UNIVERSITY OF ALBERTA

THE RELATIONSHIPS BETWEEN MICROHABITAT VARIATION AND THE PERFORMANCE OF *PICEA MARIANA* AND *LARIX LARICINA* SEEDLINGS IN A RICH FEN.

BY

KEVIN ASTRIDGE ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of **MASTER OF SCIENCE.**

DEPARTMENT OF RENEWABLE RESOURCES

Edmonton, Alberta
FALL 1996

ISBN 0-612-18230-4

Canada

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Name of Author: Kevin Astridge

Title of Thesis: The relationships between microhabitat variation and performance of *Picea mariana* and *Larix laricina* seedlings in a rich fen.

Degree: Master of Science

Year this Degree Granted: 1996

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled **The relationships between microhabitat variation and performance of *Picea mariana* and *Larix laricina* seedlings in a rich fen**, submitted by Kevin Astridge in partial fulfillment of the requirements for the degree of Master of Science.

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For My Parents and Family

ABSTRACT

The microhabitats of individual black spruce (*Picea mariana*), and tamarack (*Larix laricina*) seedlings, growing in a moderately rich fen in central Alberta, were characterized on the basis of microtopography, depth to water table, nutrient availability, soil temperature, aeration depth, and pH. The seedlings did not occur on distinct microhabitats, but rather across a range of continuous, interconnected microhabitat gradients. Both species grow on the same range of microhabitats and did not show niche separation among the factors measured. Measurements of gas exchange, foliar nutrient concentration, and growth rate were correlated with the microhabitat characteristics for each species. Strong relationships between foliar nutrients and gas exchange suggest non-stomatal factors were limiting photosynthesis. Foliar nitrogen concentration in black spruce was more influenced by nitrate availability, while tamarack was more influenced by ammonium, and this influence was also reflected in gas exchange for both species.

ACKNOWLEDGEMENTS

I would like to thank the following people:

Lee Martens (the Martenizer) for slogging around in the peatland with me.

Ellen Macdonald, my supervisor, for her support in all facets of this study.

Simon Landhäusser, Ken Greenway, Michael Hunt-Jones, Uldis Silins, Pete Tollestrup, Barb Thomas, and Ken Stadt for making it all the more enjoyable.

Annette Constabel for her help in the field, and for persuading me to finally get this finished!

Funding was provided by:

Dept. of Forest Science, U of A.
NSERC (Ellen Macdonald)
Canadian Circumpolar Institute

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CHAPTER I

INTRODUCTION

Plants are dependent on the physical and chemical environment in which they establish for the resources they require for survival, growth and development. Environmental heterogeneity, both small and large scale, can affect the structure and function of plant communities. Differences in the way species interact with their environment at different life stages can lead to spatial separation of species and of communities. Examining such niche separation can provide insight into adaptation of individual species.

Delcourt *et al.* (1983) suggest three different space-time domains in which environmental factors can be perceived to influence vegetational processes: mega-scale, macroscale; and microscale. The mega-scale domain encompasses continental differences which affect global terrestrial vegetation patterns; the circumpolar boreal forest, for example, could be considered a vegetational unit at the mega-scale. The macro-scale domain includes regional variation and landscape level variation. The effects of environmental factors, such as soil temperature and moisture, on the composition of boreal forest communities can be examined at a macro-scale. In Canadian boreal forests cold and wet sites are dominated by black spruce and tamarack; warmer and drier, mesic sites are dominated by paper birch, trembling aspen, balsam poplar, white spruce, and balsam fir; and dry sites by lodgepole and jack pine (Bonan and Shugart 1989).

The examination of individual plants at a microsite level, the environment directly surrounding an individual, can be considered micro-scale observations (Delcourt *et al.* 1983).

Small scale heterogeneity of the physical environment can affect the distribution (Beatty 1984), individual fitness (Hartgerink and Bazzaz 1984; Lechowicz *et al* 1988) and competitive ability (Latham 1992) of seedlings. Because of its influence on distribution, fitness, and competitive ability, microscale variation in the physical environment influences both community composition (Latham 1992), and population structure (Hartgerink and Bazzaz 1984) at the time of seedling establishment and into the future. Environmental heterogeneity exists at the microsite scale within forests (Beatty 1984; Bell *et al* 1991; Boerner and Koslowsky 1989; Lechowicz and Bell 1991) and has important effects on the establishment and development of tree seedlings, and community and population structure.

Grubb (1977) defines the niche of a plant as its total relationship with both its physico-chemical and biotic environment, and divides it into four components: habitat; life-form; phenology; and regeneration niches. Niche differentiation between species can occur in any of these components. Differentiation in the regeneration niche occurs in all stages of the regeneration cycle, including germination, seedling establishment and further development of the immature plant. Evidence suggests the physical environment is the most important influence in the regeneration niche with only minor effects from biotic factors. The regeneration niche sets the stage for future population and community development.

Forest Microhabitats

Variation in forest microhabitats affects both the establishment and performance of tree seedlings. Tree seedlings in oak-pine forests establish in microhabitats with less litter and more light (Collins and Good 1987). Litter also can affect establishment in mature spruce-fir forests where Engelmann spruce (*Picea engelmannii*) establishment is more successful than subalpine

fir (*Abies lasiocarpa)* on microhabitats with thinner litter layers (Knapp and Smith 1982). Shading and moss cover were found to significantly favour the establishment of western larch (*Larix occidentalis*) (Oswald and Neuenschwander 1993). Microtopography affects the distribution of northern hardwoods; the proportion of yellow birch (*Betula alleghaniensis* Britton) stems growing on mounds, versus pits, was higher than either beech (*Fagus grandifolia* Ehrh.) or sugar maple (*Acer saccharum* Marsh.) (Ruel *et al.* 1988). Microtopography also can affect the height growth (Messier and Kimmins 1992). Western red cedar (*Thuja plicata* Donn) growth was greater in depressions (50 cm below mean ground level) than on flats or mounds, but no relationship was found between forest floor nutrient status and growth. In contrast forest floor nutrient content was found to contribute to variation in height growth of understory Scots pine (*Pinus sylvestris* L.) seedlings in addition to spatial heterogeneity of above and below-ground factors, including size and proximity of canopy trees, and humus layer thickness (Kuuluvainen 1993). More fertile microsites were found to result in improved growth of individual Sitka spruce (*Picea sitchensis)* trees in clearcuts (Adams 1974). It is, therefore, important to consider variability in microhabitat when evaluating the performance of seedlings within a population.

Peatlands

Peatlands cover approximately 12.6 million ha in Alberta, or about 20 % of the total land area. (Tarnocai 1984, Zoltai 1988). Peatlands, in general, have high water tables, poorly aerated soils, low nutrient contents, and low soil temperatures (Payandeh 1973). These environmental factors have a variety of impacts on the physiological processes of plants. High water tables and anaerobic soil conditions impair root growth and function which leads to

reduced water and nutrient uptake (Kozlowski 1986). This can influence stomatal aperture, photosynthesis, and mineral relations (Kozlowski 1982), and result in a reduction in net assimilation and transpiration, a decline in shoot elongation (Zaerr 1983), height growth (Kozlowski 1986), and poor root development (Lieffers and Rothwell 1986). Cold soils and low root temperatures reduce stomatal conductance and net photosynthesis (DeLucia and Smith 1987; Lawrence and Oechel 1983; Day *et al.* 1991), decrease the photosynthetic utilisation of internal CO_2, and reduce the apparent quantum yield (Delucia 1986) and growth rate (Anderson and McNaughton 1973; Brand 1990). Clearly peatlands represent a harsh environment for tree growth.

Peatland Microhabitat

Small scale variations in microhabitat exist within peatlands. In many peatlands, surfaces are dominated by hummock/hollow microtopography, with hummocks as much as 50 cm above surrounding hollows, which are occasionally water filled. Soil water pH has been found to decrease as one moves along the hollow to hummock gradient (Karlin and Bliss 1984; Vitt et al. 1975), and there is a reduction in mineral content and bulk density (Karlin and Bliss 1984). The depth to water table increases from hollow to hummock (Lindholm and Markula 1984; Karlin and Bliss 1984) and this probably results in a decline in moisture (along this gradient) (Karlin and Bliss 1984; Vitt et al. 1975) and an increase in soil water tension (Lindholm and Markula 1984). Differential decay rates of hummock versus hollow bryophyte species (Johnson and Damman 1991) may result in differences in nutrient availability between the two positions. Peatland hummocks have a different thermal regime than surrounding hollows (Swanson and Rothwell 1989). Frost thickness,

in the spring, is greater in hummocks than in hollows. Frost was also found to accumulate in hummocks following snowpack melt. The thermal conductivity of peat decreases with reduced water content, as a result the transport of heat differs between the drier hummock tops and the wetter hollows (Swanson and Rothwell 1986). Heat transport in drier peat would be more dependent on convective processes which can be slow.

