A COMPARISON OF PRODUCTIVITY AND RELATED TRAITS FOR EUROPEAN LARCH (*Larix decidua* Miller) AND RED PINE (*Pinus resinosa* Ait.) ACROSS A SITE QUALITY GRADIENT IN THE GREAT LAKES REGION

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ABSTRACT

A comparison of productivity and related traits
for European larch (*Larix decidua* Miller) and red pine (*Pinus resinosa* Ait.)
across a site quality gradient in the Great Lakes region.

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Productivity and related traits were compared for European larch (*Larix decidua* Miller) and red pine (*Pinus resinosa* Ait.) in 27 forest stands, per species, that collectively represented a broad range of site quality. There were two general objectives: 1) determine site factor vs. productivity relationships for each species, and 2) examine the interrelationships of soil, leaf/canopy and productivity characteristics over a range of resource availabilities for species that differ in leaf life span and related traits.

Productivity (site index and overstory annual net primary production) were most strongly related to the single variables of soil moisture (sign of the coefficient +) and nitrogen availability (+). Using stepwise multiple regression models with p=0.15 for addition and removal, the combination of growing season temperature (July T +, growing degree days -) and site water balance (+) accounted for 71% of the variation in site index for European larch. The combination of growing degree days (-) and foliar %N (+) explained 32% of the variation in site index for red pine.

Larch had greater leaf N, specific leaf area, leaf area index, and productivity than red pine and leaf N was the single species trait most strongly related to productivity for both species. Over a gradient of increasing soil moisture holding capacity, productivity and leaf N increased for both European larch and red pine and the rate of increase was modestly greater for European larch. Despite these interactions, there was no trade-off in productivity since European larch maintained higher productivity over the entire gradient.

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Chapter 1

**Predicting Productivity of European larch
and red pine in the Great Lakes region**

Abstract   Site factor-productivity relationships were examined for European larch (*Larix decidua* Miller) and red pine (*Pinus resinosa* Ait.) using twenty-seven, even-aged monoculture plantations for each species distributed across the Great Lakes region. Plantations for each species were geographically paired and averaged 36 and 38 years old for European larch and red pine, respectively. Productivity was estimated as site index obtained from stem analyses and as overstory annual net primary production ($ANPP_o$) obtained with field measurements and published allometric biomass equations. The range and averages for physical soil characteristics and climate were similar for European larch and red pine stands, but European larch stands had less forest floor depth, higher soil temperatures, and greater rates of nitrogen mineralization and nitrification. Average site index (base age 15) and $ANPP_o$ values were, on average, 42 and 31% greater, respectively, for European larch than red pine. The single variables most strongly associated with productivity for both species were indices of soil moisture (sign of the coefficient +) and nitrogen availability (+). The relationships of combinations of soil, leaf/canopy, and climate characteristics to productivity were determined with multiple linear regression (MLR). For European larch, growing season temperature (+ July T, - Growing degree days) and site water balance (+) were the best combined predictors of productivity, accounting for 71% of the variation in site index. For red pine, growing degree days (-) and foliar %N (+) explained 32% of the variation in site index. Since climate variables were strong predictors of productivity, site effects on productivity were isolated by extracting climate effects from the data (i.e. using the residuals of the MLR relationship of productivity vs. climate as the predicted variable). For climate residuals, water balance (+) and foliar $^{13}C/^{12}C$ ratio (-) explained 48% of the variation in European

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larch site index and foliar nitrogen (%N, +) explained 28% of the variation in red pine site index. For $ANPP_o$, a combination of soil (A horizon depth (+), pH (-), organic matter (-) and growing degree days(-) variables explained 51% of variation in $ANPP_o$ for red pine. For European larch $ANPP_o$, 27% of the variation in $ANPP_o$ was explained by nitrification rates (+) and specific leaf area (+). In general, these relations demonstrate that both temperature and site/vegetation variables related to water and nitrogen availability can explain a large percent of the variation in red pine and European larch productivity across the Great Lakes region, and that each species and measure of productivity respond uniquely to these variables.

INTRODUCTION

European larch (*Larix decidua* Miller) and red pine (*Pinus resinosa* Ait.) have long been associated with reforestation and paper/pulp production due to their rapid growth on some sites (McComb 1955, Wilde et al. 1965, Valade 1998). However, productivity varies markedly across sites and little is known about the site factors responsible for this variation, especially for European larch in the Great Lakes region (Carmean 1975). Qualitative evidence suggests that European larch productivity is highly sensitive to site quality whereas red pine is less sensitive. Thus, red pine may have greater productivity on poor sites than European larch and vice versa on rich sites. Quantifying comparative site-productivity relationships for European larch and red pine may be important for silvicultural planning, if maximizing productivity on any given site is the focus. The goals of this study were to 1) measure the site-productivity relationships for two commercially important species for a collection of stands in the Great Lakes region, and 2) quantify below- and above-ground site variables that drive variation in productivity.

A popular method for determining the relationship between site factors and growth is the use of multiple regression equations that use some combination of soil, vegetation, topography, and climate variables as predictors of species productivity (usually estimated as site index: the height of a dominant/co-dominant tree at a given base age) for data collected across a broad range of sites. Several researchers studying various species have had mixed success in developing strong predictive relations between site index and a host of both below- and above-ground site variables. Some studies have found only moderately strong relationships between site factors and site index despite exhaustive

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sampling efforts (e.g. Gaiser 1950, Broadfoot 1969, Payandeh 1986, Harding et al. 1985, Monserud et al. 1990). Conversely, Wang (1995) explained 83% of the variation in white spruce (*Picea glauca* (Moench) Voss) site index by using combinations of soil chemical/physical, understory vegetation, and tree foliage chemistry variables. Chen et al. (1998) explained nearly 80% of the variation in aspen (*Populus tremuloides* Michx.) site index with chemical and physical soil properties alone, and using a combination of soil chemical and climatic variables, nearly 94% of variation was explained. There may be several reasons for variability in site-productivity relationships: site index is an imprecise estimate of productivity, and the predictor variables chosen may not be the factors that truly drive variation in productivity.

One way to improve the determination of site-productivity relationships is to simultaneously assess site index and alternative measures of site productivity. One such alternative is aboveground net primary production (ANPP; Aber and Melillo 1991). In the Great Lakes region, and across broad site productivity and stand composition gradients, ANPP has been found to be highly correlated with nitrogen (N) mineralization and soil texture (Pastor et al. 1984, Reich et al. 1997) as well as forest floor nitrogen (%N) and carbon (C)/N ratios (Fassnacht and Gower 1997). For closed canopy forests, ANPP of the overstory tree species ($ANPP_o$) is an estimate of productivity per unit ground area. For forestry, it is unlikely that $ANPP_o$ will replace site index as a measure of stand productivity since the latter is easy to determine and almost universal in usage. However, our basic understanding of the factors most important in driving variation in productivity across forested landscapes will be strengthened by the simultaneous consideration of site index and $ANPP_o$ as indices of forest productivity.

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Another reason for the often relatively weak relationships found between collections of site variables and site index is that some of the important factors driving variation in productivity may have been overlooked (Monserud et al. 1990). In the Great Lakes region, and throughout much of North America, forest productivity is likely to be physiologically limited by: an over-abundance or lack of water; mineral nutrients such as N; the base cations magnesium (Mg), calcium (Ca), and potassium (K) in some regions; and/or temperature. It is rare that site-productivity studies consider a set of predictor variables that encompass these potential limitations. Several studies have found at least moderately strong relationships of soil chemistry, foliage chemistry, physical soil properties, climatic and topographic characteristics with forest productivity, but few have simultaneously considered these variables (but see Wang 1995, Fassnacht and Gower 1997, Chen et al. 1998). Examples of specific variables found closely related to forest productivity include:

- soil/forest floor nutrients
    nitrogen (Fassnacht and Gower 1997, Reich et al. 1997, Chen et al. 1998)
    potassium (Fassnacht and Gower 1997, Chen et al. 1998)
    calcium (Chen et al. 1998)
    phosphorous (Alban 1972)
- foliar nutrients
    nitrogen (Wang 1995, Hebert and Jack 1998, Chen 1998)
    iron/potassium/magnesium (Truong 1975a, Truong 1975b)
- depth of mineral soil to an impermeable layer (Gaiser 1950, Coile 1952, Aird and Stone 1955, Gilmore 1992, Wang 1995)
- silt+clay content (Stoeckeler 1948, Fassnacht and Gower 1997)
- topography (e.g. slope, elevation, aspect) (Day 1947, Brown and Duncan 1990,

Monserud et al. 1990, Chen et al. 1998)

• temperature or precipitation (Cook 1941, Grier and Running 1977, Gholz 1982, Monserud et al. 1990, Churkina and Running 1998)

Efforts have been made to identify factors limiting red pine growth with soil-site studies. In a soil-site study involving 200 sites in Connecticut, Hickock et al. (1931) found that no single soil variable was well correlated with site index at age 15. They also noted that nearly all sites used would have been classified as "favorable" for tree growth and that it was only on the sandiest sites, which had lower water holding capacity, that height growth productivity declined. In Massachusetts, Mader and Owen (1961) concluded that red pine height and volume growth was significantly related to soil organic matter, nutrient supply, and texture. In the Great Lakes region, van Eck and Whiteside (1963) found that red pine growth in lower Michigan was uniform on sites across 27 soil series in lower Michigan, but high clay content was associated with a sharper growth decline than expected after 25 years. Also in lower Michigan, Hannah and Zahner (1970) found that red pine stemwood production as well as site index of jack pine (*Pinus banksiana* Lamb.) and bigtooth aspen (*Populus grandidentata* Michx.) were significantly higher on soils with fine textural banding due to an increased supply of moisture and nutrients. Wilde et al. (1965) found soil texture and soil nutrient concentrations had the strongest influence in predicting site index for pine plantations in Wisconsin. Alban (1972) showed that red pine site index in Minnesota plantations was significantly related to soil P content.

For European larch, there are no site-productivity studies for the Great Lakes region. However, in the northeast United States, Aird and Stone (1955) and Gilmore (1992)

found that soil depth was the most reliable site variable in predicting site index, accounting for 82% and 57% of the variation in larch growth, respectively.

Notably, most of these site characteristics are indices, and not direct measures of nutrient/water availability and temperature. For example, the combination of soil depth and texture are important indices of a trees soil water environment. Texture largely determines water-holding capacity while shallow soils can restrict root access to water and/or result in water logging, either of which negatively impact productivity (Pritchett and Fisher 1987). Thus, site-productivity studies often use several variables that are indirectly related to stand productivity. If site variables are chosen that collectively comprise, and closely index, the actual variables driving differences in productivity (e.g. nutrients, water, temperature), then these combinations of site factors may more closely predict productivity across forest landscapes (e.g. Wang 1995, Chen et al. 1998).

The objectives of this study were to determine the relationships of site variables to European larch and red pine productivity and their interactions using a collection of fifty-four stands (twenty-seven of each species) distributed across the Great Lakes region. The predictor variables selected were considered to be close indices of the resource/environmental variables responsible for limiting growth. Variables also were selected with regard to the ease of collection in hopes that simple, applied silvicultural tools could be developed (e.g. species selection criteria in plantation establishment given certain site characteristics to increase productivity.) Predictor variables included soil physical (depth to impermeable layers, texture, color, available water holding capacity, bulk density), soil chemical (rates of N mineralization/nitrification, pH), foliar chemical (carbon isotope ratios, %N), regional climate (water balance, growing degree-days), and

site topography (aspect, slope) characteristics. The specific hypothesis that was tested was: Some combination of the site factors and tree characteristics (e.g. soil texture, soil depth, water balance, growing degree-days, foliar nitrogen concentrations) in multiple regression will explain a large proportion of the variation in productivity for both European larch and red pine.

METHODS

Field Sites

The study consisted of paired stands, twenty-seven of each species, distributed in the Great Lakes region from north-central Minnesota to eastern Ontario (See Figure 1.1.). Stands were geographically paired ranging from directly adjacent to one another to <30 kilometers (km) apart. Selection criteria for stands included closed canopy, monoculture plantations from ~15-50 years old that were even-age and uniform in height and diameter. Stands with records or evidence of past damage (e.g. *Erethizon dorsatum dorsatum* (Linnaeus), porcupine; *Pristiphora erichsonii* (Hartig), larch sawfly) were avoided. The collection of stands was intended to span a site fertility gradient with local pairs subject to similar climate and on sites of similar glacial history.
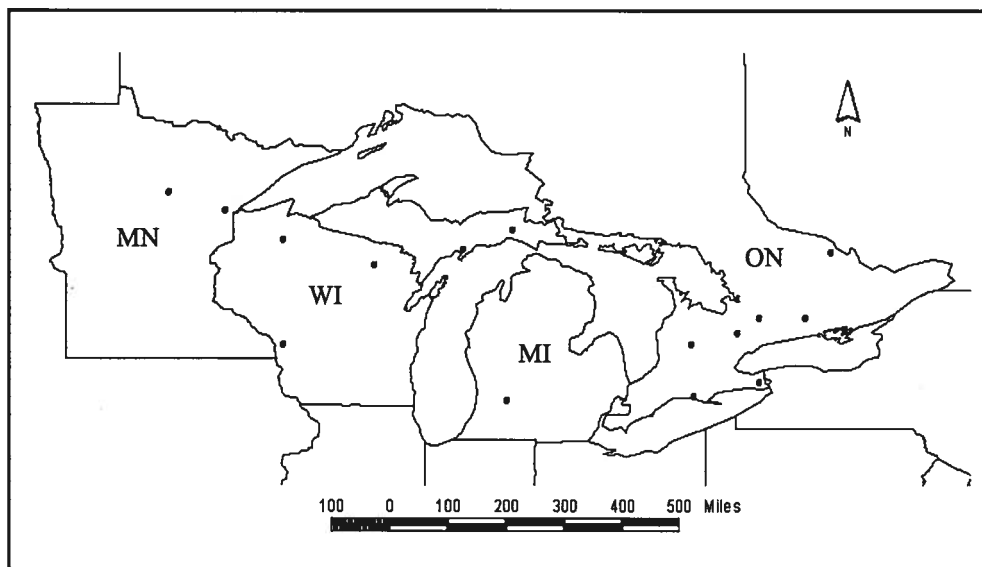
Figure 1.1. Study locations (n =15) containing the 54 study stands.

Field data were collected in 1999 and 2000 from one 10 m radius plot in each stand. Samples were collected from within that plot systematically using predetermined random distances from plot center at random compass bearings.

Site Productivity

In each stand, productivity was estimated with two indices: site index and overstory aboveground net primary productivity ($ANPP_o$).

Site index. Site index (the height of co-dominant trees at a given index age) was determined by stem analyses on three felled undamaged, co-dominant trees. Stem disks (5 cm thick 'cookies') were collected at the base, breast height (1.37 m), and every 1.5 m from breast height to the top of the tree. Disks were labeled, grouped by tree, returned to the laboratory, and then sanded until all rings were readily visible. Ages for all cookies were determined by counting rings along two or more radii until a common age was determined for a given cookie. Disks with slow radial growth (i.e. tight rings) were cross-dated to identify any potential 'locally absent' rings (Stokes and Smiley 1996) using WinDendro 6.5c Software (Regent Instruments, Quebec, QC, Canada).

Before constructing a height by age curve for each stand, error in partitioning the bole was addressed because the true total height associated with the ring count of a given disk is most-likely higher than the sampled height (Dyer and Bailey 1987). First, for all sections except the section above than the highest sampled cookie, a method developed by Carmean (1972) was applied. This method assumes that 1) on average, a cookie will be sampled in the middle of a given year's height growth, and

2) height growth per year between cookies is constant. This method has been shown

to be the most accurate (Dyer and Bailey 1987) and is described by Newberry (1991)

as follows (Eq. 1.1.):

$$H_{ij} = h_i + \frac{\left[\dfrac{(h_{i+1} - h_i)}{(r_i - r_{i+1})}\right]}{2} + (j-1) \times \left[\frac{(h_{i+1} - h_i)}{(r_i - r_{i+1})}\right] \tag{1.1.}$$

H_{ij} = estimated height for growth ring j based on point i
h_i = height at the ith section point
r_i = number of growth rings at the ith point
j = growth ring number (with pith as starting point)

For the section above the highest sampled cookie, the following correction after

Newberry (1991) was applied to avoid underestimating the corrected height of the

ring associated with the highest cookie (Eq. 1.2.):

$$H_{ij} = h_i + \frac{\left[\dfrac{(h_{i+1} - h_i)}{(r_i - r_{i+1} - 0.5)}\right]}{2} + (j-1) \times \left[\frac{(h_{i+1} - h_i)}{(r_i - r_{i+1} - 0.5)}\right] \tag{1.2.}$$

With the corrected data, a height versus age graph was plotted for each stand.

Using JMP statistical software (SAS Institute, Cary, NC, USA), a sigmoid curve and

a second order polynomial were fit using the *Nonlinear* and *Fit Y by X* platforms,

respectively. Both methods utilize least squares regression to fit a curve to the data.

The curve that produced less error (sum of squares error) was selected as being the

best descriptor of height growth for a given stand. Richards' (1959) nonlinear

function, a flexible option for summarizing growth data, was used in fitting the data

non-linearly. The equation, as described by Monserud (1984a), was as follows (Eq. 1.3.):

$$H = b_1 \times (1 - e^{-b_2 \times A})^{b_3} \qquad (1.3.)$$

H = total height minus 1.37 meters (height at breast height)
A = age at breast height
e = base of the natural logarithm
b_i = parameters estimated for each stand

To avoid error associated with plantation establishment or anomalous early growth unrelated to site characteristics, the index age was based on breast height age rather than basal cookie age (see Carmean 1972, Monserud 1984a, Monserud et al. 1990, Gilmore 1992). The resulting index curves represent height growth over time and at one or more base/index ages (Carmean 1975, Monserud 1984b). Final selection of a base age for a stand was set at <5 years from calculated base age (e.g. 21 year old stand extrapolated to base age 25 but site index for a 20 year old stand reported at base age of 15).

ANNP$_o$. Overstory annual net primary production (ANPP$_o$) also was calculated as a measure of productivity. It was estimated as stem/branch biomass increment plus foliage production of the overstory species (either European larch or red pine). To estimate stem/branch biomass increment, published species-specific allometric equations of stem and branch mass as a function of diameter at breast height were used for European larch (Gower et al. 1993) and red pine (Perala and Alban 1994 as cited by Ter-Mikaelian and Korzukhin 1997). Equations for European larch were developed in southwestern Wisconsin in three, 28-year old replicate stands using 15

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trees (Gower et al. 1993). As reported by Ter-Mikaelian and Korzukhin (1997), Perala and Alban (1994) harvested 69 trees (dbh range 2-46 cm) from the Upper Great Lakes region (e.g. Minnesota, Michigan) in the development of the latter set of equations. The equations were as follows (Eq. 1.4. and 1.5.):

Gower et al. 1993

$$\log_{10}Y = a + b\log_{10}X \qquad (1.4.)$$

Y = component dry mass (kg)
X = tree dbh (cm)
a, b = regression coefficients for different components/species

Perala and Alban 1994 as cited by Ter-Mikaelian and Korzukhim 1997

$$M = aD^b \qquad (1.5.)$$

M = component dry mass (kg)
D = tree dbh (cm)
a, b = regression coefficients for different components

Dbh for 1999, 1998, and 1997 was measured on the cookie collected at breast height for stem analysis by subtracting ring widths from the field measurement of dbh in 2000. Ring widths were measured using WinDendro 6.5c Software (Regent Instruments, Quebec, QC, Canada). Stem and branch biomass increments were calculated as the difference of biomass accumulation between 1999-1998 (i.e. 1999 increment) and 1998-1997 (i.e. 1998 increment).

Leaf litter was collected in three 61 x 61 x 15 cm traps in November 1999. After being returned to the laboratory within three days, litter was dried at 70 °C for 48 hours. Litter was then separated for each trap to remove non-targeted species' litter (i.e. not European larch or red pine litter.) Samples were then re-dried at 70°C

to a constant mass and weighed. Litter produced per trap [grams (g) per 0.3721 square meter(m^2)] was extrapolated to megagrams per hectare (Mg/ha) and averaged across traps for a stand value.

Foliage biomass production based on 1999 litter mass was added to 1998 and 1999 stem plus branch increment to estimate $ANPP_o$. This value was expanded to an areal basis (i.e. Mg ha^{-1}) with tree density measurements. (For the latter see *Vegetation Characteristics* below.) Mean annual increment (Mg ha^{-1} yr^{-1}, MAI) was calculated as total biomass accumulation in 1999 divided stand age.

Predictors of productivity

Five general categories of variables assumed to be important correlates of productivity were collected. These were physical + chemical soil properties, and vegetation, topographic, and regional climate characteristics.

Physical soil characteristics. In August 1999, a composite (n=18) soil sample that included friable litter (~O_e/O_a; Brady and Weil 1996) was collected from 0-15 cm with an Oakfield-type sampler. A second composite soil sample (n=4) was collected from 15 to 150 cm using a bucket auger. Where 150 cm in depth was not attainable due to impervious substrate, the depth attained was recorded. All soil was field sieved to 4 mm, mixed thoroughly to promote homogenization, and a subsample was collected. Samples were air dried in the field, air dried at the laboratory (within 10 days of original sampling), and then sieved to 2mm. Litter layer (O_i, O_a, O_e) depth (cm) also was measured in each stand and averaged (n=9).

Soil samples from the two strata described above were used to determine the percent sand/silt/clay using a modified hydrometer method (Grigal 1973). A

proportionate amount of soil was taken from each sample stratum to total ~ 75 g and ~ 50 g air-dry soil for sandy and clayey soils, respectively. Also, a 10 g sample was weighed and dried at 105 °C for 24 hours to determine the oven-dry/air-dry ratio used to convert air dried samples used in textural analyses to an oven dry mass.

One hundred milliliters (ml) of a 5% sodium hexametaphosphate [$(NaPO_3)_6$] solution, a dispersing agent, and ~ 200 ml of deionized water was added to each sample and allowed to stand for 30+ minutes. Samples were then mixed for exactly 5 minutes using an electric mixer. The mixed solution was transferred to a settling jar and the total volume was increased to 1000 ml. The solution was stirred thoroughly and two measurements were taken using an ASTM No. 152H hydrometer with a Bouyoucos scale in g per liter (l). The first measurement, taken at 40 seconds, measures the sand content. The second measurement, taken at 4 hours, measures clay content. After each measurement, a hydrometer reading in a 'blank' settling jar containing 100 ml of dispersing agent and 900 ml deionized water was taken to adjust for temperature and the viscosity of the dispersing agent. The "corrected" reading is the initial reading minus the subsequent blank reading. Temperature was also monitored with a StowAway®Tidbit® temperature data logger (Onset Computer Corporation, Bourne, MA, USA) every 4 seconds in the 'blank' jar to ensure changes in solution temperature were detected. Textural class (e.g. sandy loam vs. loamy sand) was defined following Soil Survey Staff (1975) protocol. Calculations of each textural component was as follows (Eq. 1.6., 1.7., and 1.8.):

% sand = [1 – (corrected 40 second reading/sample oven dry weight)] x 100 (1.6.)

% clay = (corrected 4 hour reading/sample oven dry weight) x 100   (1.7.)

