	59	36	62	2
M - Huckleberry	915	3.2	SL	60	206	28.6	46	42	52	6
M - Huckleberry	880	3.2	SiL	35	173	27.3	66	51	41	8
M - Huckleberry	950	3.2	L	40	205	29.1	71	32	58	10
R – Oak fern	908	5.1	L	15	180	31.4	58	25	67	8
R – Oak fern	920	6.6	SL	35	179	32.1	90	5	90	5
R – Oak fern	905	12.6	L	35	188	31.5	71	26	36	38
R – Oak fern	860	5.6	L	0	177	30.5	60	7	79	14
R – Oak fern	900	7.2	L	30	207	32.6	70	4	52	44
VR - Devil's Club	980	6.3	L	25	174	35.3	109	23	64	13
VR - Devil's Club	910	4.1	L	10	185	34.6	97	22	62	16
VR - Devil's Club	895	4.4	SL	20	178	37.8	98	19	64	17
VR - Devil's Club	920	7.2	L	10	206	35.9	114	12	77	12

Notes: Soil nutrient regimes 'P' poor, 'M' medium, 'R' rich, 'VR' very rich. Soil texture 'S' = sand; 'Si' = silt; 'L' = loam. F + H forest floor horizon depths do not include decayed wood. 'C.F.' = coarse fragment content of soil pit, estimated to 50 cm depth. Canopy composition % cover estimated visually and includes co-dominant and subdominant canopies. 'Pl' = lodgepole pine, 'Bl' = subalpine fir and 'Sx' = hybrid white spruce.

Table 2.2: Selected stand and soil characteristics of four plant associations and corresponding soil nutrient regimes (mean and SE in brackets).

Plant association†	Stand ht (m)	Bl foliar N (g kg <sup>-1</sup> )	FF depth (cm)	FF N <sub>o</sub> (mg kg <sup>-1</sup> )	Mineral N <sub>o</sub> (mg kg <sup>-1</sup> )	Profile N <sub>o</sub> (kg ha <sup>-1</sup> )	FF moist (w/w)	Min. moist (w/w)
P - Cladonia	21.2a‡ (1.4)	10.5a (0.5)	1.3a (0.1)	244a (84)	5.7a (2.3)	10a (2.2)	108a (12)	21a (1.7)
M - Huckleberry	27.8b (0.5)	11.8b (0.5)	3.3b (0.2)	624b (74)	6.4a (2.4)	30b (5.0)	155b (12)	25a (2.0)
R - Oak fern	31.6c (0.4)	12.5bc (0.4)	7.4c (1.0)	656b (136)	17.3b (5.0)	69c (10.4)	150b (10)	31b (2.0)
VR - Devil's club	35.9d (0.7)	13.7c (0.5)	5.5c (0.7)	1243c (66)	56.8c (9.4)	158d (23.0)	134b (11)	31b (2.2)

† soil nutrient regimes 'P' poor, 'M' medium, 'R' rich, 'VR' very rich

‡ Means within columns sharing the same letter are not significantly different (Tukey HSD  $P < 0.05$ )

Table 2.3: Soil chemical properties for forest floors (F and H horizons only) and mineral soils (0 to 20 cm) across plant associations (mean with SE in brackets).

Plant association†	Total C (g kg <sup>-1</sup> )	Total N (g kg <sup>-1</sup> )	C:N ratio	Min-N (mg kg <sup>-1</sup> )	Total S (g kg <sup>-1</sup> )
<b>Forest floor</b>					
P – Cladonia	410 (20)	9.6a (0.6)	43a (1.4)	319a (33)	0.79a (0.03)
M - Huckleberry	482 (11)	13.0b (0.5)	38b (1.0)	501b (20)	1.13b (0.04)
R - Oak fern	416 (24)	12.8b (0.8)	33c (1.0)	451b (35)	1.29bc (0.08)
VR - Devil's club	359 (23)	15.0b (0.7)	24d (1.3)	543b (36)	1.44c (0.05)
<b>Mineral soil</b>					
P – Cladonia	22.6a (1.8)	0.67a (0.04)	34a (1.2)	7.1a (1.4)	0.077a (0.007)
M - Huckleberry	21.9a (1.5)	0.70a (0.05)	32a (0.7)	5.7a (0.7)	0.084ab (0.007)
R - Oak fern	27.6b (2.1)	1.07b (0.10)	26b (0.7)	20.6b (2.6)	0.145b (0.030)
VR - Devil's club	32.1b (2.1)	1.75c (0.15)	19c (0.9)	48.2c (4.8)	0.217c (0.018)

† soil nutrient regimes 'P' poor, 'M' medium, 'R' rich, 'VR' very rich

‡ Means within columns sharing the same letter are not significantly different (Tukey HSD  $P < 0.05$ ); forest floors and mineral soils tested separately.

Table 2.3, continued.

Plant association	CEC (cmol kg <sup>-1</sup> )	Exch. Ca (cmol kg <sup>-1</sup> )	Exch. Mg (cmol kg <sup>-1</sup> )	Exch. K (cmol kg <sup>-1</sup> )	pH (H <sub>2</sub> O)
<b>Forest floor</b>					
P – Cladonia	23.2a (1.3)	12.7a (1.4)	2.2 (0.1)	2.2a (0.2)	4.0a (0.05)
M - Huckleberry	30.6a (2.9)	21.3a (2.7)	3.2 (0.3)	2.6a (0.1)	4.1a (0.07)
R - Oak fern	55.0b (5.0)	47.6b (5.4)	4.3 (0.4)	1.6b (0.2)	4.7b (0.15)
VR - Devil's club	51.9b (3.7)	43.6b (3.6)	5.4 (0.5)	1.4b (0.2)	4.8b (0.14)
<b>Mineral soil</b>					
P – Cladonia	3.3a (0.3)	0.74a (0.07)	0.16a (0.01)	0.12 (0.01)	4.8 (0.06)
M - Huckleberry	4.5a (0.2)	1.18a (0.18)	0.28a (0.04)	0.15 (0.02)	4.6 (0.05)
R - Oak fern	10.0b (1.6)	7.13b (1.85)	0.70b (0.10)	0.12 (0.02)	5.2 (0.20)
VR - Devil's club	11.7b (0.9)	9.09b (0.98)	1.48c (0.17)	0.15 (0.02)	5.3 (0.09)

Table 2.4: Bulk soil extraction (concentration and mass per area) of dissolved organic nitrogen, amino acid N and microbial biomass N across plant associations (mean and SE in brackets).

Plant association†	Dissolved organic N			Amino acid N			Microbial N		
	Forest floor	Mineral soil	Profile	Forest floor	Mineral soil	Profile	Forest floor	Mineral soil	Profile
	(mg kg <sup>-1</sup> )	(mg kg <sup>-1</sup> )	(kg ha <sup>-1</sup> )	(mg kg <sup>-1</sup> )	(mg kg <sup>-1</sup> )	(kg ha <sup>-1</sup> )	(mg kg <sup>-1</sup> )	(mg kg <sup>-1</sup> )	(kg ha <sup>-1</sup> )
P - Cladonia	300ab‡ (28)	12.1 (1.1)	18.9a (1.5)	64.8ab (8.2)	2.64 (0.3)	4.1a (0.4)	187 (16)	25.0 (3.6)	34a (4)
M - Huckleberry	448b (33)	10.4 (0.6)	28.2b (1.7)	94.2b (7.7)	2.00 (0.3)	5.7b (0.4)	227 (15)	18.7 (1.6)	32a (2)
R - Oak fern	233a (26)	10.8 (1.3)	31.5bc (3.6)	44.7a (7.5)	2.17 (0.3)	6.2b (1.1)	188 (21)	18.6 (2.4)	41b (2)
VR - Devil's club	257a (35)	17.3 (1.7)	41.1c (4.2)	45.5a (12.7)	3.71 (0.5)	8.0b (0.8)	168 (21)	22.8 (3.3)	45b (4)
<i>p</i> > F	0.046	0.066	0.001	0.027	0.116	0.030	0.509	0.322	0.005

† soil nutrient regimes 'P' poor, 'M' medium, 'R' rich, 'VR' very rich

‡ Means within columns sharing the same letter are not significantly different (Tukey HSD  $P < 0.05$ )

Table 2.5: Concentration and mass per area of dissolved organic nitrogen (DON) and inorganic nitrogen (DIN) across plant associations after a 5 week in situ incubation (mean and SE in brackets).

Plant association†	In situ DON			In situ DIN		
	Forest floor	Mineral soil	Profile	Forest floor	Mineral soil	Profile
	(mg kg <sup>-1</sup> )	(mg kg <sup>-1</sup> )	(kg ha <sup>-1</sup> )	(mg kg <sup>-1</sup> )	(mg kg <sup>-1</sup> )	(kg ha <sup>-1</sup> )
P - Cladonia	247a‡ (15)	10.7 (1.1)	16.7a (2.7)	48.4 (10)	0.25a (0.08)	0.9a (0.2)
M - Huckleberry	387b (29)	11.0 (0.8)	27.1b (1.6)	84.2 (26)	0.34a (0.09)	3.2b (1.0)
R - Oak fern	242a (18)	10.9 (1.1)	33.1b (1.4)	73.7 (11)	1.66b (0.35)	7.7c (1.0)
VR - Devil's club	171c (21)	14.6 (1.3)	32.0b (3.3)	105.3 (14)	5.91b (1.40)	14.8c (3.6)
<i>p</i> > F	0.001	0.441	0.001	0.069	0.001	< 0.001

† soil nutrient regimes 'P' poor, 'M' medium, 'R' rich, 'VR' very rich

‡ Means within columns sharing the same letter are not significantly different (Tukey HSD  $P < 0.05$ )

Table 2.6: Nitrogen availability indices correlated with asymptotic stand height (significant  $p$  values include  $r^2$  of the correlation;  $n = 19$ ).

Parameter	Substrate	Equation, $p > F$ and $r^2$
Total soil N (kg ha <sup>-1</sup> )	profile	Ht = 19.5 + 0.0046(Soil N); $p < 0.001$ ; $r^2 = 0.75$
Mineralizable N (kg ha <sup>-1</sup> )	profile	Ht = 7.2 + 6.06LN[Min-N]; $p < 0.001$ ; $r^2 = 0.69$
Soil C:N ratio	Forest floor	Ht = 52.7 - 0.68(C:N); $p < 0.001$ ; $r^2 = 0.82$
	Mineral	Ht = 52.0 - 0.83(C:N); $p < 0.001$ ; $r^2 = 0.80$
Microbial N (kg ha <sup>-1</sup> )	profile	$p = 0.085$
Microbial C:N ratio	Forest floor	Ht = 9.7 - 0.16(C:N); $p = 0.003$ ; $r^2 = 0.42$
	Mineral	$p = 0.495$
DON of bulk soil (kg ha <sup>-1</sup> )	profile	Ht = 16.0 + 0.47(DON); $p = 0.001$ ; $r^2 = 0.58$
Amino acid N (kg ha <sup>-1</sup> )	profile	Ht = 18.4 + 1.76(AA); $p = 0.004$ ; $r^2 = 0.40$
5 wk <i>in situ</i> DON (kg ha <sup>-1</sup> )	profile	Ht = 15.4 + 0.50(DON); $p = 0.001$ ; $r^2 = 0.50$
5 wk <i>in situ</i> DIN (kg ha <sup>-1</sup> )	profile	Ht = 23.7 + 4.03LN[DIN]; $p < 0.001$ ; $r^2 = 0.68$
5 wk DON+DIN (kg ha <sup>-1</sup> )	profile	Ht = 16.4 + 0.38(DON+DIN); $p < 0.001$ ; $r^2 = 0.70$

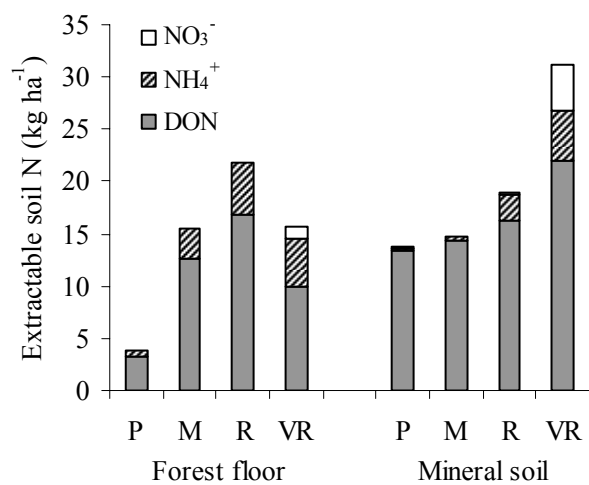


Figure 2.1: Distribution of extractable soil N forms (kg ha<sup>-1</sup> of DON, NH<sub>4</sub><sup>+</sup> and NO<sub>3</sub><sup>-</sup>) by forest floor and mineral soil after a 5 week in situ incubation across poor ('P' – Cladonia), medium ('M' - Huckleberry), rich ('R' - Oakfern), and very rich ('VR' – Devil's club).



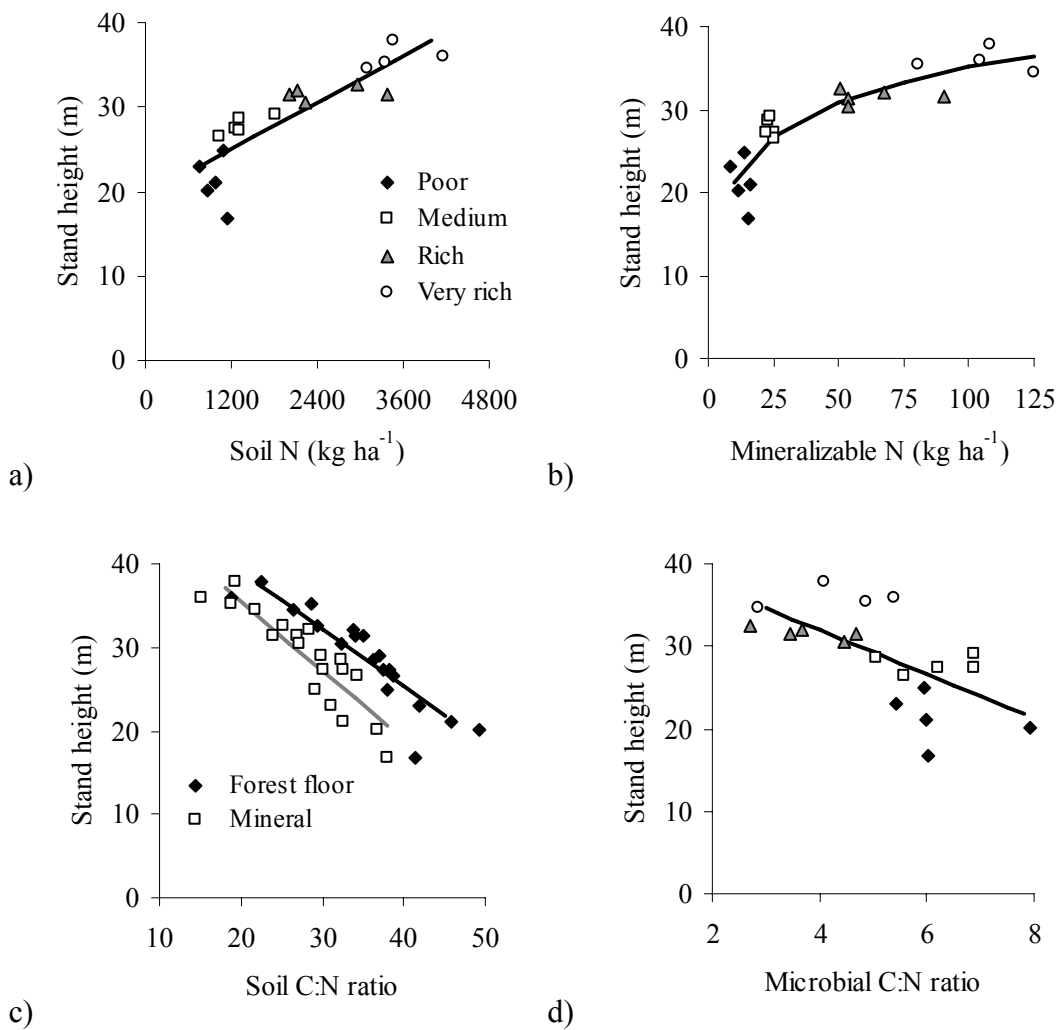


Figure 2.2: Correlation of asymptotic stand height with N indices of bulk soils: a) total soil N of the profile; b) mineralizable N of the profile; c) C:N ratios of forest floor and mineral soils; and d) microbial C:N ratios of forest floors; for poor (P – Cladonia), medium (‘M’ - Huckleberry), rich (‘R’ - Oakfern), and very rich (‘VR’ – Devil’s club).

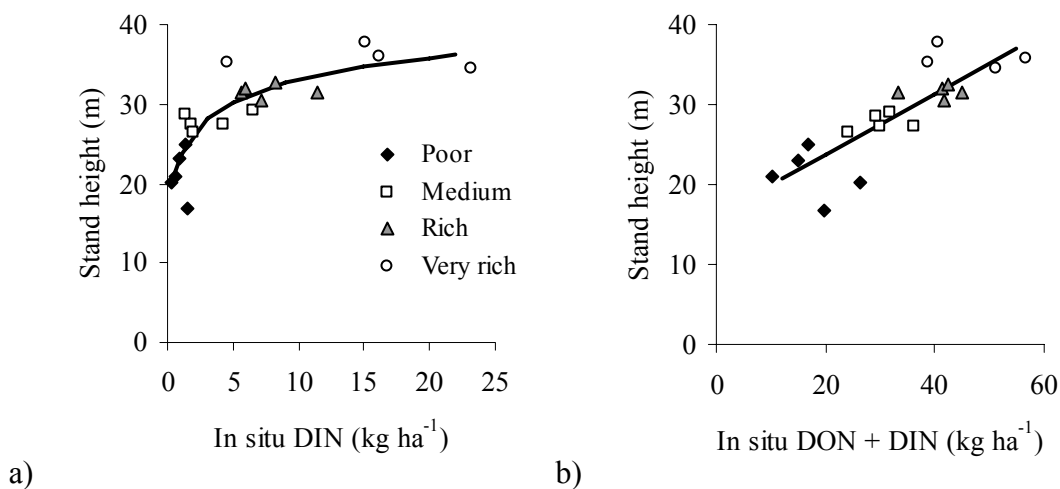


Figure 2.3: Correlation of asymptotic stand height with a) 5 wk in situ DIN ( $\text{NH}_4^+$  and  $\text{NO}_3^-$ ), and b) 5 wk in situ DON,  $\text{NH}_4^+$  and  $\text{NO}_3^-$  for poor (P – Cladonia), medium (M – Huckleberry), rich (R – Oakfern), and very rich (VR – Devil’s club) sites.

Equations for fitted regressions listed in Table 2.6.

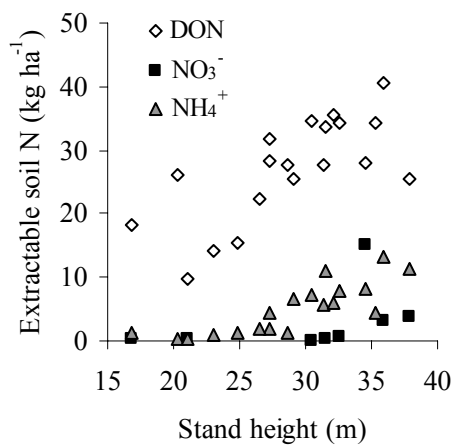


Figure 2.4: Distribution of extractable N forms (DON,  $\text{NH}_4^+$  and  $\text{NO}_3^-$  after a 5 week in situ incubation) of the soil profile across asymptotic stand height.

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### **3 Trade-offs between understory light and foliar nitrogen along productivity gradients of boreal forests<sup>2</sup>**

#### **Introduction**

Forest understory plants face multiple limitations to growth, primarily light, nutrients (especially nitrogen, N) and water (Chapin et al. 1987). Determining the response of tree species to combinations of resource limitations has been a central theme in forest ecology research, often through controlled greenhouse studies (e.g. Canham et al. 1996). Extrapolating results to forests requires quantifying limiting resources and species response across biophysical gradients of landscapes, as well as through time following cycles of disturbance. Continuous monitoring of site conditions and leaf photosynthetic rates can be difficult, however, and assessments through foliar attributes, especially N concentration (N%) and leaf morphology, can more simply quantify and integrate the multiple resource limitations affecting growth (Reich et al. 1997). Such simple indicators may become increasingly useful for assessing species response to rapid shifts in growing environments from anthropogenic influences such as CO<sub>2</sub> emissions and climate change (Norby and Iverson 2006).

With respect to biophysical gradients, Coomes and Grubb (2000) described how limiting resources in mature forest understories can covary in a predictable manner with soil fertility. They reviewed studies showing that nutrient-poor or droughty sites typically have higher levels of light in the understory than richer sites because of more open canopies of early-successional, less productive overstory trees. Conversely, light is likely more limiting to growth than deficiencies in N and water in the darker understories of more productive stands on richer sites. Understory resource interactions in boreal or temperate forests have been evaluated primarily by sapling growth rates among different forest types (Carter and Klinka 1992, Walters and Reich 1997, Drever and Lertzman 2001, Kobe 2006), but few studies have extended the analysis to relationships among light, soil resources and foliar attributes of understory trees across a wide edaphic range in unmanaged, mature forests.