Variations in peatland microhabitat affect both vascular and non-vascular plant species. Distributional patterns of vascular plant species in weakly minerotrophic peatlands are primarily a result of gradients in substrate moisture, while those in more strongly minerotrophic peatlands are more influenced by gradients in substrate chemistry (Karlin and Bliss 1984). Peatlands in northwestern Europe have vegetation gradients which are related to the microtopography of the peatland surface (Malmer 1986). Vertical zonation of *Sphagnum* species has been found along hummock-hollow gradients (Andrus et al. 1983; Vitt et al. 1975) and bryophyte growth and production is lower on hummocks than in hollows. (Moore 1989; Vitt 1990). The germination and establishment of coniferous tree species can be affected by microhabitat, bryophyte composition, or microtopography. Coniferous seeds germinated better on some species of bryophyte than on others (St. Hilaire and Leopold 1995; Ohlson and Zackrisson 1992). Seedling mortality, within one year of germination, also differs among bryophyte-defined microhabitats (Ohlson and Zackrisson 1992). St. Hilaire and Leopold (1995) found that coniferous seedlings establishement was more successful on hummocks and high hummocks than on low hummocks and in hollows. It is clear that variation in peatland

microhabitat occurs at a level which is significant for the establishment and performance of non-vascular plants, and herbaceous and woody vascular plants.

Evergreen vs. Deciduous

It is hypothesized that an evergreen habitat should provide a selective advantage in a harsh environment due to greater annual carbon gain and greater efficiency of nutrient use (Chabot and Hicks 1982). As discussed earlier, the high water tables, poorly aerated soils, low nutrient content, and low soil temperatures of peatlands represent a harsh environment for plant growth. Estimates of potential photosynthate production per unit of nitrogen are much greater for peatland evergreen versus peatland deciduous species (Small 1972a, 1972b). Simulations using two co-occurring oak species, one evergreen and one deciduous indicate that, under conditions of low water or low nitrogen, canopies of the evergreen Oak (*Quercus agrifolia*) should have higher annual production than the deciduous oak (*Quercus lobata*) (Hollinger 1992). Low nitrogen availability or poor conditions for nutrient uptake in peatlands may result in a similar relationship between evergreen and deciduous trees. Due to the increased time in which nutrients are available for photosynthesis (both seasonally and over the years), evergreen needles should be an advantage in a nutrient poor environment because of their retention. Peatland deciduous species have been found to reabsorb more nutrients from their foliage before leaf fall than non-peatland species (Small 1972a). This resorption may increase the nutrient efficiency of deciduous peatland species, by allowing nutrients to be reused and thus increasing the amount of time nutrients are available for photosynthesis.

Black spruce (*Picea mariana* (Mill.) B.S.P.), an evergreen conifer, and tamarack (*Larix laricina* (Du Roi) K. Koch), a deciduous conifer, co-occur on minerotrophic peatlands in the boreal forest. Besides leaf habit there are other differences between black spruce and tamarack, as well as some similarities. Tyrrell and Boerner (1987) found that relative growth rates and nutrient growth efficiencies are similar for black spruce and tamarack, but resorption of nitrogen is higher in tamarack. In contrast, other studies have found that tamarack shows faster growth (Mead 1978) and has greater photosynthetic nitrogen use efficiency than black spruce (Macdonald and Lieffers 1990). In both species soil flooding depresses photosynthesis (Macdonald and Lieffers 1990), and fine root biomass is positively correlated with depth to water table (Lieffers and Rothwell 1986). The relative abundance of tamarack has been found to increase along gradients of increasing soil pH, Mg, Ca, and N; while that of black spruce has been found to increase with an increase in depth to water table, and soil K and P. This leads to spatial separation as one moves along water and nutrient gradients associated with the transitions from poor to rich fens (Montague and Givnish in press)

When their roots are faced with anoxia and low temperature black spruce and tamarack show a greater increase in fermentation than other boreal forest conifers, but the increase is greater in black spruce (Conlin and Lieffers 1993). Tamarack also can transport some oxygen to root tissue, as shown by a redox dye test, and thus may be able to sustain respiration under these conditions; while black spruce roots are solely dependent on fermentative glycolysis in low temperature anoxic conditions. Both species have been found to experience water stress at midday on peatlands, but tamarack had greater diurnal

reductions in xylem pressure potential and higher photosynthetic water use efficiency (Dang et al. 1991). Because of their different responses to the peatland environment and different leaf life spans it seems reasonable to hypothesize that black spruce and tamarack respond differently to the microhabitat heterogeneity found in peatlands

The growth of conifers on peatlands is quite variable, and even aged trees on the same peatland can vary greatly in size (Jeglum 1972; Lieffers 1986; Yin 1992). Lieffers (1986) found that variation in growth rate in a peatland black spruce stand was not strongly correlated with above ground competition from crowding and shading. Drainage of peatlands lowers the water table and increases soil temperatures (Lieffers and Rothwell 1987). For both black spruce and tamarack, post-drainage release of trees in the same age class, in an open canopy low-density stand, was greater for trees in smaller size classes; the response of tamarack to drainage was sooner and greater than for black spruce (Yin 1992). This suggests that the smaller trees may have been more severely limited by their environment and thus that size variation in even age peatland trees may be due to microhabitat heterogeneity, with more favourable microhabitats resulting in better performance of trees established on them. The larger release of smaller size classes after drainage could have been the result of a greater improvement in the conditions in poorer microsites versus those in better microsites.

Objectives

The objectives of this study were to answer the following questions: 1) Are tree seedlings established on differing microhabitats within a peatland?; 2) Do black spruce

and tamarack seedlings grow on different microhabitats within peatlands?, 3) How do black spruce and tamarack respond to variation in microhabitat?

To answer these questions a field study was conducted in an Alberta peatland, where the microhabitats of black spruce and tamarack were characterized and related to the foliar nutrients, gas exchange, and growth rates of the seedlings.

CHAPTER II

STUDY SITE

The peatland selected for this study was a forested, moderately rich, fen near Perryvale, Alberta, Canada (54 30'N, 113 14'W) (Vitt *et al* 1995). A mixture of black spruce and tamarack, approximately 50 years old and 2 m tall, forms an open canopy with an understory of more recently established seedlings. The peat surface was characterized by well developed hummock/hollow microtopography.

METHODS

In mid-May 1993 two east-west 150 m transects were laid out 100 m apart. All black spruce and tamarack seedlings (< 1.3 m in height) occurring within 5 m of each transect, which had an approximate age of <10 years (whorls) above the peat surface, and had sufficient foliage for all measurements were identified. To ensure black spruce seedlings were of seed origin versus layering, seedlings which occurred at the base of larger trees were not included in the selections. Of the approximately 100-110 black spruce and tamarack seedlings identified, 60 of each species were randomly chosen for the study.

Microhabitat Characterization

At the base of each seedling, soil temperature, microtopographic position, depth to water table, nutrient availability, soil pH, and depth of the aerobic layer were measured.

Soil temperature was measured using copper-constantan thermocouples inserted to 25 cm below the peat surface. Measurements were taken bi-weekly from mid-June to late August (5 measurements), between 11 AM and 2 PM.

Microtopographic position was defined as the vertical distance from the base of the tree to the frozen water table. A level and height rod were used to measure the height of the base of each tree (+/- 1 cm) above the ice found in the closest hollow in early spring.

Wells constructed of 1 m long sections of 2 cm diameter PVC pipe were inserted at each tree to measure depth to water table. The depth of water table from the base of each tree was measured bi-weekly from mid-June to late August (5 measurements), by inserting a tape measure with a longitudinal line of water soluble ink on it. The depth of the water table below the top of the well was measured and then the measurement was corrected to reflect the depth of the water table from the base of the tree (at the peat surface).

Nutrient availability was measured using ion exchange resin bags buried 10 cm from the base each tree at a depth of 15 cm (Binkley and Matson 1983). Nylon stocking bags were filled with 20 g of cation (Amberlite IRC-50) and 20 g of anion (Amberlite IRA-440C) exchange resins. Before burial the bags were saturated with NaCl by being placed in 100 ml of a 1 M solution for 1 hour. The bags were removed after 2 months of

incubation in the peat (June 15 to August 15), and air dried. The resin was then removed from the bags and shaken with 100 ml of 2M KCl for 1 hour. The extract was analyzed for NH_4^+, NO_3^-, and PO_4^{3-} using a Technicon Autoanalyzer (Technicon Industrial Systems 1975, 1977). Results were expressed as μg/g of resin.

The depth of the aerobic layer was measured using 1 m long bright, mild steel rods inserted into the peat, leaving 5 cm above the peat surface, next to each tree. After two months the rods were removed and the depth from the peat surface to the boundary between the brown/orange oxidized (aerated) zone and the matte grey reduced (anaerobic) zone was measured. This boundary is considered to correspond with the average position of the top of the capillary fringe (Carnell and Anderson 1986).

At the end of the experiment the trees were excavated and peat samples were removed from the area immediately below the rootstock. One-half teaspoonful of moist peat was transferred into a glass screw top bottle in 4 ml of 0.015 M $CaCl_2$ and shaken. After 15 minutes the pH was measured using a pH meter (Day 1988).