% silt = 100 – (% sand + % clay)   (1.8.)

In May-June 2000, a 0.5 x 0.5 x 0.75m deep soil pit was dug in each stand in a central, representative location. Excavated soil from the pit was sieved to 4 millimeters (mm). Volume of coarse fragments >4 mm was determined via displacement of water in a calibrated bucket. Composite measures (across pit faces) for thickness (cm) and color (Munsell® Soil Color Charts 1992, Kollmorgen Instruments Corp., Newburgh, NY, USA) of the A horizon as well as depths (cm) to impermeable layers and/or C horizon were taken. Bulk density (D_b, dry soil g/ cubic centimeter (cm^3)) was calculated using the core method (Blake and Hartge 1986). Five mineral soil core samples of a known volume (15 cm depth @ 4.7625 cm diam = 267.2 cm^3 per core) were collected using a split core sampler with a slide hammer attachment and composited. At the laboratory, soils were dried (105 °C) to a constant mass and weighed. Bulk density for the stand was calculated as (Eq. 1.9.):

$D_b =$ *Mass of oven-dry soil (g)/volume (cm^3)*   (1.9.)

Soil organic matter was determined in mineral soil collected during bulk density sampling. Sample oven dry (105°C) mass was determined. Samples were then ashed in a 400°C muffle furnace for eight hours to determine loss of carbon (Ben-Dor and Banin 1989). After being removed from the muffle furnace and prior to weighing, samples were cooled over $CaCl_2$ for 12 hours. Percent weight loss was calculated as: ($mass_{105}$ − $mass_{400}$)/$mass_{105}$. Assuming that organic matter is 1.72

times the amount of organic carbon in the soil (Brady and Weil 1996) and that carbon was 48% of the volatilized material (Vitousek 1982), organic matter was calculated as follows (Eq. 1.10.):

$$Soil\ organic\ matter = \%\ ash\ x\ 0.48\ x\ 1.72 \qquad (1.10.)$$

Available soil water holding capacity (AWC), the difference in soil water content at field capacity (FC, -0.01 MPa) and permanent wilting point (PWP, -1.5 MPa), was estimated from % sand and % clay using the equations of Harding and Grigal (1984) (Eq. 1.11., 1.12., and 1.13.):

$$FC = 27.85 + 0.14\ (\%\ clay) - 0.27\ (\%\ sand) \qquad (1.11.)$$

$$PWP = 10.69 + 0.16\ (\%\ clay) - 0.11\ (\%\ sand) \qquad (1.12.)$$

$$AWC = FC - PWP \qquad (1.13.)$$

AWC on a volumetric basis was calculated by multiplying AWC (g water (g dry soil)$^{-1}$) and soil bulk density (g/cm^3) and then subtracting the volume of soil occupied by coarse fragments.

Soil temperature was monitored in 30 stands with StowAway®Tidbit® temperature data loggers (Onset Computer Corporation, Bourne, MA, USA) every 8 minutes from April to July 2000. One logger per stand was placed at a depth of 7.5 cm in a representative location within the 10 m fixed-radius plot.

Chemical soil characteristics. Soil pH was measured on a sample with the 0-15 and 15-150 cm strata composited (Thomas 1996). Ten g of soil and 10 ml of deionized

were mixed, allowed to stand for 30+ minutes, and measured with a calibrated Consort P601 pH meter (Consort Instruments, Belgium) by submersing the electrode into the supernatant while simultaneously stirring the solution with a glass rod.

Rates of N mineralization were calculated in three separate incubations: 1) one 28 day *ex situ* incubation for all stands with soils collected in August 1999 (the top stratum, 0-15 cm, as explained above in *Physical soil characteristics*); 2) one 35 day *in situ* incubation for 30 stands in May-June 2000; and 3) one 28 day *ex situ* incubation for 30 stands with soils collected in May 2000.

In August 1999, soils were air dried upon collection in the field and transported back to the laboratory within eight days. Two full laboratory incubation replicates were performed. Two 'initial' and two 'final' 10 g samples per stand of air dry soil were re-moistened four days prior to the start of the incubation due to the spike of microbial activity that occurs after re-wetting. This period was intended to allow a stabilization of the soil as air drying results in a portion of the microbial biomass to become lysed, thus that biomass N is a portion of the potentially mineralizable pool (Bartlett and James 1980, Campbell et al. 1993). The remaining two samples per stand were kept moist and incubated in a dark, humid environment at 25°C +/- 1°C for 28 days.

In May 2000, an *in situ* incubation was begun in 30 stands using the pipe method (Raison et al. 1987) to minimize soil disturbance (Binkley and Hart 1989). Eight polyvinyl chloride (PVC) pipes measuring 5 cm in diameter x 18 cm deep were driven to a depth of 15 cm. The tops were covered with duct tape to prevent rain or debris from entering the pipe. A small slice in the tape was cut with a knife

for ventilation. Adjacent to each pipe, another pipe was driven to 15 cm and soil was extracted by simultaneously pulling and twisting the pipe, ensuring the soil core was intact for the entire 15 cm. These eight cores of soil were sieved to 4 mm and thoroughly mixed to promote homogenization. One composite sample was collected, double-bagged in polyethylene bags to prevent drying, and kept at ~1-2°C during transport back to the laboratory. The *in situ* 'final' samples were excavated at 35 days, transported within 3 days, and extracted in the laboratory.

In addition to the 35 day *in situ* incubation, a 28 day *ex situ* incubation was begun in May 2000 with ~10 g sample per stand for the same 30 stands. Incubated samples were stored in a similar fashion to the 1999 *ex situ* samples: constantly moist in a dark, humid environment at 23°C +/- 1°C for 28 days.

All extractions of ammonium (NH_4^+) and nitrate (NO_3^-) were carried out following Mulvaney (1996). One hundred ml 2 M KCl and 10 g soil were combined in a 250 ml Erlenmeyer flask, shaken on an orbital shaker for 1-2 hours, and filtered through Whatman #42 filter paper after 30 minutes of settling. Samples were kept cold (1-2°C) until analyzed for NH_4^+ and NO_3^- with a continuous- or segmented-flow AutoAnalyzer (OI Analytical, College Station, Texas, USA). 'Initial' samples (T_0) were extracted to determine standing pools of NH_4^+ and NO_3^-. 'Final' samples (T_F) were extracted to determine the amount of NH_4^+ and NO_3^- produced during the incubation. Oven dry mass (g) was determined after drying (105°C) a subsample (~10g) of soil and calculating the air-dry (1999)- or fresh(2000)-/oven-dry ratio. Calculation of the NH_4^+ and NO_3^- concentrations on a gravimetric basis after Robertson et al. (1999) was as follows (Eq. 1.14.)

$$\mu g \text{ ion/g soil} = (C \times V) / W \qquad\qquad (1.14.)$$

C = concentration of ion in extract (mg/l)
V = volume of extract (KCl plus moisture in soil sample) (ml)
W = oven-dry mass of soil (g)

NOTE: $\mu g\ g^{-1} = \text{ppm} = \text{mg kg}^{-1}$

Net N mineralization was calculated as the difference between $NH_4^+ + NO_3^-$ concentrations of the incubated ('final') and original ('initial') soil samples, or $(NH_4^+ + NO_3^-)_F - (NH_4^+ + NO_3^-)_0$. Net nitrification was calculated as the difference between nitrate concentrations of the incubated and original soil samples, or $(NO_3^-)_F - (NO_3^-)_0$. To express rates for both net mineralization and nitrification on a daily basis, each was divided by the total incubation duration in days.

Vegetation Characteristics. Stand, canopy, and leaf characteristics for each stand were measured as follows.

Basal area and trees per hectare. Stand basal area (BA, $m^2\ ha^{-1}$), the cross sectional area of trees at dbh, was determined as the average of four 20 basal area factor (BAF) variable-radius plots using a CRUZ-ALL angle gauge (Forestry Suppliers, Inc. Jackson, MS, USA). Average BA was converted to $m^2\ ha^{-1}$ from the following calculation after Avery and Burkhart (1994) (Eq 1.15.):

$$BA\ per\ acre = (total\ \#\ of\ trees\ tallied/4\ plots)\ x\ 20\ BAF \qquad (1.15.)$$

Trees per ha was also determined for each stand. The average BA per tree was determined for the three selected plus trees. Total trees ha^{-1} was then calculated on the basis of the BA ha^{-1} as calculated above.

Leaf life span. Leaf life span was determined for red pine by counting the cohorts of needles present on a subsample of branches in July and August 2000. For European larch, a leaf life span of approximately six months was assumed (Gower et al. 1993, Reich et al. 1999) but not needed in any canopy calculations.

Foliar nitrogen. Foliar samples were collected during the growing season after nutrient concentrations had stabilized (Myre and Camiré 1996) and sampled consistently with regard to crown position between trees. For all collections, needles were separated from branches immediately and only needles were retained. Samples for 1999 were collected using a shotgun to retrieve sun-exposed, canopy branches from two of the three selected co-dominant trees. Larch samples consisted of short shoot needles. Pine samples consisted of second year foliage.

Samples for 2000 were collected from the co-dominant trees felled for stem analyses. Canopies of two trees were vertically stratified into thirds by canopy length. Needles were proportionately collected between and within these strata and composited (i.e. each stratum selected proportionately to volume of canopy *and* needles from each branch sampled proportionately to abundance of foliage on that branch). Larch samples consisted of short shoot needles. Each cohort for pine (n=3 or 4) was sampled separately. Collected samples were stored at 1-2 °C during transport. After being returned to the laboratory, samples were dried at 70 °C.

Subsamples were taken for specific leaf area (SLA) and subsequent measures as described below (See *Canopy leaf area and mass* and *Nitrogen retranslocation.*). Other subsamples were ground using a tissue pulverizer (Kinetic Laboratory Equipment Co., Visalia, CA, USA) and analyzed for total percent N (%N) with an elemental analyzer (Carlo Erba NA-1500 Series II or NC-2500; CE Elantech, Lakewood, NJ, USA). This was expressed on a mass ($N_{leaf \cdot mass}$, mg g^{-1}) and area ($N_{leaf \cdot area}$, mmol m^{-2} x 10^2) basis.

Photosynthesis. Rates of light saturated photosynthesis (A_{max}) were measured in the field using a portable photosynthesis system in an open-system configuration (LI-6400, LI-COR, Lincoln, NE, USA). Measurements were taken in the field during July and August 2000, the point in the growing season when needles are considered to have fully developed and nutrient concentrations have stabilized (Myre and Camiré 1996). Measurement protocol included the following settings: incoming stream flow rate equal to 400 μmol s^{-1}, ambient carbon dioxide (CO_2) concentrations set at 370 μmol CO_2 mol^{-1} air, and saturating photon flux densities of 1500 μmol quanta m^{-2} s^{-1} via an enclosed LED light source in the cuvette. Following Ellsworth and Liu (1994), measurements were taken on foliage from a subset of branches removed from sun exposed areas of canopies. Stems from three trees were rehydrated after removal by cutting them underwater prior to taking measurements. Measurements were taken on short shoots for European larch and second year foliage for red pine.

Canopy leaf area and mass. Leaf area was measured using WinSeedle 5.0 (Regent Instruments, Quebec, QC, Canada) for litterfall (1999) and live samples (2000). The samples were then dried at 70° C and weighed to determine dry mass (g). (See *Foliar nitrogen* and *ANNP$_o$* above for live and senesced foliage sampling protocols, respectively.) SLA was then calculated as fresh area (cm^2) per unit dry mass (g).

Leaf area index (LAI) was calculated by two methods: 1) converting litter mass to canopy mass by correcting for mass lost during senescence and then converting to LAI via SLA for the live canopy, and 2) extrapolating the area of the litter caught without any correction factor assuming that the area of live and senesced tissue is the same. LAI was also measured in the field via LAI 2000 Plant Canopy Analyzers (PCA; Li-Cor, Inc., Lincoln, NE, USA) in August 1999. For both calculation methods, LAI was calculated for each litter trap in a stand and averaged. The following equations summarize the calculations (Eq. 1.16. and 1.17.):

$$1) LAI = \frac{SLA_{can-avg} \times \left(litter \times \dfrac{ML_{can-avg}}{ML_{lit}} \right)}{Trap_{area}} \times cohorts \qquad \text{(Eq 1.16.)}$$

$SLA_{can-avg}$ = average canopy SLA (cm^2 g^{-1})*
$ML_{can-avg}$ = live canopy foliage mass per length (mg mm^{-1})*
$litter$ = litter collected in fall 1999 (g)
ML_{lit} = senesced needle foliage mass per length (mg mm^{-1})
$Trap_{area}$ = area of litter trap (cm^2)
$cohorts$ = number of cohorts counted in July/August 2000

*NOTE: $SLA_{can-avg}$ and $ML_{can-avg}$ calculated across all red pine cohorts.

$$2) LAI = \frac{SLA_{lit} \times litter}{Trap_{area}} \times cohorts \qquad \text{(Eq. 1.17.)}$$

SLA_{lit} = senesced needle SLA (cm^2 g^{-1})

litter	= litter collected in fall 1999 (g)
Trap$_{area}$	= area of litter trap (cm^2)
cohorts	= number of cohorts counted in July/August 2000

Standing canopy biomass also was calculated for each stand by correcting for the mass loss of live to senesced foliage for litter captured in fall 1999 and then extrapolating to Mg ha^{-1}. This was done for each trap and then averaged for the stand. The equation is as follows (Eq. 1.18.):

$$Biomass = litter \times \frac{ML_{can-avg}}{ML_{lit}} \times cohorts \qquad \text{(Eq. 1.18.)}$$

Biomass	= standing ('fresh') canopy mass (Mg ha^{-1})
litter	= litter collected in fall 1999 (g)
ML$_{can-avg}$	= live canopy foliage mass per length (mg mm^{-1})*
ML$_{lit}$	= senesced needle foliage mass per length (mg mm^{-1})
cohorts	= number of cohorts counted in July/August 2000

*NOTE: *ML$_{can-avg}$* calculated across all red pine cohorts.

Nitrogen retranslocation. Live canopy foliage (1999 and 2000) and senesced tissue (1999) were used to determine percent N retranslocated. (See *Foliar nitrogen* and *ANNP$_o$* above for live and senesced foliage sampling protocols, respectively.) First, on a mass basis, mass per unit length for both live and senesced foliage was determined for both species using WinSeedle 5.0 (Regent Instruments, Quebec, QC, Canada) to measure needle length. These samples were then dried at 70°C to a constant mass and weighed. Average mass per unit length was then calculated. The percent N retranslocated (*% retrans$_{mass}$*) was determined as follows (Eq. 1.19.):

$$\%retrans_{mass} = \left(\frac{\left(ML_{can} \times N_{can} \right) - \left(ML_{lit} \times N_{lit} \right)}{ML_{can} \times N_{can}} \right) \times 100 \qquad (1.19.)$$

ML_{can} = live canopy foliage mass per length (g mm^{-1})*
N_{can} = live canopy needle nitrogen content (mg g^{-1})*
ML_{lit} = senesced needle foliage mass per length (g mm^{-1})
N_{lit} = senesced needle nitrogen content (mg g^{-1})

*Note: ML_{can} and N_{can} for oldest red pine cohort.

On an area basis, this was determined using nitrogen concentrations (g kg^{-1}) and the specific leaf mass (SLM - g cm^2, the inverse of SLA) for both live and senesced foliage. The *% retrans$_{area}$* was calculated as follows (Eq. 1.20.):

$$\%retrans_{area} = \left(\frac{\left(N_{can} \times SLM_{can} \right) - \left(N_{lit} \times SLM_{lit} \right)}{N_{can} \times SLM_{can}} \right) \times 100 \qquad (1.20.)$$

N_{can} = live canopy needle nitrogen content (g kg^{-1})‡
SLM_{can} = live canopy needle SLM (g cm^2 g^{-1})‡
N_{lit} = senesced needle nitrogen content (g kg^{-1})
SLM_{lit} = senesced needle SLM (g cm^2 g^{-1})

‡Note: N_{can} and SLM_{can} for oldest red pine cohorts.

The calculations above which involve a live needle/senesced needle mass per unit length correction factor (e.g. LAI equation #1, standing canopy biomass, and % retrans$_{mass}$) assume that needle length does not change when needles senesce. It also assumed throughout that red pine senesces only the oldest cohort each season.

Total foliar N lost in 1999 was calculated by converting litter N (mg g^{-1}) per litter trap area (0.3721 m^2) to N loss (kg ha^{-1}) and averaged across litter traps for a stand measure.

Water use efficiency. Carbon isotope discrimination (Δ) was determined on all live foliar samples (n=54) collected in July and August 2000 and a subsample (n=10) of those collected in August 1999. Samples collected in 2000 were composited across cohorts providing one sample per stand. Samples for 1999 were only short shoots for European larch and second year cohort needles for red pine. All samples were collected fresh, immediately separated from the branch, and stored at 1-2°C until being returned to the laboratory. At the laboratory, samples were dried at 70°C and ground using a tissue pulverizer (Kinetic Laboratory Equipment Co., Visalia, CA, USA). A 2-3 mg subsample was then prepared and analyzed for carbon isotope content using a isotope ratio mass spectrometer (IRMS, Finnigan Delta Plus, Bremen, Germany) interfaced with an elemental analyzer (NC2500, CE Elantech, Lakewood, NJ, USA). The molar abundance ratio of carbon isotopes ($^{13}C/^{12}C$) of CO_2 was measured against a reference calibrated against the standard, PDB-belemnite (*Belemnitella americana*). The carbon isotope composition (δ) relative to the PDB standard in parts per thousand (‰) was calculated using the sample and standard ratios, R_{sample} and $R_{standard}$, respectively: (Eq. 1.21.):

$$\delta^{13}C_{sample} = \left(\frac{R_{sample}}{R_{s\tan dard}} - 1 \right) \times 1000 \qquad (1.21.)$$

The molar abundance ratio was then expressed as the carbon discrimination by the leaf (Δ) in ‰. As noted by Ehleringer (1991), data presented in such a way "directly expresses the consequences of biological processes". The following equation was used in calculating Δ (Eq. 1.22.):

$$\Delta = \frac{\delta^{13}C_{air} - \delta^{13}C_{sample}}{1 + \delta^{13}C_{sample}} \qquad (1.22.)$$

The carbon concentration of air ($\delta^{13}C_{air}$) was assumed to be –8‰ following

Farquhar et al. (1989) as cited by Marshall and Zang (1994), Ehleringer (1991),

Schlesinger (1997), Sparks and Ehleringer (1997), and Lambers et al. (1998).

Topographic characteristics. Stand topographical characteristics were measured in

May-June 2000. Data collected included percent slope using a clinometer. If slope

was >0°, description of slope (Grigal et al. 1999) and aspect of the plot equal to the

azimuth as measured via a compass were also recorded.

Regional climatic characteristics. Daily precipitation and temperature data for 1998

and 1999 were obtained from weather stations (n=18) 1~30 km in distance from

respective stands (Environment Canada 2000, National Oceanic and Atmospheric

Administration 2000). With these data, total annual precipitation and daily

temperature records were obtained. From temperature data, growing degrees days

(sum °C-day; GDD) were calculated as (Eq. 1.23.):

$$GDD = \left[\frac{Temp_{max} + Temp_{min}}{2} \right] - Temp_{base} \qquad (1.23.)$$

where $Temp_{max}$ and $Temp_{min}$ are daily maximum and minimum temperatures (°C),

respectively. The base temperature *($Temp_{base}$)*, the temperature below which the

species of interest are expected to be dormant, was set at 5 °C (Perala 1985). If the mean temperature for a day was less than $Temp_{base}$, it was set equal to $Temp_{base}$ and the equation was evaluated as zero GDD for that day ("Method 2", McMaster and Wilhelm 1997).

Water balance (WB) was estimated for each stand as the difference between the annual moisture potential (precipitation, PRECIP; soil water storage capacity equal to field capacity minus percent coarse fragments, FC) and outputs of moisture (potential evapotranspiration, PET) (Stephenson 1990) as (Eq. 1.24.):

$$WB = PRECIP + FC - PET \qquad (1.24.)$$

Each component is commonly expressed in cm of water addition or loss (e.g. Grier and Running 1977, Jenny 1980, Gholz 1982, Yin 1993, Hebert and Jack 1998). PRECIP and PET are summed for the year while FC is a constant capacity for each stand. Precipitation data described above were used to calculate annual sums of PRECIP. FC was calculated using Eq. 8 as described in *Physical soil characteristics* above after Harding and Grigal (1984). PET was calculated after Bonan (1989) and is described therein as follows (Eq. 1.25.):

$$E_p = \left[38 - \left(\frac{2 \times E}{305}\right) + \frac{380}{(e_2 - e_1)}\right]^{-1} \times \left[T_a + (2.5) + 0.14(e_2 - e_1) + \frac{E}{550}\right] \times R_s \qquad (1.25.)$$

E_p = PET (cm)*
E = elevation of measuring weather station (m)
T_a = mean monthly air temperature (°C)
e_2 = saturation vapor pressure (mbar) at mean maximum daily temperature
     (°C) of the warmest month of the year

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e_1 = saturation vapor pressure (mbar) at mean minimum daily temperature
        (°C) of the warmest month of the year

e_s = $33.8639[(0.00738T_a + 0.8072)^8 - 0.000019 |1.8T_a + 48| + 0.001316]$[**]

R_s = mean monthly solar radiation (cal cm^{-2} day^{-1} converted to MJ m^2 day^{-1})

Note:

[*]   Data were converted to cm from original cal cm^{-2} day^{-1} by the Jenson-Haise method (Jenson et al. 1990) as cited by Hogg (1994). Dividing the R_s by λ, the latent heat of vaporization (24.54 MJ m^{-2} cm^{-1}), provides PET in cm.

[**]   Vapor pressures were calculated after Bosen (1960) per Bonan (1989).

Solar radiation data were available for six locations in the United States from 1961 – 1990 Normal Data (National Renewable Energy Laboratory 2000) and one location in Ontario for 1998 – 1999 (Environment Canada 2000). All data were global radiation data collected on a flat-plate collector with a tilt angle of 0°.

Statistical analyses

JMP (4.0) statistical software (SAS Institute, Cary, NC, USA) was used to examine relationships between indices of stand productivity, site predictor variables, and their interrelationships.

Pearson product-moment correlation analyses were performed to relate soil, vegetation, and climate characteristics to site index (base ages 15, 25, and 50) and annual biomass increment ($ANPP_{o-total}$). The Pearson product-moment correlation coefficient (r), a measure of the strength of the linear relationship between each pair of variables (Sokal and Rohlf 1969), between predictor variables also was examined for evidence of collinearity. The linear relationship between potentially confounding variables (e.g. average stand age and/or climate) and productivity also was assessed in bivariate plots and strength of pairwise correlation coefficients. The residuals of those bivariate relationships were used in some analyses when regressing productivity by predictor variables to 'extract' that source of error.