One of the more fundamental yet poorly documented patterns is the relationship between soil fertility and foliar N status of understory trees. Under full light, foliar N concentration and leaf size generally parallel the supply of N from soil (van den Driesche

<sup>2</sup>A version of this chapter has been accepted with revisions by Can. J. For Res. as: Kranabetter, J.M., and Simard, S.W. Tradeoffs between understory light and foliar nitrogen along productivity gradients of boreal forests.

1974, Ingestad 1982), and correlate strongly with leaf photosynthetic capacity and productivity (Reich et al. 1995). These gradations in foliar N% have been widely applied in the diagnosis of site limitations for even-aged stands (Walker and Gessel 1991, Carter 1992, Brockley 2001). With shading, however, foliar N% of saplings could be reduced irrespective of soils because of biomass allocation to shoots rather than roots, by losses in the potential of roots to absorb nutrients, or by reductions in N demand under low growth rates (Chapin 1991a, 1991b). Little consensus on foliar interpretations have been provided from experiments in partially-cut forests, where neutral, positive, or negative effects of light availability on foliar N% of understory saplings have been reported (e.g. Niinemets 1997, Lusk and Reich 2000, Kaelke et al. 2001, Kazda et al. 2004). Very few of these studies include measures of soil resources, however, which may be problematic if large fluctuations in soil N availability and foliar N% occur after overstory trees are removed (Walters et al. 2006, Titus et al. 2006).

A second uncertainty in understory tree response is the interpretation of leaf morphology under dual resource gradients of soil fertility and light availability. There are large potential ranges in leaf mass and surface area due to the phenotypic plasticity of sun- and shade-adapted leaves for most tree species (Givnish 1988). In addition, foliar response to soil N availability, especially after fertilization, often includes a change in leaf size (Binkley 1986), and foliar N status may be more relevant when interpreted on the basis of leaf content (such as N per unit leaf area [ $N_a$ ]), rather than concentration. With this index, however, it becomes potentially difficult to separate the effects of soils on foliar N status from the concurrent influence of shading on leaf morphology (Niinemets et al. 2001, Fownes and Harrington 2004, Portsmouth and Niinemets 2007). Consequently, the influence of soil fertility on understory saplings may be best isolated and quantified using foliar N concentrations (Kobe 2006), but ideally this relationship should be validated for each species of interest.

In this study, I report on the relationships between natural gradients in soil productivity and understory light availability in the southern boreal forests of British Columbia, and the corresponding patterns in understory foliar attributes (N% and  $N_a$ ) of subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.). I tested the hypothesis that an inverse relationship exists between light attenuation and soil N availability along productivity

gradients, and explored the effects of shading and suppressed growth on foliar N status by comparing understory subalpine fir trees with codominant overstory trees (both subalpine fir and lodgepole pine [*Pinus contorta* Dougl. ex Loud]). The results of this study will contribute to our understanding of the trade-offs (a reduction of one resource in return for another) between understory light and N availability inherent to climax forests, and provide insights into the interpretation of foliar nitrogen status.

## Materials and Methods

### Site descriptions

The southern boreal forest of British Columbia is designated as the Sub-Boreal Spruce biogeoclimatic zone (SBS), and is located in the montane landscape of the central interior, within the closed forest portion of the Cordilleran boreal region (Pojar 1996). The SBS has a continental climate characterized by severe, snowy winters and relatively short, warm, moist summers. Upland coniferous forests are comprised of lodgepole pine (Pl), hybrid white spruce (Sx) (*Picea glauca* x *Picea engelmannii* [Moench] Voss) and subalpine fir (Bl). Soils are free of permafrost and are predominantly deep blankets of lacustrine sediments, glacialfluvial deposits or glacial tills with coarse fragments of mixed lithology.

The study sites were located in the moist cold (mc) subzone of the SBS near Smithers, British Columbia, Canada (54°49'N 127°10'W; elevation 522 m). Smithers has a mean annual air temperature of 3.9°C and mean annual precipitation of 513 mm (354 mm as rainfall) (Environment Canada 2006). Four site series (represented by climax plant communities corresponding to different soil moisture and nutrient regimes; Pojar et al. 1987) were sampled to provide a wide range in upland edaphic conditions: (02) xeric and poor Pl – Cladonia; (01) mesic and medium Sx – Huckleberry; (06) subhygric and rich Sx – Oak fern; and (09) subhygric and very rich Sx – Devil's club (Banner et al. 1993). Site series are hereafter referred to by their nutrient regime and plant association name (e.g. poor - Cladonia).

Five transects, each containing one replicate of each site series, were located along a 25 km portion of the McDonnell Forest Service Road (54°40' to 47'N and 127°16' to 36'W) at approximately 900 m elevation. We were unable to find a suitable

very rich – Devil’s club plot on the fourth transect, however, so the study was limited to 19 plots. Each plot was 50 m x 30 m (0.15 ha) in size. Plots were separate and generally < 200 m apart within a transect. Stands within plots were mostly multicohort due to gap-phase disturbance caused by bark beetles, root pathogens and wind throw, as well as a small amount of partial harvesting (ranging from 0-10% of the basal area) that occurred through the valley in the 1950’s. Further descriptions of stand, soil and vegetation characteristics of the study plots are listed in Chapter 2.

### **Soil nitrogen and moisture availability**

The mass per ha (forest floor and mineral soil) of dissolved organic N + inorganic N extracted after a 5 wk in-situ incubation was used as a index of soil nitrogen availability as reported in Chapter 2. Briefly, the in situ buried bag soil incubation was initiated June 5-9, 2006. Forest floor F and H horizons were sampled as intact cores, avoiding pure decayed wood, and mineral soils were sampled down to 20 cm with an auger. Mineral soils were sealed in a polyethylene bag within the sample hole, and forest floors were placed on top of this sample in a separate bag. This was repeated at five random microsites per plot. After five weeks, the bags were retrieved and gently run through a 5-mm sieve, followed by an analysis of dissolved organic N and inorganic N.

Gravimetric soil moisture content (w/w) of the forest floor and mineral soil (0-20 cm depth) was measured every three weeks from mid May to early September (total of six times). Forest floors (F, H horizons and buried wood) were sampled with a 15 cm diameter template to the mineral soil interface, and mineral soils were sampled to a 20 cm depth using a stony soil auger (4-cm in diameter). Three random microsites were sampled and bulked together per plot, and different microsites were chosen on each sample day. Moisture content was determined by drying soils at 105°C for 24 hours. Mineral soils were then ground and sieved to determine gravimetric moisture content of the fine fraction (< 2-mm).

Forest floor and mineral soil N concentration data was converted to mass per ha using depth and bulk density values as reported in Chapter 2. We derived an index for soil moisture content ( $\text{kg m}^{-2}$ ) of each plot using the average gravimetric moisture concentration (average of the six measurements over the summer) of each substrate type and the same values for F + H depth, bulk densities and coarse fragment content of the

soil profile as for nutrient capital. We tested N or moisture parameters using a single variable for the soil profile by adding forest floor and mineral soil amounts ( $\text{kg ha}^{-1}$ ) together.

### **Forest measures**

The old-growth forests (~ 180 years) on our sites had ceased height growth (i.e. reached an asymptote) decades earlier. The full extent of tree height closely reflects site index (Ryan and Yoder 1997), and we used the asymptotic or ‘maximum obtainable’ stand height of the old-growth forests as a measure of site potential. The heights of three mature trees of each species were measured with a Forester Vertex (Haglöf, Sweden), along with diameter at 1.3 m (DBH), for a total of nine trees per plot where possible (in some of the poor - *Cladonia* stands only lodgepole pine comprised the overstory). From the upper canopy, we selected codominant trees with good form (no broken tops, forks, large sweeps, etc.) and no evidence of ongoing height growth. Where numerous candidate trees were available, we selected trees widely spaced across the plot to obtain the best stand average.

### **Understory light and foliar attributes**

Available light (400-700 nm) in the understory over the growing season (mid-May to mid-September) was assessed at each plot using hemispherical canopy photographs. The photographs were taken in mid-July during overcast, homogeneous gray sky conditions. Five sample points per plot were systematically chosen at 10 to 15 m spacing to cover the entire area of the plot. A Nikon Coolpix 5000 digital camera with an attached Nikon FC-E8 Fisheye converter lens was set with a tripod at a 1 m height for each picture. Any nearby understory trees or shrubs were tipped back, away from the lens, to allow for a measure of light levels reaching the understory layer. The growing season light availability (direct + diffuse light sources), was expressed as a percentage of full sun and was computed from each photograph using the Gap Light Analyser (GLA) 2.0 software, following Frazer et al. (2000). Parameters included a solar constant of  $1367 \text{ Wm}^{-2}$ , a cloudiness index of 0.5 kt, a spectral fraction of 0.5, a beam fraction of 0.5, and a clear-sky transmission coefficient of 0.65.

Foliage was sampled from five randomly selected codominant (trees of equivalent height forming the main stand canopy) lodgepole pine and subalpine fir in September 18-

21, 2006, except in poor - Cladonia plots where subalpine fir was only found in the subcanopy. Current year foliage in the upper 1/3 of each selected tree was retrieved by removing small branches (using a 12-gauge shotgun), and the five sample trees were combined for one bulk sample per species per plot. At the same time, fifteen subalpine fir saplings from the naturally-regenerated understory, which ranged in height from 1 to 2.5 m, were randomly selected at each plot. Current year foliage was clipped from three lateral branches in the top quarter of each sapling. Foliage from five trees was bulked together to form three subsamples per plot for analysis.

### **Laboratory analysis**

Dissolved organic nitrogen (DON) and inorganic  $\text{NH}_4\text{-N}$  and  $\text{NO}_3\text{-N}$  (DIN) were determined colorimetrically using a modified persulphate solution, as described in Chapter 2. Foliar samples were oven-dried ( $70^\circ\text{C}$  for 24 hours) and 100 needles used to determine specific mass and one-sided projected leaf area (LI-COR 3100, Lincoln, Neb.). The lodgepole pine fascicles were split into single needles for the mass and leaf area measures. The samples were ground with a Wiley mill and foliar N was analyzed by dry combustion with a Fisons/Carlo-Erba NA 1500 NCS analyzer (Thermo Fisher Scientific, Waltham, MA). Macro- and micro- nutrients were analysed by inductively coupled plasma-atomic emission spectroscopy following microwave digestion (Kalra and Maynard 1991).

### **Statistical analysis**

Light, soil and foliar parameters were compared among plant associations in a randomized incomplete block design with five replicate transects (blocks). Height and diameter was also compared between plant associations and overstory species using a split-plot design in the ANOVA. I used Proc Mixed in SAS (SAS Inc. 2004) with block and block interactions set as random factors. Residuals from the analyses were examined and found to meet the assumptions of equal variance. Significant differences between least square means of each plant association were tested using pairwise *t* tests at a significance level of 0.05.

Regression analysis was used to examine relationships between understory attributes and site conditions, which were expressed in two ways: (1) asymptotic stand height, representing site potential, and (2) indices for light availability, soil moisture

supply and N availability, representing combinations of limiting resources. The GLM procedure in SAS using Type 1 Sums of Squares was used to test linear and curvilinear regressions between plot means of dependent and independent variables ( $n = 19$ ). Relationships between foliar attributes and site factors (light, soil moisture and N availability) were tested using multiple linear regressions with step-wise elimination of variables (based on  $r^2$  values). The  $r^2$  value of curvilinear correlations was calculated using the corrected sums of squares through Proc NLIN in SAS.

## Results

### Stand and soil characteristics

Site potential, as determined by asymptotic stand height, ranged from 17 m to 38 m, and differed significantly among plant associations ( $p < 0.001$ , Table 3.1). Hybrid spruce was significantly taller than lodgepole pine ( $p = 0.026$ ) on medium to very rich sites (Fig. 3.1a), but the 5% average difference was relatively small (poor – Cladonia sites were excluded from the species comparison because too few Bl and Sx were codominant in the canopy). Larger species effects were found for bole diameter ( $p = 0.011$ ), with subalpine fir almost 30% larger in DBH than lodgepole pine on very rich sites (Fig. 3.1b). Lodgepole pine was the dominant species on nutrient-poor, xeric sites, and was less abundant than subalpine fir or hybrid spruce on moister and richer sites (Table 3.1).

Moisture differences among plant associations were greatest in mineral soils, which averaged 31% w/w on subhygric sites (rich - Oakfern and very rich - Devil's Club) through the summer compared to 25% and 21% for medium - Huckleberry and poor - Cladonia sites, respectively. Soil N availability (dissolved organic and inorganic N) ranged from 10 to 55 kg ha<sup>-1</sup> across sites, and was strongly correlated with average soil moisture content over the growing season (Fig. 3.2).

### Understory light and foliar attributes

Understory light availability of microsites ranged from 12% to 35% full sunlight across these forests. Light availability was greatest on poor - Cladonia sites and was half as much on very rich – Devil's club sites (Table 3.1). Understory light declined with site potential, and was expressed either as a linear correlation with soil N availability, or as a curvilinear correlation with stand height (Fig. 3.3).

Foliar N concentrations of the understory subalpine fir ranged from 8.9 to 14.7 g N kg<sup>-1</sup> for subsamples, and differed significantly among plant associations (Table 3.2). Step-wise regressions with soil N availability, soil moisture and light availability revealed the best fit between foliar N<sub>%</sub> and soil N alone as a linear correlation (Fig. 3.3a); neither light nor soil moisture explained additional variance in foliar N<sub>%</sub> over and above soil N availability. Understory foliar N<sub>%</sub> was also strongly correlated with stand height (Fig. 3.3b).

Understory needle mass and surface area did not increase across plant associations in the same pattern as foliar N<sub>%</sub>; saplings on rich - Oak fern sites, for example, tended to have the smallest needles (Table 3.2). Increasing N<sub>%</sub> along with shifting needle size resulted in no difference in foliar N per unit leaf area (N<sub>a</sub>) among poor to rich plant associations (Table 3.2). In keeping with this trend, understory N<sub>a</sub> increased only slightly with soil N availability (Fig. 3.4a) or stand height ( $p = 0.039$ ,  $r^2 = 0.26$ ).

### **Overstory foliar attributes**

Foliar N concentrations of the overstory subalpine fir and lodgepole pine also increased from poor to very rich plant associations, although more so for subalpine fir than lodgepole pine (Table 3.3). Other nutrients did not vary as strongly as N<sub>%</sub>; foliar P and K concentrations were constant across plant associations, while foliar S and Mg increased slightly from poor to very rich sites for subalpine fir and lodgepole pine, respectively (Table 3.4).

For both species of overstory trees, foliar N<sub>%</sub> was linearly correlated with soil N availability, but the slope for subalpine fir was steeper than lodgepole pine (Fig. 3.5a). Foliar mass of overstory subalpine fir also increased significantly with soil fertility, but lodgepole pine did not (Table 3.3). Foliar N<sub>a</sub> of subalpine fir increased with soil fertility, more so than that of lodgepole pine (Table 3.3), and the positive linear relationship between N<sub>a</sub> and soil N availability was slightly steeper for subalpine fir than lodgepole pine (Fig. 3.4b).

Foliar N<sub>%</sub> of the overstory was more variable than the understory, perhaps due to the smaller sample size, but the correlation with soil N availability was similar (Fig. 3.5b). In contrast, foliar N<sub>a</sub> of the illuminated overstory was generally higher and was more closely correlated with soil N availability than the shaded understory (Fig. 3.4).



## Discussion

### The link between soil fertility and understory light

The inverse relationship between soil fertility and light attenuation to the understory that I described was consistent with many forest ecosystems in the absence of large-scale disturbance (Coomes and Grubb 2000). Understory light availability declined predictably with soil N supply due to the observed increase in crown size with taller trees and the increased cover of subalpine fir and hybrid spruce, which both cast more shade than lodgepole pine (Messier et al. 1998). The shift in tree species composition was most significant on medium - Huckleberry sites, accentuating the decline in light from poor – Cladonia to very rich – Devil’s club sites, as indicated by the curvilinear correlation with stand height. A minor amount of tree mortality resulting from bark beetles, root pathogens and wind throw had occurred, and these small gaps contributed to microsite variability and perhaps limited the degree of shading on the most productive sites. In general, light limitations in these old-growth boreal stands were not as severe as in some temperate and coastal forests (e.g., < 10%; Lieffers et al. 1999), and may not have been low enough to restrict survival or N uptake by the understory saplings (Parent and Messier 1995, Walters and Reich 2000).

Predicting light response to soil fertility gradients might have required testing the effects of moisture and N limitations separately, but in these boreal landscapes the two resources are strongly interconnected (Kimmins et al. 1990). This is largely because soil attributes determining moisture regime (soil texture, slope position, coarse fragment content) also affect nutrient cycling (microbial activity, ion diffusion, leaf litter quality; Gosz 1981, Chapin 1991, Scott and Binkley 1997, Giesler et al. 1998), such that no plant association in the SBS has been described with relatively dry yet N-rich soils. Rich to very rich sites, where moisture was less limiting, were further differentiated by base cation supply and pH (Giesler et al. 1998). Collectively, these site factors (moisture and geochemistry) driving fertility were well integrated by an in-situ DIN + DON index or related measure of soil N availability (e.g., N mineralization potential, total N content, C:N ratios, mineralizable N) (Chapter 2). There are also imperfectly drained, less productive sites in the SBS (dominated by black spruce [*Picea mariana*] and labrador tea

[*Ledum groenlandicum*]), which could be included for a more complete range of soil moisture regimes than represented by the four plant associations included in this study.

### **Understory foliar attributes as indices of site resources**

Foliar N concentrations (N%) were uniformly correlated with soil N availability for both understory and overstory subalpine fir, despite the differences in light exposure and tree size, which suggests there were no physiological constraints on N uptake. The consistency in foliar N% for this shade-tolerant, late-seral species reflects perhaps consistent biomass allocation and root-shoot ratios between shaded and illuminated trees (Van Hees and Clerkx 2003, Machado et al. 2003). Nitrogen is well recognized as the leading nutritional constraint to conifer growth, and the strong relationship we found between foliar N% of the understory and overstory asymptotic stand height ran parallel to those for saplings in tropical rain forests (Thomas and Bazzaz 1999). The physiological mechanism responsible for developmental decline in height growth of trees is not yet certain, but the foliar N% correlation affirms the strong influence of soil fertility on tree size (Ryan et al. 2006). In addition, the divergence in foliar N% between overstory lodgepole pine and subalpine fir along the fertility gradient mirrored the differences in bole diameter, and this competitive disadvantage in N uptake by pine (perhaps caused by lower rates of inorganic N uptake; Hangs et al. 2003) would help explain the shift in stand composition along the productivity gradient (Canham et al. 2006).

A number of other forest nutrition studies have reported positive correlations between foliar N% and conifer productivity or soil fertility (e.g., Radwan and Harrington 1986, Wang and Klinka 1997, Kranabetter et al. 2003), but this has not been universally found for all tree species, especially in extensive regional surveys (Bauer et al. 1997, Ollinger et al. 2002). The relationship between foliar N% and tree productivity is likely strongest within localized areas, and becomes more obscure across wider landscapes because of climatic gradients (Yin 1993, Bauer et al. 2000). In addition, some landscapes with narrower ranges in N% and smaller nutritional effects on tree growth possibly lack the extremes in soil fertility that were evident in our stands (Finzi and Canham 2000).

The combined foliar attribute of N per unit leaf area ( $N_a$ ) is typically well correlated with  $A_{max}$  (light-saturated assimilation rate) in conifers (reviewed by Duursma et al. 2005) and could be potentially useful in integrating both soil fertility and light

constraints on understory trees. The patterns in foliar  $N_a$  reflect in part the dual influence of these resources on needle mass; subalpine fir had smaller needles in the understory than overstory, where light levels were lower, while overstory foliage increased in both mass and  $N_{\%}$  with soil N availability. Combinations of high light and high soil fertility led to foliar  $N_a$  levels approaching an upper limit of  $4.0 \text{ g N m}^{-2}$  for overstory subalpine fir. In comparison, the suppressed understory was under inverse constraints of both light and N availability, resulting in quite consistent  $N_a$  values that were as low as  $1.5 \text{ g N m}^{-2}$  along the productivity gradient, corresponding with very poor rates of growth (consistent with other *Abies* spp.; Lusk and Reich 2000, Grassi and Bagnaresi 2001). We suspect the slight positive trend in understory  $N_a$  with soil fertility was due to a few plots, especially on very rich sites, where saplings were not completely suppressed and shading was insufficient to reduce  $N_a$  to the gradient average ( $\sim 2.0 \text{ g N m}^{-2}$ ). More definitive relationships between sapling  $N_a$  and light/soil resource availability would require further testing after partial-harvesting treatments, but patterns from these unmanaged stands suggest assessments of understory resource constraints, at least for this shade-tolerant species, could be quite effective with foliar analysis.