After excavation the distance from the base of the tree at the peat surface to the root stock was measured. Because of peat accumulation the root stock occurs below the surface of the peat. This distance was used to correct the depth to water table, microtopographic position, and the depth of the aerobic layer measurements so that they reflected the position of these variables in relation to the tree's rootstock.

Gas Exchange

Gas exchange parameters were measured for both species; a healthy lateral branch was chosen and the most recent cohort of needles was used for black spruce and short shoots were used for tamarack. A portable infrared gas analyzer (LCA-3) and leaf chamber (PLC-C) (Analytical Development Corporation, Hoddesdon, England) were used and light levels were maintained at saturating levels (1200 μmols m^{-2} sec^{-1}) using a 12 volt quartz halogen lamp (MR-16, Phillips, Sommerset, NJ, USA) attached to the leaf chamber. Flow rate was maintained at 300 ml/min and incoming relative humidity at approximately 20%. Net assimilation (NA, μmol $CO_2/m^2/s$), stomatal conductance to water vapour (gs, mmol/m^2/s), photosynthetic water-use efficiency (WUE, μmol CO_2 fixed/mmol H_2O transpired), and residual conductance (g_r, mmol/m^2/s) were determined using standard calculations (Caemmerer and Farquhar 1981; Jones 1985). Leaf temperature was assumed to be equal to the air temperature in the cuvette. Leaf area was calculated from dry weight using relationships derived by Macdonald and Lieffers (1990) for each species (Black spruce: 99.44 cm^2/g dry weight; Tamarack: 363.13 cm^2/g dry weight).

Each tree was measured 4 times during the season. The 60 trees of each species were split into 3 blocks of 20 trees. One block of each species was measured each day for three days, in each of four measuring periods: July 15-17; July 26-28; August 9, 11-12; August 27-28, 30). Measurements were made in the morning once the dew on the leaves had dried (9:30 AM - 12:00 PM). Immediately after measurement, the measured branch was removed and xylem pressure potential was determined using a Scholander type

pressure bomb. Tissue was then returned to the lab and shoots were dried at 70 C for 24 hours, and needles removed and weighed for leaf area calculations.

Foliar Nutrients

To minimize the amount of tissue removed from the seedlings and to provide sufficient tissue for analysis, the needles used for gas exchange measurements in July (two sampling times) were pooled for each tree and used for determination of nitrogen, phosphorous and potassium concentration. Needles were ground in a Wiley mill to pass a 20 mesh screen. Samples were digested in concentrated sulphuric acid followed by oxidation with hydrogen peroxide (Lowther 1980). Total N and P in digests were determined with an autoanalyzer (Technicon Instruments 1977) and expressed as a concentration (percent dry weight). Potassium levels were determined using flame emission spectrophotometry (Perkin-Elmer Model 503, Perkin-Elmer Corp., Analytical Instruments, Norwalk, CT) and also expressed as a concentration (percent dry weight).

Average Annual Growth Rate and Relative Growth Rate

Heights of trees (root stock to top of terminal shoot) were measured at the end of the experiment when the trees were excavated. Leader growth from the current year was measured and relative growth rate (cm leader growth/cm of tree height * 100) was determined using the total height of the tree. For the purposes of analysis relative growth rate was transformed by adding 0.5 to the value and taking the square root, because the data consisted of small percentage data (Steele and Torrie 1980). Trees were cut just

above the root stock and ages were determined by ring counts. Age and total height were used to calculate average annual growth rate over the life of the tree (cm/year).

Analysis

For the purposes of statistical analysis measurements of depth to water table and soil temperature for each tree were ranked within each day and an average rank (over all measurement times) was computed for each tree. Soil temperatures were ranked from highest to lowest, starting with a rank of 1; this resulted in warmer sites having lower temperature indices. Depth to water table was ranked from lowest to highest, with higher water tables having lower water table ranks. These average ranks were used as indices of depth to water table and soil temperature, because depth to water table and soil temperature were monitored on different days and at different times than the gas exchange measurements, so the gas exchange measures could not be related directly to them.

A canonical discriminant analysis was carried out on the microhabitat characteristics (index of depth to water table, index of soil temperature, nutrient availabilities, pH, microtopographic position, and depth of the aerobic layer) to determine whether black spruce and tamarack were growing on different microhabitats.

Pearson correlation coefficients were generated to examine the relationship between any two microhabitat variables. A probability test for each correlation was performed. A principle components analysis was carried out on the microhabitat characteristics to find any distinct associations of variables that could be considered to define discrete microhabitats. The principle components analysis was derived from a

correlation matrix of the microhabitat variables. Projection of each tree onto each principal component could be used to determine the distribution of trees in habitat space (Collins 1990; Collins and Good 1987). Separation of trees (sampling points) within the habitat space defined by the principal component axes would indicate the presence of discrete microhabitats.

One way analysis of variance was used to look for differences between species in average annual height growth, relative height growth rate, and age.

The remainder of the analyses were carried out using setwise regression, to examine how black spruce and tamarack respond to variation in microhabitat. Setwise regression is an alternative to stepwise regression where separate regressions are computed for all possible combinations of Independent Variables in order to choose the optimal subset of variables (Tabachnick and Fidell 1989). The criteria used for choosing the optimal subset of independent variables was maximum adjusted R^2. Setwise regressions (described below) were carried out for each species separately.

Setwise regressions were carried out for each foliar nutrient concentration, and each growth rate as dependent variables and the microhabitat characteristics: index of soil temperature; nutrient availabilities; pH; microtopographic position; and depth of the aerobic layer; as independent variables, to determine if the physical/chemical environment had a significant influence on foliar nutrients. Index of depth to water table was not used as a possible independent variable because of the high degree of collinearity between it and microtopographic position (height above frozen water table). Essentially they are

measures of the same variable- depth of water table, albeit frozen in the case of microtopographic position.

To determine whether gas exchange was influenced by the physical/chemical environment, setwise regressions were carried out for each gas exchange parameter as the dependent variable and: 1) all combinations of foliar N, P, and K concentrations and water potential as independent variables; and 2) all combinations of microhabitat characteristics (excluding index of depth to water) as independent variables. The optimal subset of independent variables was chosen based on adjusted R^2. Dummy variables were used to account for the variation in the gas exchange measures, due to the measurements being on 12 separate days throughout the season. Eleven (n-1) dummy variables (D2-D12) were created. High day to day variation in gas exchange was expected due to changes in factors such as air temperature and soil water conditions. It was necessary to account for and remove this variability in order to examine how the trees differed and how this was related to microhabitat conditions. Each measurement day corresponds with one dummy variable and trees measured on that day are given a value of 1 for that dummy variables and 0 for all others. As there are 12 measurement days and only 11 dummy variables, the remaining measurement day, which does not have a corresponding dummy variable, is coded with -1 for all dummy variables. In the setwise regressions with gas exchange parameters as dependent variables the dummy variables were included in all subsets of independent variables. Similar setwise regressions with xylem pressure potential as the dependent variable, and the dummy variables and varying combinations of the microhabitat

characteristics as independent variables were also carried out and the optimal subset of variables chosen, as above.

Finally, to determine whether growth was influenced by the physical/chemical environment setwise regressions were also carried out for both average annual growth rate, and relative growth rate as independent variables and the microhabitat characteristics as dependent variables. The optimal subset of dependent variables were again selected based on adjusted r^2.

All analyses utilized SAS for PC (SAS Institute Inc., North Carolina). All data was checked for normality and homogeneity of variance. With the exception of relative growth rate (described previously), no data transformations were required. A significance level of $p<0.05$ was used in all instances.

CHAPTER III

RESULTS

Characterization of Microsites

Significant correlations among groups of the microhabitat characteristics (Table 2) suggested the existence of a range of microhabitats within the peatland. Higher microtopographic positions had, not surprisingly, greater depths of aeration and deeper water tables, and were accompanied by higher soil temperatures (lower temperature ranks) and lower NH_4^+ and PO_4^{-3} availability. In turn, microsites with higher water tables also had higher PO_4^{-3} and NH_4^+ availability. pH of the peat surrounding the roots was higher for cooler microsites, and for those with higher water tables. Cooler microsites had shallower depths of aeration and higher water tables (lower water table ranks). The principle components analysis failed to show clear distinctions among microhabitats. Axis I, II, and III of the PCA accounted for 39%, 15%, and 13% of the variance of the microhabitat characteristics respectively (Table 1). Plots of the distribution of the seedlings in the space defined by the principal components analysis of the 8 microhabitat characteristics failed to separate them into discrete microhabitats (Fig. 1 and 2).

There was no evidence of niche partitioning between the two species along microhabitat gradients. The canonical discriminant analysis indicated that there was no significant difference between the species in their microhabitat characteristics ($p = 0.54$). This can also be seen in the distribution of each species along the axes defined by the

principal components analysis (Fig. 1 and 2), where black spruce and tamarack fail to separate from one another in terms of microhabitat.