Multiple regression models (MLR) were constructed using soil variables (% clay, available soil water holding capacity, bulk density, % coarse fragment, depth of A/C/forest floor horizons, % organic matter, pH, rates of mineralization/nitrification), climatic variables (growing degree days 1999, water balance, average July temperature 1998-1999), vegetation variables (carbon isotope discrimination, foliar nitrogen, specific leaf area) or all (n = 17) of the above as predictor variables. To conserve degrees of freedom in the regression procedures, only predictor variables which had values for all stands were selected (n = 27 of each species). Separate models were constructed for European larch and red pine in four analyses with the above predictors and the predicted variable (Y) defined as follows:

1) Y = productivity data as Site Index (15 & 25)
2) Y = residuals of Site Index (15 & 25) by climate[*]
3) Y = residuals of ANPP$_{o\text{-total}}$ by average stand age
4) Y = residuals of (*ANPP$_{o\text{-total}}$ x AGE residuals*) by climate[*]

> [*]NOTE: Climate variables included were precipitation and temperature to 'extract' effect of climate. Water balance was retained as a predictor due to it being calculated with site variables.

The 'mixed' selection method (SAS Institute, Inc. 2000) was used in variable selection as it has been shown to be a the most successful selection method compared with 'forward' and 'backward' selection (Miller 1990) and an "objective screening procedure" (McClave and Dietrich 1991). The entry/exit alpha (α) was set at 0.10 as recommended by Draper and Smith (1981). After the variable selection process, a least squares regression was performed to determine the amount of variation (adjusted for degrees of freedom, R_a^2) in the predicted variable that was explained by the predictor variable(s). Residual plots were examined for variance heteroscedasticity. Final model mean square error (MSE), R_a^2, and p-value were recorded.

Another set of MLR models was run using a subset of 'simple' (i.e. easy to measure/collect) soil variables to predict site index. Variables selected included each component of texture (sand, silt, and clay) grouped with bulk density, pH, and horizon (e.g. A, C, forest floor) depth. Selection of the best subset of variables in these three sets of four variables followed the 'stepwise' methods described above. European larch and red pine site index were modeled separately.

RESULTS

General Stand Characteristics

For the study stands, the mean age (years) ranged from 12.5 years to 67 years for European larch and 11.5 to 65 years for red pine (Table 1.1.). For both species, most of the younger stands were in the northern portion of the study area including Michigan's Upper Peninsula, northern Wisconsin, and Minnesota. Most of the older stands were in southern Michigan and southern Ontario. Average age was similar for both species; 36.5 and 37.8 years old for European larch and red pine respectively. Average stand diameter and height for European larch (24.6 cm and 19.5 m) were greater than for red pine (23.1 cm and 17.2 m) whereas stand density was much greater for red pine (963 trees ha^{-1}) than for European larch (619 trees ha^{-1}). Despite red pine having greater stand density and overstory production in 1999 ($ANPP_{o-total}$, Mg ha^{-1}) was on average 85% greater in European larch than red pine stands (Table 1.3.). In general, $ANPP_{o-total}$ (Table1.1.) and site index (not shown) for both species was greatest for young stands at sites in the northwest part of the study area.

Table 1.1. Stand location (nearest town), mean age, trees per hectare, diameter at breast height (dbh) , total height, and aboveground production ($ANPP_o$ - 1999) for the 54 study stands.

stand	spp.	location	mean age	trees per hectare	mean dbh[‡] (cm)	mean height[‡] (m)	$ANPP_o$ (Mg ha^{-1})
1	larch	Augusta, MI	59	421.1	30.6 (0.6)	24.8 (0.5)	4.6
2	pine	Augusta, MI	46.5	800.6	29.6 (1.6)	21.3 (0.4)	1.6
3	larch	Augusta, MI	60.5	523.7	32.5 (3.0)	24.9 (1.1)	7.4
4	pine	Augusta, MI	48.5	764.9	29.0 (1.4)	20.8 (0.2)	2.6
5	pine	Bangor, WI	27	1008.6	22.8 (1.6)	15.7 (0.1)	3.7
6	larch	Bangor, WI	21	666.6	24.8 (0.6)	19.8 (1.1)	9.9
7[§]	larch	Bangor, WI	34	397.1	28.1 (6.7)	24.3 (1.0)	7.9
8	pine	Bangor, WI	36	1441.2	20.1 (0.4)	19.4 (0.5)	2.5
9[§]	larch	Bangor, WI	34	227.6	36.7 (1.6)	23.3 (0.7)	5.8
10	pine	Bangor, WI	35	1179.1	20.7 (1.9)	18.4 (0.8)	2.8
11	larch	Argonne, WI	17	607.5	21.9 (2.0)	14.4 (1.1)	9.7
12	pine	Argonne, WI	20.5	713.1	21.2 (1.4)	11.8 (0.3)	6.1
13	larch	Libby, MN	15	312.1	17.6 (5.2)	13.3 (1.8)	5.2
14	pine	Libby, MN	13	2063.2	12.1 (1.9)	8.5 (0.2)	7.0
15	larch	Cloquet, MN	17	1135.1	15.1 (2.3)	12.6 (1.6)	8.8
16	pine	Cloquet, MN	17.5	1615.1	17.3 (0.7)	10.3 (0.7)	7.7
17	larch	Winter, WI	17.5	386.4	21.2 (2.5)	13.7 (1.5)	4.3
18	pine	Winter, WI	17	1415.6	15.4 (1.4)	10.0 (0.2)	6.7
19	larch	Brampton, MI	13	701.0	17.0 (1.6)	11.5 (0.6)	11.0
20	larch	Brampton, MI	12.6	789.1	18.2 (2.2)	10.9 (0.6)	9.2
21	larch	Brampton, MI	13	800.8	17.6 (0.75)	11.9 (0.4)	14.5
22	pine	Trenary, MI	27	950.5	22.7 (3.6)	17.1 (0.9)	4.0
23	pine	Cornell, MI	21.5	1362.0	19.4 (0.7)	12.2 (0.3)	5.6
24	pine	Cornell, MI	11.5	1195.7	15.6 (1.8)	7.6 (0.4)	8.2
25	larch	Newberry, MI	39	352.3	29.4 (3.1)	18.6 (1.4)	3.1
26	pine	Newberry, MI	38	562.2	22.2 (1.1)	18.0 (0.3)	4.4
27	larch	Turkey Point, ON	49	343.7	30.3 (4.7)	24.2 (0.9)	2.6
28	larch	Turkey Point, ON	56	431.2	24.1 (2.4)	19.9 (1.1)	2.3
29	pine	Walsingham, ON	36	831.4	23.6 (1.4)	17.8 (0.4)	2.7
30	pine	Turkey Point, ON	65	431.5	35.4 (1.6)	25.7 (1.0)	1.2
31	larch	Fonthill, ON	58	557.6	33.5 (2.6)	28.6 (1.2)	4.1
32	pine	Fonthill, ON	29	502.4	20.2 (0.8)	15.1 (1.1)	1.4
33	pine	Elizabethville, ON	35.5	1501.5	20.4 (1.8)	15.9 (0.7)	2.2
34	pine	Elizabethville, ON	28.5	1863.4	17.5 (1.0)	14.3 (0.5)	2.7
35	pine	Elizabethville, ON	33.5	1487.8	17.4 (2.1)	12.0 (0.04)	1.8
36	larch	Elizabethville, ON	41	572.5	29.8 (3.3)	24.3 (0.03)	8.6
37	larch	Fenella, ON	67	389.1	26.6 (3.4)	23.5 (0.2)	3.0
38	larch	Fenella, ON	46.5	482.0	30.9 (2.5)	22.2 (1.1)	5.2

Table 1.1. (cont'd)

stand	spp.	location	mean age	trees per hectare	mean dbh[‡] (cm)	mean height[‡] (m)	ANPP$_o$ (Mg ha^{-1})
39	larch	Petawawa, ON	35.5	719.6	19.6 (1.5)	20.0 (1.1)	3.6
40	larch	Petawawa, ON	44.5	577.6	24.1 (1.9)	23.5 (1.3)	3.7
41	pine	Petawawa, ON	63	312.1	30.3 (5.2)	25.0 (1.5)	1.3
42	pine	Petawawa, ON	64	731.8	22.3 (2.2)	20.3 (0.7)	2.1
43	larch	Petawawa, ON	24	2049.4	15.6 (0.3)	16.8 (0.5)	8.3
44	pine	Petawawa, ON	61.5	818.4	26.4 (1.2)	23.3 (0.7)	2.8
45	larch	Siloam, ON	45	396.5	25.0 (1.4)	17.8 (0.5)	3.1
46	pine	Siloam, ON	47	676.7	23.9 (4.5)	19.9 (0.5)	2.2
47	larch	Coppins Cs., ON	59.5	434.0	27.1 (3.5)	20.5 (0.6)	4.2
48	pine	Coppins Cs., ON	64.5	298.6	32.5 (5.5)	24.2 (2.0)	2.7
49	larch	Palgrave, ON	33	926.7	20.9 (3.0)	18.4 (1.6)	8.8
50	pine	Palgrave, ON	32	986.7	22.4 (0.5)	16.5 (1.1)	3.7
53	larch	Monticello, ON	37	950.4	22.4 (3.2)	20.5 (1.5)	8.6
54	pine	Bellwood, ON	51	214.8	34 (0.7)	22.0 (0.8)	1.3
55	pine	Bellwood, ON	50	281.8	29.6 (2.2)	21.3 (0.4)	1.5
56	larch	Stirton, ON	35.5	570.5	25.2 (3.2)	23.7 (1.3)	3.8

Note: Age, dbh, and total height are means of the three selected co-dominant trees selected for stem analysis. ANPP$_o$ is calculated with published allometric equations assuming that the co-dominant stem analysis trees are representative of the overall stand.

[‡] mean (± 1 standard deviation)

[§] Two co-dominate trees sampled.

Table 1.2. Definition of terms and units.

Acronym	Parameter	Units
$SI_{15, 25, 50}$	site index (base ages 15, 25, or 50)	m
$ANPP_{o\text{-}total}$	total overstory annual net primary production	$Mg\ ha^{-1}\ 1999^{-1}$
$ANPP_{o\text{-}stem}$	stem component of $ANPP_{o\text{-}total}$	$Mg\ ha^{-1}\ 1999^{-1}$
% sand	sand fraction soil texture	%
% silt	silt fraction of soil texture	%
% clay	clay fraction of soil texture	%
AWC	available water holding capacity	$cm^3\ m^{-3}$
D_b	bulk density of soil	$g\ cm^{-3}$
pH	pH of soil	--
% CF	soil coarse fragments (> 4 mm)	%
A_{depth}	depth to A horizon	cm
C_{depth}	depth to C horizon	cm
FF_{depth}	depth of forest floor	cm
% OM	organic matter fraction of soil	%
NMIN	nitrogen mineralization	$mg\ kg^{-1}\ day^{-1}$
NIT	nitrification	$mg\ kg^{-1}\ day^{-1}$
Δ	foliar carbon isotope discrimination	‰
leaf %N	nitrogen fraction of leaf	%
$N_{leaf\cdot mass}$	mass-based leaf nitrogen	$mg\ g^{-1}$
$N_{leaf\cdot area}$	area-based leaf nitrogen	$mmol\ m^{-2}\ x\ 10^2$
annual N loss	annual nitrogen loss through litterfall	$kg\ ha^{-1}$
canopy biomass	mass of fresh canopy	$Mg\ ha^{-1}$
SLA_{canopy}	live canopy specific leaf area	$cm^2\ g^{-1}$
SLA_{litter}	senesced tissue specific leaf area	$cm^2\ g^{-1}$
LAI	leaf area index	$m^2\ m^{-2}$
JULY	average July temperature	°C
GDD	growing degree days	count (°C)
WB	site water balance	cm

Productivity

ANPP$_{o\text{-total}}$ (stems + foliage) and ANPP$_{o\text{-stem}}$ (bole and branches) ranged seven fold within species. Over 75% of annual aboveground production was in bole and branches for both species. Site index at a base age of 15 (SI$_{15}$) ranged two fold within species and was approximately 50% greater for European larch than red pine. Sample size was smaller for site index at base age 25 (SI$_{25}$) and 50 (SI$_{50}$), but values were still greater for European larch than for red pine. (Table 1.3.)

Table 1.3. Measures of productivity for European larch and red pine species.

	European larch			red pine		
	n	mean	range	n	mean	range
mean annual increment (Mg ha^{-1} yr^{-1})	27	**4.66**	1.82 - 8.65	27	**3.56**	1.36 - 6.53
ANPP$_{o\text{-total}}$ (Mg ha^{-1} 1999^{-1})	27	**6.35**	2.32 -14.51	27	**3.43**	1.18 - 8.21
ANPP$_{o\text{-stem}}$ (Mg ha^{-1} 1999^{-1})	27	**4.84**	1.67 - 11.96	27	**2.74**	0.95 - 6.60
SI$_{15}$ (base age 15, m)	27	**13.22**	9.36 - 17.61	27	**9.34**	6.57 - 13.24
SI$_{25}$ (base age 25, m)	18	**17.70**	13.85 - 22.21	23	**14.21**	10.24 - 17.69
SI$_{50}$ (base age 50, m)	7	22.88	18.70 - 28.04	10	21.92	18.20 - 23.49

Boldface indicates significantly different means (Tukey-Kramer HSD, $\alpha = 0.05$).

Physical Soil Characteristics

For both species, the majority of the stands were found on sandy loam soils (n = 11 and 10 of 27 stands for European larch and red pine each, respectively.) There was a weak trend for European larch stands to be on lighter (i.e. lower bulk density), more developed (i.e. greater horizon depth) soils, with fewer coarse fragments, than red pine stands. Soil supporting European larch stands also had, on average, greater available

water holding capacity (AWC), higher % organic matter, greater spring temperatures, and lower forest floor depth than red pine stands. However, only forest floor depth and mean soil temperature, characteristics primarily due to species effects, were significantly different between species (Table 1.4.).

Table 1.4. Physical soil characteristics in 27 stands each of European larch and red pine.

	European larch		red pine	
	mean	range	mean	range
sand (%)	63.90	16.28 – 94.67	67.90	12.81 – 95.99
silt (%)	27.05	3.33 – 63.69	24.20	2 – 55.76
clay (%)	9.05	0.67 – 41.86	7.90	1.34 – 39.79
AWC (cm^3 m^{-3}) ‡	7.74	2.44 – 16.82	6.95	2.04 – 17.24
bulk density (g cm^{-3})	1.18	0.83 – 1.41	1.22	0.9 – 1.51
coarse fragments (%)	3.47	0 – 25.62	4.09	0 – 30.58
depth to A (cm)	15.15	3 – 33	13.81	4 – 36
depth to C (cm)	47.52	19 – 80	44.93	14 – 75
forest floor depth (cm)	**2.81**	1.17 – 5.56	**4.53**	2.61 – 6.5
organic matter (%)	3.37	1.54 – 6.20	3.32	1.16 – 7.23
mean soil temp (°C) §	**5.32**	-0.22 – 11.15	**4.37**	-0.3 – 9.98

Boldface indicates significantly different means (Tukey-Kramer HSD, $\alpha = 0.05$).
‡ Available water holding capacity.
§ Mean daily temperature at 7.5 cm depth from 4/13/00 to 4/30/00 for 14 stands of European larch and 15 stands of red pine.

Chemical soil characteristics

In laboratory incubations, nitrogen mineralization and nitrification rates were greater for soils from European larch stands than red pine stands (Table 1.5). Rates were greater in 1999 versus 2000. This discrepancy may be due to the different times the soils were collected (August 1999 versus May 2000) or by differences in handling protocol (air dried and remoistened in 1999 versus field-fresh samples in 2000). There was a weak trend of slightly higher soil pH in European larch than red pine stands. (Table1.5.)

Table 1.5. Mean chemical soil characteristics of species across stands.

	European larch		red pine	
	mean	range	mean	range
1999 N mineralization (mg kg^{-1} day^{-1})[†]	1.50	0.41 – 3.11	1.15	0.35 – 5.30
1999 nitrification (mg kg^{-1} day^{-1})	**1.63**	0 – 3.15	**0.94**	0 – 3.52
2000 N mineralization (mg kg^{-1} day^{-1})[†]	0.66	-0.13 – 1.16	0.45	0.05 - 0.97
2000 nitrification (mg kg^{-1} day^{-1})	**0.65**	0 – 1.27	**0.26**	0 – 0.62
pH	5.83	4.64 – 7.39	5.74	4.27 – 7.55

Boldface indicates significantly different means (Tukey-Kramer HSD, α = 0.05).
[†] Removing red pine outliers in 1999 (1 of n = 54) and 2000 (2 of n = 30), rates of N mineralization in European larch soils were significantly greater than red pine (1999; mean = 0.989 mg kg^{-1} day^{-1}; 2000, mean = 0.3816 mg kg^{-1} day^{-1}).

Vegetation characteristics

Compared to red pine, European larch foliage had greater carbon isotope discrimination (Δ), mass-based fresh canopy and senesced leaf litter N, canopy and litter SLA, leaf area index, and %N retranslocated but lower area-based N and mean canopy biomass versus red pine (Table 1.6.).

Table 1.6. Vegetation characteristics of European larch and red pine in all stands.

	European larch		red pine	
	mean	range	mean	range
foliar Δ (‰) [§]	**21.03**	19.33 – 22.22	**20.02**	18.76 – 21.18
foliar nitrogen (%)	**1.94**	1.26 – 2.66	**0.96**	0.77 – 1.42
foliar nitrogen (mmol m^{-2} x 10^2)	**1.13**	0.79 – 1.66	**1.91**	1.38 – 2.92
litter nitrogen (%)	**0.57**	0.30 – 1.09	**0.37**	0.29 – 0.53
foliar N turnover (kg ha^{-1} yr^{-1})	**12.23**	5.65 – 23.45	**7.05**	1.89 – 14.20
canopy SLA (cm^2 g^{-1}) [‡]	**123.86**	102.29 – 161.71	**36.09**	32.02 – 43.24
litter SLA (cm^2 g^{-1}) [‡]	**117.29**	90.26 – 145.96	**36.25**	31.39 – 44.30
leaf area index	**4.08**	1.99 – 6.24	**2.82**	0.63 – 4.56
canopy biomass (Mg ha^{-1})	**3.31**	1.72 – 5.46	**7.95**	1.73 – 14.25
% nitrogen retranslocated	**79.55**	58.50 – 93.21	**72.05**	58.16 – 83.08

Boldface indicates significantly different means (Tukey-Kramer HSD, α = 0.05).
[§] Carbon isotope discrimination.
[‡] Specific leaf area.

Topographical characteristics

Nearly half of the stands for each species had a slope of 0%; 60-80% of the remaining stands were located on a shoulder slope with a mean slope of ~4% and a southeast aspect. Due to the very skewed distribution (mostly 0's) and small % slope in the remaining stands, topographical characteristics were not used in further analyses (Table 1.7.).

Table 1.7. Topographical characteristics of study stands by species.

	European larch		red pine	
	mean	range	mean	range
slope (%)	4.37	0 – 14	4.81	0 – 12
aspect (azimuth)	161.33	6 – 346	150.19	18 – 360

Climatic Characteristics

The climate across the sites can be generally characterized by cold winters and warm, humid summers (Table 1.8.). Sites in the northwestern part of the study (e.g. Minnesota and Wisconsin) were generally coldest (average Jan. temp –9.83 °C). The lowest average precipitation and stand water balance were in southwestern Ontario, 763.19 mm and 41.48 cm, respectively.

Table 1.8. Mean climatic characteristics for 1998 – 1999 across the study area.

	mean	range
annual precipitation (mm)	833.74	675.3 – 970.15
January temp (°C)	- 7.30	-10.89 – -2.77
July temp (°C)	21.11	18.50 – 22.98
growing degree days	2390.84	1925 – 2823.06
water balance (cm)	48.80	24.70 – 70.41

Note: Data are from 18 climate stations <30 km from study areas.

Predicting productivity

Three approaches were taken to predict productivity: 1) investigate the effects of single variables in predicting $ANPP_{o-total}$ and SI_{25}, 2) use combinations of variables in stepwise multiple linear regression to predict $ANPP_{o-total}$ and SI_{25}, and 3) use a subset of simple to measure variables to predict SI_{25}.

Relationships of individual soil, vegetation, and climate variables with productivity. In general, correlations of site index to soil, climate, and vegetation variables were stronger for SI_{25} than for SI_{15} or SI_{50} (Table 1.9.; See Table 1.2. for definition of terms.). Average July temperature and Δ were associated with both SI_{25} and SI_{50} for European larch. NIT, %clay, and FF_{depth} were all associated with SI_{15} and SI_{25} for European larch. No predictor variable was significantly correlated with SI_{15} or SI_{50} for red pine. Temperature variables (e.g. average July, GDD) were positively correlated with SI_{25} and SI_{50} for European larch but negatively correlated with $ANPP_{o-total}$ and the $ANPP_{o-total}$ – age residuals for red pine. NIT, SLA, and C_{depth} and temperature variables were associated with $ANPP_{o-total}$ and the $ANPP_{o-total}$ – age residuals for European larch and red pine, respectively.

Pearson correlation analysis was used to examine collinearity among predictor variables. Some variables exhibited strong co-linearity. AWC was correlated with sand ($r = -0.9711$, $r = -0.9714$) and clay ($r = 0.7467$, $r = 0.8699$) for European larch and red pine, respectively. The correlation between average July temperature and GDD was also strong ($r = 0.9573$).

Predictor variables were also correlated with the residuals of a smoothing spline (λ = 3000) fit to $ANPP_{o\text{-}total}$ versus age since there was a strong negative relationship of $ANPP_{o\text{-}total}$ with stand age for both European larch ($R^2 = 0.473$) and red pine ($R^2 = 0.846$) stands. The correlation between site index and stand age was not significant as is expected since it is determined retrospectively at a common base age (e.g. 15, 25, 50) with stem analysis. In general, the same variables that were correlated with $ANPP_{o\text{-}total}$ were correlated with the residuals of $ANPP_{o\text{-}total}$ versus age.

Table 1.9. Pearson product-moment correlation coefficients for measures of productivity and predictor variables reported by species.