## Conclusions

When I compared relationships between light levels and foliar  $N_{\%}$ , I identified contrasting and predictable resource limitations, from relatively high light with low  $N_{\%}$  on poor sites to low light with high  $N_{\%}$  on very rich sites. The near consistent and relatively low values in understory foliar  $N_a$  along the productivity gradient indicated that resource constraints were close to a balanced trade-off in the quantities of both light and soil N supply. Given these relationships, we suggest that models of gap dynamics utilizing light availability as a primary driver in the understory of boreal forests (Messier et al. 1999), while correct, should also consider the potential influence of sapling N nutrition on growth response to light (Kobe 2006). The approach taken in this study, where site constraints were well characterized by plant association or asymptotic stand height, demonstrate that soil and light resources could be relatively easily quantified across spatial scales for analyzing and modelling multicohort stands (Duursma et al. 2005). The linkage between soil moisture and fertility, and the resulting differences in

light attenuation and species N nutrition, are fundamental relationships in forest ecology that will need periodic reassessment given the anticipated changes in climate and tree species distributions (Hamann and Wang 2006).

Table 3.1: Forest stand and soil characteristics among four plant associations comprising the productivity gradient (mean and SE in brackets).

Plant association*	Stand height (m)	Relative cover (%)			Soil N availability (kg ha <sup>-1</sup> )	Soil moisture (kg m <sup>-2</sup> )	Light availability (%)
		Pl	Bl	Sx			
P - Cladonia	21.2a† (1.4)	80a (3)	15a (4)	5 (2)	17.6a (2.7)	13.4a (1.2)	28.6a (0.8)
M - Huckleberry	27.8b (0.5)	44b (5)	49b (5)	7 (1)	30.2b (1.9)	18.7a (1.5)	20.0b (0.6)
R - Oak fern	31.6c (0.4)	13c (5)	65b (9)	22 (8)	40.8c (2.0)	29.3b (2.1)	18.4bc (0.6)
VR - Devil's club	35.9d (0.7)	19c (2)	67b (3)	15 (1)	46.7c (4.3)	27.6b (2.0)	16.7c (0.6)

\* soil nutrient regimes 'P' poor, 'M' medium, 'R' rich, 'VR' very rich

† Means within columns sharing the same letter are not significantly different (Tukey HSD  $P < 0.05$ )

Table 3.2: Understory subalpine-fir foliar attributes (N concentrations, needle size, N per unit leaf area) across plant associations (mean and SE in brackets).

Plant association*	N <sub>%</sub> (g kg <sup>-1</sup> )	Needle mass (g 100 <sup>-1</sup> )	Needle area (cm <sup>2</sup> 100 <sup>-1</sup> )	N <sub>a</sub> (g m <sup>-2</sup> )
M - Huckleberry	11.5b (0.17)	0.47 (0.02)	27.6bc (0.8)	1.98a (0.11)
R - Oak fern	12.6c (0.14)	0.43 (0.02)	25.3ab (0.9)	2.11ab (0.10)
VR - Devil's club	13.6d (0.17)	0.52 (0.02)	29.5c (1.3)	2.44b (0.14)
$p > F$	$< 0.001$	0.060	0.022	0.027

\* soil nutrient regimes 'P' poor, 'M' medium, 'R' rich, 'VR' very rich

† Means within columns sharing the same letter are not significantly different (Tukey HSD  $P < 0.05$ )

Table 3.3: Foliar attributes (N concentrations, needle size, and N per unit leaf area) of overstory subalpine fir and lodgepole pine across plant associations (mean and SE in brackets).

Plant association*	N <sub>%</sub> (g kg <sup>-1</sup> )	Needle mass (g 100 <sup>-1</sup> )	Needle area (cm <sup>2</sup> 100 <sup>-1</sup> )	N <sub>a</sub> (g m <sup>-2</sup> )
<b>Subalpine fir</b>				
P - Cladonia	10.5a† (0.5)	0.56a (0.04)	22.4 (2.0)	2.62a (0.13)
M - Huckleberry	11.8b (0.5)	0.61ab (0.04)	24.4 (1.4)	2.94a (0.08)
R - Oak fern	12.5bc (0.4)	0.70b (0.05)	26.1 (1.8)	3.39b (0.23)
VR - Devil's club	13.7c (0.5)	0.74b (0.07)	27.3 (1.9)	3.68b (0.12)
<i>p</i> > F	0.003	0.039	0.194	0.003
<b>Lodgepole pine</b>				
P - Cladonia	9.7a (0.1)	2.24ab (0.09)	68.7 (1.8)	3.16 (0.09)
M - Huckleberry	10.5ab (0.4)	1.92a (0.16)	63.9 (5.3)	3.15 (0.17)
R - Oak fern	10.7bc (0.4)	1.91a (0.14)	58.9 (4.0)	3.48 (0.15)
VR - Devil's club	11.5c (0.5)	2.52b (0.15)	76.3 (4.9)	3.68 (0.12)
<i>p</i> > F	0.020	0.036	0.090	0.057

\* soil nutrient regimes 'P' poor, 'M' medium, 'R' rich, 'VR' very rich

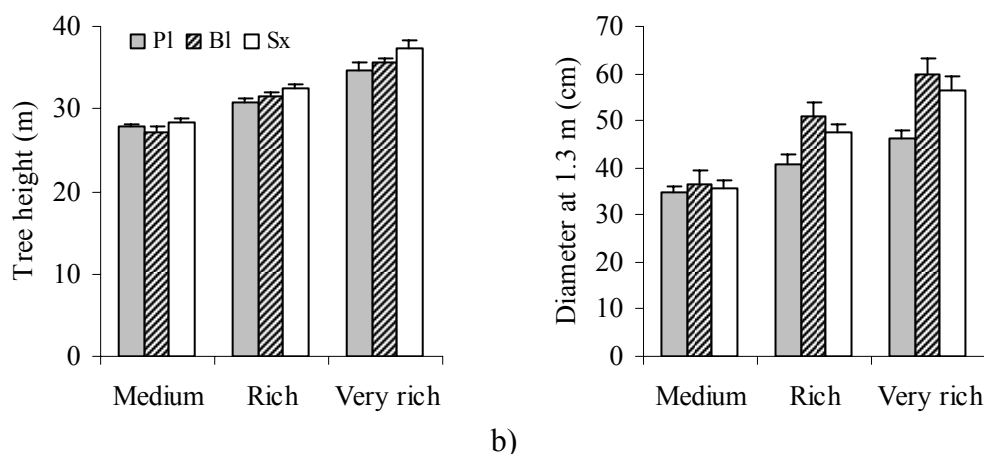
† Means within columns sharing the same letter are not significantly different (Tukey HSD  $P < 0.05$ )

Table 3.4: Foliar nutrient concentrations of overstory subalpine fir and lodgepole pine across plant associations (mean and SE in brackets).

Plant association*	P (g kg <sup>-1</sup> )	S (g kg <sup>-1</sup> )	K (g kg <sup>-1</sup> )	Mg (g kg <sup>-1</sup> )	Ca (g kg <sup>-1</sup> )	B (mg kg <sup>-1</sup> )	Cu (mg kg <sup>-1</sup> )	Fe (mg kg <sup>-1</sup> )	Mn (mg kg <sup>-1</sup> )	Zn (mg kg <sup>-1</sup> )
<b>Subalpine fir</b>										
P - Cladonia	2.0 (0.04)	0.87a† (0.03)	7.7 (0.5)	0.81 (0.08)	3.6 (0.3)	11.8 (3.4)	2.5 (0.3)	43a (6)	1581a (181)	29a (1)
M - Huckleberry	1.9 (0.10)	0.98ab (0.05)	7.6 (0.3)	1.05 (0.07)	4.9 (0.4)	9.2 (1.4)	2.7 (0.1)	31b (3)	1322a (100)	34a (3)
R - Oak fern	2.0 (0.06)	1.03b (0.05)	8.6 (0.2)	1.09 (0.05)	4.8 (0.5)	10.4 (2.1)	2.9 (0.2)	29b (2)	528b (119)	39ab (4)
VR - Devil's club	2.0 (0.13)	1.12b (0.03)	7.9 (0.5)	1.03 (0.05)	4.7 (0.5)	8.8 (1.3)	3.2 (0.3)	26b (2)	467b (119)	52b (12)
<b>Lodgepole pine</b>										
P - Cladonia	1.1 (0.03)	0.76 (0.03)	4.5 (0.1)	0.78a (0.04)	1.8 (0.2)	4.7 (0.8)	3.2a (0.9)	34 (3)	643a (48)	41a (2)
M - Huckleberry	1.1 (0.07)	0.80 (0.04)	4.7 (0.3)	0.87ac (0.05)	1.7 (0.1)	6.4 (0.5)	2.8a (0.1)	28 (2)	515a (39)	36a (2)
R - Oak fern	1.2 (0.10)	0.80 (0.03)	4.9 (0.2)	1.01b (0.05)	1.6 (0.2)	7.3 (0.9)	2.9a (0.9)	31 (3)	295b (38)	40a (3)
VR - Devil's club	1.2 (0.10)	0.88 (0.03)	5.3 (0.5)	0.92bc (0.08)	1.5 (0.2)	6.6 (1.2)	3.8b (0.3)	24 (2)	232b (51)	56b (10)

\* soil nutrient regimes 'P' poor, 'M' medium, 'R' rich, 'VR' very rich

† Means within columns sharing the same letter are not significantly different (Tukey HSD  $P < 0.05$ )



a) b)  
 Figure 3.1: a) Tree height and b) diameter by species across medium, rich and very rich plant associations (Pl = lodgepole pine; Bl = subalpine fir; Sx = hybrid spruce). SE of the mean indicated by error bars.

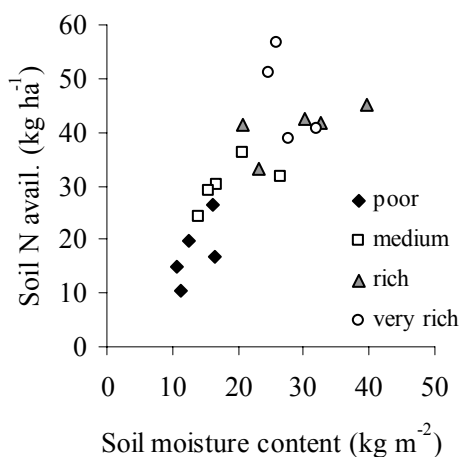


Figure 3.2: Correlation of nitrogen availability with moisture content of the soil profile (forest floor and 0 - 20 cm mineral soil) across plant associations (poor - Cladonia, medium - Huckleberry, rich - Oak fern, and very rich - Devil's club).

$$\text{Soil N availability} = 6.2 + 0.81(\text{Moisture}) + 0.04(\text{Exch. Mg} + \text{K}); p < 0.001, r^2 = 0.73$$



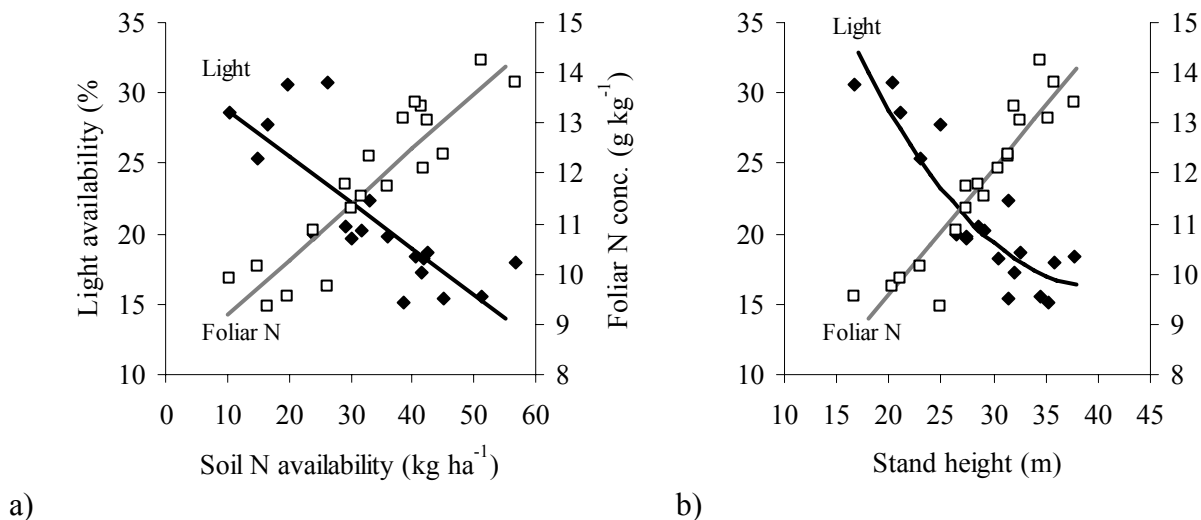


Figure 3.3: Light availability (black diamonds and black line) of the forest understory and foliar N concentrations of the subalpine fir understory (white square and gray line) along the gradient of a) soil N availability, and b) asymptotic stand height.

$$\text{Light availability (\%)} = 31.9 - 0.33(\text{Soil N}); p < 0.001, r^2 = 0.65$$

$$\text{Light availability (\%)} = 66.8 - 2.54(\text{Ht}) + 0.032(\text{Ht}^2); p < 0.001, r^2 = 0.87$$

$$\text{Understory foliar N}_{\%} = 8.1 + 0.11(\text{Soil N}); p < 0.001, r^2 = 0.84$$

$$\text{Understory foliar N}_{\%} = 4.6 + 0.25(\text{Ht}); p < 0.001, r^2 = 0.87$$

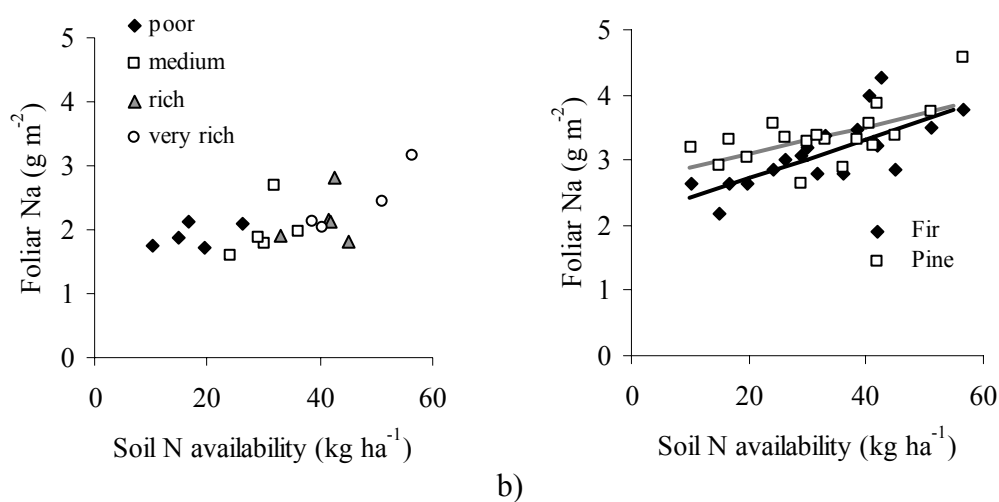


Figure 3.4: Foliar N per unit leaf area along the gradient of soil N availability for a) understory subalpine fir, and b) overstory subalpine fir and lodgepole pine.

Understory foliar  $N_a = 1.47 + 0.02(\text{Soil N})$ ;  $p = 0.008$ ;  $r^2 = 0.36$

Overstory subalpine fir foliar  $N_a = 2.1 + 0.03(\text{Soil N})$ ;  $p = 0.001$ ;  $r^2 = 0.55$

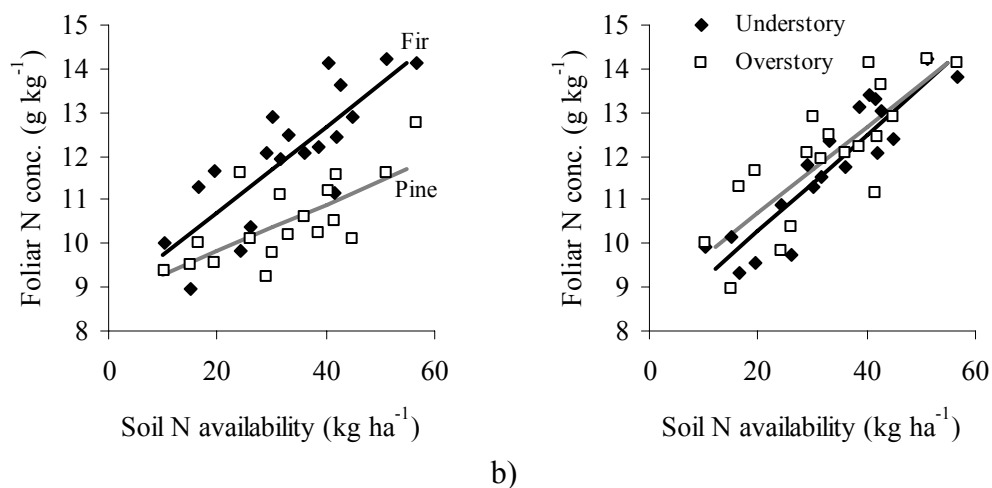


Figure 3.5: Foliar N concentrations of overstory subalpine-fir along a soil N availability gradient compared to a) lodgepole pine and b) understory subalpine fir.

Overstory subalpine fir foliar  $N\% = 8.8 + 0.10(\text{Soil N})$ ;  $p < 0.001$ ;  $r^2 = 0.66$

Overstory lodgepole pine foliar  $N\% = 8.7 + 0.05(\text{Soil N})$ ;  $p = 0.001$ ;  $r^2 = 0.51$

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## 4 Species patterns in foliar nitrogen concentration, nitrogen content and $^{13}\text{C}$ abundance for saplings along light gradients<sup>3</sup>

### Introduction

In forests, light availability and soil fertility typically constrain understory tree growth, and differences in species responses are important drivers in regeneration success and stand dynamics (Catovsky and Bazzaz 2002a, Catovsky et al. 2002b, Kobe 2006). Monitoring and interpreting interactions between the understory environment (e.g., soils, microclimate and light) and photosynthesis is challenging, and scientists have often utilized foliar attributes to integrate and quantify the multiple resource constraints acting upon plants. In particular, foliar nitrogen concentration ( $\text{N}_\%$ ), specific leaf area, and natural carbon isotope abundance ( $\delta^{13}\text{C}$ ) have proven to be effective indices for comparing intra- and interspecific responses to resource gradients (Reich et al. 1997, Dawson et al. 2002). Establishing understory foliar  $\text{N}_\%$ , SLA and  $\delta^{13}\text{C}$  as tools for interpreting complex forest environments would facilitate future research on shade tolerance and growth potential, and could be used to validate process models characterizing multi-species responses to disturbance in complex stands (Coates et al. 2003).

Foliar  $\text{N}_\%$  defines the photosynthetic capacity and growth potential of many tree species (Reich et al. 1995, Wright et al. 2004) and is an effective index for comparing soil fertility across localized forested landscapes, especially those with even-aged stands (Radwan and Harrington 1986, Wang and Klinka 1997). In complex stands, however, interpreting foliar  $\text{N}_\%$  is complicated by its potential interaction with reduced light availability, which may affect foliar  $\text{N}_\%$  irrespective of soil N supply. In general, shade-intolerant species appear to have negative interactions between foliar nutrition and shade, perhaps due to declining rates of N uptake and shifts in biomass allocation under reduced light (Niinemets 1998, Lusk and Reich 2000, Kaelke et al. 2001, Kazda et al. 2004). Shade tolerant tree species, by contrast, have more consistent foliar  $\text{N}_\%$  across light levels, where shading results in increased specific leaf area ( $\text{cm}^2 \text{g}^{-1}$ ) and decreased foliar N content ( $\text{N}_a, \text{g m}^{-2}$ ) (Niinemets et al. 1998, Grassi and Bagnaresi 2001, Kranabetter and Coates 2004, Lapointe et al. 2006). Foliar  $\text{N}_\%$  status may be a useful index for predicting

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growth potential of understory saplings (Kobe 2006), but whether foliar N% can be used as an independent index of soil fertility (see Chapter 3) or an integrator of soil and light constraints, must be determined for each tree species.

Natural abundance of  $^{13}\text{C}$  is another useful and well established index in ecophysiology studies, and is based on discrimination against the heavier  $^{13}\text{C}$  isotope during  $\text{CO}_2$  gas exchange and photosynthesis (Farquhar et al. 1989). Foliar  $\delta^{13}\text{C}$  is depleted under shaded conditions due to a reduction in carboxylation caused by diminished regeneration of ribulose biphosphate at lower light levels (Broadmeadow and Griffiths 1993, Le Roux et al. 2001). Both light and nitrogen can affect the balance of  $\text{CO}_2$  supply (stomatal conductance) and demand (assimilation rate), however, and consequently  $\delta^{13}\text{C}$  can be well correlated with foliar  $N_a$  (Duursma and Marshall 2006). Interpretation of foliar  $\delta^{13}\text{C}$  patterns can be confounded because of stratification of atmospheric  $\text{CO}_2$  by soil and canopy respiration (Sternberg et al. 1989, Buchmann et al. 1997), as well as by vertical gradients in light availability with tree height (Burgess and Dawson 2007). These potentially confounding factors should be minor, however, in the narrow range of canopy positions for understory trees. To understand and predict understory tree responses to changes in resource availability in complex stands, there is a need to develop species-specific relationships between foliar  $\delta^{13}\text{C}$  and  $N_a$ .