Foliar Nutrients and Microhabitat

The setwise regressions demonstrated that variation in microhabitat conditions had a weak but significant influence on seedling nutrition for both black spruce (Table 3) and tamarack (Table 4). While foliar nitrogen concentration was most closely related to NO_3^- availability for black spruce this variable was not significant in explaining variation in foliar nitrogen in tamarack. The multiple regression predicting foliar nitrogen concentration in black spruce included NO_3^- availability, pH, and temperature as independent variables. ($r^2 = 0.16$, $p = 0.023$). NO_3^- availability was the only independent variable with a sizable effect on foliar nitrogen ($p = 0.005$, $sr^2 = 0.13$). Black spruce foliar nitrogen was positively correlated with NO_3^- availability. With tamarack foliar nitrogen as a dependent variable the multiple regression included PO_4^{3-} availability, NH_4^+ availability, temperature, microtopographic position, pH, depth of aeration, and NO_3^- availability ($r^2 = 0.368$, $p = 0.002$). Available PO_4^{3-} ($p = 0.003$, $sr^2 = 0.13$) and NH_4^+ ($p = 0.005$, $sr^2 = 0.11$) had the greatest impact on foliar nitrogen. Foliar nitrogen concentration was positively correlated with NH_4^+ availability, and temperature rank ($p = 0.023$, $sr^2 = 0.07$), and negatively correlated with PO_4^{3-} availability, microtopographic position ($p = 0.029$, $sr^2 = 0.07$), and pH ($p = 0.032$, $sr^2 = 0.06$).

The relative temperature of the microhabitat was the most important variable in the setwise regressions predicting foliar phosphorous concentration for both black spruce (Table 3) and tamarack (Table 4). For black spruce foliar phosphorous concentration the

regression contained PO_4^{3-} availability, temperature, and depth of aeration as independent variables ($r^2 = 0.19$, $p = 0.012$). Temperature rank had the largest effect on phosphorous concentration ($p=0.002$, $sr^2 = 0.16$). Phosphorous concentration was positively correlated with the relative warmth of microhabitats (negatively correlated with temperature rank). For tamarack there was a significant relationship correlating foliar phosphorous with temperature rank, NO_3^- availability, microtopographic position and pH ($r^2 = 0.30$, $p= 0.001$). Temperature rank ($p = 0.001$, $sr^2 = 0.20$), and NO_3^- availability ($p = 0.047$, $sr^2 = 0.05$) had the greatest contribution to the variance explained by the regression. As with black spruce phosphorous concentration was higher in warmer microsites (negatively correlated with temperature rank) and negatively correlated with NO_3^- availability.

Foliar potassium concentration in black spruce was significantly influenced by several microhabitat characteristics (Table 3), while only PO_4^{3-} availability had a significant correlation with tamarack foliar potassium concentration (Table 4). Black spruce foliar potassium concentration was predicted in a multiple regression that included microtopographic position, pH, temperature, and depth of aeration ($r^2 = 0.21$, $p = 0.016$). With the exception of pH, all of the independent variables had an important effect on potassium concentration. Potassium concentration was positively correlated with microtopographic position ($p = 0.043$, $sr^2 = 0.06$), and negatively correlated with temperature rank ($p = 0.036$, $sr^2 = 0.07$), and depth of aeration ($p = 0.004$, $sr^2 = 0.14$). The regression describing foliar potassium concentration in tamarack included PO_4^{3-} availability, temperature, and pH ($r^2 = 0.19$, $p = 0.012$). Only PO_4^{3-} availability had an

appreciable contribution to the variance explained by the regression ($p = 0.028$, $sr^2 = 0.08$). Foliar potassium concentration was negatively correlated with available PO_4^{3-}.

The relationships between tamarack foliar nitrogen, phosphorous, and potassium concentrations with microhabitat were stronger than those for black spruce, as measured by the r^2 values of the above regressions.

Gas Exchange and Foliar Nutrients

All of the multiple regressions used to analyze the effects of varying foliar nutrient concentration and xylem pressure potential on gas exchange contain dummy variables and varying combination of other independent variables. The dummy variables were used to capture variance due to different measurement dates. As expected there was high day to day variation between measurement dates such that, in all cases, the bulk of the variation in gas exchange variables is accounted for by the dummy variables. Once the contribution of the dummy variables is considered the effects of foliar nutrients can be examined separately, and their importance as independent variables gauged by the size of their semi-partial correlation coefficient (sr^2).

As expected foliar nutrient concentration had a significant impact on gas exchange in both black spruce (Table 5) and tamarack (Table 6). Nitrogen was the most influential nutrient, having a large impact on the net assimilation, water use efficiency, and residual conductance of both species.

Table 5 summarizes the multiple regressions used to analyze the effect of differing foliar nutrient concentrations and xylem pressure potential on gas exchange of black spruce. Net Assimilation was significantly related to the nitrogen and phosphorous

concentration of the foliage ($r^2 = 0.60$, $p = 0.0001$). Foliar nitrogen was positively correlated with net assimilation ($p = 0.0001$, $sr^2 = 0.14$). Foliar phosphorous concentration had little effect ($p = 0.009$, $sr^2 = 0.01$). There was a significant relationship between stomatal conductance and foliar nitrogen and phosphorous concentration, and water potential ($r^2 = 0.21$, $p = 0.0001$). Stomatal conductance was positively correlated with foliar nitrogen concentration ($p = 0.0002$, $sr^2 = 0.06$). Xylem pressure potential and foliar phosphorous explained little of the variation. Water use efficiency was also significantly related to foliar nitrogen and phosphorous concentration, and xylem pressure potential ($r^2 = 0.38$, $p = 0.0001$). Water use efficiency was positively correlated with foliar nitrogen concentration ($p = 0.0001$, $sr^2 = 0.08$) and negatively correlated with xylem pressure potential ($p = 0.0001$, $sr^2 = 0.06$). Foliar phosphorous did not have a sizable impact ($p = 0.195$, $sr^2 = 0.01$). Residual conductance was related to foliar nitrogen and phosphorous concentrations ($r^2 = 0.57$, $p = 0.0001$). Residual conductance was positively correlated with foliar nitrogen ($p = 0.0001$, $sr^2 = 0.16$) and negatively correlated with foliar phosphorous concentration ($p = 0.005$, $sr^2 = 0.02$), although the influence of phosphorous was quite small.

A similar group of setwise multiple regressions were used to analyze the effect of foliar nutrients and xylem pressure potential on gas exchange in tamarack (Table 6). There was a significant relationship between the concentration of all three foliar nutrients and net assimilation ($r^2 = 0.63$, $p = 0.0001$). Of the three foliar nutrients only nitrogen explained an appreciable amount of the variance. Net assimilation was positively correlated with foliar nitrogen ($p=0.0001$, $sr^2 = 0.11$). The foliar phosphorous and

potassium concentration explained little of the variance in net assimilation ($p = 0.016$, $sr^2 = 0.01$; $p = 0.260$, $sr^2 = 0.002$ respectively). There was no relationship between stomatal conductance and foliar nutrients or xylem pressure potential. The water use efficiency of the tamarack seedlings was significantly related to xylem pressure potential and foliar nitrogen concentration ($r^2 = 0.56$, $p = 0.0001$). As xylem pressure potential ($p = 0.001$, $sr^2 = 0.07$) and foliar nitrogen concentration increased ($p = 0.0001$, $sr^2 = 0.04$), water use efficiency increased. Variation in residual conductance was related to differences in nitrogen, phosphorous, and potassium concentrations in the foliage ($r^2 = 0.61$, $p = 0.0001$). Nitrogen was the most influential foliar nutrient; residual conductance was positively correlated with nitrogen concentration ($p = 0.0001$, $sr^2 = 0.14$). The influence of phosphorous was minor ($p = 0.015$, $sr^2 = 0.01$) as was that of potassium ($p = 0.141$ sr $= 0.004$)

Gas Exchange and Microhabitat

As with the analysis of gas exchange and foliar nutrients above, the setwise multiple regressions used to analyze the effects of varying microhabitat on gas exchange included dummy variables to account for the high variance between differing measurement days. The dummy variables were included in all regressions as independent variables, along with differing combinations of microhabitat characteristics. In all cases the dummy variables were responsible for the majority of the variance accounted for in the regressions.

The setwise regressions indicated that variations in microhabitat had significant, but minimal, effects on the gas exchange of both black spruce (Table 7) and tamarack

(Table 8) seedlings. As with foliar nitrogen, there was a difference in the form of available nitrogen which affected the response of black spruce vs. tamarack. Net assimilation, water use efficiency and residual conductance of black spruce were influenced by NO_3^- availability, while for tamarack they were influenced by NH_4^+ availability. For both species net assimilation and residual conductance were higher in lower microhabitats (closer to hollows).