	European larch					pine				
	ANPP$_{o\text{-}total}$ − age resid. (Mg ha⁻¹ 99⁻¹)§	ANPP$_{o\text{-}total}$ (Mg ha⁻¹ 99⁻¹)	SI$_{15}$	SI$_{25}$	SI$_{50}$	ANPP$_{o\text{-}total}$ − age resid. (Mg ha⁻¹ 99⁻¹)§	ANPP$_{o\text{-}total}$ (Mg ha⁻¹ 99⁻¹)	SI$_{15}$	SI$_{25}$	SI$_{50}$
% sand	-0.260	-0.269	-0.237	**-0.549**	-0.4	0.311	0.18	-0.141	**-0.384**	0.25
% silt	0.277	0.246	0.095	0.352	0.288	**-0.398‡**	-0.229	0.08	0.316	-0.313
% clay	0.149	0.207	**0.398**	**0.662**	**0.555**	-0.109	-0.066	0.206	**0.402**	0.214
AWC	0.306	0.316	0.259	**0.502**	0.335	**-0.355‡**	-0.141	0.207	**0.441**	0.223
D$_b$	0.312	0.244	0.205	0.061	-0.325	-0.081	0.115	0.108	0.06	0.125
% CF	-0.003	-0.158	-0.135	0.04	0.27	0.148	0.081	-0.071	-0.015	0.035
A$_{depth}$	-0.261	**-0.528**	**-0.413**	-0.332	-0.103	0.245	-0.256	-0.241	-0.142	0.045
C$_{depth}$	**-0.364**	**-0.405**	-0.231	0.096	0.224	-0.152	-0.243	-0.322	**-0.457**	0.005
FF$_{depth}$	-0.019	**-0.442**	**-0.467**	**-0.464**	-0.126	0.040	-0.209	-0.284	-0.105	0.037
% OM	0.095	0.248	0.083	0.319	**0.645**	0.092	-0.277	-0.198	0.091	-0.144
99 MIN	0.105	0.041	-0.077	0.154	0.132	0.046	-0.077	0.09	**0.442**	-0.108
99 NIT	**0.494**	**0.543**	**0.349**	**0.415**	0.211	-0.146	-0.164	0.018	**0.372**	0.132
pH	**0.379**	0.284	-0.069	-0.285	**-0.754**	**-0.488**	-0.244	-0.164	-0.038	0.192
Δ	0.022	0.224	-0.089	**-0.59**	**-0.812**	-0.213	**0.345**	0.243	0.149	-0.154
%N	**0.397**	0.284	0.245	**0.598**	-0.092	-0.044	-0.056	0.313	**0.477**	0.506
SLA	**0.434**	**0.44**	0.156	-0.018	-0.202	-0.266	0.174	0.056	-0.205	**-0.494**
avg July	0.224	-0.108	0.2	**0.624**	**0.67**	**-0.387**	**-0.459**	-0.005	-0.061	0.3
99 GDD	0.196	-0.25	0.013	**0.46**	**0.628**	**-0.469**	**-0.582**	-0.108	-0.146	0.33
99 WB	0.036	0.25	-0.005	0.182	0.051	-0.125	0.079	0.079	0.355	-0.325

§Residuals of ANPP$_{o\text{-}total}$ by average stand age fit with a spline ($\lambda = 3000$). ‡Correlation not significant with one point removed. **Boldface** indicates significant correlation ($\alpha = 0.10$).
See Table 1.2. for definition of terms.

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Multiple Linear Regression. Climate variables JULY and GDD as well as WB (a combination of climate and soil characteristics), explained the most variation (71.9%) in European larch SI_{25} (Table 1.10., Y group 1). For red pine, the combination of GDD and foliar %N was the best predictive model for SI_{25} explaining over 30% of the variation in site index (Table 1.10., Y group 1). Removing the effects of climate by using the residuals of SI_{25} predicted by JULY, and GDD; Δ and WB explained 48.2% of the variation in SI_{25} residuals for European larch (Table 1.10., Y group 2). Regressed against the same residuals for red pine, foliar %N alone explained 28.2% of the variation in SI_{25} (Table 1.10., Y group 2). Notably, models predicting SI_{15} could not be developed in most cases since no variables met stepwise criteria of $P < 0.10$ to enter and $P > 0.10$ to exit.

For European larch, NIT and SLA explained 27% of variation in the $ANPP_{o-total}$ residuals of the $ANPP_{o-total}$ versus age relationship (Table 1.10., Y group 3) whereas, for red pine, the combination of A_{depth}, pH, % OM, and GDD explained 51.3% of the variation in $ANPP_{o-total}$ residuals (Table 1.10., Y group 3). An age and climate extracted data set was obtained by first obtaining residuals from the $ANPP_{o-total}$ versus age relationship (smoothing spline fit, $\lambda = 3000$). The next step was to regress these residuals using stepwise multiple linear regression on climate variables and finally saving the residuals of the model as an 'age then climate extracted' data set. When "extracting" the effects of both age and climate from $ANPP_{o-total}$ for red pine, Δ and pH were still able to explain 38.7% of the variation in productivity (Table 1.10., Y group 4).

Table 1.10. Strongest multiple regression equations for predicting productivity of European larch and red pine.

Y	spp.	Type	Model	R_a^2	MSE	P
1	larch	A, S	$SI_{15} = 15.912 - 0.962(FF_{depth})$	0.187	5.16	0.014
		C	$SI_{25} = -46.937 + 4.506(July) - 0.015(GDD) + 0.101(WB)$	0.719	1.87	<0.0001
	pine	--	$SI_{15} = N/A$	--	--	--
		A	$SI_{25} = 14.651 - 0.003(GDD) + 7.739(\%N)$	0.322	2.23	0.0079
2	larch	--	$SI_{15} = N/A$	--	--	--
		A	$SI_{25} = 17.600 + 0.088(WB) - 1.058(\Delta)$	0.482	1.432	0.0028
	pine	V	$SI_{15} = -2.994 + 3.113(\%N)$	0.109	1.316	0.0513
		V	$SI_{25} = -5.090 + 5.239(\%N)$	0.282	1.54	0.0053
3	larch	A	$ANPP_{o\text{-}total} = -8.239 + 0.732(NIT) + 0.057(SLA)$	0.273	3.74	0.0083
	pine	A	$ANPP_{o\text{-}total} = 6.084 + 0.041(A_{depth}) - 0.507(pH) - 0.001(GDD) - 0.007(\%OM)$	0.513	0.330	<0.0001
4	larch	--	$ANPP_{o\text{-}total} = N/A$	--	--	--
	pine	A	$ANPP_{o\text{-}total} = 10.54 - 0.416(\Delta) - 0.387(pH)$	0.387	0.351	0.0028

NOTE: Predicted variable (Y): 1 – all data; 2 – climate extracted; 3 – age extracted; 4 – age and climate extracted. Type (of predictor variables): S = soil, C = climate, V = vegetation, A = all. See Table 1.2. for definition of terms. All variables significant ($P < 0.10$).

To build simpler models intended as silvicultural tools, relatively easy to measure site factors were used to predict SI_{25}. Variables considered included % sand, % clay, % silt, Db, pH, A_{depth}, C_{depth}, FF_{depth}. Using these variables, % sand and pH were the best predictors of SI_{25} for European larch. A model with only %clay was the best predictor of SI_{25} for red pine but explained variance was low (Table 1.11.).

Table 1.11. Multiple regression equations for 'simple' measures of predicting productivity (SI_{25}) for European larch and red pine.

spp.	Model	R_a^2	MSE	P
larch	$SI_{25} = 29.18 - 0.074(\%SAND) - 1.19(pH)$	0.469	3.56	0.0034
pine	$SI_{25} = 13.631 + 0.067(\%CLAY)$	0.122	2.89	0.0573

NOTE: Model components: %SAND – percent sand of soil texture; pH – soil pH, %CLAY – percent clay of soil texture. All variables significant ($P < 0.10$).

Given the potential confounding effects of climate across the geographic gradient of sites, the same predictor variables were regressed against the residuals of SI_{25} predicted by climate for a conservative analysis of soil variables predicting SI_{25}. The amount of variation explained for predicting European larch and red pine SI_{25} decreased (model R_a^2 = 0.15 and 0.116, P = 0.0602 and 0.0624, respectively). Percent sand and % clay were the only significant variables selected via stepwise regression for European larch and red pine, respectively. However, both were significant with or without the effect of climate in the data.

DISCUSSION

Productivity

Compared to red pine, European larch achieved greater net productivity and greater height growth rates, especially in earlier stages of plantation growth. In only one study area did the height growth of red pine exceed that of European larch at the age of 15 or 25 (SI $_{15}$ for stands #54 @ 16.11 m and #53 @ 14.72 m, respectively.) At 50 years, in one of three study areas with both species old enough for SI_{50} calculations, red pine height growth surpassed that of neighboring European larch (21.8 m vs. 18.7m. for stands #46 and #45, respectively.) However, the mean annual increment (MAI, Mg ha^{-1} yr^{-1}) for both species was 2.23 Mg ha^{-1} yr^{-1}. In other study areas European larch stands generally had higher rates of growth than red pine at all ages. For example, for two neighboring ~40 year old stands mean annual increment (MAI) for European larch was over 20% greater than the MAI of red pine stands (stands #36 and #33: 5.8 vs. 4.6, Mg ha^{-1} yr^{-1} at 41 and 35.5 years, respectively).

Measures of productivity for both species for this study are in the range of estimates found in other studies (Table 1.12.). Results reported from Miller et al. (1993) are from European larch plantations on shallow peat soil and had been thinned regularly. Gower et al. (1993) data are from one study area used in this study (southwest Wisconsin.) Alban and Laidly (1982) and Schlaegel (1975) data are from Minnesota.

Table 1.12. Comparison of biomass production data for European larch and red pine.

	Productivity (Mg ha^{-1} yr^{-1})	Stand Age (years)	Study
European larch	1.82 – 8.65	12 – 67	this study
	6.82	28	Gower et al. 1993
	1.77	63	Miller et al. 1993
	1.63	19	Miller et al. 1993
red pine	1.36 – 6.53	12 – 65	this study
	5.85	28	Gower et al. 1993
	4.56	43	Alban and Laidly 1982
	3.68	40	Schlaegel 1975

Predictors of productivity – comparison by species

Although the two species occupied a similar range of soils in terms of physical mineral soil characteristics, differences in species leaf litter chemistry and leaf habit may have been largely responsible for species differences in microclimate, organic soil components, and N mineralization. However, differences in soil are modest compared to differences in site index and ANPP$_o$. Red pine leaf litter was significantly deeper, a result of more recalcitrant, lower N material necessary for foliage to persist for 3 to 4 years (Scott and Binkley 1997, Fassnacht and Gower 1999). During leaf off, the deciduous habit of European larch promotes insolation throughout the winter and early spring – increasing soil temperature and increasing the amount of moisture infiltration (Sartz and Tolsted 1976). The combination of higher litter quality (higher N) and higher spring temperatures promotes higher NMIN and NIT for European larch as warmer, moister soils are beneficial for the soil microorganisms which control soil N availability in forest ecosystems (Linn and Doran 1984, Barnes et al. 1998, Zak et al. 1999). Thus, the significantly different FF$_{depth}$ and NMIN/NIT rates are likely species influenced given the higher N$_{leaf·mass}$, litter N, annual N turnover, and deciduous habit of European larch.

Correlation of soil, vegetation, and climate variables with productivity

In general, moisture as well as the physical soil factors controlling moisture were strong predictors of productivity for both species. The correlation of higher productivity with greater moisture availability in the largely sandy soils encountered should not come as a surprise because tree growth and microbial activities providing nutrients are moisture dependent (Zak et al. 1994). Other studies have reported increased productivity with moisture in the Great Lakes region (e.g. Pastor et al. 1984, Fassnacht and Gower 1997). Results of this study also follow Marshall and Zhang (1994) and Kloeppel et al. (1998) with an evergreen coniferous species (red pine) exhibiting greater water use efficiency (defined as lower Δ) compared to a deciduous conifer. This suggests that European larch uses water less efficiently on a leaf area basis relative to red pine.

There are many reasons why some predictor variables were not correlated with all of the chosen measures of productivity. First, sample sizes differed between measures (e.g. site index at different base ages.) An explanation of why SI_{15} was not sufficient in differentiating site quality may be due to the fact that forest plantations are still relatively young at 15 years. Variation inherent in site fertility/quality, may not yet be fully expressed. Resources (e.g. nutrients, moisture) even on relatively poor sites may be relatively abundant in young, monoculture plantations as compared with older stands since conditions are right for high mineralization rates and demand is low.

The productivity of both species also was correlated with NMIN and/or NIT. There was a stronger correlation of productivity with NIT than with NMIN for European larch, while the opposite was true for red pine. The results for European larch are

opposite of what Zak et al. (1989) observed in nine upland deciduous forests in northern Lower Michigan. Similar to Zak et al. (1989), rates of NMIN and NIT from this study are from *ex situ* incubations that represent a potential versus a field measure. One explanation for the stronger correlation between NIT and productivity for European larch than red pine is that European larch is more efficient in NH_4^+ and NO_3^- uptake compared to some species (e.g. Scots pine, *Pinus sylvestris* L.) (Malagoli et al. 2000). Thus, European larch may be able to utilize both forms of inorganic nitrogen more effectively than red pine.

One of the puzzling outcomes of correlating European larch productivity with site variables was the consistent negative correlation with A_{depth} or C_{depth}. Aird and Stone (1955) and Gilmore (1992) found measures of soil depth as their best positive predictors of European or Japanese/European larch site index, respectively. However, Aird and Stone (1955) used log transformed soils depth data that excluded soils "characterized by coarse texture or shallowness to rock". The predicted variable, SI_{50}, was developed anamorphically from pure or mixed European and Japanese larch stands spread across southern New England (mostly New York) with an average age of 20 and 15 years, respectively. Gilmore (1992) noted that there was no significant correlation between solum thickness (~depth to C) and SI_{20}, but it was found to be an important factor in site quality assessment with discriminant analysis.

Lastly, another sharp contrast in the correlation analyses was the positive association of temperature variables with European larch SI_{25} productivity but the opposite for red pine $ANPP_{o-total}$. While no clear explanation is available, the answer may be related to moisture supply for red pine more sensitive in warmer temperatures.

Prediction of productivity in multiple linear regression

Similar to the correlation analyses, connections can be drawn with moisture and the best predictors of European larch productivity and, to a lesser extent, red pine. The best model for European larch explained over 70% of variation in SI_{25} using climate variables, including an increase in WB. However, this model involves an increase in one temperature variable (JULY), a decrease in the other temperature variable (GDD), and greater WB occurring simultaneously. This may be a result of two collinear factors (e.g. average July temperature and GDD) being used as predictor variables. When 'extracting' the effect of climate, an increase in WB and greater water use efficiency (decrease in Δ) both involve increased moisture and explain nearly half of the variation in SI_{25} for European larch. Regarding the predictor variables for red pine SI_{25} or $ANPP_{o\text{-}total}$, a decrease in temperature (GDD) could be related to increases in moisture as evapotransporation would be lower.

In this study foliar %N was a significant predictor of red pine site index, a result similar to what Wang (1995) and Chen et al. (1998) found for white spruce and trembling aspen, respectively. For European larch productivity, the increase of both SLA and NIT explain 27% of variation in $ANPP_{o\text{-}total}$. Potential explanation of this relationship could be increased productivity related to an increase in the canopy area available for photosynthesis but also increased inorganic N supply from higher NIT.

Conclusion

On average, European larch was more productive than red pine. The only average site variables that differed between species were greater FF_{depth} and lower NMIN/NIT rates for red pine than European larch. These characteristics may have been strongly influenced by differences in species foliar chemistry. Compared to red pine, European larch had higher Δ, $N_{leaf \cdot mass}$, litter N, annual N turnover, SLA_{canopy}, SLA_{litter}, LAI, % N retranslocated and lower $N_{leaf \cdot area}$ and canopy biomass.

In multiple linear regression analyses, up to ~70% and ~50% of the variation in productivity was explained for European larch and red pine, respectively. In more conservative analysis, where potential confounding effects were removed (e.g. average stand age and/or climate), ~40-50% of variation in growth was explained. However, excluding climate also may remove some of the effects of site variables that covary with climate, and thus should be interpreted with caution.

While the majority of variation in productivity was unexplained for certain models using multiple linear regression, moisture and nitrogen avaialability were identified as important predictors of productivity. For species selection criteria in plantation establishment, European larch outgrew red pine consistently over a broad range of site qualities.

REFERENCES

Aber, J.D. and J.M. Melillo. 1991. *Terrestrial Ecosystems*. Saunders College Publishing, Philadelphia. 429 pp.

Aird, P. L. and E. L. Stone. 1955. Soil characteristics and the growth of European and Japanese larch in New York. *J. For.* 53: 425-429.

Alban, D. H. 1972. The relationship of red pine site index to soil phosphorus extracted by several methods. *Proc. Soil Sci. Amer.* 36: 664 – 667.

Alban, D.H. and P.R. Laidly. 1982. Generalized biomass equations for jack and red pine in the Lake States. Can. J. For. Res. 12: 913 – 921.

Avery, T.E. and H.E. Burkhart. 1994. *Forest Measurements*. 4th ed. McGraw-Hill, Inc., New York. 408 pp.

Barnes, B.V., D.R. Zak, S.R. Denton, and S.H. Spurr. 1998. *Forest Ecology*, 4th ed. John Wiley & Sons, Inc., New York. 774 pp.

Bartlett, R. and B. James. 1980. Studying dried, stored soil samples – some pitfalls. *Soil Sci. Soc. Am. J.* 44: 721-724.

Ben-Dor, E. and A. Banin. 1989. Determination of organic matter content in arid-zone soils using a simple "loss-on-ignition" method. *Commun. In Soil Sci. Plant Anal.* 20: 1675-1695.

Binkley, D. and S.C. Hart. 1989. The components of nitrogen availability assessments in forest soils. *Adv. Soil Sci.* 10: 57 – 112.

Blake, G.R. and K.H. Hartge. 1986. Bulk Density. *In* A. Klute (ed.) *Methods of Soil Analysis*. Agron. Monog. 9, Part I. American Society of Agronomy. Madison, WI.

Bonan, G.B. 1989. A computer model of the solar radiation, soil moisture, and soil thermal regimes in boreal forests. *Ecol. Modell.* 45: 275 – 306.

Bosen, J.F. 1960. A formula for approximation of the saturation vapor pressure over water. *Mon. Weather Rev.* 88: 275 – 276.

Brady, N.C. and R.R. Weil. 1996. *The Nature and Properties of Soils*. 11th ed. Prentice Hall, Upper Saddle River, NJ. 740 pp.

Broadfoot, W.M. 1969. Problems in relating soil to site index for southern hardwoods. *For. Sci.* 15: 354-364.

Brown, J.H. and C.A. Duncan. 1990. Site index of red pine in relation to soils and topography in the Allegheny Plateau of Ohio. *North. J. Appl. For.* 7: 129 – 133.

Campbell, C.A., B.H. Ellert, and Y.W. Jame. 1993. Nitrogen Mineralization Potential in Soils. *In* M.R. Carter (ed.) *Soil Sampling and Methods of Analysis.* Lewis Publishers, Boca Raton. 823 pp.

Carmean, W.M. 1972. Site index curves for upland oaks in the central states. *For. Sci.* 33: 3-13.

Carmean, W. H. 1975. Forest site quality evaluation in the United States. *Adv. Agronomy* 27: 209-269.

Chen, H.Y.H., K. Klinka, and R.D. Kabzems. 1998. Site index, site quality, and foliar nutrients of trembling aspen: relationships and predictions. *Can. J. For. Res.* 28: 1743 – 1755.

Churkina, G. and S.W. Running. 1998. Contrasting climatic controls on the estimated productivity of global terrestrial biomes. *Ecosystems* 1: 206 – 215.

Coile, T.S. 1952. Soil and the growth of forest. *Adv. Agronomy* 4: 329-398.

Cook, D.B. 1941. Five seasons' growth of conifers. *Ecology* 22: 285-296.

Day, W.R. 1947. On the effect of changes in elevation, aspect, slope, and depth of free-rooting material on the growth of European larch, Japanese larch, Sitka spruce, and Scots pine in Mynydd Ddu Forest. *Forestry* 20: 7-20.

Draper, N.R. and H. Smith. *Applied regression analysis,* 2nd edition. John Wiley & Sons, New York, 709 pp.

Dyer, M.E. and R.L. Bailey. 1987. A test of six methods for estimating true heights from stem analysis data. *For. Sci.* 33(1): 3-13.

Ehleringer, J.R. 1991. $^{13}C/^{12}C$ Fractionation and Its Utility in Terrestrial Plant Studies. *In* D.C. Coleman and B. Fry (eds) *Carbon Isotope Techniques.* Academic Press, Inc. San Diego. 274 pp.

Ellsworth, D.S. and X. Liu. 1994. Photosynthesis and canopy nutrition of four sugar maple forests on acid soils in northern Vermont. *Can. J. For. Res.* 24: 2118-2127.

Environment Canada. 2000. Temperature, precipitation, and solar radiation data. Ontario Climate Centre. Downsview, Ontario.

Farquhar, G.D., J.R. Ehleringer, and K.T. Hubick. 1989. Carbon isotope discrimination and photosynthesis. *Annu. rev. plant physiol. plant mol. biol.* 40: 503 - 537.

Fassnacht, K.S. and S.T. Gower. 1997. Interrelationships among the edaphic and stand characteristics, leaf area index, and aboveground net primary production of upland forest ecosystems in north central Wisconsin. *Can. J. For. Res.* 27: 1058-1067.

Fasshacht, K.S. and S.T. Gower. 1999. Comparison of the litterfall and forest floor organic matter and nitrogen dynamics of upland forest ecosystems in north central Wisconsin. *Biogeochemistry* 45: 265 – 284.

Gaiser, R.N. 1950. Relation between soil characteristics and site index of loblolly pine in coastal region of Virginia and the Carolinas. *J. For.* 48:271-275.

Gholz, H.L. 1982. Environmental limits on aboveground net primary production, leaf area, and biomass in vegetation zones in the Pacific Northwest. *Ecology* 63: 469-481.

Gilmore, D.W. 1992. Soil-site relationships for European larch plantations in Maine. University of Maine Thesis.

Gower, S.T., P. B. Reich, Y. Son. 1993. Canopy dynamics and aboveground production of five tree species with different leaf longevities. *Tree Physiol.* (12): 327-345.

Grier, C.G. and S.W. Running. 1977. Leaf area of mature northwestern coniferous forests: relation to site water balance. *Ecology* 58: 893 – 899.

Grigal, D.F. 1973. Hydrometer method of particle analysis. Minnesota Forestry Research Note 245. University of Minnesota, St. Paul.

Grigal, D.F., J.C. Bell, R.J. Ahrens, R.D. Boone, E.F. Kelly, H.C. Monger, P. Sollins. 1999. Site and landscape characterization for Ecological Studies. *In* G.P. Robertson, D.C. Coleman, C.S. Bledsoe, and P. Sollins (eds.), *Standard soil methods for long-term ecological research.* Oxford University Press, New York. 462 pp.

Hannah, P.R. and R. Zahner. 1970. Nonpedogenetic texture bands in outwash sands of Michigan: their origin, and influence on tree growth. *Proc. Soil Sci. Amer.* 34: 134 – 136.

Harding, R.B. and D.F. Grigal. 1984. Prediction equations for water-holding capacity of some Minnesota forest soils. Minnesota Forestry Research Note 293. University of Minnesota, St. Paul.

Harding, R.B., D.F. Grigal, and E.H. White. 1985. Site quality evaluation for white spruce plantations using discriminant analysis. *Soil Sci. Soc. Amer. J.* 49: 229-232.

Hebert, M.T. and S.B. Jack. 1998. Leaf area index and site water balance of loblolly pine (Pinus taeda L.) across a precipitation gradient in East Texas. *For Ecol. Manage.* 105: 273-282.

Hicock, H.W., M.F. Morgan, H.J. Lutz, H. Bull, and H.A. Lunt. 1931. The relation of forest composition and rate of growth to certain soil characters. *Connecticut Agric. Expt. Sta. Bul.* 300.

Hogg, E.H. 1994. Climate and the southern limit of the western Canadian boreal forest. *Can. J. For. Res.* 24: 1835- 1845.

Jenny, H. 1980. *The Soil Resource: Origin and Behavior.* Springer-Verlag, New York. 377 pp.

Jenson, M.E., Burman, R.D., and R.G. Allen (Editors). 1990. *Evapotranspiration and irrigation water requirements.* American Society of Civil Engineers, New York. Man. Rep. Eng. Pract. 70.