Partial-cutting regimes that retain live trees and add structural diversity to managed stands will directly alter light availability in the understory (Coates and Burton 1997), and will also influence soil nutrient cycling over time (Prescott 2002). It is important that inferences of light effects on saplings via partial cutting also consider possible concurrent changes in soil resources, especially the short-term (approx. 5 years) post-harvest peak in N availability typical for coniferous forests (Walters et al. 2006, Titus et al. 2006). In addition, there are ontogenetic changes in foliar attributes, such as leaf mass, in the early years after seedling establishment that can confound the attributes associated with shade tolerance (Niinemets 2006). Given these issues, the characterization of species response to light gradients via foliar attributes could be more effective in the medium term (> 10 years post-harvest), when the initial perturbation to soil fertility and seedling size effects are less conspicuous.

The objective of the study was to establish relationships between foliar  $N_{\%}$ ,  $N_a$ , and  $\delta^{13}C$  across light gradients and examine the consistency in these patterns among tree species of varying shade tolerance. The tree species, in order of decreasing shade tolerance, were western redcedar (*Thuja plicata* Donn ex D. Don in Lamb), western hemlock (*Tsuga heterophylla* [Raf.] Sarg.), hybrid spruce (*Picea glauca* x *Picea sitchensis* [Moench] Voss) and paper birch (*Betula papyrifera* Marsh.) saplings. The study was conducted in 12-year-old partial-cut treatments at the Date Creek research forest, where the experimental range of gap sizes provided a broad gradient in light availability. I hypothesized that soil N mineralization rates would be unaffected by canopy removal, resulting in consistent foliar  $N_{\%}$  across a broad range of light levels. In addition, I predicted foliar  $N_a$  and  $\delta^{13}C$  would vary directly with light availability, helping to explain shading constraints on growth of understory saplings.

## Materials and methods

### Site description

The 4000-ha Date Creek Research Forest is located in the coast-interior transitional forests in the moist-cold subzone of the Interior Cedar-Hemlock zone (Banner et al. 1993) near Hazelton, British Columbia, Canada (55°22' N, 127°50' W, elevation 450 m). The average climatic characteristics of Hazelton are 535 mm annual precipitation (238 mm during the growing season), 4.4°C mean annual temperature, 1267 growing degree days > 5°C, and 176 frost-free days (Banner et al. 1993). The research forest is comprised mostly of western hemlock (65% of the basal area) with smaller amounts of western redcedar (18%), hybrid spruce (8%), subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) (2%), paper birch (5%), and lodgepole pine (*Pinus contorta* Dougl. Ex Loud. var. *latifolia* Engelm.) (2%). Mesic ecosystems (Western Hemlock - Step moss; Banner et al. 1993) predominate in the research forest and are characterized by a continuous cover of mostly coniferous trees, sparse shrub and herb layers, and a continuous and well-developed ground cover of feathermosses. Soils are Eluviated/Orthic Dystric Brunisols and Orthic Humo-Ferric Podzols developed in morainal blankets, with soil textures ranging from sandy loam to clay loam (Soil Classification Working Group 1998). Forest floors are 4- to 14-cm thick Hemimors

(Green et al. 1993). Soil nutrient characteristics of the forest floors and mineral soils in unharvested and partial-cut treatments are listed in Kranabetter and Coates (2004).

### **Experimental design**

The study was conducted in the heavy-removal (60% of the basal area) treatment at Date Creek (Coates et al. 1997). This treatment is comprised of small patch cuts (1000-5000 m<sup>2</sup> in size) interspersed with forest containing single-tree to small group-selection cuts. This heavy-removal treatment unit was replicated four times in a randomized complete block design. Each treatment unit is approximately 20 ha in size. The blocks were defined by successional stage (mature stands of 145 years and oldgrowth of 355 years) and ecological site units (relative soil moisture/nutrient regime; Banner et al. 1993): block A, mature stand 100% mesic; block B, mature stand 70% mesic - 30% submesic; block C, 70% mesic - 30% subhygric; and block D, oldgrowth 100% mesic. The four blocks are between 3 and 7 km apart. Treatment units were harvested (whole-tree removal) in the summer and fall of 1992 using ground-skidding equipment. Western redcedar, hybrid spruce, western hemlock, subalpine fir and lodgepole pine were planted throughout the treatment units in 1993.

In the summer of 2004, I searched the heavy-removal treatment units for candidate trees under four classes of estimated light: 20, 40, 60 and 80% full sunlight. The juvenile trees were a mixture of 10 to 12-year-old planted and naturally-regenerated western redcedar, western hemlock, hybrid spruce and paper birch. I selected three well-dispersed replicate trees of each species for the four light classes (4 species x 4 light classes x 3 replicates = 48 trees per experimental block; 192 trees in total).

Available light (400-700 nm) over the growing season (mid-April to mid-September) was assessed using hemispherical canopy photographs for each sample tree. The digital photograph was taken at 1.5 m height, either above the tree or, in the case of larger trees, adjacent to it in the same light environment. The larger juvenile trees were either briefly bent back, away from the camera, or edited out of the digital photograph to allow for an estimation of light conditions. The growing season light availability, expressed as a percentage of full sun, was computed from each photograph using the Gap Light Analyser (GLA) 2.0 software, following Frazer et al. (2000).

### **Soil nitrogen availability**

Beginning June 9 and 10<sup>th</sup>, 2004, during the early growing season, five trees (regardless of species) at each light level were selected as sample points to determine mineral soil and forest floor N availability using in-situ buried bags. Soils were collected outside the crown dripline of the selected tree. Intact forest floor was sampled using a 15-cm diameter template, avoiding pure decayed wood, and humus depth was noted at each sampling spot. Mineral soils were too rocky to extract as an intact core, so a stony auger was used to sample down to 20 cm. Mineral soils were gently poured back into a polyethylene bag lining the sample hole, and the bag was sealed with a twist tie. Forest floor cores were put into a separate polyethylene bag, which was placed on top of the mineral soil bag, and covered with moss or leaf litter. After 5 weeks, the bags were retrieved and gently run through a 5 mm sieve, and a subsample taken for moisture content (105°C for 24 hours). A second subsample was frozen for an analysis of inorganic N.

### **Foliage sampling and tree growth attributes**

Foliar samples were taken from the current year's growth of three lateral shoots in the top quarter of each tree (all sides of the tree), and bulked into one sample. Birch leaves (petioles removed) were sampled August 24, 2004, before colour loss, avoiding any leaves damaged by insects or disease. Conifer needles were sampled on September 20 and 21<sup>st</sup>, 2004, when tree growth had ceased. The leaves were assessed for N concentrations,  $\delta^{13}\text{C}$ , oven-dried mass (24 hours at 70°C) and one-sided projected leaf area (LI-COR 3100, Lincoln, Neb.) based on 10 leaves for birch, 50 needles for western hemlock and hybrid spruce, and five branchlets for western redcedar (Radwan and Harrington 1986). Tree height, root-collar diameter and height increment were measured on each tree in late September, 2004.

Inorganic  $\text{NH}_4\text{-N}$  and  $\text{NO}_3\text{-N}$  were determined using KCl extraction of a 5-g and 2-g dry-soil equivalent of mineral soil and forest floor, respectively (Hart et al. 1994). The extracts were immediately frozen (-80°C), allowing all pre-incubation and post-incubation samples to be analysed together. The  $\text{NH}_4\text{-N}$  and  $\text{NO}_3\text{-N}$  in the extracts were measured colorimetrically using an Alpkem Flow System IV analyzer (OI Analytical, College Station, Tex.). Nitrogen results are presented as total mineralized N

concentrations (inorganic N extracted after 5 weeks incubation) and converted to mass for the soil profile. For this conversion, forest floor depth at each sample point with a bulk density of  $100 \text{ kg m}^{-3}$  was used, along with a mineral soil depth of 20 cm and bulk density of  $1000 \text{ kg m}^{-3}$  (corrected for average coarse fragment content of the treatment block; J. M. Kranabetter, unpublished).

Foliar N was analysed by dry combustion with a Leco CHN-600 analyser (LECO Corp., St. Joseph, Mich.) (Kalra and Maynard 1991). The natural abundance of  $^{13}\text{C}$  was determined using an AS autosampler of a Thermoquest NC 2500 elemental analyser (Carlo Erba Instruments, Milan, Italy) coupled to a Finnigan DELTAplus (Thermo Electron Corp., Boston, U.S.A.) isotope ratio mass spectrometer. Lab standards were calibrated against the international calcium carbonate standards NBS 19 (1.95‰) and NBS 20 (-1.06‰). Carbon isotopic values are expressed relative to Vienna Peedee Belemnite (vpdb) (Wolf et al. 1994).

### **Statistical analyses**

The data were analysed as a randomized block design, where the light class treatment was tested as a continuous variable (using measured % light availability) against foliar attributes or soil properties using the GLM procedure in SAS (SAS Inc. 1988). The relationship between foliar attributes and light availability was examined separately for each tree species because of the significant species  $\times$  light interactions ( $p < 0.001$ ) for almost all variables. These relationships were explored by fitting linear or nonlinear regressions (Type III exponential function) with block and block\*light interactions removed if nonsignificant. Fitted curves in the figures represent an average of the four blocks. It was not possible to directly test soil N measures against individual trees because only a subset of the light gradient was sampled for soil N availability.

### **Results**

Light availability ranged from 10% to 75% full sunlight, which included canopy gaps resulting from single-tree removal, to approximately 80-m diameter openings (0.5 ha) resulting from small patch cuts. The regenerating conifers 12 years postharvest ranged in height from 0.5 to 6 m, and in annual height increment from 2 cm to 70 cm, across the gradient of light availability. Paper birch saplings were as tall as 7 m, but were

more variable in size than conifers across light gradients because of regeneration delays and browse damage from wildlife.

### **Soil N mineralization along light gradients**

Soils were at field moisture capacity across the light gradients at the onset of the buried-bag incubation (averaging 250% w/w and 40% w/w for forest floors and mineral soils, respectively). After 5 weeks, concentrations of mineralized N did not vary with light availability for either forest floors or mineral soils ( $p = 0.951$  and  $0.369$ , respectively), but differed significantly among treatment blocks, with the highest values in block C ( $p < 0.05$ ) (Table 4.1). Inorganic N occurred almost entirely as  $\text{NH}_4^+$ ; 93% and 99% of the forest floors and mineral soil samples, respectively, had undetectable concentrations of  $\text{NO}_3^-$  after the incubation. Forest floor depth averaged 4.7 cm (SE 0.3), and did not differ significantly across light levels ( $p = 0.360$ ). When converted to mass, soil N mineralization rates of the profile did not change with light availability ( $p = 0.210$ ), but were again significantly greater in block C, reflecting comparatively richer, subhygric microsites around some of the sample trees in this treatment unit (Table 4.1).

### **Foliar attributes along light gradients**

We found a significant species  $\times$  light interaction for foliar N concentration ( $p = 0.003$ ). Foliar N% declined in the shade by approximately 40% (14.5 to 8.5 g kg<sup>-1</sup>) for western redcedar and 20% (23.0 to 18.0 g kg<sup>-1</sup>) for paper birch, in curvilinear and linear regressions, respectively (Table 4.2, Fig. 4.1a, d). Shading had no effect on foliar N% of western hemlock or hybrid spruce, where N concentrations averaged 12.1 and 11.7 g kg<sup>-1</sup>, respectively, across light levels (Table 4.2, Fig. 4.1b, c). There was also a significant block effect overall (all species and light levels combined) due to elevated foliar N% in block C ( $p = 0.015$ ) (Table 4.1).

Specific leaf area declined with light for western redcedar, paper birch and, less consistently, for western hemlock (significant block  $\times$  light interactions) (Table 4.2, Fig. 4.2a, b, d). Hybrid spruce had variable leaf morphology and we were unable to detect any pattern in SLA with light availability (Table 4.2, Fig. 4.2c). Species and light availability interacted significantly in their effects on foliar N<sub>a</sub>, which was highest in blocks C and D (Table 4.1). Foliar N<sub>a</sub> was positively correlated with light availability for

all species except hybrid spruce, with significant block x light interactions for western hemlock (Table 4.2).

The natural abundance of  $^{13}\text{C}$  was strongly positively correlated with light availability for all species, with the best fit as an exponential curve for conifer species and a linear relationship for paper birch (Table 4.2, Fig. 4.3). Isotopic discrimination was reduced under higher levels of light availability, with relatively small differences among conifer species at light levels > 40%. Average  $\delta^{13}\text{C}$  values across light levels also varied significantly among species, following traditional shade tolerance rankings:  $\delta^{13}\text{C}$  was least depleted for western redcedar (-27.7‰), followed by western hemlock - hybrid spruce (-29.5‰ and -29.7‰, respectively), and then paper birch (-31.7‰).

Foliar  $N_a$  was linearly correlated with  $\delta^{13}\text{C}$  for western redcedar, western hemlock and paper birch ( $p < 0.001$ ), with no significant effect of block or block interactions (Fig. 4). There was no correlation between foliar  $N_a$  and  $\delta^{13}\text{C}$  for hybrid spruce, but a weak positive relationship occurred between foliar N mass (g N per 100 needles) and  $\delta^{13}\text{C}$  values ( $p = 0.028$ ,  $r^2 = 0.32$ ).

## Discussion

### Effects of light gradients on soil N supply

The initial flush of N after harvest treatments at Date Creek was apparently short-lived, as Walters et al. (2006) concluded, and by year 12, I could find no differences in N supply indices along these gradients in canopy openings. The total amount of inorganic N produced in situ may not include all relevant forms of plant-available N (Chapter 2, Schimel and Bennett 2004), but nevertheless should provide an effective index of N supply for comparing harvesting treatments (Grenon et al. 2005; Högberg et al. 2006). The nonsignificant differences in post-harvest N supply I found along light gradients in the mid-term (> 10 years) are consistent with other coniferous and deciduous stands utilizing similar silviculture systems (Jerabkova et al. 2006). The variation in soil N supply (ranging from 2.5 to 35 kg ha<sup>-1</sup>) and foliar N<sub>%</sub> among saplings (e.g. hybrid spruce ranging from 8 to 16 g kg<sup>-1</sup>) within the research forest was considerable, however, reflecting a mix of microsite quality (submesic to subhygric soils) among transects and experimental blocks.



### **Species interactions between foliar N% and light**

The relationship between soil N supply and foliar N% across light gradients differed among species in our study, consistent with other multi-species comparisons (Niinemets 1998, Lusk and Reich 2000, Kaelke et al. 2001, Kazda et al. 2004). Foliar N% was more uniform across light levels for western hemlock and hybrid spruce, suggesting that these shade-tolerant species maintain similar rates of N uptake and root/shoot ratios across a wide range of light conditions (Machado et al. 2003). Regeneration success and N uptake of shade-tolerant or intolerant species likely require at least a minimum amount of light, however, and in these stands it is uncommon for saplings to survive at < 15% light. Our intolerant species, paper birch, responded to partial cutting with shade-avoidance strategies, including increasingly etiolated stems under low light levels. This shift in biomass allocation from roots to stems, as is typical of shade-intolerant species (Messier et al. 1999), could have reduced N uptake rates, thus explaining the pattern of declining foliar N% with shade. Western redcedar's response was more puzzling, as this too is a shade-tolerant species and we did not expect to see declining foliar N% of such magnitude with shade. Respiration costs increase with foliar N% (Reich et al. 1998b), so a reduction in N uptake under low light (< 40% light) might be an adaptation to lower light compensation points, thus enhancing survival potential. However, many of the cedar saplings under deep shade were in very poor condition by year 12, especially on submesic-mesic microsites, and they appeared unlikely to survive in the long-term. Western redcedar is a temperate species limited to < 780 m elevation in the northwest interior (Banner et al. 1993), and the combined stresses of deep shade and poor soil fertility at this elevation (450 - 600 m for Date Creek) may truncate its distribution relative to that predicted by climate models (Hamann and Wang 2006).

### **An assessment of leaf photosynthetic activity**

Studies of leaf-level photosynthesis typically demonstrate a light saturation point at approximately 40% full light (Mitchell and Arnott 1995, Man and Lieffers 1997), and we found a similar asymptotic relationship in the field with  $\delta^{13}\text{C}$  for the three conifer species. This plateau in  $\delta^{13}\text{C}$  suggests that the gains in sapling growth at > 40% light could be attributed to increases in leaf area rather than higher rates of photosynthesis. Paper birch had a unique linear correlation between light and leaf  $\delta^{13}\text{C}$  abundance that

likely reflected both the reduced N uptake and losses in photosynthetic capacity with shading. Some of the variation in leaf  $\delta^{13}\text{C}$  abundance for individual saplings across light levels could be attributed to microsite differences in soil moisture and N supply (Brown et al. 1996, Sun et al. 1996), along with possible genetic differences in  $\text{CO}_2$  assimilation/transpiration efficiency (Guy and Holowachuk 2001). The difference in average leaf  $\delta^{13}\text{C}$  abundance between species was also noteworthy, and presumably indicates greater water use efficiency in more shade tolerant species (Marshall and Zhang 1994, Brooks et al. 1997).

The possible stratification of atmospheric  $\text{CO}_2$  through soil and canopy respiration did not appear to affect foliar  $\delta^{13}\text{C}$  patterns. Air circulation was less restricted in our heavy-removal (60% volume) cutblocks than the primal forest, and sample trees were often only a few metres apart at contrasting light levels (e.g., along gap edges). Other studies have shown significant stratification of  $\text{CO}_2$  between ground level and mature forest canopies (Sternberg et al. 1989, Buchmann et al. 1997), but our sampled foliage differed in height by 5 m at most, minimizing this confounding effect. In general, the utility of foliar attributes in interpreting understory resource constraints is ideal for saplings since the relatively narrow range in size should minimize possible effects of tree height on water use efficiency, specific leaf area and foliar  $\text{N}_\%$  (Rijkers et al. 2000, Niinemets et al. 2002, Burgess and Dawson 2007).

Expressing foliar N status on a leaf-area or mass basis generally provides insights into patterns in photosynthetic capacity (Reich et al. 1995, Niinemets 1997b, Kloeppel et al. 2000, Katahata et al. 2007), which was supported here by the strong linear correlations with leaf  $\delta^{13}\text{C}$  abundance for hemlock, cedar and birch (Duursma and Marshall 2006). Hybrid spruce was an exception, with only weak correlations between  $\text{N}_\text{m}$  and leaf  $\delta^{13}\text{C}$  abundance, and this may have resulted from greater intraspecific variation in needle and shoot morphology with light (Niinemets 1997a). For the other tree species, foliar  $\text{N}_\text{a}$  values correlated primarily with light gradients, with some additional influence of microsite variation in N supply, and this simple parameter was the best integrator and predictor of both resource limitations on the regenerating saplings (i.e., Reich et al. 1998a). An example is provided by an outlier population of western hemlock saplings in

the D block, which caused significant interactions with light in the analysis but nevertheless was quite well characterized by foliar  $N_a$  levels (Fig. 4.4b).

### **Significance of light interactions on foliar N status in forest understories**

The ability to maximize N uptake under shade to compensate for reduced light availability is likely an important attribute of shade tolerance (Niinemets 1997b). In Chapter 3, I suggested that the inability of lodgepole pine to match the foliar  $N_{\%}$  of subalpine fir could partly explain its absence from the understory on moderate and highly productive sites. Likewise, I predict that paper birch is at a higher risk of mortality in the understory at Date Creek because of its inability to maintain N nutrition under shade. This could also apply to western redcedar, perhaps demonstrating physiological constraints in shade tolerance at the northern edge of its distribution. In general, the inherent differences in how well species exploit soil N supply (amino acids, ammonium and nitrate) (Lucash et al. 2007) and how effective N uptake is under shade are likely key parameters to examine in sapling physiology and understory dynamics across landscapes.

### **Conclusions**

Foliar  $N_{\%}$ ,  $N_a$ , and  $\delta^{13}C$  were useful indices for explaining the dual constraints of light and nutrition on understory sapling physiology. I found that foliar  $N_{\%}$  characterized soil fertility well across light gradients (down to ~ 15% light) for spruce and hemlock, and could therefore be a useful tool in quantifying the effects of harvesting and site quality on N dynamics (Mitchell et al. 2007). For birch and cedar (at least at the elevation in this study), declining foliar  $N_{\%}$  with shading reduces the utility of  $N_{\%}$  as an index of soil fertility, but may also explain higher rates of mortality in the forest understory. In general, the best growth of all species occurred on the richest microsites where there was ample N supply to compensate for reduced light levels. Consistent with this were significant linear correlations between foliar  $N_a$  ( $N_m$  for spruce) and sapling height increment (data not shown), but a more precise model of understory sapling growth might also consider differences in biomass allocation with tree size over time (Delagrange et al. 2004, Claveau et al. 2005). Using these foliar attributes to examine the influence of N nutrition on light utilization for each species, as well as for inherent

differences in species exploitation of soil N supply, would be the next steps in accurately modelling regeneration dynamics in complex stands and landscapes.

Table 4.1: Treatment block averages of forest floor and mineral soil N mineralization, foliar N concentrations and foliar N per unit area (all species) (mean and SE in brackets).