The multiple regressions used to analyze black spruce gas exchange in varying microhabitats are summarized in Table 7. Net assimilation of the black spruce seedlings was significantly related to NO_3^- availability, PO_4^{3-} availability, microtopographic position and depth of aeration ($r^2 = 0.49$, $p = 0.0001$). Net assimilation was positively correlated with NO_3^- availability ($p = 0.004$, $sr^2 = 0.021$), which had the largest impact and negatively correlated with PO_4^{3-} availability ($p = 0.037$, $sr^2 = 0.01$), and microtopographic position ($p = 0.042$, $sr^2 = 0.01$). Depth of aeration, although positively correlated with net assimilation, explained little of the variance ($p=0.207$, $sr^2 = 0.004$). There was a relationship between stomatal conductance and the independent variables ($r^2 = 0.157$, $p = 0.0008$), but little of the variation was explained by microhabitat. The significant relationship was the result of the dummy variable contribution. Water use efficiency was significantly related to temperature and NO_3^- availability ($r^2 = 0.32$, $p = 0.001$). As the temperature increased (temperature rank decreased) ($p = 0.001$, $sr^2 = 0.035$) and the availability of NO_3^- increased, the water use efficiency of the seedlings improved. A significant portion of the variance in residual conductance was explained by setwise regression including NO_3^- availability, microtopographic position, and PO_4^{3-} availability (r^2

= 0.45, p = 0.0001). Residual conductance was positively correlated with NO_3^- availability (p = 0.002, sr^2 = 0.025), and negatively correlated with microtopographic position (p = 0.035, sr^2 = 0.021) and PO_4^{3-} availability (p=0.039, sr^2 = 0.011), although PO_4^{3-} had little effect.

Table 8 summarizes the regressions used to examine the effects of variation in microhabitat on the gas exchange of the tamarack seedlings. The variation in net assimilation of the tamarack seedlings was best explained by a combination of NH_4^+ availability, PO_4^{3-} availability, pH, NO_3^- availability, microtopographic position, depth of aeration (r^2 = 0.51, p = 0.0001). Net assimilation was positively correlated with the availability of NH_4^+ (p = 0.0001, sr^2 = 0.04), and negatively correlated with pH (p = 0.0008, sr^2 = 0.03) and PO_4^{3-} availability (p = 0.0006, sr^2 = 0.03). The other independent variables had negligible contributions to the variation in net assimilation. Stomatal conductance was significantly related to PO_4^{3-} availability, NH_4^+ availability, and temperature rank. Stomatal conductance was positively correlated with PO_4^{3-} availability (p = 0.009, sr^2 = 0.02) and negatively correlated with NH_4^+ availability (p = 0.039, sr^2 = 0.01). Water use efficiency (p=0.0001, r^2= 0.50) was negatively correlated with pH (p = 0.024, sr^2 = 0.01) and positively correlated with depth of aeration (p= 0.079, sr^2 = 0.01). The variation in residual conductance of the tamarack seedlings was best related to a combination of NH_4^+ availability, PO_4^{3-} availability, pH, NO_3^- availability, microtopographic position, and depth of aeration (r^2 = 0.48, p = 0.0001). Residual conductance was positively correlated with NH_4^+ availability (p = 0.0001, sr^2 = 0.04), and

negatively correlated with PO_4^{3-} availability ($p = 0.0002$, $sr^2 = 0.04$) , pH ($p = 0.0003$, $sr^2 = 0.04$), and microtopographic position ($p = 0.025$, $sr^2 = 0.01$).

Variation in microhabitat did not have a significant effect on either black spruce (Table 9) or tamarack (Table 10) xylem pressure potential.

Overall the relationships between microhabitat and gas exchange were weak, as the variation in microhabitat did not explain a large amount of the variation in gas exchange.

Growth Rates

There was a weak relationship between the relative growth rate of black spruce and the temperature and microtopographic position of its microsite ($r^2 = 0.11$, $p = 0.05$) (Table 11). As the microsite became warmer ($p=0.01$, $sr^2 = 0.10$) the relative growth rate increased. Microtopographic position did not have a significant impact on the growth rate. There was a significant relationship between the average annual growth rate of black spruce and a combination of a number of microhabitat characteristics ($r^2 = 0.28$, $p = 0.004$), but only temperature had a significant impact ($p = 0.003$, $sr^2 = 0.14$). Average annual growth rate was higher on warmer microsites (with a lower temperature rank).

There were no significant relationships between either the relative growth rate, or the average annual growth of tamarack and microhabitat characteristics (Table 12).

Tamarack seedlings had a significantly higher average annual growth rate (4.78 +/- 0.17) than black spruce (Table 16, 4.30 +/- 0.18) (Table 13, $p = 0.053$), but a lower relative growth rate (Table 16, 7.47 +/- 0.47 vs. 9.30 +/- 0.42, Table 14, $p = 0.003$). On average the tamarack seedlings were one year older than the black spruce (13 vs. 12, $p = 0.032$, Table 15).

Table 1. Correlation coefficients for 8 microhabitat variables, measured for black spruce and tamarack seedlings, with the first 3 axes of a principal components analysis of their correlation matrix.

Microhabitat variable	PC I	PC II	PC III
(1) Microtopographic position	0.48	0.04	0.24
(2) NO_3^- Availability	-0.08	0.04	0.94
(3) NH_4^+ Availability	-0.21	0.51	0.05
(4) PO_4^{-3} Availability	-0.32	0.49	0.07
(5) pH	-0.20	-0.50	0.18
(6) Temperature (Rank)	-0.25	-0.49	0.02
(7) Aeration Depth	0.49	0.07	-0.07
(8) Water Table Depth (Rank)	0.51	-0.02	0.14
Eigenvalue	3.17	1.24	1.02
% Variance	40	16	13

Table 2. Pearson correlation matrix for the microhabitat variables measured for black spruce and tamarack seedlings in a treed peatland.

Microhabitat variable	1	2	3	4	5	6	7	8
(1) Microtopographic position	1.00							
(2) NO_3^- Availability	0.01	1.00						
(3) NH_4^+ Availability	-0.19*	0.03	1.00					
(4) PO_4^{-3} Availability	-0.38***	0.08	0.36***	1.00				
(5) pH	-0.18	0.06	0.07	-0.02	1.00			
(6) Temperature (Rank)	-0.33**	0.04	0.01	0.08	0.26**	1.00		
(7) Aeration Depth	0.67***	-0.18	-0.16	-0.43***	-0.30**	-0.33***	1.00	
(8) Water Table Depth (Rank)	0.88***	-0.06	-0.25**	-0.45***	-0.25**	-0.24*	0.78***	1.00

* P=0.05
**P=0.01
***P=0.001

Table 3. Multiple regressions for black spruce foliar nutrient concentrations versus microhabitat characteristics

Dependent Variable	Independent Variables	B	β	p	sr^2
Nitrogen (% dry wt.)					
	NO_3^- Availability	0.076	0.368	0.005	0.13
	pH	0.014	0.134	0.309	0.01
	Temperature (Rank)	-0.001	-0.194	0.146	0.03
Intercept = 0.569	$r^2 = 0.16$ adj $r^2 = 0.12$	P>F = 0.023			
Phosphorous (% dry ....)					
	PO_4^{3-} Availability	0.002	0.161	0.223	0.02
	Temperature (Rank)	-0.001	-0.441	0.002	0.16
	Depth of Aeration	-0.001	-0.176	0.229	0.02
Intercept = 0.112	$r^2 = 0.19$ adj $r^2 = 0.14$	P>F = 0.012			
Potassium (%dry wt.)					
	Microtopographic position	0.002	0.364	0.043	0.06
	pH	-0.010	-0.149	0.261	0.02
	Temperature (Rank)	-0.001	-0.306	0.036	0.07
	Depth of Aeration	-0.004	-0.544	0.004	0.14
Intercept = 0.570	$r^2 = 0.21$ adj $r^2 = 0.14$	P>F = 0.016			

Note: NO_3^-, and PO_4^{3-} availabilities are µg/g resin. Depth of aeration and microtopographic position are in cm. Values of B are regression coefficients, β are standardized regression coefficients, p are prob>F, and sr^2 are squared semi-partial correlation coefficients for each regression component.

Table 4. Multiple Regressions for tamarack foliar nutrient concentrations versus microhabitat characteristics.

Dependent Variable	Independent Variables	B	β	p	sr^2
Nitrogen (% dry wt.)					
	PO_4^{3-} Availability	-0.045	-0.464	0.003	0.13
	NH_4^+ Availability	0.018	0.392	0.005	0.11
	Temperature (Rank)	0.001	0.300	0.023	0.07
	Microtopographic position	-0.004	-0.349	0.029	0.07
	pH	-0.035	-0.283	0.032	0.06
	Depth of Aeration	0.004	0.329	0.057	0.05
	NO_3^- Availability	0.083	0.217	0.078	0.04
Intercept = 1.341	r^2 = 0.368 adj r^2 = 0.275	P>F = 0.002			
Phosphorous (% dry wt.)					
	Temperature (Rank)	-0.001	-0.478	0.001	0.20
	NO_3^- Availability	-0.020	-0.242	0.047	0.05
	Microtopographic position	-0.001	-0.227	0.073	0.05
	pH	-0.004	-0.131	0.293	0.02
Intercept = 0.226	r^2 =0.30 adj r^2 = 0.24	P>F = 0.001			
Potassium %(dry wt.)					
	PO_4^{3-}	-0.013	-0.282	0.028	0.08
	Temperature (Rank)	-0.001	-0.215	0.102	0.04
	pH	-0.010	-0.176	0.178	0.03
Intercept = 0.553	r^2 =0.19 adj r^2 = 0.14	P>F = 0.012			

Note: NO_3^-, PO_4^{3-}, and NH_4^+, availabilities are μg/g resin. Depth of aeration and microtopographic position are in cm. Values of B, β, p, and sr^2 as in Table 3.