Lambers, H., F. S. Chapin III, and T.L. Pons. 1998. *Plant physiological ecology.* Springer-Verlag, New York. 540 pp.

Linn, D.M., and J.W. Doran. 1984. Effect of water-filled pore space on carbon dioxide and nitrous oxide production in tilled and non-tilled soils. *Soil Sci. Soc. Am. J.* 48: 1267-1272.

Kloeppel, B.D., S.T. Gower, I.W. Treichel, and S. Kharuk. 1998. Foliar carbon isotope discrimination in *Larix* species and sympatric evergreen conifers: a global comparison. *Oecologia* 114: 153-159.

Mader, D.L. and D.F. Owen. 1961. Relationships between soil properties and red pine growth in Massachusetts. *Proc. Soil Sci. Amer.* 25: 62 – 65.

Malagoli, M., A. Dal Canal, S. Quaggiotti, P. Pegoraro and A. Bottacin. 2000. Differences in nitrate and ammonium uptake between Scots pine and European larch. *Plant and Soil* 221: 1-3.

Marshall, J.D. and J. Zhang. 1994. Carbon isotope discrimination and water-use efficiency in native plants of the north-central Rockies. *Ecology* 75: 1887 – 1895.

McClave, J.T. and F.H. Dietrich, II. 1991. *Statistics*, 5th edition. Macmillan Publishing, San Francisco. 928 pp.

McComb A.L. 1955. The European larch: its race, site requirements and characteristics. *For. Sci.* 1: 298-318.

McMaster, G.S. and Wilhelm, W.W. 1997. Growing degree-days: one equation, two interpretations. *Agric. For. Meteor.* 87: 291-300.

Miller, A.J. 1990. *Subset Selection in Regression.* Chapman and Hall, London. 229 pp.

Miller, J.D., J.M. Cooper, and H.G. Miller. 1993. A comparison of above-ground component weights and element amounts in four forest species at Kirkton Glen. J. Hydrol. 145: 419 – 438.

Mulvaney, R.L. 1996. Nitrogen – Inorganic forms. *In* D.L. Sparks, A.L. Page, P.A. Helmke, R.H. Loeppert, P.N. Soltanpour, M.A. Tabatabai, C.T. Johnston, M.E. Sumner. (eds.) *Methods of Soil Analysis*, Part 3. Chemical Methods. SSSA Book Ser. 5. SSSA and ASA, Madison, WI.

Myre, R. and C. Camiré. 1996. The effect of crown position and date of sampling on biomass, nutrient concentrations, and contents of needles and shoots in European larch. *Trees* 10: 339-350.

Monserud, R.A. 1984a. Height growth and site index curves for inland Douglas-fir based on stem analysis data and forest habitat type. *For. Sci.* 30: 943 – 965.

Monserud, R.A. 1984b. Problems with site index: an opinionated review. *In* J.G. Bockheim (ed.) Symp. Proc. *Forest Land Classification: Experiences, Problems, Perspectives.* NCR-102 North Central For. Soils Com., Soc. Am. For., USDA For. Serv., and USDA Soil Cons. Serv.

Monserud, R.A., U. Moody, and D. W. Breuer. 1990. A soil-site study for inland Douglas-fir. *Can. J. For. Res.* 20: 686-695.

National Oceanic and Atmospheric Administration. 2000. Temperature and precipitation data. National Climatic Data Center. Asheville, North Carolina.

National Renewable Energy Laboratory. 2000. Solar radiation Normal Data (1961 – 1990). Golden, Colorado.

Newberry, J.D. 1991. A note on Carmean's estimate of height from stem analysis data. *For. Sci.* 37: 368-369.

Pastor, J., J.D. Aber, C.A. McClaugherty, and J.M. Melillo. 1984. Aboveground production and N and P cycling along a nitrogen mineralization gradient on Blackhawk Island, Wisconsin. *Ecology* 65: 256-268.

Payandeh, B. 1986. Predictability of site index from soil factors and lesser vegetation in northern Ontario forest types. Canadian For. Serv. Great Lakes For. Cent. Inf. Rep. O-X-373.

Perala, D.A. 1985. Predicting red pine shoot growth using growing degree days. *For. Sci.* 31: 913-925.

Perala, D.A. and D.H. Alban. 1994. Allometric biomass estimates for aspen-dominated ecosystems in the Upper Great Lakes. U.S. For. Serv. Res. Pap. NC-134.

Pritchett, W.L. and R.F. Fisher. 1987. *Properties and Management of Forest Soils*. John Wiley and Sons, New York.

Raison, R.J., M.J. Connell, and P.K. Khanna. 1987. Methodology for studying fluxes of soil mineral-N *in situ*. *Soil Biol. Biochem.* 19: 521 – 530.

Reich, P.B., D.F. Grigal, J.D. Aber, and S.T. Gower. 1997. Nitrogen mineralization and productivity in 50 hardwood and conifer stands on diverse soils. *Ecology* 78: 335-347.

Reich, P.B., D.S. Ellsworth, M.B. Walters, J.M. Vose, C. Gresham, J.C. Volin, and W.D. Bowman. 1999. Generality of leaf trait relationships: a test across six biomes. *Ecology* 80: 1955-1969.

Richards, F.J. 1959. A flexible growth function for empirical use. *J. Exp. Botany* 10: 290 - 300.

Robertson, G.P., P. Sollins, B.G. Ellis, K. Lajtha. 1999. Exchangeable Ions, pH, and Cation Exchange Capacity. *In* G.P. Robertson, D.C. Coleman, C.S. Bledsoe, and P. Sollins (eds.), *Standard soil methods for long-term ecological research*. Oxford University Press, New York. 462 pp.

Sartz, R.S. and D.N. Tolsted. 1976. Snowmelt runoff from planted conifers in southwestern Wisconsin. U.S. For. Serv. Res. Pap. NC-205.

SAS Institute, Inc. 2000. *JMP® Statistics Guide*, Version 4. SAS Institute, Inc., Cary, North Carolina.

Schlaegel, B.E. 1975. Yields of four 40-year-old conifers and aspen in adjacent stands. Can. J. For. Res. 5: 278- 280.

Schlesinger, W.H. 1997. *Biogeochemistry*, 2nd edition. Academic Press, San Diego. 588 pp.

Scott, N.A. and D. Binkley. 1997. Foliage litter quality and annual net N mineralization: comparison across North American forest sties. *Oecologia* 111: 151 – 159.

Soil Survey Staff. 1975. Soil taxonomy: a basic system of soil classification for making and interpreting soil surveys. USDA-SCS Agric. Handbook No. 436. U.S. Government Printing Office. Washington, D.C.

Sokal, R.R. and F.J. Rohlf. 1961. *Biometry; The Principles and Practice of Statistics in Biological Research*. W.H. Freeman and Company, San Francisco. 776 pp.

Sparks, J.P. and J.R. Ehleringer. 1997. Leaf carbon isotope discrimination and nitrgen content for riparian trees along elevational transects. *Oecologia* 109: 362 – 367.

Stephenson, N.L. 1990. Climatic control of vegetation distribution: the role of the water balance. *Am. Nat.* 135: 649-670.

Stoeckeler, J.H. 1948. The growth of quaking aspen as affected by soil properties and fire. *J. For.* 46: 727-737.

Stokes, M.S. and T.L. Smiley. 1996. *An Introduction to Tree-Ring Dating.* The University of Arizona Press. 73 pp.

Ter-Mikaelian, M.T. and M.D. Korzukhin. 1997. Biomass equations for sixty-five North American tree species. *For. Ecol. Manage.* 97: 1-24.

Thomas, G.W. 1996. Soil pH and soil acidity. *In* D.L. Sparks et al. (ed) *Methods of Soil Analysis*, Part 3. Chemical Methods. SSSA Book Ser. 5. SSSA and ASA, Madison, WI.

Truong, dinh Phu. 1975a. Nutrient requirements of planted European larch in Quebec. *Plant Soil* 42:109-117.

Truong, dinh Phu. 1975b. Potassium et magnésium: deux éléments limitant la croissance en hauteur du pin rouge au Québec. *Can. J. For. Res.* 5: 73 – 79.

Valade, J.L. 1998. The potential use of larch in the Canadian pulp and paper industry: A review. *Pulp Paper Can* 99: 156-158.

van Eck, W.A. and E.P. Whiteside. 1963. Site evaluation studies in red pine plantations in Micigan. *Proc. Soil Sci. Amer.* 27: 709 – 714.

Wang, G. 1995. White spruce site index in relation to soil, understory vegetation, and foliar nutrients. *Can. J. For. Res.* 25: 29-38.

Wilde, S.A., J.G. Iyer, C. Tanzer, W.L. Trautmann, and K.G. Watterston. 1965. Growth of Wisconsin coniferous plantations in relation to soils. Univ. Wis. Res. Bull. 262.

Yin, X. 1993. Variation in foliar nitrogen concentration by forest type and climatic gradients in North America. *Can. J. For. Res.* 23: 1587-1602.

Zak, D.R., G.E. Host, and K.S. Pregitzer. 1989. Regional variability in nitrogen mineralization, nitrification, and overstory biomass in northern Lower Michigan. *Can. J. For. Res.* 19: 1521-1526.

Zak, D.R., D. Tilman, R.R. Parmenter, C.W. Rice, F.M. Fisher, J. Vose, D. Milchunas, C.W. Martin. 1994. Plant production and soil microorganisms in late-successional ecosystems: a continental-scale study. *Ecology* 75: 2333

Zak, D.R., W.E. Holmes, N.W. MacDonald, and K.S. Pregitzer. 1999. Soil temperature, matric potential, and the kinetics of microbial respiration and nitrogen mineralization. *Soil Sci. Soc. Am. J.* 63: 575-584.

A comparison of site factors, productivity, species traits, and their interrelationships for European larch and red pine in the Great Lakes region

Abstract The objectives of this study were to 1) examine the interrelationships of soil site factors, leaf/canopy characteristics and measures of productivity (site index and overstory annual net primary production, $ANPP_o$) for European larch (*Larix decidua* Miller) and red pine (*Pinus resinosa* Ait.) over an array of stands that constitutes a broad landscape scale moisture/nutrient gradient, and 2) compare species productivity for species with different leaf life spans and associated traits to examine if a trade-off exists such that red pine (long leaf life span) has greater productivity than European larch (short leaf life span) on poor sites and vice versa. The relationships between soil, vegetation characteristics, and productivity were examined using least squares regression. Site index for European larch and red pine were strongly correlated with indices of moisture (available water holding capacity - AWC, $r = 0.502$ and 0.441, respectively) and nitrogen availability (nitrification, $r = 0.415$ and 0.372, respectively). Species traits correlated with site index productivity for European larch and red pine were foliar nitrogen (%N, $r = 0.598$ and 0.477, respectively) and specific leaf area of senesced foliage ($r = 0.400$ and 0.506, respectively). Because the study species affected chemical and organic soil characteristics, I compared species productivity and related traits over the physical soil resource availability gradient, AWC. Both species productivity increased with AWC and the rate of increase was weakly, and not significantly, greater for European larch than for red pine. Over the entire range of AWC, European larch maintained greater productivity, indicating that there no trade-offs in productivity due to differences in species traits, as was predicted.

INTRODUCTION

On well-drained sites in the Great Lakes region, tree productivity is limited by nutrient and water supply and by differences in species' abilities to utilize those resources. Differences in species' abilities to use resources may be due to species-specific variation in physiological and morphological traits. Among these traits are leaf life span and associated characteristics. In general, species with short leaf life span also have high light-saturated photosynthetic rates (A_{max}), leaf nitrogen (N_{leaf}), leaf area per unit mass (specific leaf area, SLA), and canopy nitrogen (N) loss rates, and low canopy mass and water use efficiency (WUE), whereas species with long leaf life span have low A_{max}, N_{leaf}, and canopy N loss rates and high canopy foliage mass and WUE (Reich et al. 1992, 1995, 1997a, 1999; Kloeppel et al. 2000). These collections of traits, and observed abundances of evergreen (long leaf life span) vs. deciduous (short leaf life span) species across landscape to global-scale fertility gradients suggest that evergreen species have relative productivity advantages over deciduous species on sites of low fertility/moisture status and vice versa; deciduous species have productivity advantages on high moisture/fertility sites. The goals of this study were to consider a species of short (European larch (*Larix decidua* Miller), ~6 months) and long (red pine (*Pinus resinosa* Ait.), ~40 months) leaf life span and address the following questions: (1) what are the importance of differences in leaf life span and associated traits (e.g. N_{leaf}; N turnover; leaf area index, LAI) to productivity for trees growing across fertility/moisture availabilities, and (2) do differences in these traits represent a trade-off such that evergreen trees have

greater productivity on poor sites and vice versa. If so, what is the specific nature of these trade-offs?

European larch and red pine have leaf life spans averaging 6 and 40 months, respectively. Gower and Richards (1990) speculate that deciduous larch spp. can have similar productivity in the marginally productive environments that favor the conservative characteristics of evergreen conifers due to a number of characteristics (e.g. the deciduous habit, architecture, relatively high rates of photosynthesis). While larch needles have higher A_{max}, they also have relatively high rates of leaf and N loss (Gower and Son 1992) and lower foliage mass compared with evergreen conifers (Gower et al. 1993). Conversely, red pine often has a denser canopy (higher LAI and canopy mass) and retains its needles longer, but has lower A_{max} (Reich et al. 1999).

Table 2.1. Comparison of characteristics for European larch and red pine on a moderately high fertility site in Wisconsin.[†]

	European larch	red pine
leaf life span (growing seasons)	--	3-4 times greater
leaf area index (leaf area/ground area)	--	1.2 times greater
Annual leaf loss (mass)	~ the same	
leaf N concentrations	2 times greater	--
annual N losses	1.8 times greater	--
maximum rates of photosynthesis ($A_{max \cdot mass}$)	2.5-4 times greater	--
specific leaf area (leaf area/leaf dry mass)	3.5 times greater	--
overstory biomass production ($ANPP_o$)	1.2 times greater	--

[†](Data from Gower et al. 1993 and Reich et al. 1999.)

Common garden studies have shown levels of productivity can be similar for species with different leaf habits on a given site (e.g. Matyssek 1986, Tyrrell and Boerner 1986, Gower et al. 1993). Matyssek (1986) found that despite larch spp. maintaining higher N_{leaf} and $A_{max \cdot (mass\ \&\ area)}$ and lower WUE than spruce, the two species attained similar stem increment. In another larch and spruce comparison, Tyrell and Boerner (1986)

reported that both species had similar relative growth rates and growth efficiency (wood produced per nutrient loss in litter) despite vastly different leaf life spans. Gower et al. (1993) also reported that productivity, measured as aboveground tree biomass, was not significantly different for larch, spruce, and pine species despite large species differences in SLA, leaf N, and LAI. These studies compared functionally different species on similar sites. However, it is unclear how these relationships may change across a broad range of site fertilities. Because of this limitation, Gower et al. (1993) could only suggest that differences in leaf traits may result in trade-offs in productivity across a soil moisture/fertility gradient.

Other studies have aimed to quantify how a single species acclimates to variation in resource availability by assessing species' attributes across a gradient of resources. Bockheim et al. (1989) measured changes in foliar nutrient concentrations and productivity of red pine across a precipitation-chemistry gradient in Wisconsin. While within-site variation was too large to be able to draw conclusions about differences in precipitation chemistry affects among-sites they did find that needle N was significantly and positively related to site index. Hebert and Jack (1998) quantified variation in LAI and site water balance in loblolly pine (*Pinus taeda* L.) plantations across a historically-based precipitation gradient in Texas. They reported that anomalous precipitation patterns just prior to study masked the gradient, but they did find a significant correlation between LAI and foliar N and P.

Past studies also have investigated multiple species over a range of sites. Pastor et al. (1984) reported increased productivity (ANPP) across an N mineralization gradient on a 70 ha island but the design did not allow a comparison of the six species along its

entirety. Kloeppel et al. (1998) compared physiological traits of *Larix* spp. (including European larch) and co-occurring evergreen conifers (not including red pine) at various locations in the northern hemisphere. They reported that, despite lower WUE, *Larix* spp. can have similar rates of productivity compared to those of evergreen conifers. Again, all species were not present at all locations. In another study, Kloeppel et al. (2000) compared leaf-level resource use for western larch (*Larix occidentalis* Nutt.), a deciduous conifer, and two sympatric evergreen conifers, Douglas fir (*Pseudotsuga menziessi*, Beissn., Franco) and lodgepole pine (*Pinus contorta* Engelm.) along a resource availability gradient in Montana. Contrary to Kloeppel et al. (1998), they found that both types of conifers were equally water limited as measured with carbon isotopes. Kloeppel et al. (2000) were able to show that the deciduous conifer had higher SLA, mass-based photosynthetic rates and foliar N but evergreen conifers exhibited higher N-use efficiency. Yin (1993) found that differences in foliar N concentrations were strongly correlated with climatic factors (e.g. mean July temperature, light availability). Neither Kloepplel et al. (2000) nor Yin (1993) measured productivity.

Studies have also assessed the relationships of regional variation in N mineralization (Reich et al. 1997b), LAI (Fassnacht and Gower 1997), potential net nitrification and mineralization (Zak et al. 1989), or soil microbial biomass (Zak et al. 1994) with stand productivity (measured as ANPP or $ANPP_o$) for multiple species. These studies reported significant and positive relationships between their respective predictor variables and stand productivity, yet the designs did not permit a separation of species from site.

The Extended COllaboration to Link Ecophysiology And forest Productivity (ECOLEAP) project is an effort initiated in 1996 to improve the understanding of site-

level controls on boreal and sub-boreal forest productivity as extracted by multispectral satellite data on a landscape scale in Canada (Bernier et al. 1999). While this study is directed towards estimating forest productivity, it is too coarse in focus to identify species' trade-offs.

In review, studies have provided fragments of information, but have lacked a design that quantitatively assesses interrelationships among soil moisture/fertility, leaf traits, and productivity for species with contrasting leaf traits. The goals of this study were to compare leaf and canopy traits of European larch and red pine and their relationship to productivity across a broad soil resource gradient in the Great Lakes region. In addition to furthering basic understanding of the interrelationships of species' traits, resource availability, and productivity, this information could be used as a silvicultural tool for improving productivity through better species selection in plantation establishment. Pinpointing the bottlenecks of productivity for a species also improves the possibility that genetically superior stock could be developed for enhanced production. Original predictions and general hypotheses are:

- European larch will be more productive than red pine on fertile sites. In addition, European larch will have higher N_{leaf} and A_{max} than red pine if moisture is not limiting (Gower et al. 1993). On less fertile sites, European larch will have much lower N_{leaf}, A_{max}, and LAI due to high N turnover (Gower et al. 1993). European larch will also be more sensitive to droughty sites with a less efficient use of water (Kloeppel et al. 1998).

- On less fertile sites, red pine productivity will be higher than European larch due to characteristics leading to greater nutrient conservation: longer leaf life span leading to greater foliage mass, LAI and WUE, and lower N turnover than European larch (Gower and Son 1992). Extended leaf life span for red pine will compensate for lower N uptake rates, thus maintaining productivity by maintaining relatively high $N_{leaf \cdot area}$, $A_{max \cdot area}$, LAI, and foliage mass. On high fertility sites, red pine will not have greater productivity than European larch due to inherent A_{max} limits. Overall, due to its plasticity in leaf life span, the productivity of red pine will be less sensitive to changes in fertility or moisture than European larch.
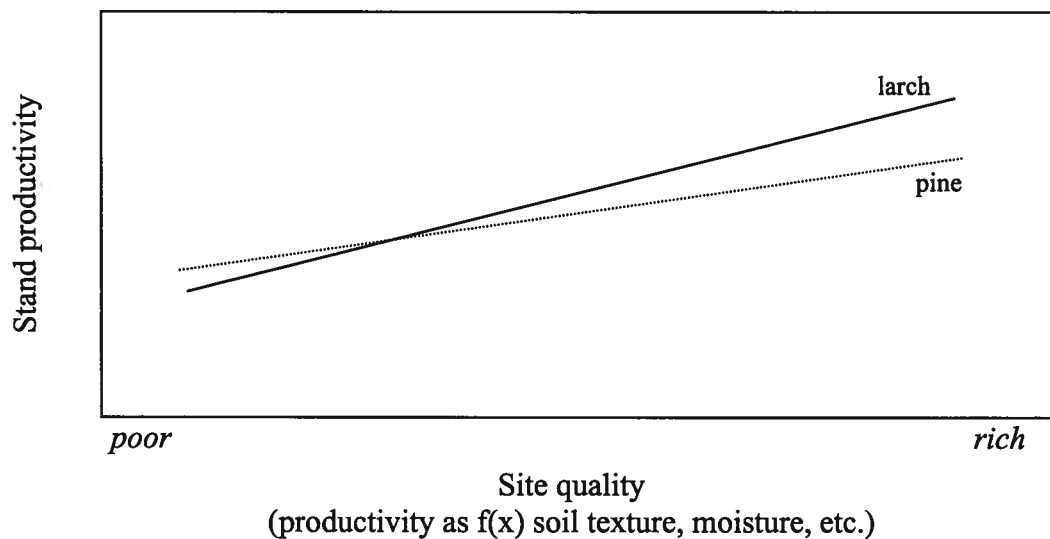

Figure 2.1. Hypothesized relationship between stand productivity and site quality (as defined by productivity being a function of site factors – e.g. soil texture, moisture, etc.)

Specific hypotheses that are tested include:

- Leaf N will scale closely with light-saturated photosynthesis (A_{max}.)

- European larch will have higher $ANPP_o$ than red pine on rich sites (see Fig. 2.1.) because of higher $N_{leaf \cdot mass}$ (Fig. 2.2.d) and $A_{max \cdot mass}$ (f), despite only slightly higher $A_{max \cdot area}$ (e) and LAI (h) and a lower foliage mass (g) than red pine.

- Red pine will be have higher $ANPP_o$ than European larch on poor sites (see Fig. 2.1.) due to much greater leaf life span (Fig. 2.2.a) and foliage mass (g), moderately higher LAI (h), $A_{max \cdot area}$ (e), and WUE (j), and lower annual N losses (i), despite much lower $N_{leaf \cdot mass}$ (d) and $A_{max \cdot mass}$ (f) than European larch.

- Compared to poor sites, European larch on rich sites will have similar leaf life span (Fig. 2.2.a), slightly lower SLA (b), lower WUE (j), and greater $N_{leaf \cdot (area \& mass)}$ (c & d), $A_{max \cdot (area \& mass)}$ (e & f), annual foliage turnover, N losses (i), and foliage mass (g) and area (LAI; h) per unit ground area.