	5-wk in-situ N mineralization				
	Forest floor (mg kg <sup>-1</sup> )	Mineral soil (mg kg <sup>-1</sup> )	Profile (kg ha <sup>-1</sup> )	Foliar N <sub>%</sub> (g kg <sup>-1</sup> )	Foliar N <sub>a</sub> (g m <sup>-2</sup> )
Block A	109a† (15)	6.9a (1.0)	13.7a (2.0)	13.4a (0.7)	1.88a (0.1)
Block B	97a (14)	8.4ab (1.3)	14.3a (2.1)	13.6a (0.6)	1.89a (0.1)
Block C	181b (21)	15.1b (3.0)	23.8b (3.4)	14.8b (0.7)	3.01b (0.3)
Block D	209b (18)	7.0a (1.6)	15.4ab (1.9)	13.1a (0.6)	2.70b (0.2)

† Means within columns sharing the same letter are not significantly different (Tukey HSD  $P < 0.05$ )

Table 4.2: Linear and curvilinear correlations ( $p > F$  and  $r^2$ ) for foliar attributes across light levels for each tree species ( $n = 48$  for each species). Values in bold are significant ( $p < 0.05$ ).

Source	Foliar N <sub>%</sub> (g kg <sup>-1</sup> ) ( $p > F$ )	SLA (cm <sup>2</sup> g <sup>-1</sup> ) ( $p > F$ )	Foliar N <sub>a</sub> (g m <sup>-2</sup> ) ( $p > F$ )	$\delta^{13}C$ (‰) ( $p > F$ )
<b>Western redcedar</b>				
Block	0.689	0.075	0.711	0.431
Light	<b>&lt; 0.001</b>	<b>&lt; 0.001</b>	<b>&lt; 0.001</b>	<b>&lt; 0.001</b>
Block x light	0.978	0.224	0.219	0.705
<b>Western hemlock</b>				
Block	0.754	<b>0.002</b>	<b>0.027</b>	0.168
Light	0.602	<b>&lt; 0.001</b>	<b>&lt; 0.001</b>	<b>0.002</b>
Block x light	0.864	<b>0.023</b>	<b>0.049</b>	0.611
<b>Hybrid spruce</b>				
Block	0.505	0.087	0.195	0.740
Light	0.519	0.688	0.421	<b>0.001</b>
Block x light	0.427	0.600	0.959	0.779
<b>Paper birch</b>				
Block	0.709	0.175	0.429	0.108
Light	<b>0.004</b>	<b>&lt; 0.001</b>	<b>&lt; 0.001</b>	<b>&lt; 0.001</b>
Block x light	0.455	0.499	0.263	0.141

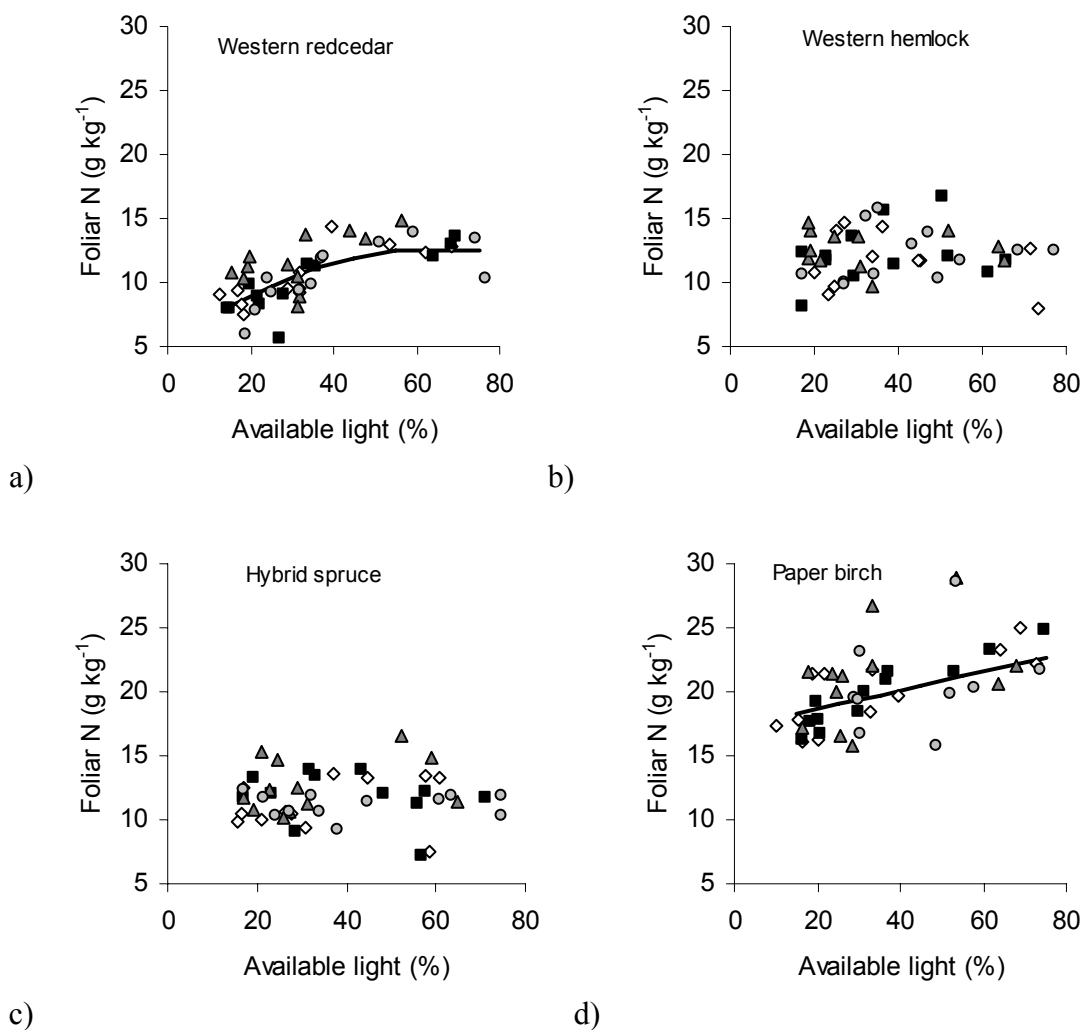


Figure 4.1: Correlation between light availability and foliar N% ( $\text{g kg}^{-1}$ ) for a) western redcedar, b) western hemlock, c) hybrid spruce and d) paper birch ( $n = 48$  for each species; blocks differentiated by symbols).

$$\text{Western redcedar foliar N}_{\%} = 4.9 + 0.24(\text{Light avail.}) - 0.0019(\text{Light avail.})^2; r^2 = 0.51$$

$$\text{Paper birch foliar N}_{\%} = 17.2 + 0.073(\text{Light availability}); r^2 = 0.38$$

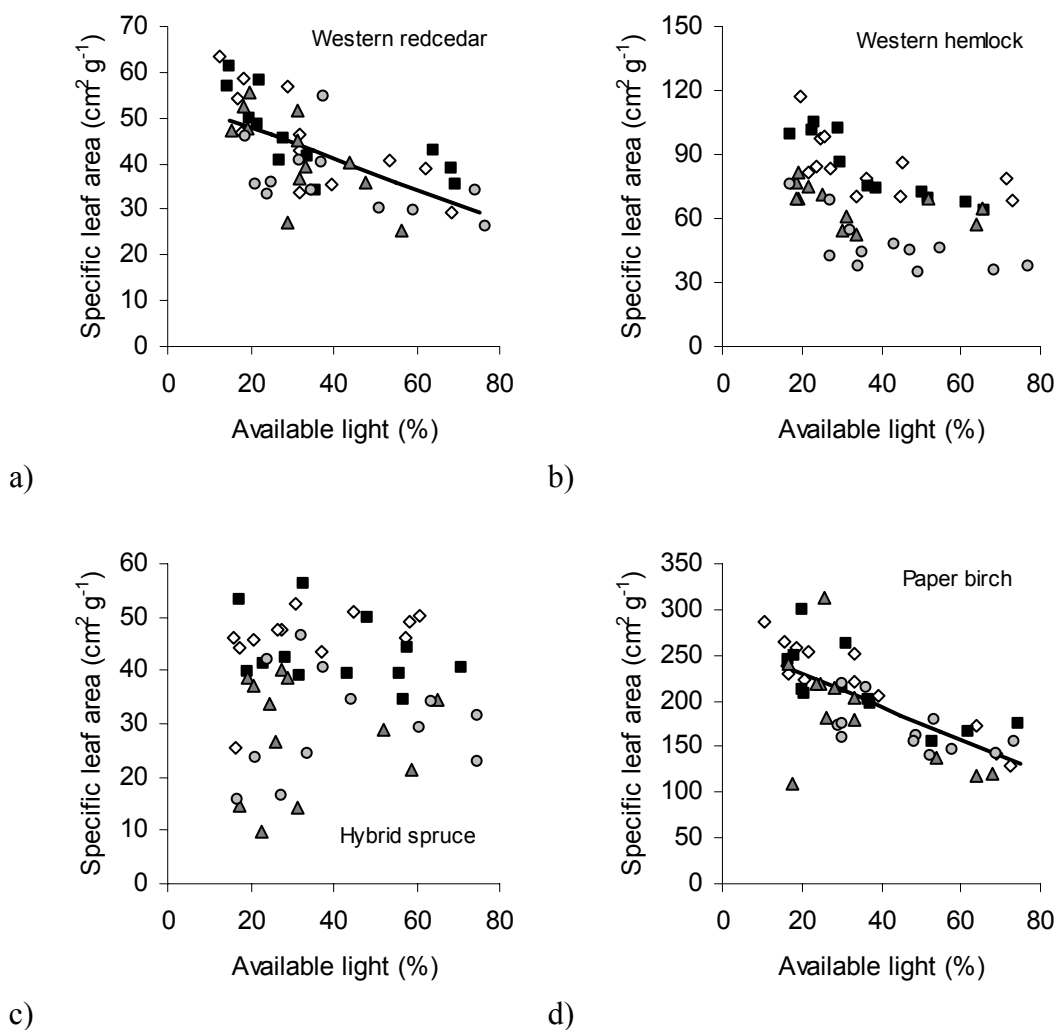


Figure 4.2: Correlation between light availability and specific leaf area ( $\text{cm}^2 \text{g}^{-1}$ ) for a) western redcedar, b) western hemlock, c) hybrid spruce and d) paper birch ( $n = 48$  for each species; blocks differentiated by symbols).

Western redcedar foliar SLA =  $54.7 - 0.34(\text{Light availability})$ ;  $r^2 = 0.52$

Paper birch foliar SLA =  $264 - 1.77(\text{Light availability})$ ;  $r^2 = 0.61$

No correlation is shown for Hw because of block x light interactions.

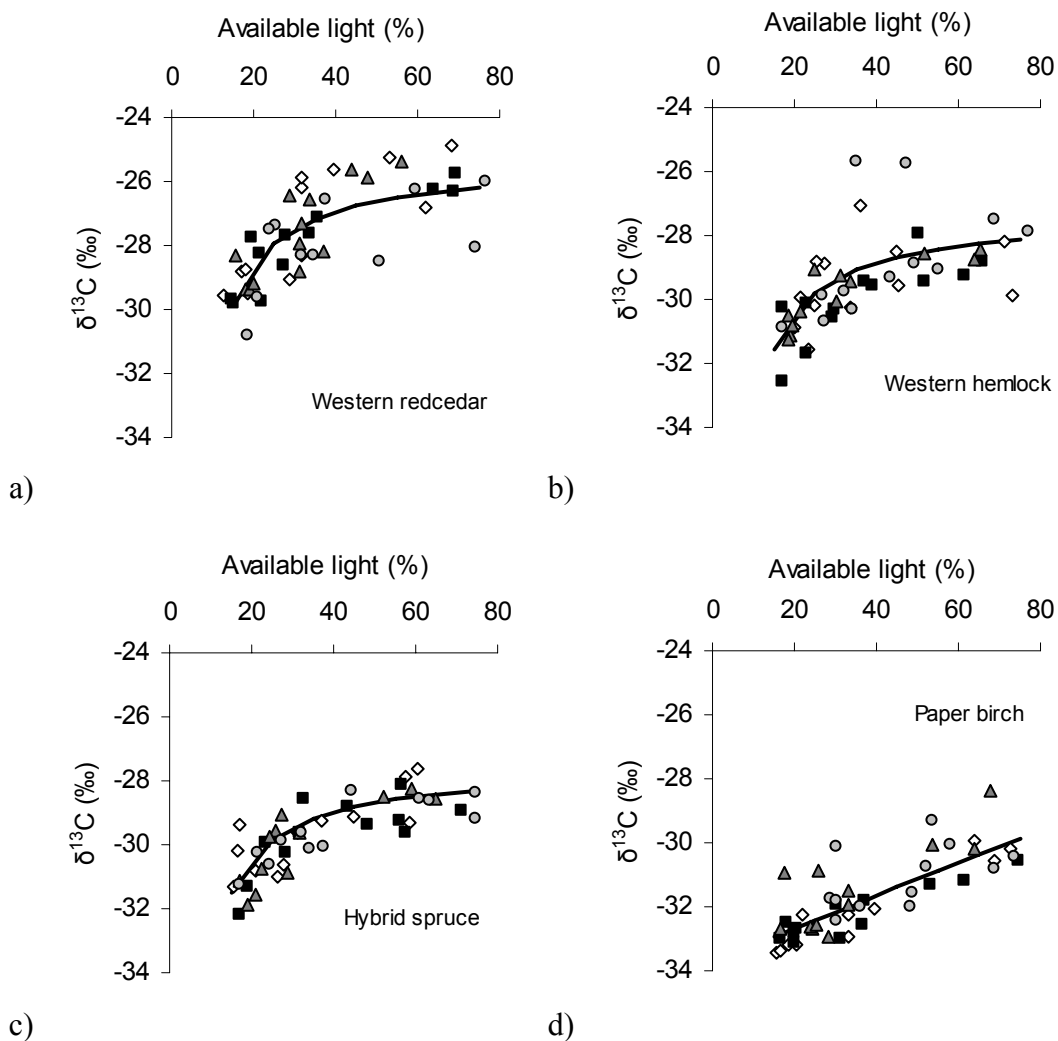


Figure 4.3: Correlation between light availability and  $\delta^{13}\text{C}$  for a) western redcedar, b) western hemlock, c) hybrid spruce and d) paper birch (n = 48 for each species; blocks differentiated by symbols).

Western redcedar foliar  $\delta^{13}\text{C} = -25.3 - 67.8(1/\text{Light availability})$ ;  $r^2 = 0.66$

Western hemlock foliar  $\delta^{13}\text{C} = -27.3 - 65.0(1/\text{Light availability})$ ;  $r^2 = 0.50$

Hybrid spruce foliar  $\delta^{13}\text{C} = -27.7 - 60.3(1/\text{Light availability})$ ;  $r^2 = 0.70$

Paper birch foliar  $\delta^{13}\text{C} = -33.7 + 0.051(\text{Light availability})$ ;  $r^2 = 0.76$



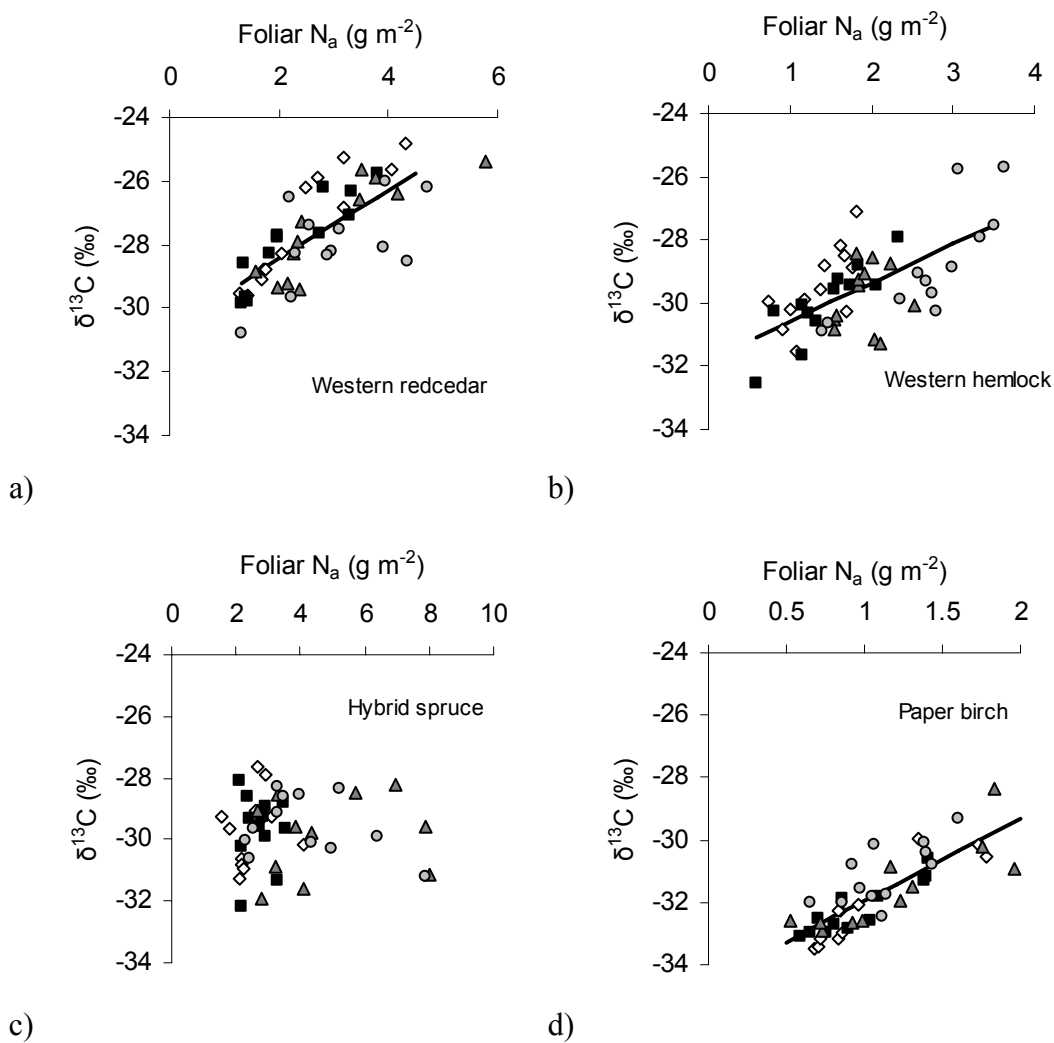


Figure 4.4: Correlation between foliar  $N_a$  and  $\delta^{13}C$  for a) western redcedar, b) western hemlock, c) hybrid spruce and d) paper birch ( $n = 48$  for each species; blocks differentiated by symbols).

$$\text{Western redcedar foliar } \delta^{13}C = -30.6 + 1.08(\text{Foliar } N_a); r^2 = 0.58$$

$$\text{Western hemlock foliar } \delta^{13}C = -31.1 + 1.95(\text{Foliar } N_a); r^2 = 0.57$$

$$\text{Paper birch foliar } \delta^{13}C = -34.6 + 2.65(\text{Foliar } N_a); r^2 = 0.70$$

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## **5 Understory sapling foliar and growth response to nitrogen treatments along gradients of light availability<sup>4</sup>**

### **Introduction**

The dual resource constraints of light and N availability differentially affect species survival and growth in forest understories (Catovsky and Bazzaz 2002, Kobe 2006), and models of regeneration and stand development in multi-species, uneven-aged forests require more precise information on these species interactions. Different approaches to develop this information include greenhouse experiments (Mitchell and Hinkley 1993, Evans et al. 2001, Thompson et al. 1992, Fownes and Harrington 2004), field experiments (Catovsky and Bazzaz 2002, Machado et al. 2003, Walters et al. 2006), and retrospective studies of natural site gradients (Carter and Klinka 1992, Drever and Lertzman 2001, Finzi and Canham 2000, Kobe 2006). None of these approaches are without flaws: greenhouse settings require extrapolation from seedlings that may or may not be valid; field manipulations are also short-term, and include artificial treatments, especially N fertilization, that might not accurately reflect complex soil processes; and natural site gradients cannot control for other factors, such as moisture availability, that could confound light-nitrogen interactions. A variety of research approaches will likely be necessary to reach some consensus on species interactions with light and N availability.

Having examined natural N gradients with no alteration in understory light (Chapter 3), I undertook a reciprocal field experiment with light gradients where I sought to alter the soil N supply. My experimental approach to light/nitrogen interactions was novel in using established saplings, rather than planted seedlings, which I felt would be an improvement in methodology. The primary disadvantage with seedlings is the time needed to recover from transplanting stress, and the slow growth rates under shade that could delay the full expression of site resources. At the Date Creek Research Forest, juvenile saplings are clearly expressing light constraints to growth, with some variation in response contributed by microsite variation in soil fertility (Chapter 4). Adjusting the soil N availability around this light gradient, where root systems are already well established, should allow for a more immediate integration of N status on species response than

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seedlings would offer. A second advantage with older field installations is the consistency in soil N availability and conifer nutrition across canopy openings, when the confounding issues of an assart flush or seedling size effects have passed (Chapter 4).

In this experiment, saplings (~ 12 years old) were selected from under a range of canopy opening sizes (e.g. 15% to 85% of available light), and nitrogen availability was manipulated around these trees either by an addition of N as fertilizer or by immobilization of N in sawdust. The experimental treatments were applied to four tree species of declining shade tolerance: western redcedar (*Thuja plicata* Donn ex D. Don in Lamb), western hemlock (*Tsuga heterophylla* [Raf.] Sarg.), hybrid spruce (*Picea glauca* x *Picea sitchensis* [Moench] Voss) and paper birch (*Betula papyrifera* Marsh.) (Kobe and Coates 1997).