Table 5. Multiple regressions for black spruce gas exchange parameters versus foliar nutrient concentrations and xylem pressure potential.

Dependent Variable	Independent Variables	B	β	p	sr^2
NA $\mu mol\ CO_2/m^2/s$					
	Nitrogen	2.954	0.403	0.0001	0.14
	Phosphorous	-4.809	-0.137	0.009	0.01
Intercept = 0.511	$r^2 = 0.60$ adj $r^2 = 0.57$	P>F= 0.0001	D_2-D_{12} Σsr^2 = 0.47		
g_s $mmol/m^2/s$					
	Nitrogen	117.713	0.257	0.0002	0.06
	Phosphorous	-309.676	-0.141	0.058	0.01
	Ψ	-1.492	-0.095	0.194	0.01
Intercept = 6.593	$r^2 = 0.21$ adj $r^2 = 0.16$	P>F = 0.0001	D_2-D_{12} Σsr^2= 0.15		
WUE $\mu mol\ CO_2$ fixed/ mmol H_2O transpired					
	Nitrogen	2.248	0.316	0.0001	0.08
	Ψ	0.072	0.297	0.0001	0.06
	Phosphorous	-2.889	-0.085	0.195	0.01
Intercept = 2.145	$r^2 = 0.38$ adj $r^2 = 0.24$	P>F = 0.0001	D_2-D_{12} Σsr^2= 0.29		
g_r $mmol/m^2/s$					
	Nitrogen	8.928	0.433	0.0001	0.16
	Phosphorous	-15.245	-0.154	0.005	0.02
Intercept = 1.471	r^2 =0.57 adj $r^2 = 0.55$	P>F = 0.0001	D_2-D_{12} Σsr^2 = 0.29		

Note: Foliar nutrient concentrations are % dry weight. Xylem pressure potential (Ψ) is in bars. Values of B, β, p, and sr^2 as in Table 3.

Table 6. Multiple regressions for tamarack gas exchange parameters versus foliar nutrient concentrations and xylem pressure potential.

Dependent Variable	Independent Variables	B	β	p	sr^2
NA $\mu mol\ CO_2/m_2/s$					
	Nitrogen	1.261	0.421	0.0001	0.11
	Phosphorous	1.722	0.124	0.016	0.01
	Potassium	0.341	0.054	0.260	0.002
Intercept = -0.179	$r^2 = 0.63$ adj $r^2 = 0.60$	P>F= 0.0001	D_2-D_{12} Σsr^2 = 0.41		
g_s $mmol/m^2/s$					
	Phosphorous	214.373	0.1	0.154	0.01
	Nitrogen	41.36	0.089	0.215	0.01
Intercept = 20.559	$r^2 = 0.26$ adj $r^2 = 0.21$	P>F = 0.0001	D_2-D_{12} Σsr^2 = 0.24		
WUE $\mu mol\ CO_2$ fixed/ mmol H_2O transpired					
	Ψ	0.06	0.362	0.0001	0.07
	Nitrogen	0.951	0.218	0.0001	0.04
Intercept = 2.114	$r^2 = 0.56$ adj $r^2 = 0.57$	P>F = 0.0001	D_2-D_{12} Σsr^2 = 0.52		
g_r $mmol/m^2/s$					
	Nitrogen	3.877	0.465	0.0001	0.14
	Phosphorous	4.934	0.128	0.015	0.01
	Potassium	1.266	0.072	0.141	0.004
Intercept = -0.826	r^2 =0.61 adj $r^2 = 0.58$	P>F = 0.0001	D_2-D_{12} $\Sigma sr^2 = 0.36$		

Note: Foliar nutrient concentrations are % dry weight. Xylem pressure potentials are in bars. Values of B, β, p, and sr^2 as in Table 3.

Table 7. Multiple Regressions for black spruce gas exchange parameters versus microhabitat characteristics.

Dependent Variable	Independent Variables	B	β	p	sr^2
NA $\mu mol\ CO_2/m^2/s$					
	NO_3^- Availability	0.242	0.159	0.004	0.021
	PO_4^{3-} Availability	-0.103	-0.118	0.037	0.010
	Microtopographic position	-0.012	-0.152	0.042	0.010
	Depth of Aeration	0.008	0.095	0.207	0.004
Intercept = 2.224	$r^2 = 0.49$ adj $r^2 = 0.45$	P>F= 0.0001	D_2-D_{12} Σsr^2= 0.45		
g_s $mmol/m^2/s$					
	NH_4^+ Availability	-1.853	-0.105	0.122	0.010
	PO_4^{3-} Availability	-5.545	-0.102	0.164	0.008
	Microtopographic position	-0.254	-0.052	0.453	0.002
Intercept = 113.13	$r^2 = 0.157$ adj $r^2 = 0.101$	P>F = 0.0008	D_2-D_{12} Σsr^2= 0.15		
WUE $\mu mol\ CO_2$ fixed/ $mmol\ H_2O$ lost					
	Temperature (Rank)	-0.004	-0.202	0.001	0.035
	NO_3^- Availability	0.282	0.192	0.001	0.035
Intercept = 2.19	$r^2 = 0.32$ adj $r^2 = 0.28$	P>F = 0.0001	D_2-D_{12} Σsr^2= 0.27		
g_r $mmol/m^2/s$					
	NO_3^- Availability	0.756	0.177	0.002	0.025
	Microtopographic position	-0.035	-0.163	0.035	0.021
	$PO4^{3-}$ Availability	-0.297	-0.121	0.039	0.011
Intercept = 6.54	r^2 =0.45 adj $r^2 = 0.41$	P>F = 0.0001	D_2-D_{12} Σsr^2= 0.41		

Note: NO_3^-, PO_4^{3-}, and NH_4^+ availabilities are in μg/g resin. Microtopographic position and depth of aeration are in cm. Values of B, β, p, and sr^2 as in Table 3.

Table 8. Multiple Regressions for tamarack gas exchange parameters versus microhabitat characteristics.

Dependent Variable	Independent Variables	B	β	p	sr^2
NA $\mu mol\ CO_2/m^2/s$					
	NH_4 Availability	0.031	0.225	0.0001	0.04
	PO_4 Availability	-0.067	-0.231	0.0006	0.03
	pH	-0.069	-0.184	0.0008	0.03
	NO_3^- Availability	0.110	0.095	0.0644	0.01
	Microtopographic position	-0.005	-0.122	0.07	0.01
	Depth of Aeration	0.003	0.084	0.250	0.003
Intercept = 2.13 $r^2 = 0.51$ adj $r^2 = 0.47$ P>F=0.0001 D_2-D_{12} $\Sigma sr^2 = 0.45$					
g_s $mmol/m^2/s$					
	PO_4 Availability	-8.783	-0.194	0.009	0.02
	NH_4 Availability	3.041	0.142	0.039	0.01
	Temperature (rank)	-0.161	-0.073	0.268	0.004
Intercept = 107.66 $r^2 = 0.28$ adj $r^2 = 0.23$ P>F = 0.0001 D_2-D_{12} $\Sigma sr^2 = 0.27$					
WUE $\mu mol\ CO_2$ fixed/ mmol H_2O transpired					
	pH	-0.067	-0.123	0.024	0.01
	Depth of Aeration	0.006	0.099	0.079	0.01
Intercept = 2.40 $r^2 = 0.50$ adj $r^2 = 0.47$ P>F = 0.0001 D_2-D_{12} $\Sigma sr^2 = 0.48$					
g_r $mmol/m^2/s$					
	NH_4 Availability	0.095	0.248	0.0001	0.04
	PO_4 Availabiiity	-0.215	-0.264	0.0002	0.04
	pH	-0.219	-0.208	0.0003	0.03
	Microtopographic position	-0.017	-0.156	0.025	0.01
	NO_3^- Availability	0.300	0.094	0.078	0.01
	Depth of Aeration	0.012	0.113	0.134	0.01
Intercept = 6.44 $r^2 = 0.48$ adj $r^2 = 0.44$ P>F = 0.0001 D_2-D_{12} $\Sigma sr^2 = 0.43$					

Note: NO_3^-, NH_4^+, and PO_4^{3-} and avavilabilities are in µg/g resin. Microtopographic position and depth of aeration are in cm. Values of B, β, p, and sr^2 as in Table 3.

Table 9. Multiple Regression for black spruce xylem pressure potential versus microhabitat characteristics.