- Compared to poor sites, red pine on rich sites will have shorter leaf life span (Fig. 2.2.a), slightly lower WUE (j), and higher SLA (b), $N_{leaf \cdot (area \& mass)}$ (c & d), $A_{max \cdot (area \& mass)}$ (e & f), foliage mass (g) and area (LAI; h) per unit ground area, annual foliage turnover, and N losses (i).

a)
leaf life span

pine

larch

b)
SLA

larch

pine

c)
$N_{leaf \cdot area}$

pine

larch

d)
$N_{leaf \cdot mass}$

larch

pine

e)
$A_{max \cdot area}$

larch

pine

f)
$A_{max \cdot mass}$

larch

pine

g)
foliage
mass/area

pine

larch

h)
LAI

pine

larch

i)
annual
N
losses

larch

pine

j)
WUE

pine

larch

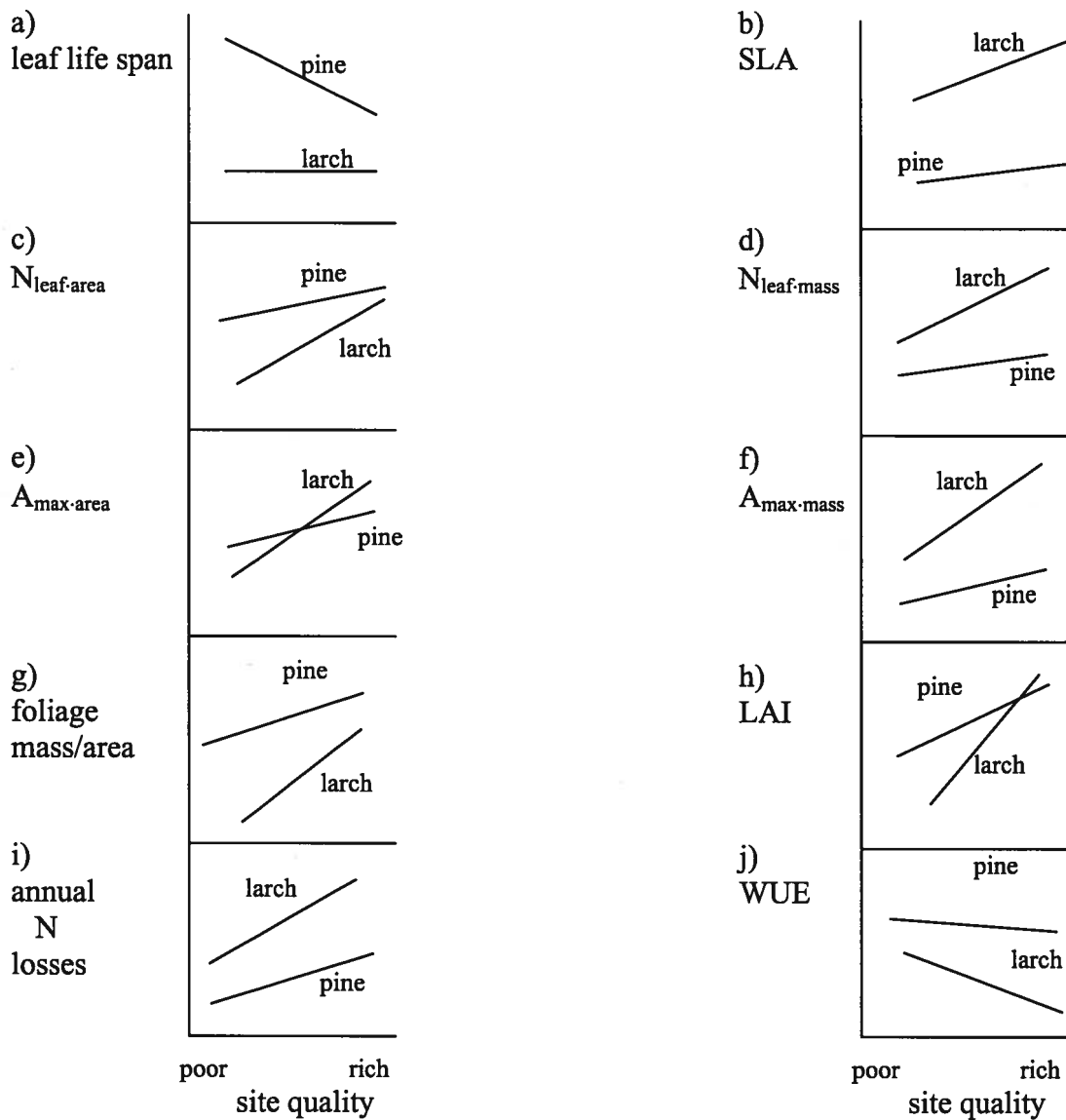poor   rich
site quality

poor   rich
site quality

Figure 2. 2. Hypothesized responses of foliar and canopy characteristics and productivity to site quality (~moisture/nutrient gradients) for European larch ("larch") and red pine ("pine").

- ANPP$_o$ is a function of the product of foliage (mass (Figure 2.3.a) or area (Figure 2.3.b)) times foliar N (mass or area) per unit ground area and these relationships will be similar for European larch and red pine.

a)
ANPP$_o$

foliage mass x N$_{leaf \cdot mass}$

b)
ANPP$_o$

LAI x N$_{leaf \cdot area}$

Figure 2. 3. Hypothesized relationship between productivity (ANPP$_o$) and foliage mass (either mass or area basis) and foliage N per unit ground area.

- The combination of (foliage mass x N$_{leaf \cdot mass}$) and $^{13}C/^{12}C$ ratio explains more variation in ANPP$_o$ than (foliage mass x N$_{leaf \cdot mass}$) alone (Figure 2.4.).

ANPP$_o$

(foliage mass x N$_{leaf \cdot mass}$)
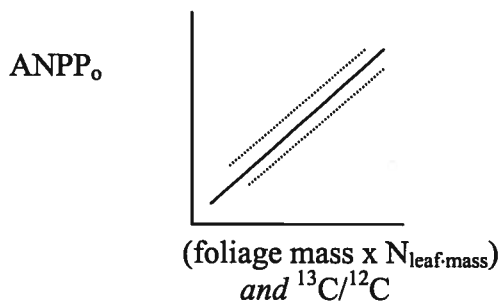*and* $^{13}C/^{12}C$

Figure 2.4. Hypothesized result of multiple regression ANPP$_o$ and [(foliage mass and foliage N per unit ground area)] and $^{13}C/^{12}C$].

- Species' productivity relative to one another will be greater for red pine than European larch on low fertility sites whereas productivity will be greater for European larch than red pine on high fertility sites (Figure 2.1)

METHODS

Measurements were made to determine physical soil characteristics, foliar/canopy traits, and productivity as described in Chapter 1. These data were used to test and model interrelationships as well as the success of foliar/canopy traits to predict productivity.

Statistical methods.

Pearson product-moment correlation analyses were performed to relate soil and vegetation characteristics to site index (base ages 15, 25, and 50) and annual biomass increment ($ANPP_{o\text{-}total}$). The Pearson product-moment correlation coefficient (r), a measure of the strength of the linear relationship between each pair of variables (Sokal and Rohlf 1969), between predictor variables also was examined for evidence of collinearity.

Two-factor models were used to test the effects of pairs of predictor variables and their interactions on productivity. If interactions had $P > 0.25$, the variances were pooled (Bancroft 1964). The coefficient of determination (R^2) adjusted for degrees of freedom, Mean Square, and model P value were reported.

Least squares regression models were used to exam the relationship of physical soil variables with productivity. Variables were chosen with their independence from species in mind (e.g. % sand instead of forest floor depth since the latter is influenced by species.) The variable with the largest average coefficient of determination with productivity among species was then substituted as a gradient across which changes in physiology/morphology for each species could be compared. This was done by

regressing leaf/canopy traits (e.g. carbon isotope discrimination, foliar nitrogen, canopy biomass) by the physical site factor to assess changes in species' attributes given a change in inherent site productivity.

RESULTS

Relations of soil variables with productivity

For both European larch and red pine, site index at base age 25 (SI_{25}) was positively

correlated with available water holding capacity (AWC) and the textural characteristics

that determine it (i.e. % sand , silt, and clay) (Table 2.2.; See Table 2.3. for definition of

terms). In addition, rates of nitrification (NIT) and total N mineralization (NMIN)

obtained from laboratory incubations were positively related to SI_{25} for red pine, whereas,

for European larch, only nitrification rates were positively associated with SI_{25}. No soil

variables were significantly correlated with red pine $ANPP_{o-total}$ and only NIT and FF_{depth}

were correlated with European larch $ANPP_{o-total}$.

Table 2.2. Pearson product-moment correlation coefficients for measures of physical soil attributes and productivity by species.

	European larch		red pine	
	$ANPP_{o-total}$ (Mg ha^{-1} 99^{-1})	SI_{25}	$ANPP_{o-total}$ (Mg ha^{-1} 99^{-1})	SI_{25}
% sand	-0.269	**-0.549**	0.18	**-0.384**
% silt	0.246	0.352	-0.229	0.316
% clay	0.207	**0.662**	-0.066	**0.402**
AWC	0.316	**0.502**	-0.141	**0.441**
D_b	0.244	0.061	0.115	0.06
FF_{depth}	**-0.442**	**-0.464**	-0.209	-0.105
% OM	0.248	0.319	-0.277	0.091
99 NMIN	0.041	0.154	-0.077	**0.442**
99 NIT	**0.543**	**0.415**	-0.164	**0.372**
pH	0.284	-0.285	-0.244	-0.038
WB	0.250	-0.005	0.079	0.307

Boldface indicates significant correlation ($\alpha = 0.10$).

To investigate if soil attributes in addition to AWC explain additional variance in productivity, single factors were combined in regressions with AWC to predict SI_{25}. AWC was chosen as the first variable in these regressions since it explained, on average

Table 2.3. Definition of terms and units.

Acronym	Parameter	Units
$SI_{15, 25, 50}$	site index (base ages 15, 25, or 50)	m
$ANPP_{o\text{-}total}$	total overstory annual net primary production	$Mg\ ha^{-1}\ 1999^{-1}$
$ANPP_{o\text{-}stem}$	stem component of $ANPP_{o\text{-}total}$	$Mg\ ha^{-1}\ 1999^{-1}$
% sand	sand fraction soil texture	%
% silt	silt fraction of soil texture	%
% clay	clay fraction of soil texture	%
AWC	available water holding capacity	$cm^3\ m^{-3}$
D_b	bulk density of soil	$g\ cm^{-3}$
pH	pH of soil	--
% CF	soil coarse fragments (> 4 mm)	%
A_{depth}	depth to A horizon	cm
C_{depth}	depth to C horizon	cm
FF_{depth}	depth of forest floor	cm
% OM	organic matter fraction of soil	%
NMIN	nitrogen mineralization	$mg\ kg^{-1}\ day^{-1}$
NIT	nitrification	$mg\ kg^{-1}\ day^{-1}$
Δ	foliar carbon isotope discrimination	‰
leaf %N	nitrogen fraction of leaf	%
$N_{leaf\text{-}mass}$	mass-based leaf nitrogen	$mg\ g^{-1}$
$N_{leaf\text{-}area}$	area-based leaf nitrogen	$mmol\ m^{-2}\ x\ 10^2$
annual N loss	annual nitrogen loss through litterfall	$kg\ ha^{-1}$
canopy biomass	mass of fresh canopy	$Mg\ ha^{-1}$
SLA_{canopy}	live canopy specific leaf area	$cm^2\ g^{-1}$
SLA_{litter}	senesced tissue specific leaf area	$cm^2\ g^{-1}$
LAI	leaf area index	$m^2\ m^{-2}$
JULY	average July temperature	°C
GDD	growing degree days	count (°C)
WB	site water balance	cm

across species, a high % of variation in SI_{25}, and because, compared to % clay and % sand (other strong predictors of SI_{25}), it was more normally distributed. For red pine, AWC, % OM, and their interactions explained more variation in SI_{25} than AWC alone ($R^2 = 0.16$) and all three terms were significant (P=0.01, 0.099, and 0.04 respectively). However, explained variance was relatively low for the combined model ($R^2 = 0.26$). No other variable in combination with AWC explained appreciably more variation in red pine SI_{25} than AWC alone. In contrast, for European larch, the combination of pH and AWC explained 49.4% of the variation in SI_{25} compared to 20% for AWC alone and both AWC (P=0.0012) and pH (P=0.006) were significant.

Although NMIN and NIT rates were important corollaries of SI_{25} for red pine, inclusion of NMIN or NIT did not markedly increase the amount of variation explained by AWC alone. This may be due to the generally strong collinearity of NMIN and NIT with AWC (data not shown).

Table 2.4. Analysis of variance for regressing SI_{25} by physical soil attributes, available soil water holding capacity (AWC), and their interactions. Mean Square, P value, and adjusted R^2 are reported.

		MS	(P>F)	R^2
	% organic matter	7.25	0.099	
red pine	AWC	19.59	0.010	0.264
	%OM*AWC	11.76	0.040	
European larch	pH	34.38	0.006	0.494
	AWC	53.795	(0.0012)	

NOTE: For interactions $P>0.25$ variances were pooled (Bancroft 1964). R^2 reported are adjusted for degrees of freedom (R_a^2).

Interrelations of soil physical and chemical variables

Nitrogen mineralization and AWC, the soil characteristics most strongly related to SI_{25} for both species, were themselves strongly positively related (Table 2.5.). This relationship was stronger for NIT than for total NMIN rates. Of all variables correlated with NMIN, % OM was the strongest. Percent OM is a characteristic related to both soil moisture holding capacity (but notably not incorporated into the AWC calculation) and to the supply of organic material for NMIN. Forest floor depth was negatively associated with all measures of nitrogen cycling, but was only significant with nitrification for red pine. In part the weak relations could be an artifact of the laboratory incubation technique since forest floor material was mostly screened and removed from the soils. In a mixed model of the effects of % OM, species and their interactions on N mineralization, species affected NMIN independent of % OM (both effects P < 0.001) but interactions were not significant (P>0.10). For any given % OM larch sites had higher NMIN rates, and NMIN increased with % OM for soils from both European larch stands and red pine stands in parallel. Similarly AWC and Species both affected NIT strongly (both effects P<0.001), and interactions were not significant (P>0.10). At any AWC, NIT was greater for soils from larch stands and NIT increased with AWC for soils from larch and red pine stands in parallel.

Table 2.5. Pearson product-moment correlation coefficients for measures of physical soil attributes and rates of soil nitrogen mineralization and nitrification.

	European larch		red pine	
	N mineralization (mg kg^{-1} day^{-1})	nitrification (mg kg^{-1} day^{-1})	N mineralization (mg kg^{-1} day^{-1})	nitrification (mg kg^{-1} day^{-1})
% sand	**-0.570**	**-0.519**	**-0.409**	**-0.676**
% silt	**0.617**	**0.422**	**0.411**	**0.635**
% clay	0.260	**0.493**	0.319	**0.596**
AWC (cm^3 m^{-3})	**0.495**	**0.583**	0.304[‡]	**0.639**
D_b	-0.109	0.029	**-0.358**	-0.263
pH	0.175	**0.499**	-0.283	0.318
% OM	**0.665**	**0.407**	**0.541**	0.271
WB 1999 (cm)	**0.383**	0.134	**0.411**	**0.421**
FF$_{depth}$ (cm)	-0.230	-0.319	-0.011	**-0.346**

[‡]Correlation significant (r = **0.393**) when one outlier removed. Note: Rates of mineralization ('N MIN') and nitrification ('NIT') are from laboratory incubations (1999). **Boldface** indicates significant correlation ($\alpha = 0.10$).

Relations of vegetation characteristics and productivity-Site index

Several leaf/canopy traits were strongly associated with SI$_{25}$ and ANPP$_{o-total}$ (Table 2.6.). Foliar N was more strongly correlated with SI$_{25}$ than any other variables. For red pine, the relationship of foliar N to SI$_{25}$ was strongest when N was expressed on a per unit leaf area basis (N$_{leaf·area}$) whereas, for European larch, foliar N expressed on a mass basis (N$_{leaf·mass}$) was most strongly related to SI$_{25}$. Carbon isotope discrimination (Δ) was negatively associated with SI$_{25}$ for European larch but was unrelated to SI$_{25}$ for red pine. Thus productive European larch stands tended to be more water use efficient in photosynthesis than less productive stands. In general, variation in leaf area per unit leaf mass (specific leaf area, SLA) was not as closely related to SI$_{25}$ as was variation in leaf N. However, SLA determined from needles senesced in autumn (SLA$_{litter}$) was strongly related to SI$_{25}$ for red pine. Furthermore, SLA$_{litter}$ was consistently more strongly related

to both SI_{25} and $ANPP_{o\text{-}total}$ than was SLA determined from foliage collected in mid-summer (SLA_{canopy}).

Out of the four foliar variables related to SI_{25} for red pine and/or European larch, only the effects of %N were independent of species (Table 2.7., Figs. 2.5., 2.6., 2.7. and 2.8.). For species pooled, % N mass explained 57% of the variation in SI_{25} (Fig. 2.6. and data not shown).

Table 2.6. Pearson product-moment correlation coefficients for leaf/canopy traits and measures of productivity (total increment 1999, $ANPP_{o\text{-}total}$; site index at 25 yrs., SI_{25}).

	European larch		red pine	
	$ANPP_{o\text{-}total}$ $(Mg\ ha^{-1}\ 1999^{-1})$	SI_{25}	$ANPP_{o\text{-}total}$ $(Mg\ ha^{-1}\ 1999^{-1})$	SI_{25}
Δ	0.224	**-0.590**	**0.345**	0.149
$N_{leaf\text{-}mass}$	0.284	**0.598**	-0.056	**0.477**
$N_{leaf\text{-}area}$	-0.005	**0.471**	-0.132	**0.553**
SLA_{canopy}	**0.440**	-0.018	0.174	-0.205
SLA_{litter}	**0.444**	0.400	**0.800**	**0.506**
LAI	**0.597**	-0.046	-0.318	0.155
canopy biomass	**0.431**	-0.027	**-0.364**	0.201
annual N loss	**0.339**	-0.016	**-0.371**	0.227

Boldface indicates significant correlation ($\alpha = 0.10$). See Table 2.3. for definition of terms.
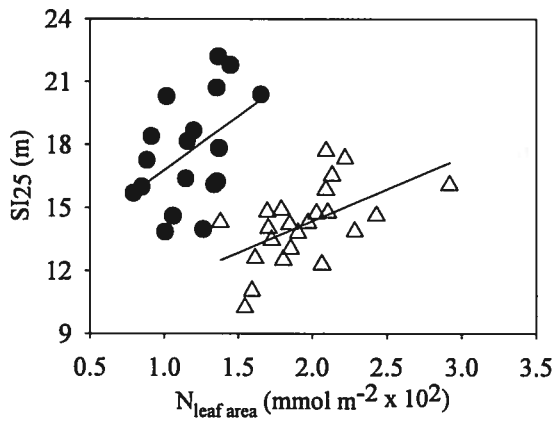
Figure 2.5. Area-based leaf nitrogen ($N_{leaf \cdot area}$) in relation to site index (SI_{25}) for European larch and red pine.
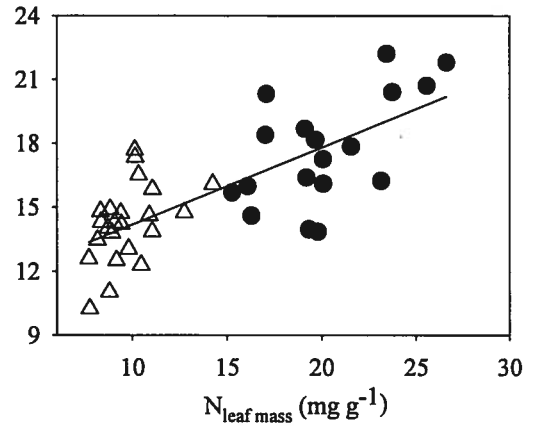
Figure 2.6. Mass-based leaf nitrogen ($N_{leaf \cdot mass}$) in relation to site index (SI_{25}) for European larch and red pine.
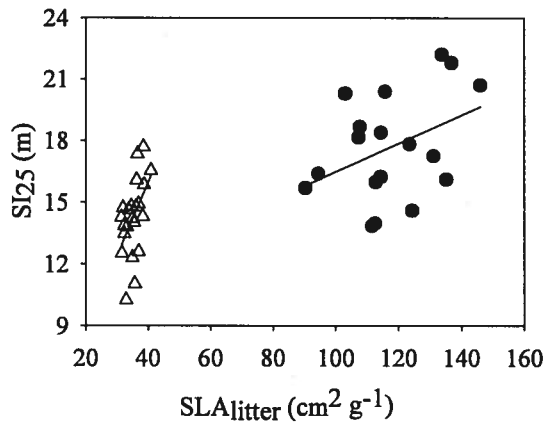
Figure 2.7. Senesced tissue specific leaf area (SLA_{litter}) in relation to site index (SI_{25}) for European larch and red pine.
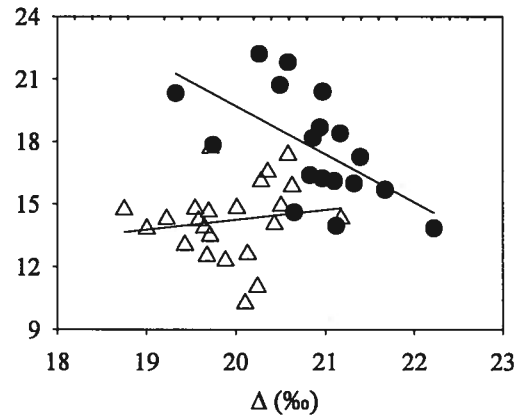
Figure 2.8. Foliar carbon isotope discrimination (Δ) in relation to site index (SI_{25}) for European larch and red pine.
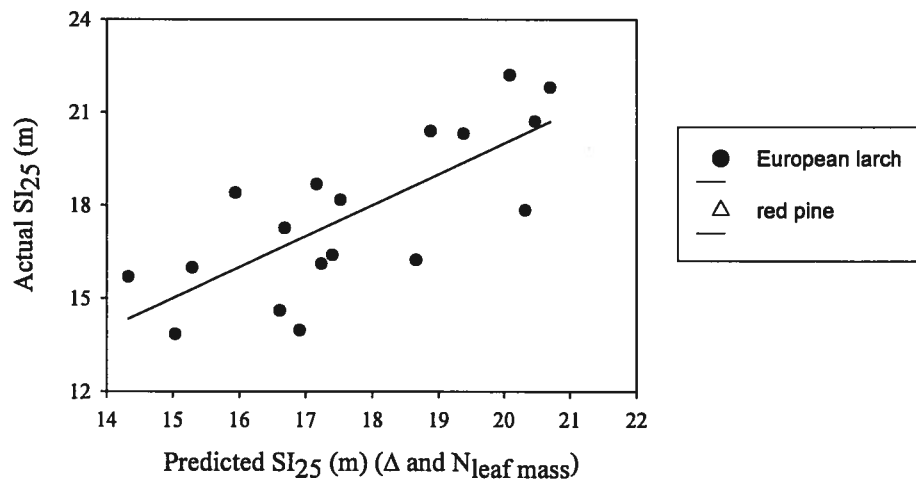
Figure 2.9. Actual SI_{25} in relation to Predicted SI_{25} for European larch. Predicted values from two factor regression of SI_{25} by carbon isotope discrimination (Δ) and mass-based leaf nitrogen ($N_{leaf \cdot mass}$).

Table 2.7. Least squares model for the effects of foliar attributes, species, and their interactions on site index at base age 25 (SI_{25}.) Mean Square, P value, and R^2 are reported.