The objectives of this study were to (1) quantify differences in growth (height and radial increment) of juvenile trees as a function of nitrogen supply across a full range in light availability; (2) to determine whether the interactive effects of nitrogen and light differed among species of varying shade tolerance; (3) to relate the combined light and N constraints on growth to leaf photosynthetic activity (foliar N per unit area); and (4) to determine an ‘optimization to stagnation range’ for each species, describing the combinations of soil N supply and light availability where growth is maximized or essentially ceases.

## **Materials and methods**

### **Site description**

The 4000-ha Date Creek Research Forest is located in the coast-interior transitional forests of the Interior Cedar-Hemlock zone, moist-cold subzone (Banner et al. 1993) near Hazelton, British Columbia, Canada (55°22' N, 127°50' W, elevation 450 m). The average climatic characteristics of Hazelton are 535 mm annual precipitation (238 mm during the growing season), 4.4°C mean annual temperature, 1267 growing degree days > 5°C, and 176 frost-free days (Banner et al. 1993). The research forest is comprised mostly of western hemlock (65% of the basal area) with smaller amounts of western redcedar (18%), hybrid spruce (8%), subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) (2%), paper birch (5%), and lodgepole pine (*Pinus contorta* Dougl. Ex Loud. var.

*latifolia* Engelm.) (2%). Mesic ecosystems (Western Hemlock - Step moss; Banner et al. 1993) predominate in the research forest and are characterized by a continuous cover of mostly coniferous trees, sparse shrub and herb layers, and a continuous and well developed ground cover of feathermosses. Soils are Eluviated/Orthic Dystric Brunisols and Orthic Humo-Ferric Podzols developed in morainal blankets, with soil textures ranging from sandy loam to clay loam (Soil Classification Working Group 1998). Forest floors are 4- to 14-cm thick Hemimors (Green et al. 1993). Soil nutrient characteristics of the forest floors and mineral soils in unharvested and partial-cut treatments are listed in Kranabetter and Coates (2004).

### **Experimental design**

The study was conducted in the heavy removal (60% of the basal area) treatment at Date Creek (Coates et al. 1997). This treatment is comprised of small patch cuts (1000-5000 m<sup>2</sup> in size) interspersed with forest containing single-tree to small group-selection cuts. This heavy-removal treatment unit was replicated four times in a randomized complete block design. Each treatment unit is approximately 20 ha in size. The blocks were defined by successional stage (mature stands of 145 years and oldgrowth of 355 years) and ecological site units (relative soil moisture/nutrient regime; Banner et al. 1993): block A, mature stand 100% mesic; block B, mature stand 70% mesic - 30% submesic; block C, 70% mesic - 30% subhygric; and block D, oldgrowth 100% mesic. The four blocks are between 3 and 7 km apart. Treatment units were harvested (whole-tree removal) in the summer and fall of 1992 using ground-skidding equipment. Western redcedar, hybrid spruce, western hemlock, subalpine fir and lodgepole pine were planted throughout the treatment units in 1993.

In the summer of 2004, I searched the heavy-removal treatment units for candidate trees under four classes of estimated light: 20, 40, 60 and 80% full sunlight. The juvenile trees were a mixture of 10 to 12-year-old planted and naturally-regenerated western redcedar, western hemlock, hybrid spruce and paper birch. I selected five well dispersed replicate trees of each species for the four light classes (4 species x 4 light classes x 5 replicates = 80 trees per experimental block; 320 trees in total).

Available light (400-700 nm) over the growing season (mid-April to mid-September) was assessed using hemispherical canopy photographs for each sample tree.

The digital photograph was taken at 1.5-m height, either above the tree or, in the case of larger trees, adjacent to it in the same light environment. The larger juvenile trees were either briefly bent back, away from the camera, or edited out of the digital photograph to allow for an estimation of light conditions. The growing season light availability, expressed as a percentage of full sun, was computed from each photograph using the Gap Light Analyser (GLA) 2.0 software, following Frazer et al. (2000).

### **Nitrogen treatments**

Two treatment levels of reduced N supply (low wood and high wood) were implemented by an application of carbon (sawdust and sawdust + tongue depressors, respectively) to immobilize soil N through decomposition. Sawdust was obtained from bandsaw cuttings at a mill in Smithers. The sawdust was from conifer logs (lodgepole pine, hybrid spruce, subalpine fir), and the particles were between 1 mm and 2 mm in size. Sawdust was applied around each tree in a circle with a diameter corresponding to the approximate canopy 'dripline' of the four size classes: 50 cm diameter for 20% light; 75 cm for 40% light; 120 cm for 60% light; and 175 cm for 80% light. An application rate of 8.5 L sawdust per m<sup>2</sup> across all size classes was used, which resulted in an average depth of 1 cm. The sawdust was 150 g per L dry wt, with a C content of 48% and C:N ratio of 2150. The application rate equalled 1.3 kg sawdust (0.6 kg C) per m<sup>2</sup>, equivalent to 13 Mg per ha or 6000 kg C per ha. Sawdust was applied August 23-25, 2004. A second application for the high wood treatment only was applied August 12, 2005. Some moss was removed from around the tree, taking care not to damage feeder roots, and the sawdust was gently raked by hand to ensure contact with the forest floor.

The high wood treatment included birch wood pegs (tongue depressors 15 x 2 cm; 2 mm thick, Puritan Quality Medical Products), with the double application of sawdust, to immobilize N deeper in the soil. A proportional number of pegs to the dripline radius were utilized: 12 pegs at 20% light; 20 pegs at 40% light; 35 pegs at 60% light; and 70 pegs for 80% light. The pegs were pushed into the soil as deeply as possible, radiating out from the stem of the sample tree at 15-20 cm spacing. The birch wood had a C content of 48% and C:N ratio of 945. Average mass of 10 pegs is 28.5 g, which is equivalent to 1700 kg per ha or 815 kg C per ha.

Two treatment levels (low N and high N) of enhanced N supply were implemented through the application of urea fertilizer (46:0:0) at 100 kg N per ha and 200 kg N per ha, respectively. Urea was applied September 20-22, 2004. The same aerial dimensions used in the sawdust application were used for the urea fertilizer application; I applied 4.4, 10, 25, and 54 g of N for 20%, 40%, 60% and 80% light, respectively, in the low N treatment, and 8.8, 20, 50 and 108 g for the high N treatment.

#### **Soil N and foliar assessments**

Beginning May 28<sup>th</sup>, 2007, during the early growing season, mineral soil and forest floor N availability at each sample tree was assessed using in situ buried bags. Soils were collected inside the nitrogen treatment areas (within the crown dripline) of the selected tree. Intact forest floor was sampled using a 10 cm template, avoiding pure decayed wood, and humus depth was noted at each sampling spot. Mineral soils were too rocky to extract as an intact core, so a stony auger was used to sample down to 20 cm. Mineral soils were gently poured back into a polyethylene bag lining the sample hole, and the bag was sealed with a twist tie. Forest floor cores were put into a separate polyethylene bag, which was placed on top of the mineral soil bag, and covered with moss or leaf litter. After 5 weeks, the bags were retrieved and gently run through a 5 mm sieve, and a subsample taken for moisture content (105°C for 24 hours). A second subsample was immediately shipped fresh to the MOF laboratory in Victoria, B.C., for an analysis of inorganic and organic N.

Foliar samples were taken from the current year's growth of three lateral shoots in the top quarter of each tree (all sides of the tree), and bulked into one sample. Birch leaves (petioles removed) were sampled August 15, 2007, before color loss, avoiding any leaves damaged by insects or disease. Conifer needles were sampled on September 20 and 21<sup>st</sup>, 2007, when tree growth had ceased. The leaves were assessed for N concentrations, oven-dried mass (24 hours at 70°C) and one-sided projected leaf area (LICOR 3100, Lincoln, Neb.) based on 10 leaves for birch, 100 needles for western hemlock and hybrid spruce, and five branchlets for western redcedar (Radwan and Harrington 1986). Foliar N was analysed by dry combustion with a Leco CHN-600 analyser (LECO Corp., St. Joseph, Mich.) (Kalra and Maynard 1991). Tree height, root collar diameter

and height increment were measured on each tree in late September over the three years of the study (2005, 2006 and 2007).

Dissolved organic nitrogen,  $\text{NH}_4\text{-N}$  and  $\text{NO}_3\text{-N}$  were determined from a 5-g and 2-g dry-soil equivalent of mineral soil and forest floor, respectively (Hart et al., 1994; Jones and Willett, 2006). A 2 M KCl solution was added to the soils at a 1:5 w/v ratio, and samples were shaken for 1 hour at 20°C. Samples were clarified by centrifugation for 15 minutes at 850 g. The extract was pipetted from the clear supernatant into an auto-analyzer cup for analysis. The  $\text{NH}_4\text{-N}$  and  $\text{NO}_3\text{-N}$  in the extracts were measured colorimetrically using an Alpkem Flow System IV analyzer (OI Analytical, College Station, Tex.).

A modified persulphate solution (low-N potassium peroxydisulphate) was used to convert dissolved organic N of the extract to nitrate (Qualls, 1989). A 1-ml aliquot of persulphate solution was added to 1 ml of soil extract in a glass vial, which was then sealed and autoclaved (121°C for 30 minutes). Nitrate concentrations in the persulphate digests were measured colorimetrically on an Alpkem Flow System IV analyzer, and DON was calculated by subtracting DIN concentrations from the total. Colour absorption by the digest reagents were corrected for using control N blanks.

### **Statistical analyses**

The experiment is a randomized complete block design with light as a main plot factor, nitrogen as a split-plot factor, and species as a split-split-plot factor. The N treatments were tested by soil, foliar and growth attributes using proc Mixed procedure in SAS (SAS Inc. 1988) with block and block interactions set as random factors. Light and N supply were tested as continuous variables using Proc GLM and type III sums of squares to test relationships between these resources and foliar/growth response. Inorganic N mass was log transformed for this analysis because of the curvilinear relationship between DIN and site potential (Chapter 2). Correlations were examined separately for each tree species because of the significant species interactions ( $p < 0.001$ ) for almost all variables. Relationships between light and growth as well as foliar nutrient and growth, were explored by fitting linear or nonlinear regressions with block and block interactions.

## Results

### Nitrogen treatments

There was a significant decrease in extractable inorganic N mass of the soil profile with the heavy wood treatment, and an intermediate decline with the low wood treatment (Table 5.1). Dissolved organic N was not affected by the N treatments, however, and no differences in the combined index (DIN + DON) were detected for the soil profile (Table 5.1). Some reduction in forest floor DON concentration was found with harvesting treatments, as indicated by light availability (Table 5.2), which led to weak differences ( $p = 0.087$ ) in DIN + DON mass with light availability (Table 5.2). Neither forest floor nor mineral soil DIN mass was affected by light availability ( $p = 0.335$  and  $p = 0.470$ , respectively).

### Foliar attributes

There were no differences in foliar N concentrations ( $N_{\%}$ ) among the N treatments for any of the four tree species (Table 5.1). However, foliar N was strongly affected by light availability and there were significant interactions between species and light (consistent with Chapter 4). Similarly, foliar N per unit area ( $N_a$ ) did not differ between N treatments but was affected by light availability and species interactions with light (Table 5.1).

### Growth response and site attributes

Height and diameter growth responses were regressed against the inherent range in soil N supply, sapling nutrition and light availability. The growth response of the conifer saplings (both height and root collar diameter) was well correlated with light availability (Table 5.3). Paper birch sapling size was extremely variable by block due to differences in regeneration delay, snow press damage and animal browse; for this reason there were strong block interactions in height and root-collar diameter correlations with light availability (Table 5.3, height results not included). Soil fertility, as indicated by either DIN mass or combined DIN + DON, was not a significant covariant in correlations between growth and light availability (Table 5.3). Foliar  $N_a$ , as a combined index of light and N supply, was as well correlated with height growth as was light availability, and in some cases, such as western redcedar, was a better predictor of growth response (Table 5.3, Fig. 5.1).

## **Discussion**

### **An evaluation of the experiment**

The attempted manipulation of N supply to the understory trees was only partially successful, with a significant decline in N mineralization via the heavy wood applications. The reduction in N mineralization, from an average of approx. 2.5 kg ha<sup>-1</sup> to 1.4 kg ha<sup>-1</sup>, represents a loss in fertility to DIN levels corresponding with submesic ecosystems (0.9 to 3.2 kg ha<sup>-1</sup> for poor-Cladonia to medium-Huckleberry; Chapter 2). The fertilizer treatments (100 and 200 kg N ha<sup>-1</sup>) had little effect on N supply by year 3, which is not entirely unusual for the Pacific Northwest (White et al. 1988, Prescott et al. 1993, Chappell et al. 1999), and probably reflects leaching and/or immobilization of the applied N. Unfortunately for the objectives of this study, none of the N treatments led to a corresponding gradation in foliar N nutrition, either as N concentration (N<sub>%</sub>) or N content (N<sub>a</sub>).

The most likely explanation for the outcome of the N treatments was that too little area was treated around each tree to greatly affect sapling nutrition. The decision to treat only the area under the canopy dripline was in part to protect the integrity of the research forest, as many of the surrounding understory trees are also being monitored for separate studies. Secondly, the wood treatments were laborious to complete, and doubling or tripling the size of the treated area was impractical for such widely dispersed and numerous sample trees. Although I was unable to sample foliage each year after treatment, it is quite possible that there was an ephemeral increase in foliar N concentration and leaf size with the N fertilizer before returning to pretreatment conditions. Overall, the success of the wood or fertilizer treatments would probably have required larger areas treated around each sapling, with multiple applications of N fertilizer to counteract the high rates of N leaching/immobilization in soil and uptake of N by non-target plants.

### **Utilizing a DIN + DON index with treatment regimes**

The proposed index of soil fertility, a 5 week in situ incubation of dissolved organic and inorganic N content (Chapter 2), was utilized across manipulated canopy openings (corresponding to light gradients) and N treatments in this study, rather than in undisturbed forests (as in Chapter 2), and its effectiveness under these conditions is less

certain. Based on the results of this study, the traditional DIN index should continue to be used until the link between DIN, DON and tree nutrition is well established under experimental conditions. In the case of sawdust treatments, for example, the reduction in N mineralization rates was not matched by DON to the same degree, and it is possible that the combined index of DIN + DON was less sensitive to the wood treatment effects on N supply.

In the assessment of partial cutting, I found that DON of the forest floor declined with increasing gap size, in agreement with Hannam and Prescott (2003), which could reflect either a disruption in DON inputs via litter or abiotic retention of DON with increasing harvesting disturbances. There was no corresponding change in DIN levels, however, and the combined index for the soil profile (mineral soils and forest floors) declined marginally by approx. 3 kg ha<sup>-1</sup> across light classes. The consistency in profile DIN or DIN + DON across light levels supports the general consensus that there is uniform nutrition across silviculture systems in the mid-term (i.e. > 10 years after harvest) (Jerabkova et al. 2006). Interestingly, the old-growth (355 year) stand had much higher concentrations of forest floor DON than the 145-year-old stands (375 g kg<sup>-1</sup> forest floor versus 210 g kg<sup>-1</sup>, respectively), yet there were no corresponding difference in foliar N concentrations of the regenerating saplings. Possibly the organic N extract from oldgrowth forests included more recalcitrant, high-molecular-weight N compounds that did not contribute to tree nutrition. Given the effects of harvesting disturbances and stand age, it would be worth considering temporal effects in the interpretation of DON and stand nutrition, especially for forest floors.

### **Monitoring sapling response through foliar N<sub>a</sub>**

None of the soil N indices improved the correlation between light availability and growth response, and it is possible that other factors (e.g. microsite variability, genetic differences, root/foliar disease, varying belowground competition and animal damage) were affecting the linkage between soils and foliar N%. In Chapter 3, the good relationships between soils and sapling nutrition were derived from plot averages (Chapter 3), and using individual saplings likely introduces more variability, especially without the large and consistent differences in N supply characteristic of natural fertility gradients. Despite the nonsignificant link to soil N indices, the understory saplings



monitored over the duration of the study varied widely in foliar N concentrations (i.e., from 7 to 16 g kg<sup>-1</sup>), which were again negatively affected by shade for paper birch and western redcedar, and independent of light for western hemlock and hybrid spruce (Chapter 4). The combined effects of light and N on sapling growth were fairly well integrated by foliar N<sub>a</sub> for western redcedar, western hemlock and paper birch, and by foliar N<sub>m</sub> for hybrid spruce (Chapter 5). Based on the saplings from this thesis, the following N<sub>a</sub> and N<sub>m</sub> values indicate the extremes in foliar N content reflecting growth stagnation and resource optimization: western redcedar 2.0 to 5.0 g m<sup>-2</sup>; western hemlock 1.0 to 2.0 g m<sup>-2</sup>; paper birch 0.7 to 1.7 g m<sup>-2</sup>; subalpine fir 2.0 to 4.0 g m<sup>-2</sup>; and hybrid white spruce 0.0025 to 0.0075 g 100<sup>-1</sup> needles. Foliar nitrogen concentrations have long been used as a tool to rank nutritional deficiencies in even-aged stands (e.g. Walker and Gessel 1991, Carter 1992, Brockley 2001), and this similar approach with foliar N content could be used in complex stands to assess the combined limitations of light and N on understory productivity.

## Conclusions

A more complete analysis of foliar attributes and species interactions under light and N resources would require a study design with clear and prolonged differences in soil N supply. Artificially imposed N treatments may not be practical or even realistic for this objective because of the short-term response associated with N fertilizers (approx. 5 years in operational fertilization; Mika et al. 1992), as well as the more complex inorganic and organic N cycles in northern ecosystems (Chapter 2). It might be difficult, for example, to recreate the diverging foliar N<sub>a</sub> correlations between subalpine fir and lodgepole pine (Fig. 3.5a) utilizing only ammonium fertilizer. In other field experiments, it has been concluded that enhanced soil N availability is less influential at low (< 40%) light levels (Drever and Lertzman 2002, Kobe 2006), and can even hasten seedling mortality of shade-intolerant species (Catovsky and Bazzaz 2002). Neither of these conclusions were entirely supported by the sapling response in these partial-cut stands; for example, paper birch on very rich microsites (primarily the C block) had elevated foliar N<sub>a</sub>, <sup>13</sup>C abundance and relative growth rates across light gradients, all suggesting significant and positive soil N effects for this shade-intolerant species even in shade (Chapter 4). Any

experimental manipulation of N availability at low light levels (approx. 15 - 25%) has to consider the artefact the treatments create simply by slow growth rates; because of this delay, it may take a few growing seasons for the full effects of site fertility to be expressed via foliage attributes and growth response. Given these experimental design limitations, a more rigorous analysis would require a carefully selected, replicated range of sites, where gap openings could be implemented over significant gradients in soil productivity, and species establishment and growth monitored for long periods of time.

Table 5.1: Extractable inorganic (DIN) and organic N (DON) after 5 week in situ incubation, foliar nitrogen concentration (N%) and content (N<sub>a</sub>) by treatment (mean and SE in brackets).

Treatment	NH <sub>4</sub> <sup>+</sup> + NO <sub>3</sub> <sup>-</sup> (kg ha <sup>-1</sup> )	DIN + DON (kg ha <sup>-1</sup> )	Foliar N% (g kg <sup>-1</sup> )	Foliar N <sub>a</sub> (g m <sup>-2</sup> )
High wood	1.39a (0.2)	25.2 (1.5)	12.8 (0.6)	2.00 (0.14)
Low wood	2.28ab (0.5)	30.7 (2.5)	12.7 (0.6)	1.98 (0.14)
Untreated	2.45b (0.4)	29.4 (1.9)	13.0 (0.6)	2.03 (0.14)
Low N fert.	3.02b (0.6)	29.3 (1.7)	12.7 (0.5)	2.05 (0.17)
High N fert.	2.72b (0.4)	28.7 (2.1)	13.0 (0.6)	2.07 (0.16)

† Means within columns sharing the same letter are not significantly different (Tukey HSD P < 0.05)

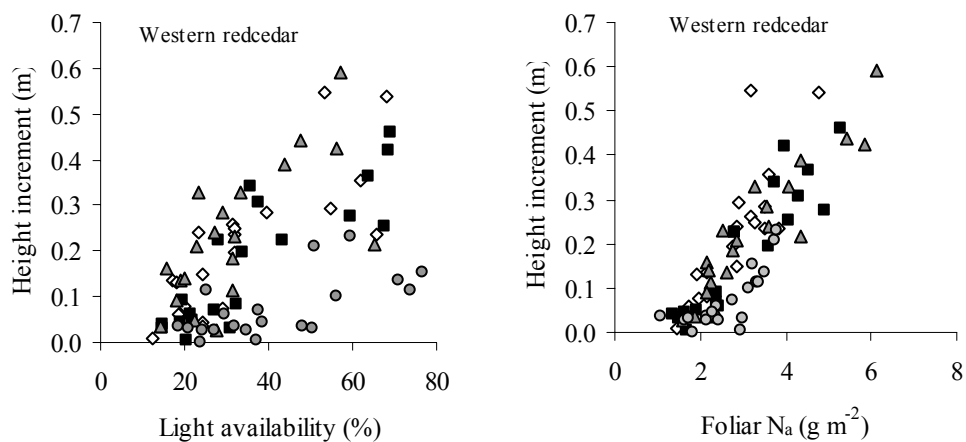
Table 5.2: Dissolved organic N (DON) and inorganic N (DIN) after 5 week in situ incubation by light class (mean and SE in brackets).