Dependent Variable	Independent Variables	B	β	p	sr^2
Ψ bars					
	NO_3^- Availability	-0.447	-0.074	0.224	0.005
	Temperature (Rank)	0.008	0.083	0.189	0.006
Intercept = 17.570	$r^2 = 0.27$ adj $r^2 = 0.23$	P>F= 0.001 D_2-D_{12} Σsr^2= 0.28			

Note: NO_3^- availability is in μg/g resin. Values of B, β, p, and sr^2 as in Table 3.

Table 10. Multiple Regression for tamarack xylem pressure potential versus microhabitat characteristics.

Dependent Variable	Independent Variables	B	β	p	sr^2
Ψ bars					
	NO_3^- Availability	0.552	0.051	0.299	0.003
	pH	-0.234	-0.070	0.170	0.004
Intercept = 17.570	$r^2 = 0.27$ adj $r^2 = 0.23$	P>F= 0.001 D_2-D_{12} Σsr^2= 0.28			

Note: NO_3^- availability is in μg/g resin. Values of B, β, p, and sr^2 as in Table 3.

Table 11. Multiple regressions for black spruce growth rates versus microhabitat characteristics.

Dependent Variable	Independent Variables	B	β	p	sr^2
Relative Growth Rate					
	Temperature (Rank)	-0.005	-0.352	0.01	0.10
	Microtopographic position	-0.007	-0.148	0.30	0.01
Intercept = 3.57	$r^2 = 0.11$ adj $r^2 = 0.07$	P>F = 0.05			
Average Annual Growth Rate					
	Temperature (Rank)	-0.017	-0.420	0.003	0.14
	PO_4 Availability	-0.215	-0.251	0.052	0.06
	pH	-0.299	-0.211	0.096	0.04
	NO_3 Availability	0.477	0.175	0.155	0.03
	Microtopographic position	-0.025	-0.180	0.191	0.02
Intercept = 7.67	r^2 =0.28 adj $r^2 = 0.21$	P>F = 0.004			

Note: Values of B, β, p, and sr^2 as in Table 3.

Table 12. Multiple regressions for tamarack growth rates versus microhabitat characteristics.

Dependent Variable	Independent Variables	B	β	p	sr^2
Relative Growth Rate					
	pH	-0.077	-0.151	0.286	0.02
	Temperature (Rank)	0.002	0.087	0.536	0.01
Intercept = 3.16	$r^2 = 0.02$ adj $r^2 < 0.01$	P>F = 0.53			
Average Annual Growth Rate					
	Depth of Aeration	-0.043	-0.385	0.047	0.07
	PO_4 Availability	-0.177	-0.216	0.165	0.03
	Temperature (Rank)	-0.007	-0.190	0.173	0.03
	Microtopographic Position	-0.017	-0.160	0.363	0.01
	pH	-0.115	-0.111	0.431	0.01
Intercept = 7.34	r^2 =0.17 adj $r^2 = 0.08$	P>F = 0.092			

Note: Values of B, β, p, and sr^2 as in Table 3.

Table 13. Anova table comparing the average annual growth rates of black spruce and tamarack seedlings.

Source	d.f.	S.S.	F	p
Species	1	6.6	3.83	0.053
Error	111	191.6		
Total	112			

Table 14. Anova table comparing the relative growth rates of black spruce and tamarack seedlings.

Source	d.f.	S.S.	F	p
Species	1	2.9	9.43	0.003
Error	111	34.0		
Total	112			

Table 15. Anova table comparing the age of black spruce and tamarack seedlings.

Source	d.f.	S.S.	F	p
Species	1	30	4.73	0.032
Error	118	747.7		
Total	119			

Table 16. Means and standard errors for all dependent and independent variables.

Variable	Black Spruce	Tamarack
Foliar Nitrogen (% dry wt.)	0.733 (0.014)	1.279 (0.021)
Foliar Phosphorous (% dry wt.)	0.091 (0.002)	0.135 (0.004)
Foliar Potassium (% dry wt.)	0.464 (0.009)	0.442 (0.009)
Net Assimilation (μmol $CO_2/m^2/s$)	2.23 (0.05)	1.83 (0.03)
Stomatal Conductance ($mmol/m^2/s$)	90.75 (3.20)	99.53 (3.03)
Water Use Efficiency (μmol CO_2 fixed/mmol H_2O lost)	2.26 (0.05)	2.07 (0.04)
Residual Conductance ($mmol/m^2/s$)	6.60 (0.14)	5.40 (0.08)
Xylem Pressure Potential (bars)	-17.7 (0.2)	-21.3 (0.3)
Relative Growth Rate	3.07 (0.06)	2.75 (0.08)
Average Annual Growth Rate (cm\year)	4.30 (0.18)	4.78 (0.17)
Height (cm)	52.6 (1.9)	63.8 (1.9)
Microtopographic Position (cm)	24.0 (1.3)	25.0 (1.5)
NO_3^- Availability (μg/g resin)	1.236 (0.067)	1.204 (0.051)
NH_4^+ Availability (μg/g resin)	5.335 (0.364)	5.522 (0.425)
PO_4^{-3} Availability (μg/g resin)	1.329 (0.214)	1.482 (0.200)
pH	6.65 (0.13)	6.45 (0.16)
Temperature (Rank)	63.3 (4.5)	55.1 (4.1)
Aeration Depth (cm)	14.1 (1.2)	16.5 (1.5)

Note: Values in parentheses are standard errors

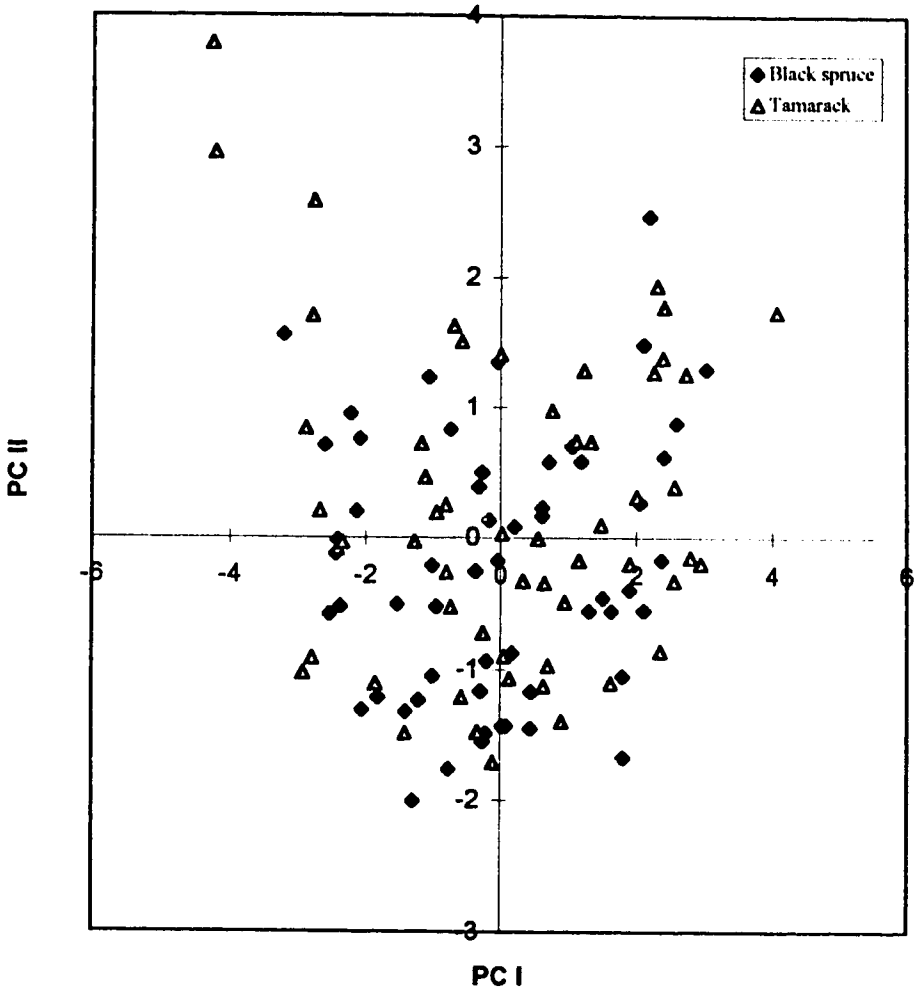

Figure 1. Principal components analysis of microhabitat for 120 seedlings (sampling points) Axis I (40 % of the variance) is a microtopographic position/water table depth-nutrient availability/temperature gradient. Axis II (16% of the variance) is a nutrient availability-temperature/ph gradient (see Table 1).