	MS	(P>F)	R^2
$N_{leaf \cdot mass}$	43.775	(0.0011)	
spp.	4.824	(0.2472)	0.581
$N_{leaf \cdot mass}$*spp.	--	--	
$N_{leaf \cdot area}$	45.661	(0.0013)	
spp.	132.767	(<0.0001)	0.541
$N_{leaf \cdot area}$*spp.	--	--	
Δ	12.795	(0.0860)	
spp.	126.687	(<0.0001)	0.493
Δ*spp.	28.145	(0.0109)	
SLA_{litter}	24.901	0.0549	
spp.	16.47	0.0190	0.467
SLA_{litter}*spp.	11.422	0.1048	

NOTE: If significant interactions P>0.25 variances were pooled (Bancroft 1964). R^2 adjusted for degrees of freedom.

Although leaf $N_{leaf \cdot area}$ and $N_{leaf \cdot mass}$ were strong, consistent predictors of SI_{25} for both species they were also strongly collinear ($N_{leaf \cdot mass}$ versus $N_{leaf \cdot area}$ — European larch, r = 0.81 P = <0.0001; red pine, r = 0.89, P = <0.0001). These relations were much stronger than those between SLA and $N_{leaf \cdot area}$ or SLA and $N_{leaf \cdot mass}$ (P never > 0.03).

There was also a strong relationship between $N_{leaf \cdot area}$ and Δ. In a least squares model of the effects of species, $N_{leaf \cdot area}$, and their interactions on Δ, $N_{leaf \cdot area}$ was strongly related to Δ but species and interaction terms were insignificant (Table 2.8.). If one red pine outlier was removed, both species and the interactions were still not significant (P = 0.6115 and 0.5315, respectively) and the model explained over half of the variation in Δ (R^2 = 0.529). This suggests that $N_{leaf \cdot area}$ is the primary determinant of variation in Δ (Table 2.8.). Thus, there was a decrease in Δ with an increase in $N_{leaf \cdot area}$ independent of

species (Figure 2.10.). This can be interpreted as water use efficiency increasing with
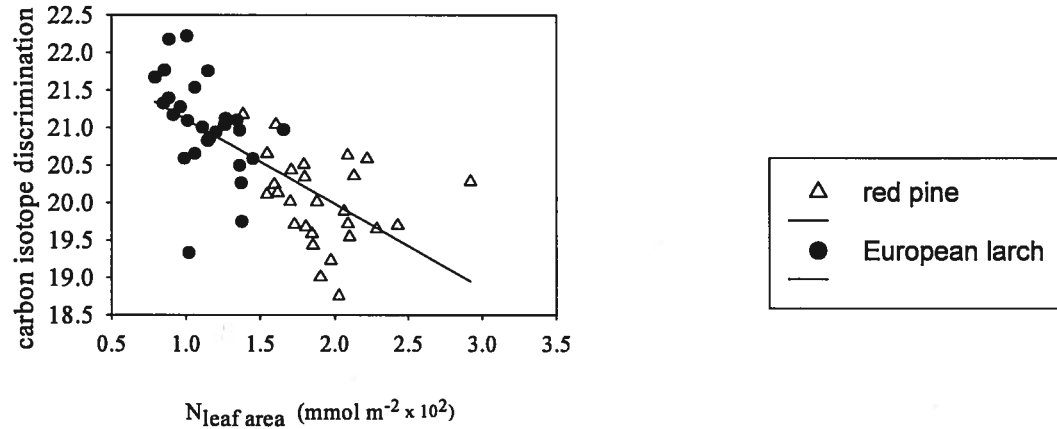
$N_{leaf \cdot area}$ independent of species.

Figure 2.10. Area-based leaf nitrogen ($N_{leaf \cdot area}$) in relation to foliar carbon isotope discrimination (Δ).

Table 2.8. Analysis of variance for testing species, leaf nitrogen ($N_{leaf \cdot area}$), and their interactions in predicting change in foliar carbon isotope discrimination (Δ). Mean Square, P value, and R^2 are reported.

	MS (P>F)	R_a^2
$N_{leaf \cdot area}$	2.82 (0.0055)	
spp.	0.3508 (0.3112)	0.500
spp. * $N_{leaf \cdot area}$	0.5839 (0.1929)	

NOTE: If significant interactions $P>0.25$ variances were pooled (Bancroft 1964). R^2 adjusted for degrees of freedom.

For both European larch and red pine, the combination of the two strongest vegetation corollaries of site index markedly increased the amount of variation explained in site index over the individual variables. For European larch, Δ and $N_{leaf \cdot mass}$ explained 51% of the variation in SI_{25} (Table 2.9. and Figure 2.9.) compared to 31% for Δ and 32%

for $N_{leaf \cdot mass}$ alone (data not shown). For red pine SLA_{litter} and $N_{leaf \cdot area}$ accounted for 46% of the variation in SI_{25} (Table 2.9.), compared to 21% for $N_{leaf\ area}$ and 20% for SLA_{litter} alone.

Table 2.9. Least squares models of site index at base age 25 (SI_{25}) as a function of carbon isotope discrimination (Δ), and leaf nitrogen ($N_{leaf \cdot mass}$) for European larch, and SLA_{litter}, and $N_{leaf\ mass}$ for red pine.

	European larch		
Predictor	MS	(P>F)	R^2
Δ	24.361	0.0153	
			0.510
$N_{leaf \cdot mass}$	25.413	0.0136	

	Red pine		
Predictor	MS	(P>F)	R^2
SLA_{litter}	14.21	0.0088	
			0.46
$N_{leaf \cdot area}$	16.10	0.0058	

Note: For both models interactions were pooled since P>0.25 (Bancroft 1964). Mean Square, *P* value, and R^2 are reported.

Relations of vegetation variables and productivity – $ANPP_{o\text{-}total}$.

For both species $ANPP_{o\text{-}total}$, was positively related to several characteristics measured on the same basis as $ANPP_{o\text{-}total}$, (i.e. per unit area of ground). These included leaf area index (LAI), canopy biomass, and annual N loss (% nitrogen in leaf litter x leaf litter mass per unit area). As expected, canopy biomass was positively associated with $ANPP_{o\text{-}total}$ for European larch, while, surprisingly, the opposite was true for red pine – increased canopy biomass was associated with decreased $ANPP_{o\text{-}total}$ (Figure 2.13).

SLA_{litter} was the single strongest predictor of $ANPP_{o-total}$ for red pine and was a significant, although weaker corollary of $ANPP_{o-total}$ for European larch.

Similar to the strong needle-level based vegetation corollaries of SI_{25} (i.e. $N_{leaf\cdot area}$, $N_{leaf\cdot mass}$, SLA_{litter}), some of the ground-area based vegetation corollaries of $ANPP_{o-total}$ were themselves correlated (e.g. annual N loss versus canopy biomass – European larch, $r = 0.36$ $P = 0.06$; red pine, $r = 0.75$ $P = < 0.0001$).

Although, within species, SLA_{canopy} is only relatively weakly correlated with $ANPP_{o-total}$, , across species it was a relatively strong predictor of $ANPP_{o-total}$ since high-SLA_{canopy} European larch has greater $ANPP_{o-total}$ than low-SLA_{canopy} red pine (Table 2.2., Figure 2.12.). For LAI, canopy biomass, and SLA_{litter}, there were both strong species effects and strong interactions with species in their relation to $ANPP_{o-total}$, indicating that these vegetation characteristics affected productivity differently for European larch and red pine (Table 2.2., Figures 2.11., 2.13., 2.14.).

Table 2.10. Analysis of covariance for foliar attributes, species, and their interactions in predicting $ANPP_{o-total}$. Mean Square, P value, and R^2 are reported.

	MS	(P>F)	R^2
Canopy biomass	27.979	(0.0392)	
spp.	94.831	(0.0003)	0.321
Can. biomass*spp.	60.136	(0.0031)	
Leaf area index	9.672	(0.1877)	
spp.	56.154	(0.0023)	0.409
LAI*spp.	71.950	(0.0006)	
SLA_{canopy}	52.382	(0.0054)	
spp.	20.657	(0.0741)	0.346
SLA_{canopy}*spp	--	--	
SLA_{litter}	100.223	(<0.0001)	
spp.	76.225	(0.0003)	0.455
SLA_{litter}*spp.	42.076	(0.0056)	

NOTE: If significant interactions $P>0.25$ variances were pooled (Bancroft 1964). R^2 adjusted for degrees of freedom.

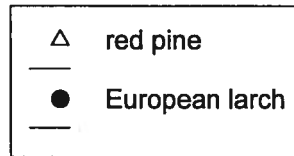(NOTE: The following figure legends are for Figures on next page.)

△   red pine

●   European larch

Figure 2.11. Leaf area index (LAI) in relation to 1999 total biomass increment ($ANPP_{o\text{-}total}$).

Figure 2.12. Canopy specific leaf area (SLA_{canopy}) in relation to 1999 total biomass increment ($ANPP_{o\text{-}total}$).

Figure 2.13. Canopy biomass in relation to 1999 total biomass increment ($ANPP_{o\text{-}total}$).

Figure 2.14. Litter specific leaf area (SLA_{litter}) in relation to 1999 total biomass increment ($ANPP_{o\text{-}total}$).

Figure 2.15. Mass-based leaf nitrogen ($N_{leaf\text{-}mass}$) in relation to 1999 total biomass increment ($ANPP_{o\text{-}total}$).

Figure 2.16. Carbon isotope discrimination (Δ) in relation to 1999 total biomass increment ($ANPP_{o\text{-}total}$).

Figure 2.17. Actual $ANPP_{o\text{-}total}$ in relation to predicted $ANPP_{o\text{-}total}$ values for European larch. Predicted values from two factor regression of $ANPP_{o\text{-}total}$ by canopy biomass and mass-based leaf nitrogen ($N_{leaf\text{-}mass}$).

Figure 2.18. Actual $ANPP_{o\text{-}total}$ in relation to predicted $ANPP_{o\text{-}total}$ values for red pine. Predicted values from two factor regression of $ANPP_{o\text{-}total}$ by carbon isotope discrimination (Δ) and litter specific leaf area (SLA_{litter}).

Fig. 2.11.

Fig. 2.12.

Fig. 2.13.

Fig. 2.14.

Fig. 2.15.

Fig. 2.16.

Fig. 2.17.

Fig. 2.18.
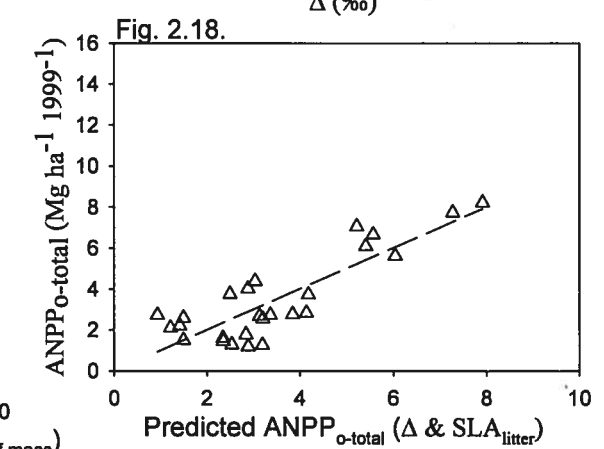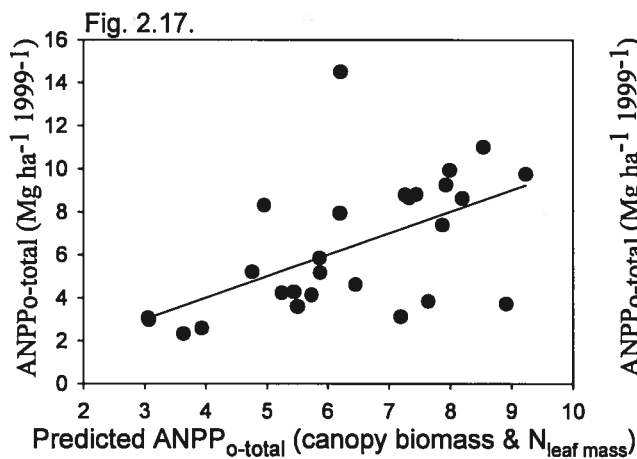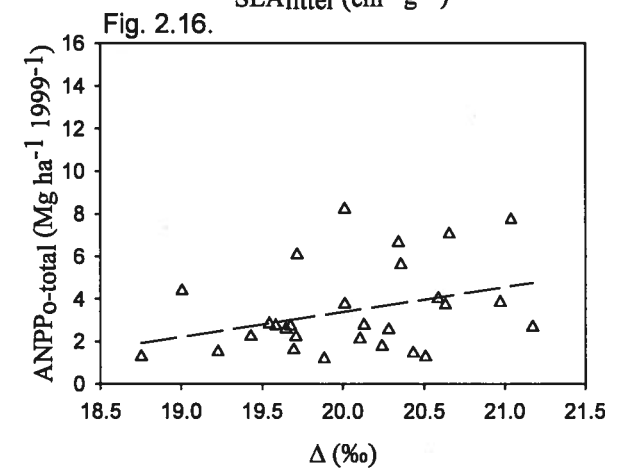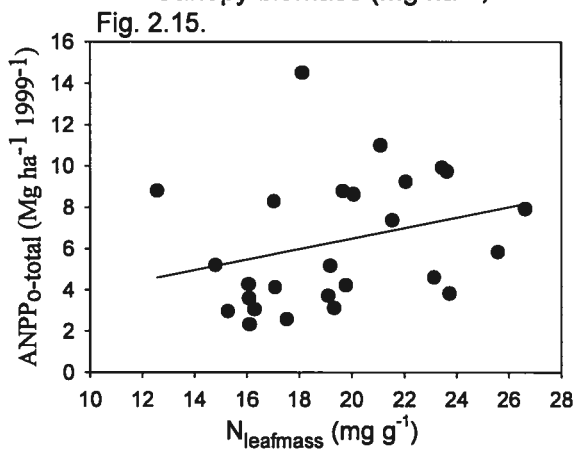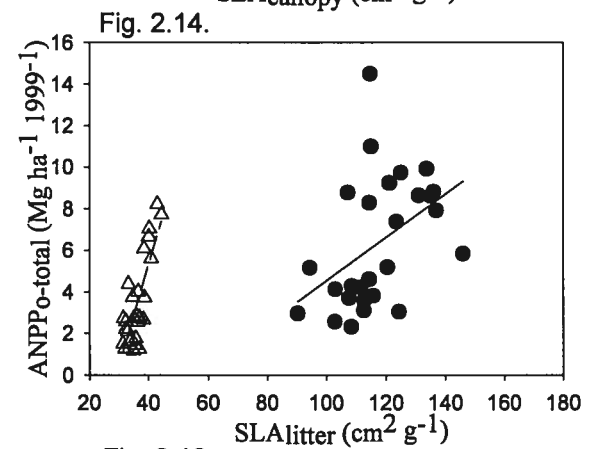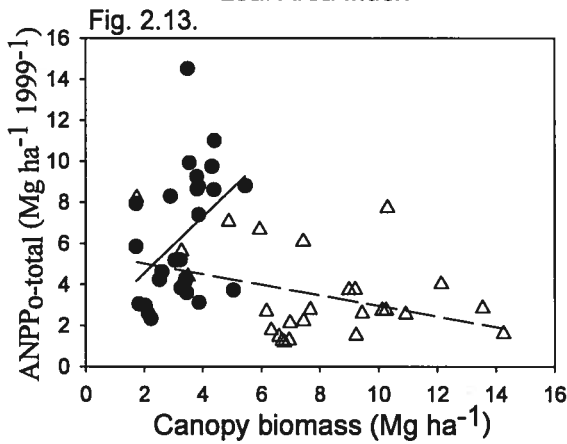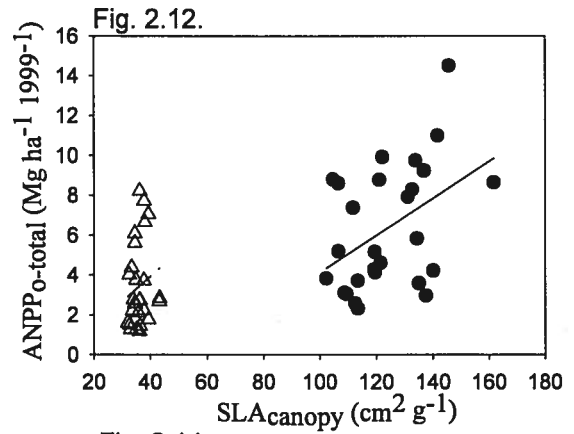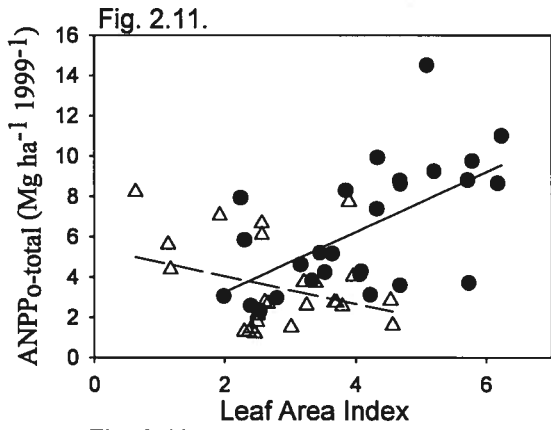
For red pine, an increase in $ANPP_{o\text{-}total}$ was associated with increases in Δ and SLA_{litter} (Figures 2.14. and 2.16., respectively). The amount of variation in $ANPP_{o\text{-}total}$ explained by the combination of Δ and SLA_{litter} (variance pooled) was greater than either variable alone (Table 2.11.), as evidenced by the close relationship between actual values of $ANPP_{o\text{-}total}$ and $ANPP_{o\text{-}total\ values}$ predicted by Δ and SLA_{litter} (Figure 2.18.). For European larch the combination of Δ and SLA_{litter} did not explain more variation in $ANPP_{o\text{-}total}$ than either variable alone (Table 2.11.). For European larch, the combination of canopy biomass and $N_{leaf\cdot mass}$ explained a greater amount of variation in $ANPP_{o\text{-}total}$. than did of canopy biomass or $N_{leaf\cdot mass}$ alone. This is illustrated by the tighter relationship of $ANPP_{o\text{-}total}$ with the $ANPP_{o\text{-}total}$ values predicted by canopy biomass and $N_{leaf\cdot mass}$ than with canopy biomass or $N_{leaf\cdot mass}$ (Figures 2.13., 2.15. and 2.17.). This relationship is not surprising since the product of canopy biomass and $N_{leaf\cdot mass}$ is the amount of foliar N per unit ground area, a characteristic which might be expected to scale with productivity. However, for red pine the combination of canopy biomass and $N_{leaf\cdot mass}$ failed to increase the amount of variation explained for $ANPP_{o\text{-}total}$ by canopy biomass or $N_{leaf\cdot mass}$ alone (Table 2.11.).

Table 2.11. Least squares models predicting total increment ($ANPP_{o\text{-}total}$) as a function of i) canopy mass and leaf nitrogen ($N_{leaf\cdot mass}$), and ii) carbon isotope discrimination (Δ) and specific leaf area of litter (SLA_{litter}) and their respective interactions. Mean Square, P value, and R^2 are reported.

	European larch		red pine	
	MS (P>F)	R^2	MS (P>F)	R^2
canopy mass	58.26 (0.0094)		16.259 (0.0613)	
$N_{leaf\cdot mass}$	31.49 (0.0489)	0.309	1.587 (0.5448)	0.146
can. mass* $N_{leaf\cdot mass}$	--		--	
Δ	19.79 (0.1217)		9.89 (0.0122)	
SLA_{litter}	57.102 (0.0118)	0.275	70.023 (< 0.0001)	0.728
$\Delta * SLA_{litter}$	--		--	

NOTE: If significant interactions $P>0.25$ variances were pooled (Bancroft 1964). R^2 adjusted for degrees of freedom.

Comparing species productivity and related traits over physical soil gradients

To compare changes in leaf and canopy traits between species and across soil resource gradients, a physical soil gradient was identified. Chemical soil variables including pH, NMIN, NIT, % organic matter and forest floor depth were not used, since these characteristics are influenced by species. AWC and % clay were, on average, the best physical soil predictors of SI_{25} (Table 2.2.). AWC was also the physical soil variable

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most closely associated with $ANPP_{o-total}$ for both species. However, it was not significant in both cases (data not shown), perhaps because the relation of site variables to ANPP is partially confounded by age (Chapter 1) and potential stand density effects (this Chapter) on $ANPP_{o-total}$.

Table 2.12. Model statistics for fitting productivity (site index at base age 25) by physical soil characteristics with least squares regression.

	European larch		red pine	
	R^2	P	R^2	P
%sand	0.302	0.018	0.147	0.070
%clay	0.439	0.002	0.162	0.057
bulk density	0.004	0.809	0.004	0.785
AWC	0.252	0.033	0.195	0.035

In addition, clay had a skewed distribution, which resulted in a few data points overly affecting regression results. For these reasons, AWC was selected as the best single measure of a physical soil productivity gradient over which both species could be compared (Figure 2.19.). In least squares models of the effects of Species, AWC and their interactions on leaf/canopy characteristics, Species effects were significant for all traits (Table 2.13.). AWC significantly affected $N_{leaf \cdot mass}$, $N_{leaf \cdot area}$ annual N loss, N-leaf mass, and SLA_{litter} independent of species. For SLA_{litter}, Species x AWC interactions were significant, indicating that for each species, SLA_{litter} responds differently to the AWC gradient.
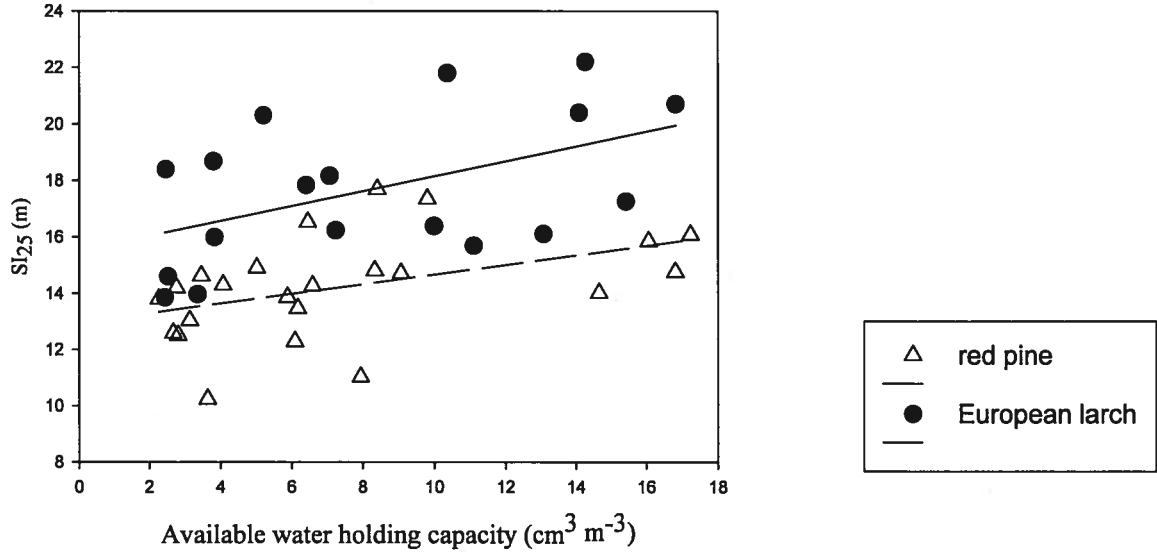
Figure 2.19. Available water holding capacity (AWC) in relation to site index (base age 25, SI_{25}).