Treatment	DON of FF (mg kg <sup>-1</sup> )	DON of min (mg kg <sup>-1</sup> )	DIN + DON (kg ha <sup>-1</sup> )
20% light	247a (14)	13.1 (0.8)	29.3 (1.6)
40% light	239a (14)	14.2 (0.9)	31.0 (2.1)
60% light	198b (12)	13.3 (1.0)	28.0 (1.7)
80% light	188b (12)	12.8 (0.8)	26.4 (1.7)

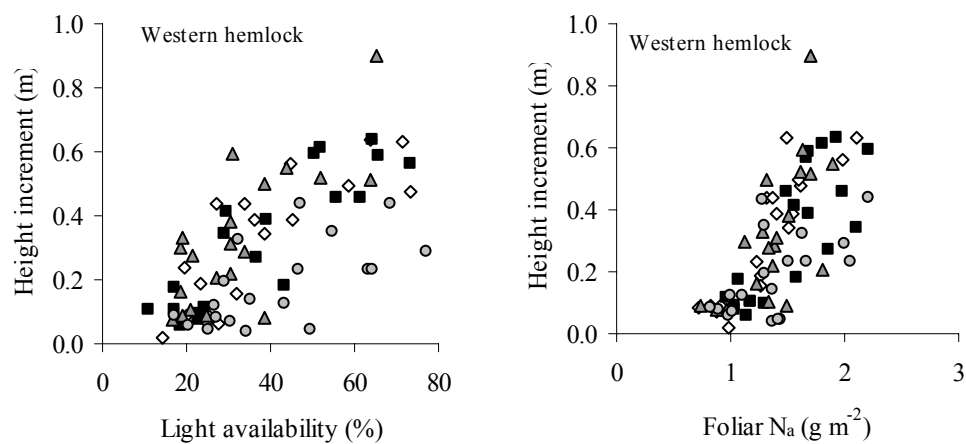
† Means within columns sharing the same letter are not significantly different (Tukey HSD P < 0.05)

Table 5.3: Statistical significance ( $r^2$ ) of annual growth response (height and root collar diameter increments) in correlation with site resources of understory light and inorganic N (DIN) supply, and in correlation with foliar N content ( $N_a$ ).

Species	Light avail. (%)	Light + DIN (%) + (kg ha <sup>-1</sup> )	Foliar $N_a$ (g m <sup>-2</sup> )
<b>Height increment</b>			
Western redcedar	$r^2 = 0.68$	$r^2 = 0.77$	$r^2 = 0.83$
Western hemlock	0.68	0.70	0.61
Hybrid spruce	0.63	0.68	0.53
<b>Root collar increment</b>			
Western redcedar	0.58	0.68	0.72
Paper birch	0.68	0.73	0.64
Western hemlock	0.54	0.56	0.52
Hybrid spruce	0.54	0.61	0.55

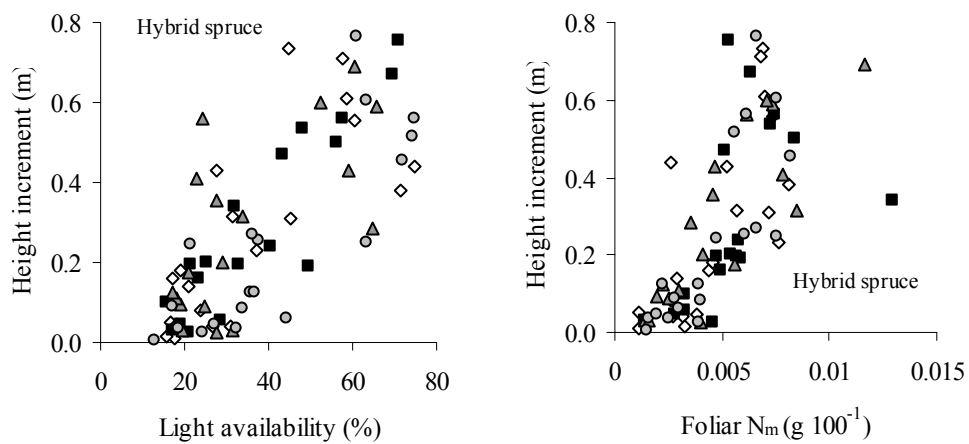


a)



b)

Figure 5.1: Correlations between height increment and light availability (1<sup>st</sup> column) or foliar N per unit area (2<sup>nd</sup> column) for a) western redcedar, b) western hemlock, and c) hybrid white spruce.



c)

Fig. 5.1: continued.

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## 6 An investigation into factors causing height suppression of understory conifers<sup>5</sup>

### Introduction

Forest scientists have long recognized that stand development patterns in multicohort forests are more complicated than in single cohort plantations (Oliver and Larson 1990). Overstory trees alter the growing environment (e.g. humidity, temperature) and compete for resources (light, moisture and nutrients), resulting in complex interactions that affect growth rates of understory trees. Because of this, the public demand for more complex silvicultural regimes, rather than predominantly clearcutting, will create challenges for forest managers in predicting and modeling growth patterns and species interactions of uneven-aged plantations (Coates and Burton 1997, Franklin et al. 2000).

One of the challenges in predicting stand development patterns is the interaction between tree size and light availability on growth rates in multicohort stands (Messier et al. 1999). Tall trees are thought to have relatively greater light requirements than shorter trees (Waring 1987, Givnish 1988), suggesting it is too simplistic to extrapolate the functional responses of small seedlings to taller individuals (Lusk 2004, Claveau et al. 2005). Similarly, tree size may be a factor leading to the suppression of understory trees in uneven-aged forest ecosystems (e.g. Canham 1990). Understory trees achieve a limited size related to the availability of light ('maximum sustainable height'; Messier et al. 1999), and growth will not resume until light conditions improve (Wright et al. 2000). These patterns in growth, and interactions between light availability and tree size, will vary among tree species, depending upon inherent differences in shade tolerance (Canham 1988, Walters et al. 1993). A clearer understanding of growth rate changes under shaded conditions and how they vary between tree species is needed to evaluate silviculture systems and to develop stand dynamic simulation models such as SORTIE (Coates et al. 2003).

The reduction in growth rates associated with shaded trees has been explained primarily through the increasing respiratory demands of nonphotosynthetic tissue and ontogenetic changes in biomass allocation and crown morphology (Messier and

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Nikinmaa 2000, Claveau et al. 2002, King 2003, Lusk 2004). There are, however, potential physiological constraints to photosynthesis and growth that might arise as seedlings get larger. For example, trees growing poorly in the shade will acquire very narrow radial increments that can reduce hydraulic conductance (Shumway et al. 1993, Sellin 1993, Protz et al. 2000). Greatly restricted water flow through narrow xylem cells could eventually cause a cessation in height growth for understory saplings, analogous to a proposed mechanism controlling height growth under full light (Ryan and Yoder 1997). A second potential mechanism for growth cessation of understory trees would be declining foliar nitrogen (N) status over time, either from shifts in aboveground and belowground allocation with sapling size, or from changes in soil N availability with canopy opening size (Prescott 2002), or from increased competition from overstory trees (Coomes and Grubb 2000). Light availability in the understory could also decline with ingress of the overstory canopy (Hibbs 1982, Runkle and Yetter 1987, Beaudet et al. 2004), leaving the older, larger saplings in increasingly shaded conditions. For all three hypotheses, the reduction in photosynthetic rates would accentuate already limited growth potential to cause complete suppression, if not mortality (Kobe and Coates 1997, Kneeshaw et al. 2006), of the forest understory.

Understory saplings in the partial-cutting treatments at the Date Creek Research Forest are, after 13 years, showing signs of suppression and reduced height growth, especially for hybrid white spruce (*Picea glauca* x *Picea sitchensis* [Moench] Voss). I examined the three hypotheses for explaining causes of height suppression of understory hybrid spruce and western hemlock (*Tsuga heterophylla* [Raf.] Sarg.) saplings: acute moisture stress, reduced foliar N concentrations, and declining light availability. I did this by comparing trees in the partial cutting treatment with trees of the same age located in large forest gaps. Total sapling biomass and allocation patterns between foliage and wood (ratios of photosynthetic to nonphotosynthetic biomass) were also evaluated. My objectives were to 1) confirm that a reduction in height growth is occurring only with understory trees in these partially cut stands; 2) evaluate whether physiological constraints to photosynthesis have contributed to the reduced growth rates; and 3) examine whether reductions in physiological function and growth rates were less severe

for western hemlock, a shade-tolerant tree species, than moderately shade-tolerant hybrid spruce.

## **Materials and Methods**

### **Site description**

The 4000-ha Date Creek Research Forest is located in the coast-interior transitional forests of the moist, cold Interior Cedar-Hemlock subzone (ICHmc) (Banner et al. 1993) near Hazelton, British Columbia, Canada (55°22' N, 127°50' W, elevation 450 m). The average climatic characteristics of Hazelton are 535 mm annual precipitation (238 mm during the growing season), 4.4°C mean annual temperature, 1267 growing degree days > 5°C, and 176 frost-free days (Banner et al. 1993). The research forest is comprised mostly of western hemlock (65% of the basal area) with smaller amounts of western redcedar (*Thuja plicata* Donn ex D. Don in Lamb) (18%), hybrid spruce (8%), subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) (2%), paper birch (*Betula papyrifera* Marsh.) (5%), and lodgepole pine (*Pinus contorta* Dougl. Ex Loud. var. *latifolia* Engelm.) (2%). Mesic ecosystems (Western Hemlock - Step moss; Banner et al. 1993) predominate in the research forest and are characterized by a continuous cover of mostly coniferous trees, sparse shrub and herb layers, and a continuous and well developed ground cover of feathermosses. Soils are Eluviated/Orthic Dystric Brunisols and Orthic Humo-Ferric Podzols developed in morainal blankets, with soil textures ranging from sandy loam to clay loam (Soil Classification Working Group 1998). Forest floors are Hemimors (Green et al. 1993), 4- to 14-cm thick.

### **Experimental design**

The study was conducted in the 60% heavy-removal treatment at Date Creek (Coates et al. 1997). This treatment is comprised of small patch cuts (1000-5000 m<sup>2</sup> in size) interspersed with forest containing single-tree to small group-selection cuts. The heavy-removal treatment was replicated four times in a randomized complete block design. Each treatment unit was approximately 20 ha in size. The blocks were defined by successional stage (mature stands of 155 years and oldgrowth of 355 years) and ecological site units (relative soil moisture/nutrient regime; Banner et al. 1993): block A, mature stand 100% mesic; block B, mature stand 70% mesic - 30% submesic; block C,

mature stand 70% mesic - 30% subhygric; and block D, oldgrowth 100% mesic. The four blocks were between 3 and 7 km apart. Treatment units were harvested (whole-tree removal) in the summer and fall of 1992 using ground-skidding equipment. Western redcedar, hybrid spruce, western hemlock, subalpine fir and lodgepole pine were planted throughout the treatment units in 1993.

In the spring of 2005, I searched the heavy-removal treatment units for candidate trees under shaded ('understory') or high-light ('gap') conditions. The majority of juvenile trees in the shade were showing some reduction in leader growth increment. From this population, I chose 2-m-tall hybrid spruce and western hemlock saplings growing under similar site conditions (soils and light availability) and within 5 m of each other. Hybrid spruce and western hemlock trees, again within 5 m of each other, were also selected near the centre of large gaps that were approximately 0.5 ha in size. All trees were located on mesic microsites as indicated by plant communities and slope position (Banner et al. 1993). The juvenile trees were a mixture of 10 to 13-year-old planted and naturally-regenerated stock. I selected three pairs of trees from both understory and gap conditions in each block (2 species x 2 light classes x 3 replicates x 4 blocks = 48 trees in total).

Available light (400-700 nm) over the growing season (mid-April to mid-September) was assessed for each tree using hemispherical canopy photographs. The digital photograph was taken at 1.5 m height, either above the tree or, in the case of larger trees, adjacent to it in the same light environment. The larger juvenile trees were either briefly bent back, away from the camera, or edited out of the digital photograph to allow for an estimation of light conditions. The growing season light availability, expressed as a percentage of full sun, was computed from each photograph using the Gap Light Analyser (GLA) 2.0 software, following Frazer et al. (2000).

### **Soil and tree measures**

Gravimetric soil moisture was determined from forest floors (10-cm-diameter core, excavated down to mineral soil) and mineral soils (0-15 cm deep) every 3 weeks from May 18 to September 1, 2005. One sample was taken from each species pair across forest and gap treatments (n = 24 per soil type per sample day). Moisture content was determined by drying soils at 105°C for 24 hours. Mineral soils were then ground and

sieved (100 mesh) to determine gravimetric moisture content of the fine fraction (< 2-mm). Field capacity was determined using intact soil cores (2-cm deep by 5-cm diameter) for both mineral soils and forest floors. Cores were extracted in July from the Fm layer (Green et al. 1993) of the forest floor and at a 10-cm depth in the mineral soil. The cores were saturated and drained on a pressure plate apparatus at -0.01 MPa tension (Kalra and Maynard 1991). Water retained in cores after reaching equilibrium was divided by the sample mass (< 2-mm mass for mineral soils) to determine gravimetric moisture content at field capacity.

Xylem water potential was determined on 1-year-old lateral branches in the top whorl of the juvenile trees. The branches were cut once near the node, and the phloem/bark tissue was peeled back approximately 2 cm to reveal the inner wood surface. The exposed branch end was inserted into a rubber stopper and placed into a pressure chamber (PMS, Corvallis, OR). Xylem water potential was determined by increasing air pressure in the chamber until just the point where water beaded on the cut surface. Xylem water potential readings were taken in mid-afternoon (2 pm) and predawn (6 am) on the trees from one experimental block per sample day (12 trees). The measurements were taken mid-month from separate blocks during the growing season (Block D in June, Block B in July and Block A in August). It was not possible to resample all of the trees each month because of the limited number of lateral branches in 1-year-old whorls.

At the end of the growing season (mid-September), I cut the trees at the ground surface and measured total height and height increments from the previous 5 years. Height increments were determined by locating the bud scars at the nodes along the stem, and by distinguishing the darker bark colouration from earlier growth. Where necessary, I also cut the stem at the node to count rings and confirm the internode length. At this time I also took foliar samples for nitrogen analysis from the current year's growth. Three lateral shoots in the top quarter of each tree (all sides of the tree) were clipped and bulked into one sample (n = 48). The foliage was oven-dried at 60° C for 24 hours, and average needle mass and area (one-sided projected leaf area using a LI-COR 3100, Lincoln, Neb.) was determined from 50 needles per tree.

Physiological constraints to photosynthesis were explored using <sup>13</sup>C natural abundance (Dawson et al. 2002) of stem wood produced in the previous 5 years. A disc

was cut from the base of each stem, oven-dried (36 hours at 105° C) and radial increments from the current year (1), year 3 and year 5 were sampled. The wood was extracted using a drill press and 1 mm carbide drill bit, taking approximately 10 subsamples within a ring (~ 5 mm depth) to obtain enough material for an adequate sample. The width of annual growth rings was also measured from these discs. The radial increment was often uneven around the stem so an average was determined from three transects, spaced equilaterally at 120°.

Total tree biomass was determined on half the experimental trees (2 blocks, 24 trees in total) because of the limitations in lab resources. The trees were taken to a heated warehouse and air-dried for 3 months, then separated into foliage and wood (branches and stem) and weighed. A subsample was taken from each component to correct for oven-dry moisture content (36 hours at 105° C). The relationship between one-sided projected leaf area and mass was determined from 100 needles (all age classes of needles) and used to calculate total leaf area of the tree.

### **Laboratory analyses**

Foliar N was analysed by dry combustion with a Leco CHN-600 analyser (LECO Corp., St. Joseph, Mich.). The natural abundance of <sup>13</sup>C was determined using an AS autosampler of a Thermoquest NC 2500 elemental analyzer (Carlo Erba Instruments, Milan, Italy) coupled to a Finnigan DELTAplus (Thermo Electron Corp., Boston, U.S.A.) isotope ratio mass spectrometer. Lab standards were calibrated against the international calcium carbonate standards NBS 19 (1.95‰) and NBS 20 (-1.06‰). Carbon isotopic values are expressed relative to Vienna Peedee Belemnite (vpdb) (Wolf et al. 1994).

### **Statistical analyses**

The treatments were organized as a split-plot, with understory/gaps as the main plot factor and tree species as the split-plot factor, in a randomized complete block design. Xylem moisture potential and foliar/wood biomass were tested without a block term because of the limited sample sizes. Effects of time on height/radial increment and  $\delta^{13}\text{C}$  were also tested with repeated measures using proc Mixed in SAS.

## Results

Available light averaged 24% (SE 1.7) and 25% (2.5) for hybrid spruce and western hemlock, respectively, in the forest understory, compared to 62% (2.6) and 63% (2.4) in the gaps. Tree height in 2005 (13 years after harvest) was 200 cm (SE 11) for hybrid spruce and 194 cm (11) for western hemlock in the forest understory, compared to 521 cm (13) and 467 cm (20), respectively, in the gaps.

### Tree growth patterns and biomass

Height increments in the gaps averaged 54 cm and 46 cm annually over the 5 year period for hybrid spruce and western hemlock, respectively, in contrast to the declining height growth for these species in the forest understory (Fig. 6.1a, Table 6.1). Hybrid spruce height increment averaged 21 cm in the forest understory in 2001, which had declined by 60%, to 8 cm, by 2005. Because of interactions between treatments and species ( $p < 0.10$  in Table 6.1), the effects of understory and gap treatments on growth were also tested separately (Table 6.2). The reduction in height growth from gaps to understories was more severe for hybrid spruce than western hemlock (27% reduction over 5 years), resulting in significant species interactions by year for understory trees (Table 6.2). Radial increment also declined in the shade, but less severely over time than height increment (by 27% for hybrid spruce and 11% for western hemlock), and with no species-by-year interactions (Fig. 6.1b, Table 6.2). Overall, height/diameter ratios in 2005 were significantly higher for shaded trees compared to gap trees, and for western hemlock compared to hybrid spruce (Fig. 6.2, Table 6.1).

Hybrid spruce had almost twice the biomass (needles, branches and stems) as western hemlock across understory and gap treatments (Table 6.3). Western hemlock had relatively more biomass as foliage compared to wood under shaded conditions, while hybrid spruce had quite consistent ratios across understory/gap treatments (species-by-treatment interactions significant for foliar mass or area ratios with wood, Table 6.3). No heartwood had yet developed in the saplings, so the entire stem was considered metabolically-active sapwood.

### Soil and tree physiological measures

Mineral-soil field-capacity was 49% (SE 2.3) and 52% (3.1) for the understory and gap treatments, respectively ( $p = 0.434$ ), while forest-floor field-capacity was 296%



(14) and 267% (16) ( $p = 0.249$ ). Both mineral soils and forest floors were near field-capacity throughout the summer, with minor differences between gaps and understories in soil moisture across sample days ( $p = 0.148$  and  $p = 0.106$  for mineral soils and forest floors, respectively; note also that treatment effects were inversed between mineral soils and forest floors) (Fig. 6.3a and 6.3b). Mid-afternoon xylem water potentials for saplings were, on average, between -0.5 and -1.5 MPa on days sampled over the summer (Fig. 6.4), while predawn xylem potential was consistently between -0.1 and -0.5 MPa (data not shown). Western hemlock had slightly higher xylem potential than hybrid spruce in July and August ( $p = 0.027$  and  $p = 0.015$ , respectively), but no differences were found between saplings in forest understories versus gaps (Table 6.4).

Foliar N concentrations in 2005 did not differ between species or treatments, but foliar mass was lower among understory than gap trees (Table 6.5). Hybrid spruce and western hemlock had 33% and 15% lower leaf mass in the understory than gaps, but the species x treatment interaction was not significant. Leaf mass per unit area was significantly lower for western hemlock than hybrid spruce under both understory and gap conditions ( $p < 0.001$ , Table 6.5).

Stem wood from gap trees had less negative  $\delta^{13}\text{C}$  values than stem wood from forest understory trees ( $p = 0.010$ ) (Fig. 6.5), with significant treatment x species x year interactions ( $p = 0.016$ ). There was evidence for a time effect on  $\delta^{13}\text{C}$  for both understory and gap trees, but  $\delta^{13}\text{C}$  did not decline in either treatment over time (Table 6.6, Fig. 6.5). I also compared year interactions separately by species, and found no significant difference in  $\delta^{13}\text{C}$  between gap and understory spruce (treatment x year  $p = 0.305$ ) or hemlock ( $p = 0.191$ ).

## **Discussion**

### **Confirmation of growth check and causes**

Growth of understory saplings at Date Creek, especially hybrid spruce, had declined during the 5-year study period, hence confirming my first hypothesis, and I expect complete suppression in height growth to occur in the near future (Canham 1990, Wright et al. 2000). However, I was unable to find evidence for a physiological mechanism that could explain the reduction in growth rates over time for shaded saplings.