For vegetation characteristics where AWC effects were significant at $P<0.2$, regression statistics further illustrate that as AWC increased, $N_{leaf \cdot mass}$ and $N_{leaf \cdot area}$ increased in parallel for both species with $N_{leaf \cdot mass}$ higher for European larch than red pine and vice versa with $N_{leaf \cdot area}$ for red pine (Figure 2.20. and 2.21.). For the two characteristics that showed significant AWC * species interactions, canopy biomass was greater for red pine than European larch at any AWC and it increased with AWC for red pine but was insensitive to AWC for European larch (Table 2.13., Figure 2.23.). For SLA_{litter}, European larch had higher values than red pine at any AWC and it increased with AWC for European larch but was insensitive to AWC for red pine (data not shown).

Table 2.13. Analysis of variance for leaf/canopy attributes as predicted by available water holding capacity (AWC), species (SPP), and their interactions. Mean Square, P value, and R^2 are reported.

	AWC	SPP	SPP x AWC	R^2
Δ (‰)	0.002 (0.9377)	14.093 (< 0.0001)	--	0.426
$N_{leaf \cdot mass}$ (mg g^{-1})	83.32 (0.0003)	1230.46 (< 0.0001)	8.712 (0.2193)	0.822
$N_{leaf \cdot area}$ (mmol m^{-2} x 10^2)	0.6304 (0.0028)	8.256 (< 0.0001)	--	0.727
annual N loss (kg ha^{-1})	128.62 (0.0035)	316.859 (< 0.0001)	--	0.420
litter N (%)	0.025 (0.2243)	0.543 (< 0.0001)	--	0.423
SLA_{canopy} (cm^2 g^{-1})	173.344 (0.2256)	99738.098 (< 0.0001)	--	0.945
SLA_{litter} (cm^2 g^{-1})	482.59 (0.0194)	85533.35 (< 0.0001)	446.39 (0.0243)	0.953
LAI	1.47 (0.2864)	21.10 (0.0002)	--	0.276
canopy biomass (Mg ha^{-1})	10.69 (0.1357)	292.31 (< 0.0001)	11.67 (0.1194)	0.550
leaf life span (# growing seasons)	0.0007 (0.9101)	58.58 (< 0.0001)	--	0.957

NOTE: If no significant interactions ($P>0.25$) variance pooled and R^2 reported. If otherwise, R^2 adjusted for degrees of freedom (R_a^2).

Table 2.14. Least squares regression results for vegetation characteristics versus AWC for each species. Model R^2, P value, and coefficients of slope (m) and intercept (b) are reported by species.

	spp.	R^2	P	m	b
$N_{leaf\cdot mass}$ (mg g^{-1})	larch	0.223	**0.013**	0.391	16.42
	pine	0.376	**0.000**	0.202	8.213
$N_{leaf\cdot area}$ (mmol m^{-2} x 10^2)	larch	0.122	**0.074**	0.018	0.991
	pine	0.215	**0.015**	0.033	1.681
canopy biomass (Mg ha^{-1})	larch	0.000	0.920	-0.004	3.35
	pine	0.104	0.109	0.215	6.43
SLA_{lit} (cm^2 g^{-1})	larch	0.192	**0.022**	1.385	106.57
	pine	0.001	0.866	0.027	36.06
annual N loss (kg ha^{-1})	larch	0.092	0.556	0.337	9.617
	pine	0.349	**0.002**	0.394	4.251

Note: **Boldface** indicate significance ($\alpha = 0.10$).

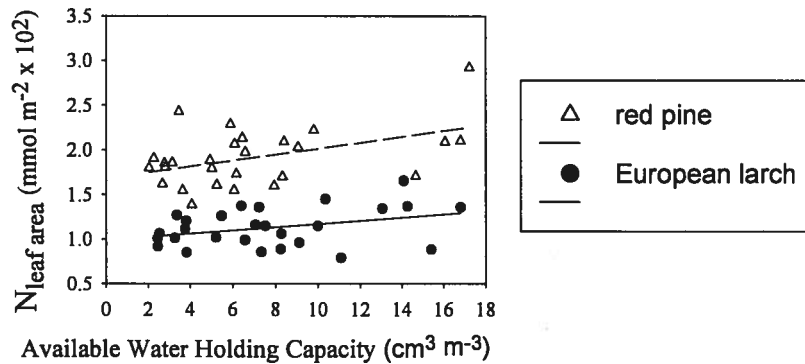

Figure 2.20. Productivity/site moisture (AWC) in relation to area-based leaf nitrogen ($N_{leaf\cdot area}$) for European larch and red pine.
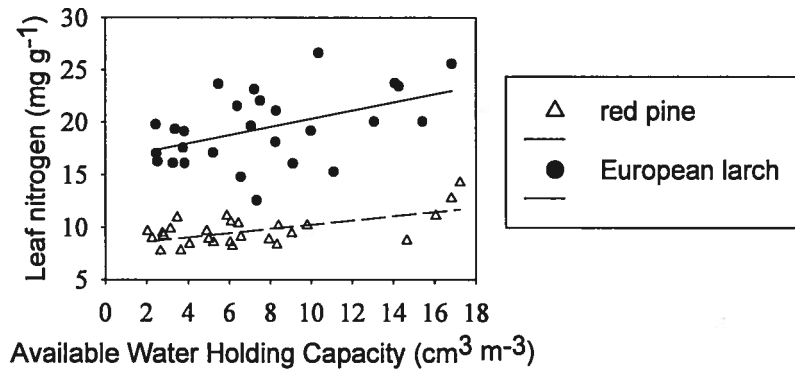
Figure 2.21. Productivity/site moisture (AWC) in relation to mass-based leaf nitrogen ($N_{leaf\cdot mass}$) for European larch and red pine.
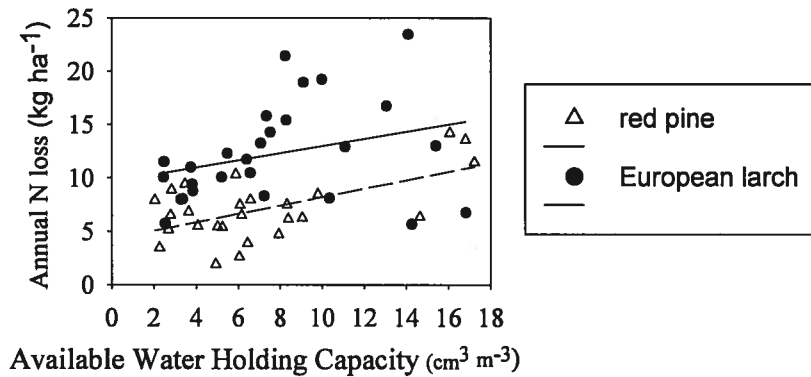

Figure 2.22. Productivity/site moisture (AWC) in relation to annual nitrogen loss for European larch and red pine.
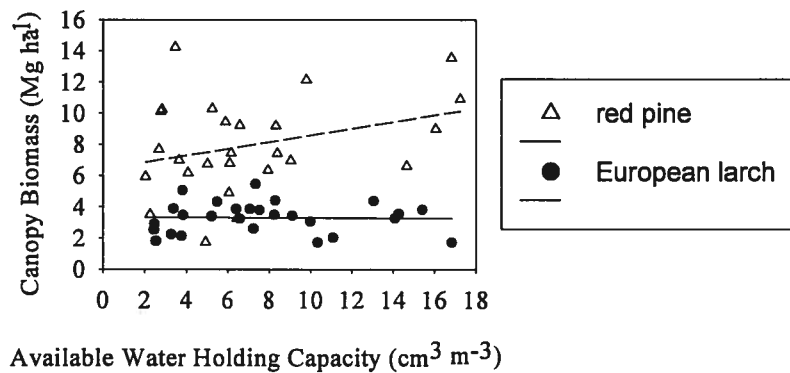

Figure 2.23. Productivity/site moisture (AWC) in relation to canopy biomass for European larch and red pine.

DISCUSSION

Relations of soil variables with productivity

Consistent with other studies in the Great Lakes region, productivity was positively correlated with soil water (e.g. Pastor et al. 1984, Fassnacht and Gower 1997) and nutrient supply (e.g. Fassnacht and Gower 1997, Reich et al. 1997b). Zak et al. (1989) showed that N supply was strongly related to productivity at low N supply, but at high N supply on morainal sites, productivity became insensitive to variation in N. Although there were strong correlations of both N cycling and soil water variables with productivity, N cycling and moisture variables were themselves highly correlated. Thus it is impossible to determine if productivity is more limited by water, nitrogen, or co-limited by both. The negative correlation between FF_{depth} and productivity ($ANPP_{o\text{-}total}$) for European larch suggests that moisture and nitrogen limitation are inextricably linked since microbial activity, which is responsible for litter decomposition, is moisture dependent (Linn and Doran 1984, Barnes et al. 1998, Zak et al. 1999).

As Sartz and Tolsted (1976) showed, spring infiltration rates of water in European larch stands can be substantially higher than in evergreen conifer stands. Field data from (Chapter 1) also show soil temperature to be warmer in critical spring periods where microbial activity could persist earlier in the season as compared with neighboring conifer stands.

Interrelations of physical and chemical soil characteristics

The interrelations of physical and chemical soil characteristics provided further evidence of a relationship between soil moisture and both productivity and N cycling. Measures of potential moisture (e.g. AWC, WB) as well as %OM, which both increases water holding capacity markedly (Brady and Weil 1996) and provides the short term source for mineralizable N, were positively associated with nitrogen cycling rates. The positive correlation between %OM and NMIN also suggests that microbial populations in these stands are carbon limited (sensu Zak et al. (1994). Similarly, NIT increased with AWC for both species – also suggesting that moisture was an important determinant of microbial nitrification. In both cases, NMIN and NIT were greater for European larch than red pine. Consistently higher NMIN and NIT rates at any given level of AWC or OM, even in potential laboratory incubations, suggest that soils supporting European larch stands have greater nitrogen supply capabilities, perhaps due to high quality % OM, higher leaf litter N, warmer soil temperature, higher spring infiltration, and less lignified, higher N litter (Chapter 1, Sartz and Tolsted 1976, Scott and Binkley 1997). Fassnacht and Gower (1999) observed that species on richer sites in northern Wisconsin tended to have higher N turnover but also higher litter quality (lower C:N), and lower nutrient and organic matter residence time. In this study, European larch supplied, on average, ~twice as much N annually than red pine but also had higher decomposition (i.e. less forest floor) and higher rates of nitrogen mineralization.

While European larch stands do have a number of characteristics that could lead to higher potential NMIN and NIT, the microbial processes ultimately responsible for mineral transformation could be pH dependent (e.g. activity of bacteria and

actinomycetes). There were positive, although weak relationships between pH and NMIN and NIT for European larch (1999: $R^2 = 0.03$ $P = 0.382$, $R^2 = 0.249$ $P = 0.008$; 2000: $R^2 = 0.217$ $P = 0.079$, $R^2 = 0.307$ $P = 0.032$). Furthermore, the combination of pH and AWC explained nearly 50% of the variation in SI_{25} for European larch.

Relations of vegetation characteristics and productivity

The vegetation characteristics that best predicted productivity for either species were measures of foliar N. The increase in productivity from increased foliar N could be parallel with the increases in productivity correlated with moisture and nitrogen supply via nitrogen mineralization. Increase N supply, N uptake, and foliar N should then scale with increased canopy photosynthesis and productivity (Matyssek 1986, Reich et al. 1995; but see Kloeppel et al. 2000). The combination of canopy biomass and N for European larch explained more variation in productivity than either component alone. This argues that greater N in a larger light-capturing, photosynthesizing canopy is positively correlated with productivity. SLA_{canopy} and SLA_{litter} were strongly related to productivity across species. This is not surprising since high SLA leaves tend to have high $N_{leaf \cdot mass}$ (at least across species) and $N_{leaf \cdot mass}$ was a strong determinant of productivity. More surprising was the fact that SLA_{litter} was more strongly related to productivity than SLA_{canopy} both within and across species. This could reflect SLA_{canopy} being more variable due to carbohydrates or non-structural material that change in amount daily or through the season and bear no direct relation to productivity. Senesced tissue, on the other hand, contains only basic structural components and may be a better quantitative measure of productivity as predicted by leaf structure. Fassnacht and Gower

(1997) also found that SLA_{litter} explained a surprisingly high proportion (76%) of variation in productivity among conifer, mixed conifer-hardwood, and hardwood stands.

For European larch, a decrease in Δ also was associated with an increase in productivity – a result opposite of that hypothesized. The decrease in discrimination against the heavier ^{13}C (lower Δ) indicates that intercellular CO_2 is lower, thus high productivity trees are more efficient in their use of water but less efficient in their use of N. The fact that $N_{leaf\cdot mass}$ not only increased independent of Δ, but contributed to explaining over 50% of variation in SI_{25} productivity also suggests that increased photosynthetic capacity was related to both increased productivity and increased water use efficiency.

However, it should be noted that, if water were never limiting, a lower intercellular CO_2 would result in lower photosynthesis per unit leaf N, and thus lower photosynthetic nitrogen use efficiency. In contrast to European larch, Δ for red pine increased with productivity. It is possible that, for red pine, low water constrained productivity on some sites as reflected by lower Δ (i.e. more closed stomata) for low productivity red pine stands. An increase in productivity for red pine was associated with other unexpected results: both a smaller canopy and lower LAI. Given the increase in Δ, this may suggest that the reduced amount of canopy improved water availability, thus opening stomata wider and discriminating more against the heavier ^{13}C. Lower LAI with increased productivity equates to a higher photosynthetic efficiency per unit needle. However, nitrogen also increased for red pine with increases in productivity. It is possible that higher N in less (lower canopy biomass) but more exposed (higher SLA) foliage resulted in higher rates of productivity.

Other limitations of the data may give a partial explanation for inconsistencies in relationships (e.g. canopy biomass for red pine decreased with higher productivity). $ANPP_o$ productivity was estimated with only three trees per stand. While the stands were even-aged, monoculture plantations, a sample size of three trees may be too small to represent the entire stand. Also, area-based measures (e.g. canopy biomass, LAI) were calculated from litter caught from August to late November. There is a chance some litter was not captured and all measurements dependent upon litterfall are underestimated.

Furthermore, another caveat for interpretation of relations of area based productivity ($ANPP_o$) with its determinants is that several of the study stands were thinned in the past. Although closed canopy conditions were a stand selection criterion, it is possible that interrelations between $ANPP_o$ and vegetation characteristics were affected by density and past thinning regimes.

Species comparison across a productivity gradient

It was hypothesized that differences in leaf life span and associated traits for two species would confer an advantage in productivity for each species at different positions along a soil resource gradient; i.e. difference in species traits would be productivity trade-offs over a resource gradient. As hypothesized, short leaf life-span species European larch, had higher $N_{leaf\cdot mass}$, SLA, and annual N losses but lower water use efficiency, $N_{leaf\cdot area}$ and canopy biomass than long leaf life-span species red pine. Leaf life span for red pine was less plastic than expected; 24 of the 27 stands carried three cohorts and only three carried four cohorts. Also, it was not hypothesized that LAI would be higher for European larch on more productive sites.

While species productivities and foliar and canopy traits were affected by resource availability (i.e. the AWC gradient) these responses were generally parallel for the species and only weak interactions were observed. Thus there was no support for the hypothesis for species productivity trade-offs based on differences in leaf traits; European larch was always more productive than red pine. Even on poor sites, European larch had higher $N_{leaf \cdot mass}$, LAI, and NMIN compared to red pine. As productivity of European larch productivity increased, not only did $N_{leaf \cdot mass}$ increase, but so did water use efficiency. Given that nitrogen and soil moisture were the strongest corollaries with productivity, the leaf/canopy traits of European larch thus were able to promote productivity across the entire site quality gradient of the study.

Conclusion

The strongest corollaries of growth for both species were foliar N, SLA_{litter}, and soil moisture. Simultaneously considering physical and chemical soil properties, the supply of moisture is undoubtedly influential in the rate of productivity for both species. Given the species effects on litter quality, and perhaps on microbial physical environments, European larch promotes higher nitrogen cycling rates than red pine. This may be part of the reason that European larch out produced red pine across the entire site quality gradient. Short leaf life span European larch was associated with high $N_{leaf \cdot mass}$, annual N turnover, and SLA. The long leaf life span of red pine may be more advantageous for productivity as stands mature (Reich 1998), but for the relatively young stands compared, productivity was lower for red pine across a broad site quality gradient despite it having higher $N_{leaf \cdot area}$, canopy biomass, and water use efficiency.

Larch had higher productivity than red pine over the entire site quality gradient. Thus there were no productivity trade-offs as was hypothesized based on species differences in leaf and canopy traits.

REFERENCES

Bancroft, T.A. 1964. Analyses and inferences for incompletely specified models involving the use of preliminary tests of significance. Biometrics 20: 427 – 442.

Barnes, B.V., D.R. Zak, S.R. Denton, and S.H. Spurr. 1998. *Forest Ecology*, 4th ed. John Wiley & Sons, Inc., New York. 774 pp.

Bernier, P.Y., R.A. Fournier, C.H. Ung, G. Robitaille, G.R. Laroque, M.B. Lavigne, R. Boutin, F. Raulier, D. Paré, J. Beaubien, and C. Delisle. 1999. Linking ecophysiology and forest productivity: An overview of the ECOLEAP project. *For. Chron.* 75: 417 – 421.

Bockheim, J.G., J.E. Leide, and L.E. Frelich. 1989. Red pine growth and chemical composition of foliage and forest floors across a precipitation-chemistry gradient in Wisconsin. *Can. J. For. Res.* 19: 1543 – 1549.

Brady, N.C. and R.R. Weil. 1996. *The Nature and Properties of Soils.* 11th ed. Prentice Hall, Upper Saddle River, NJ. 740 pp.

Fassnacht, K.S. and S.T. Gower. 1997. Interrelationships among the edaphic and stand characteristics, leaf area index, and aboveground net primary production of upland forest ecosystems in north central Wisconsin. *Can. J. For. Res.* 27: 1058-1067.

Fasshacht, K.S. and S.T. Gower. 1999. Comparison of the litterfall and forest floor organic matter and nitrogen dynamics of upland forest ecosystems in north central Wisconsin. *Biogeochemistry* 45: 265 – 284.

Gower, S.T. and J.H. Richards. 1990. Larches: deciduous conifers in an evergreen world. *Bioscience* 40: 818-826.

Gower, S.T. and Y. Son. 1992. Differences in soil and leaf litterfall nitrogen dynamics for five forest plantations. *Soil Sci. Soc. Amer. J.* 56: 1959-1966.

Gower, S.T., P. B. Reich, Y. Son. 1993. Canopy dynamics and aboveground production of five tree species with different leaf longevities. *Tree Physiol.* (12): 327-345.

Hebert, M.T. and S.B. Jack. 1998. Leaf area index and site water balance of loblolly pine (Pinus taeda L.) across a precipitation gradient in East Texas. *For Ecol. Manage.* 105: 273-282.

Kloeppel, B.D., S.T. Gower, J.G. Vogel, and P.B. Reich. 2000. Leaf-level resource use for evergreen and deciduous conifers along a resource availability gradient. *Func. Ecol.* 14: 281 – 292.

Kloeppel, B.D., S.T. Gower, I.W. Treichel, and S. Kharuk. 1998. Foliar carbon isotope discrimination in *Larix* species and sympatric evergreen conifers: a global comparison. *Oecologia* 114: 153-159.

Linn, D.M., and J.W. Doran. 1984. Effect of water-filled pore space on carbon dioxide and nitrous oxide production in tilled and non-tilled soils. *Soil Sci. Soc. Am. J.* 48: 1267-1272.

Matyssek, R. 1986. Carbon, water and nitrogen relations in evergreen and deciduous conifers. *Tree Physiol.* 2: 177-187.

Pastor, J., J.D. Aber, C.A. McClaugherty, and J.M. Melillo. 1984. Aboveground production and N and P cycling along a nitrogen mineralization gradient on Blackhawk Island, Wisconsin. *Ecology* 65: 256-268.

Reich, P.B., M.B. Walters, D. S. Ellsworth. 1992. Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. *Ecol. Monogr.* 62: 365-392.

Reich, P.B., B.D. Kloeppel, D.S. Ellsworth, and M.B. Walters. 1995. Different photosynthesis-nitrogen relations in deciduous hardwood and evergreen coniferous tree species. *Oecologia* 104: 24-30.

Reich, P.B., M.B. Walters, and D.S. Ellsworth. 1997a. From tropics to tundra: global convergence in plant functioning. Proceedings of the National Academy of Sciences USA 94: 13730-13734.

Reich, P.B., D.F. Grigal, J.D. Aber, and S.T. Gower. 1997b. Nitrogen mineralization and productivity in 50 hardwood and conifer stands on diverse soils. *Ecology* 78: 335-347.

Reich, P.B. 1998. Variation among plant species in leaf turnover rates an associated traits: implications for growth at all life stages. *In*: H. Lambers, H. Poorter, and M.M.I. Van Vuuren (eds.), *Inherent variation in plant growth.* Physiological mechanisms and ecological consequences. Backhuys Publishers, Leiden.

Reich, P.B., D.S. Ellsworth, M.B. Walters, J.M. Vose, C. Gresham, J.C. Volin, and W.D. Bowman. 1999. Generality of leaf trait relationships: a test across six biomes. *Ecology* 80: 1955-1969.

Sartz, R.S. and D.N. Tolsted. 1976. Snowmelt runoff from planted conifers in southwestern Wisconsin. U.S. For. Serv. Res. Pap. NC-205.

Scott, N.A. and D. Binkley. 1997. Foliage litter quality and annual net N mineralization: comparison across North American forest sties. *Oecologia* 111: 151 – 159.

Sokal, R.R. and F.J. Rohlf. 1961. *Biometry; The Principles and Practice of Statistics in Biological Research.* W.H. Freeman and Company, San Francisco. 776 pp.

Tyrrell, L.E. and R.E.J. Boerner. 1986. *Larix laricina* and *Picea mariana*: relationships among leaf life-span, foliar nutrient patterns, nutrient conservation, and growth efficiency. *Can. J. Bot.* 65: 1570-1577.

Yin, X. 1993. Variation in foliar nitrogen concentration by forest type and climatic gradients in North America. *Can. J. For. Res.* 23: 1587-1602.

Zak, D.R., G.E. Host, and K.S. Pregitzer. 1989. Regional variability in nitrogen mineralization, nitrification, and overstory biomass in northern Lower Michigan. *Can. J. For. Res.* 19: 1521-1526.

Zak, D.R., D. Tilman, R.R. Parmenter, C.W. Rice, F.M. Fisher, J. Vose, D. Milchunas, C.W. Martin. 1994. Plant production and soil microorganisms in late-successional ecosystems: a continental-scale study. *Ecology* 75: 2333-2347.

Zak, D.R., W.E. Holmes, N.W. MacDonald, and K.S. Pregitzer. 1999. Soil temperature, matric potential, and the kinetics of microbial respiration and nitrogen mineralization. *Soil Sci. Soc. Am. J.* 63: 575-584.