My second hypothesis, that understory trees were under more acute physiological stress than trees in gaps, was not supported by measures of reduced xylem water potential or N status, nor by reductions in  $\delta^{13}\text{C}$  over time that could reflect diminishing photosynthetic activity in the previous 5 years. Delagrange et al. (2004) also reported consistent physiological traits across tree sizes within light classes. The logical determinant of growth rate reductions in the shade would therefore be the accumulating C demands of nonphotosynthetic relative to photosynthetic biomass (Givnish 1988, Messier et al. 1999), and shifting allocations of increasingly scarce resources to foliage or roots, rather than stems (Poorter 2001, King 2003). In support of this alternative explanation, I did find greater allocation to foliage relative to shoots under shade than in gaps for western hemlock, but not for spruce. Although not measured here, some key aspects of crown morphology for understory spruce, such as leaf area ratios and needle morphology, possibly change with tree size (especially for trees less than 1 – 1.5 m) and may have contributed to the curtailment in growth as well (Niinemets and Kull 1995, Messier and Nikinmaa 2000, Claveau et al. 2002, King 2003, Delagrange et al. 2004, Claveau et al. 2005, Niinemets 2006).

### **Evidence for moisture restrictions to growth**

Soil moisture levels across the partial cutting treatments were near field capacity throughout the summer due to extensive rainfall (average of 65 mm per month in 2005; BC MOF weather station). This is not unusual as the ICHmc subzone, which is transitional to a coastal climate and typically has only minor soil moisture deficits in the growing season (Meidinger and Pojar 1991). After 13 years, the differences in soil moisture between partial forest-cover and gaps were negligible, which suggests vegetation cover in openings were contributing comparable amounts of evapotranspiration loss as forest canopies (Gray et al. 2002). With abundant soil moisture and overcast conditions throughout much of the summer, saplings were likely not tall enough to experience extreme water stress (i.e. which would occur at potentials from -2.0 to -3.0 MPa; Phillips et al. 2002, Tyree 2003, Woodruff et al. 2004), even with the narrower radial increments accrued under the shade. I did detect less moisture stress among hybrid spruce than hemlock, which might provide some advantage to spruce growth under gap conditions where light was less limiting (Maherali et al. 1997).

### **Evidence for nutritional restrictions to growth**

When the Date Creek study was initiated in 1992, soil N availability and foliar N concentrations were higher within gaps than in the forest understory (Walters et al. 2006). These differences have diminished over time, and the consistent foliar N concentrations I found across gaps and understories suggest that current differences in foliar mass and tree size are driven by light availability rather than soil fertility (Chapter 4). Declining soil N availability would have more likely affected nutrition of trees in larger gaps, especially in the first 5 years after harvest following an assart effect, rather than causing suppression in sapling growth under the less disturbed forest canopy. A key question for understanding the mechanism of understory height suppression is whether foliar N concentration, and related photosynthetic capacity, decline with increasing sapling size. However, I found that hybrid spruce and western hemlock had consistent foliar N concentrations across the range in tree sizes (2 to 5 m), suggesting that foliar N concentrations for these species may not necessarily decline as saplings grow larger (Rijkers et al. 2000, Niinemets et al. 2002; see also Chapter 3).

### **Evidence for reduction in photosynthetic activity**

Given that xylem water potential and sapling N nutrition were consistent across openings, and unlikely to have caused a curtailment in understory growth, any reductions in  $\delta^{13}\text{C}$  over time would most likely be due to a decrease in light availability. The more negative  $\delta^{13}\text{C}$  values for understory sapling wood was consistent with foliar patterns for both western hemlock and hybrid spruce at Date Creek (Chapter 4; see also Broadmeadow and Griffiths 1993, Le Roux et al. 2001), and likely indicate a reduction in carboxylation caused by diminished regeneration of ribulose biphosphate at lower light levels. Although  $\delta^{13}\text{C}$  did decline over time (approximately 0.5‰), it was too small to account (e.g. -4‰ as reported in Chapter 4) for such large reductions in growth rates of understory saplings. It is possible that overstory canopy ingress could cause the declines, and this is often expected after harvesting treatments (Beaudet et al. 2004), but these mature and old-growth forests had grown to their full height potential (~30 m), and consequently had limited expansion of tree crowns after partial-cutting. It is also possible that the potential reduction in light availability associated with canopy growth over time

has been ameliorated to some degree by the minor amounts of windthrow occurring since harvesting treatments.

## **Conclusions**

Growth patterns in height and radial increment between the understory and gap trees at 13 years after harvest demonstrated a ‘cross-over’ pattern often found between species of differing shade tolerance (Sack and Grubb 2001). The decline in growth under shade was less severe for western hemlock than hybrid spruce, perhaps due to its larger plasticity in foliage/wood allocations and height/diameter ratios (Canham 1988, Chen et al. 1996, Williams et al. 1999). The lower leaf-mass per unit area of western hemlock than spruce needles was also consistent with its greater shade tolerance (Niinemets 2006), along with other adaptations such as lower respiration rates and greater leaf life span (Reich et al. 1998, Walters and Reich 1999, Lusk 2002). For hybrid spruce to ‘sit and wait’ at this point in stand development, akin to more shade-tolerant species (Messier et al. 1999), could be less successful given the increasing risk of mortality as radial growth declines (Kobe and Coates 1997, Kneeshaw et al. 2006). For this reason, hybrid spruce may gradually be eliminated from this understory cohort, leaving only the more shade-tolerant species as a suppressed understory. The results from this study demonstrate, even under relatively stable environmental conditions, how forest managers will need to consider the rapid changes in growth patterns and ongoing species interactions that can occur in the initial decades following partial cutting.

Table 6.1: ANOVA results for height and radial increment under gap and forest understory treatments for western hemlock and hybrid spruce over a 5-year period. Values in bold are significant ( $p < 0.05$ ).

	df	Height inc.	Radial inc.	Ht / Dia ratio
		$p > F$	$p > F$	$p > F$
Treatment	1	<b>0.001</b>	<b>0.002</b>	<b>0.039</b>
Species	1	0.453	0.059	<b>0.004</b>
Treatment x Species	1	0.078	0.076	0.197
Year	4	<b>0.005</b>	<b>0.035</b>	n/a
Treatment x Year	4	0.055	0.057	
Species x Year	4	0.106	<b>0.016</b>	
Treat x Species x Year	4	0.487	<b>0.010</b>	

Table 6.2: ANOVA results for height and radial increment by species and year for forest understory and gap treatments separately. Values in bold are significant ( $p < 0.05$ ).

	df	Height inc.	Radial inc.
		$p > F$	$p > F$
<b>Understory</b>			
Species	1	<b>0.014</b>	0.612
Year	4	<b>0.001</b>	0.084
Species x Year	4	<b>0.025</b>	0.205
<b>Gaps</b>			
Species	1	0.154	<b>0.022</b>
Year	4	0.126	0.139
Species x Year	4	0.481	0.111

Table 6.3: Total biomass and projected leaf area of understory and gap trees by foliage and wood (branches + stem) components (mean and SE in brackets). Values in bold are significant ( $p < 0.05$ ).

	Foliar mass per tree (kg)	Wood mass per tree (kg)	Foliar area per tree (m <sup>2</sup> )	Foliar mass/wood (kg/kg)	Foliar area/wood (cm <sup>2</sup> /g)
<b>Understory</b>					
Hybrid white spruce	0.29 (0.05)	0.63 (0.10)	1.17 (0.15)	0.48 (0.05)	20 (3)
Western hemlock	0.13 (0.02)	0.24 (0.06)	1.06 (0.22)	0.60 (0.06)	47 (4)
<b>Gaps</b>					
Hybrid white spruce	2.84 (0.3)	5.83 (0.4)	12.45 (1.9)	0.49 (0.04)	21 (2)
Western hemlock	1.24 (0.5)	3.30 (0.8)	7.75 (2.2)	0.35 (0.05)	23 (2)
Treatment ( $p > F$ )	<b>&lt; 0.001</b>	<b>&lt; 0.001</b>	<b>&lt; 0.001</b>	0.068	<b>0.006</b>
Species	<b>0.014</b>	<b>0.008</b>	0.133	0.812	<b>0.001</b>
Treatment x Species	<b>0.036</b>	<b>0.036</b>	0.149	<b>0.004</b>	<b>0.001</b>

Table 6.4: ANOVA results for midday xylem potential (MPa) over the summer by understory and gap treatments and species. Values in bold are significant ( $p < 0.05$ ).

	June 15		July 15	August 17
	df	$p > F$	$p > F$	$p > F$
Treatment	1	0.318	0.871	0.629
Species	1	0.815	<b>0.027</b>	<b>0.015</b>
Treatment x Species	1	0.155	0.866	0.719

Table 6.5: ANOVA results for current-year foliar N concentrations and foliar size under gap and understory treatments for western hemlock and hybrid spruce. Values in bold are significant ( $p < 0.05$ ).

	Foliar N (g/kg)	Foliar mass (g per 50)	Foliar mass/area (mg/cm <sup>2</sup> )
<b>Understory</b>			
Hybrid white spruce	9.5 (0.3)	0.16 (0.01)	26.3 (1.1)
Western hemlock	10.0 (0.4)	0.11 (0.01)	12.8 (1.2)
<b>Gaps</b>			
Hybrid white spruce	10.9 (0.6)	0.24 (0.02)	25.3 (1.3)
Western hemlock	10.5 (0.4)	0.13 (0.01)	14.1 (0.6)
Treatment ( $p > F$ )	0.165	<b>0.046</b>	0.919
Species	0.819	<b>0.010</b>	<b>&lt; 0.001</b>
Treatment x Species	0.304	0.120	0.271

Table 6.6: ANOVA results for  $\delta^{13}\text{C}$  of wood increment by species and year for understory and gap treatments separately. Values in bold are significant ( $p < 0.05$ ).

	$\delta^{13}\text{C}$ (‰)	
	df	$p > F$
<b>Understory</b>		
Species	1	0.314
Year	2	<b>0.043</b>
Species x Year	2	0.236
<b>Gaps</b>		
Species	1	0.121
Year	2	0.083
Species x Year	2	0.140

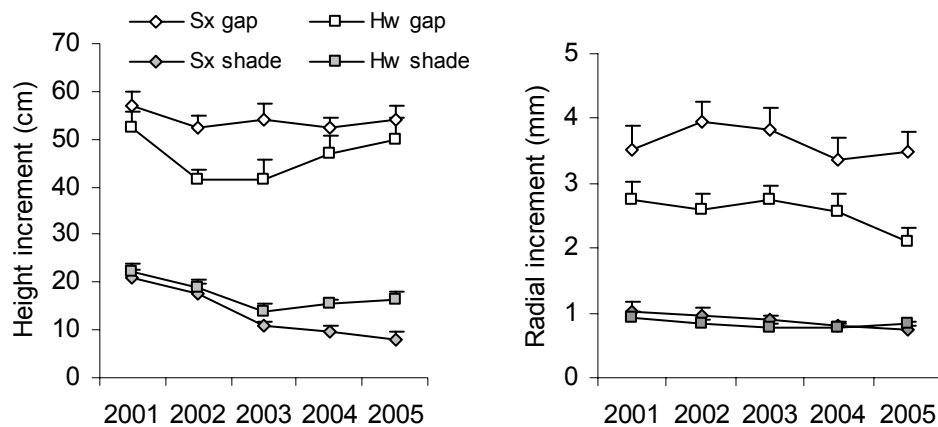


Figure 6.1: Five-year growth patterns in a) height increment and b) radial increment for hybrid spruce (Sx) and western hemlock (Hw) under understory (shade) and gap conditions (SE of the mean as error bars).

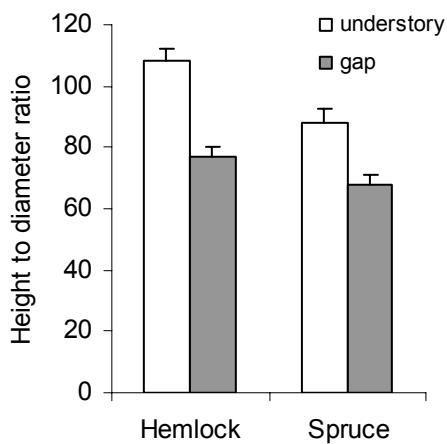
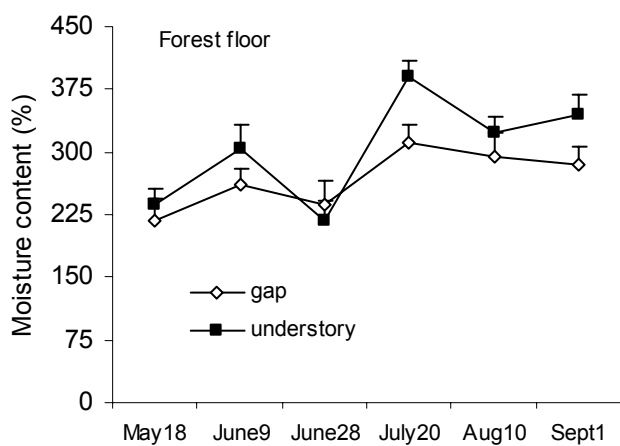
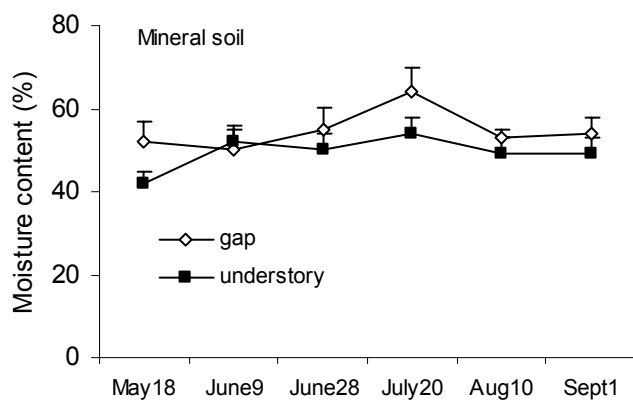


Figure 6.2: Height-to-diameter ratios (2005) for western hemlock and hybrid spruce in understory and gap conditions (SE of the mean as error bars).





a)



b)

Figure 6.3: Gravimetric moisture content for a) forest floors and b) mineral soil (< 2 mm) over the summer for understory and gap treatments (SE of the mean as error bars).

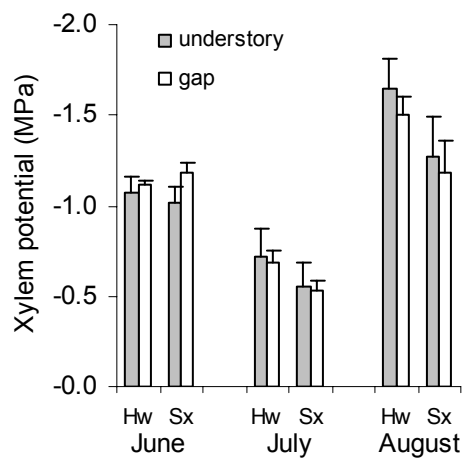


Figure 6.4: Midday xylem potentials of hybrid spruce (Sx) and western hemlock (Hw) across understory and gap treatments during summer months (means of one block per month, SE of the mean as error bars).

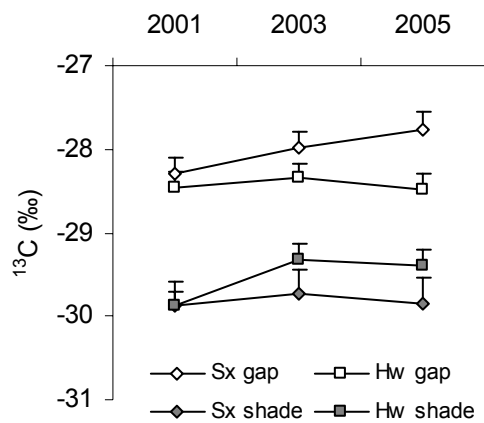


Figure 6.5: Patterns in  $\delta^{13}\text{C}$  of radial wood increments for hybrid spruce (Sx) and western hemlock (Hw) for understory (shade) and gap treatments (SE of the mean as error bars).

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## 7 Summary and conclusions

Understory light and soil N availability together affect sapling growth by constraining photosynthesis, and it was hypothesized that differences in species response to these limiting resources are largely responsible for regeneration success (Grubb 1977) and stand dynamics in multi-species, uneven-aged forests. In this thesis I explored the characterization and tradeoffs of these resources (soil N and light availability), the ability to use foliar attributes to isolate and integrate these resource constraints, and the effects of these resource combinations on species growth responses. A number of conclusions were made:

**Soil N availability characterized by a combined index of DIN and DON reveals functional differences in N cycles that are relevant for ecological studies.**

I also found that a simple inorganic N index was effective for assessing soil fertility, but investigators should recognize that DIN can have a curvilinear relationship with productivity and tree nutrition. I determined that soil N availability should be assessed using N mass over the soil profile (forest floor and mineral soil), rather than using N concentrations of either horizon, and that total N produced over an incubation period, rather than net changes, should be used in correlations with productivity.

**Foliar N% typically increases with soil N supply, but not necessarily at the same rate among species.**

Reasons for this divergence among species might include differences in their inherent physiological abilities to translocate the diverse forms of N, including amino acids,  $\text{NH}_4^+$  and  $\text{NO}_3^-$ , through roots. The diverging trends in foliar N%, and the effect on species distribution (Chapter 3), is analogous to the resource ratio theory of Tilman (1985, 1988). In my study, however, I suspect it is the differential ability to maximize N uptake that drives competition, rather than the depletion of soil N supply to a critical threshold. Further research into this fundamental relationship (soil N supply and species nutrition or productivity) would improve our understanding of species autecology, interspecific competition and stand dynamics.

**Understory foliar N% is an effective index of soil fertility and site potential for select tree species.**

In theory, foliar N% of shade-tolerant species should be more independent of light availability than shade-intolerant species, but the counterintuitive results for western redcedar (Chapter 4) emphasize how unambiguous proof of this relationship for each species of interest is needed. Size effects (understory versus overstory; Chapter 3) may not be a factor in interpreting foliar N%, which would greatly simplify this index of site potential, but again only further studies of each species of interest will confirm this.

**Light attenuation by the overstory is negatively correlated with soil N availability through differences in tree height, canopy size, and tree species composition.**

This relationship provides an important insight into tradeoffs between growth-constraining resources, and the potential response by forest understories to gap dynamics (Chapter 3). For example, a silviculture prescription for creating gaps with 40% light availability across this gradient would lead to significantly better growth responses with increasing N supply. The inability of shade-intolerant species to maintain adequate N nutrition in compensation for shading (e.g. paper birch, Chapter 4) would also likely contribute to poor growth, mortality, and consequently alter patterns of regeneration in partially-cut stands.

**Foliar N<sub>a</sub> was strongly correlated with both <sup>13</sup>C and sapling growth increment, and is the simplest integration of combined light and N effects on photosynthetic activity.**

Unfortunately I was unable to determine the full range of N<sub>a</sub> response to light-N combinations (Chapter 5), but clearly these relationships would offer insights into regeneration and stand dynamics. The ability of a species to capitalize on different N forms (amino acids, NH<sub>4</sub><sup>+</sup> and NO<sub>3</sub><sup>-</sup>), to maximize N uptake under shade, and to optimize N utilization via light harvesting or subsequent photochemistry and carbon reactions will collectively affect foliar photosynthetic capacity and growth response to light constraints.

### **Understory sapling growth rates are not a consistent function of light and N availability alone because of the effect of tree size.**

I was unable to find a physiological mechanism (moisture stress, N nutrition or light availability) to explain the declining height growth of understory hybrid spruce or western hemlock. Instead, the effect of tree size seems related to accumulating C demands of nonphotosynthetic relative to photosynthetic biomass, and shifting allocations of resources to foliage or roots, rather than stems. Forest scientists should be aware of the changes in growth patterns and ongoing species interactions that can occur in the initial decades following partial cutting.

### **Future research directions**

Short-term experiments with seedlings under controlled conditions or field settings suffer from the limitations of a reductionist approach to forest science. Understory seedlings will take some time to fully establish and express site conditions, and responses to growth constraints may be more dynamic than portrayed by initial results (Chapter 6). Artificially imposed gradients in resources, especially N supply, are difficult to create and unlikely to mimic the more complex attributes found with natural soil gradients (Chapter 5). Enough information has been gained from greenhouse studies and simple field experiments to demonstrate the basic relationships between these two resources and species response, and the next step in development would ideally be ‘model’ ecosystems (Vitousek 2004). This would entail careful selection of a wide gradient in sites, similar to the ecosystems described in Chapter 2, where partial-cutting treatments could be imposed and a mix of tree species established. Some progress has been made along these lines (Kobe 2006), but it is important to recognize that species response to soil fertility via foliar N<sub>%</sub> can diverge (Chapter 3) or be affected by light availability (Chapter 4). Rather than relying solely on foliar N<sub>%</sub> to gauge soil fertility effects, actual links between foliar N attributes and soil N supply (or a substitute measure such as plant association or asymptotic stand height) are needed to establish the site context of these species interactions.

## **Final conclusions**

I have demonstrated several tools that are effective for understanding the resource limitations and species interactions that drive stand dynamics in multi-species, uneven-aged stands across gradients of soil fertility. These include use of in-situ soil DIN + DON incubations, canopy fish-eye photographs, asymptotic stand height (as a simple measure of site potential), and foliar attributes of N%, N<sub>a</sub> and <sup>13</sup>C abundance. Key differences in species response to soil N supply were demonstrated, as well as species patterns in foliar N nutrition under light gradients. Clear relationships between inherent soil fertility, site potential, foliar N% and understory light availability provided a more thorough framework for describing and predicting species dynamics in uneven-aged stands. Future research utilizing partial-cutting treatments over a wide range of site potential will clarify and possibly confirm these species interactions.

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