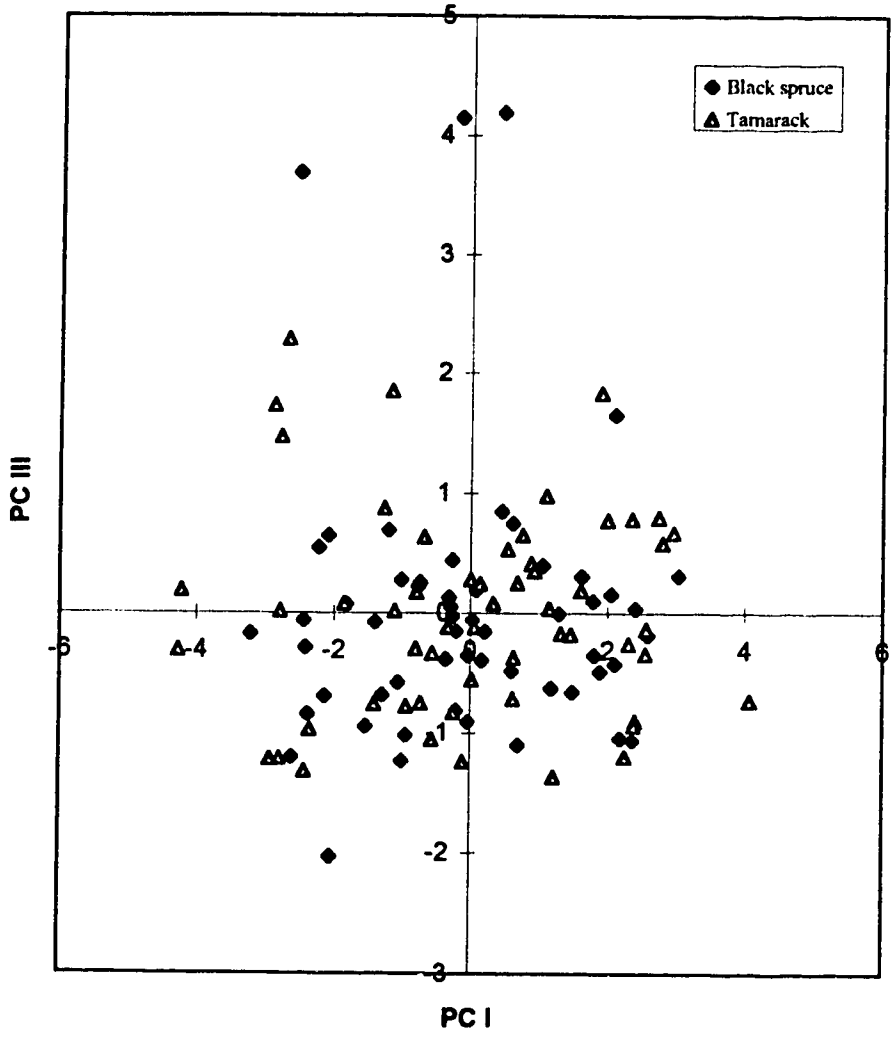

Figure 2. Principal components analysis of microhabitat for 120 seedlings (sampling points). Axis I (40% of the variance) is a nutrient availability-temperature/ph gradient (see Table 1). Axis III (13% of the variance) is a nitrate availability - microtopographic position gradient (see Table 1).

CHAPTER IV

DISCUSSION

Microhabitat

There were correlations among microhabitat variables (Table 2) and much of the variation in microhabitat was associated with changes in microtopographic position. Moving down the microtopographic gradient from high (hummock) positions to lower (towards hollows) positions there was a increase in NH_4^+ availability, and PO_4^{3-} availability, and microhabitats were cooler, wetter, and rooting depth was restricted by reductions in the aerated layer. Soil pH was not significantly correlated with microtopography as has been found with soil water pH in other studies (Karlin and Bliss 1984; Vitt *et al* 1975), but it was strongly correlated with depth of aeration, and water table depth both of which are directly affected by microtopography (Table 3).

The PCA revealed that the seedlings of both species, as a whole, did not occur on distinct microhabitats, but rather across a range of continuous microhabitat variables. Tamarack and black spruce could not be separated based on the microhabitats in which they had established. This is similar to results from a minerotrophic peatland in New York, where seedlings of four different coniferous tree species grew on the same subset of available microhabitats (St. Hilaire and Leopold 1995). Since microhabitats were only characterized where seedlings had already established, it is not known whether the seedling occurred on the whole range of microhabitats available in the peatland or, more

likely, a subset of them. It is possible that black spruce and tamarack occur across the same range of microhabitat because it is the only portion of available habitat suitable for both establishment and further tree growth.

Foliar Nutrients

The concentration of foliar nutrients was affected by microhabitat for both species (Table 4 and 5). Based on the amount of variation explained, microhabitat had a greater influence on the levels of foliar nutrients in tamarack than in black spruce. The weaker relationship between microhabitat and black spruce foliar nutrients may be due to the evergreen nature of black spruce. Older needles may act as a nutrient source, allowing translocation of nutrients to new needles during periods of high demand and when nutrient availability is low (Chabot and Hicks 1982). Although Greenway *et al* (1992) reported no evidence of an increase in nutrient retranslocation from older needle cohorts in black spruce during simulated nutrient deficiency, the normal seasonal translocation of nutrients from older needles in the spring (Tyrrell and Boerner 1987) may be sufficient to reduce the effect of varying microhabitat on foliar nutrients in black spruce.

Foliar nitrogen concentration was influenced by nitrate availability in black spruce and ammonium availability in tamarack. As ammonium and nitrate are the forms of nitrogen that can be taken up by higher plants, one would expect foliar nitrogen to be driven by the available forms of nitrogen, but a difference between the nitrogen source affecting foliar nitrogen concentration in black spruce and tamarack was not expected.

Preference for ammonium versus nitrate as a nitrogen sou ce varies between species. For example, cranberry only uses ammonium, while radish is intolerant to ammonium (Chapin *et al.* 1987). Cultivars of barley from warm and cold soils have been found to have similar ammonium influx, while nitrate influx has been found to be lower in cultivars from colder soils (Chapin 1985).

In non-photosynthetic tissue nitrate assimilation has a substantial cost (Pate 1983). A substantial amount of organic acid is required to counter OH^- generated in nitrate assimilation, resulting in a substantial amount of reduced carbon in the form of the organic acid ion (Raven and Smith 1976); this can require as much as 15 % of the energy production of the plant (Chapin *et al.* 1987). Ammonium assimilation, which must be driven by respiration in roots because respiration provides the energy (Chapin *et al.* 1987) and reductant required for glutamine and glutamate synthesis (Oaks and Hirel 1985), is less costly than nitrate assimilation. Conlin and Lieffers (1993) found that tamarack had the ability to transport oxygen to root tissues and was able to sustain limited respiration under anaerobic conditions, while black spruce did not have this ability. If tamarack is able to sustain respiration in the cold anaerobic conditions, like those found in peatlands, then this would enable it to assimilate ammonium in its roots. This may explain why tamarack foliar nitrogen had a higher correlation with ammonium availability, and black spruce foliar nitrogen was more correlated with nitrate availability. It may also play a role in the greater positive response of tamarack foliar nitrogen to urea fertilization than black spruce (Mugasha *et al* 1993), and explain how a deciduous species like tamarack is able to balance its nitrogen demand in nutrient poor peatland conditions.

Foliar concentrations of phosphorous and potassium in black spruce and phosphorous in tamarack were all negatively affected by lower soil temperatures. This could reflect the effect of cold soils on root growth and function. Low soil temperatures have been found to reduce the growth and affect the metabolism of roots (Lopushinsky and Kaufmann 1984, Conlin and Lieffers 1993). Warmer microsites may have had improved root growth and functioning, leading to an increase in the uptake of nutrients and higher foliar nutrient concentrations. Unlike phosphorous concentration, the concentration of nitrogen in tamarack foliage decreased as the relative temperature of microsites increased (Table 4). This is explained by the higher NH_4^+ availability in lower, cooler microsites, and the effect of available NH_4^+ on tamarack foliar nitrogen concentration which has previously been discussed.

Gas Exchange and Foliar Nutrients

There were strong relationships between foliar nutrients and gas exchange, suggesting non-stomatal factors play an important role in limiting photosynthesis biochemically. The strong correlations between foliar nitrogen and both net assimilation and residual conductance for both species are consistent with the results of Macdonald and Lieffers' (1990) work on black spruce and tamarack, and similarly could indicate a nitrogen limitation causing carboxylation resistance (Evans 1989). Tilton (1977) and Sherrif *et al* (1986) have also suggested that net assimilation in conifers can be limited by nitrogen. With 75% of foliar nitrogen invested in chloroplasts, and the majority of chloroplast nitrogen involved in photosynthesis (ie. light harvesting complexes, electron

transport proteins, and Rubisco) (Chapin *et al* 1987), the effect of foliar nitrogen on net assimilation and residual conductance is not surprising. Nitrogen limitation can ultimately lead to reduction in enzyme synthesis and a reduction in the rates of biochemical reactions associated with carbon dioxide fixation.

Water use efficiency was also correlated with nitrogen for both species. If higher levels of nitrogen lead to increases in net assimilation, this increase would also be reflected in an increase in water use efficiency, further supporting the contention of non-stomatal limitations of photosynthesis. Higher water use efficiency has been shown to be associated with higher leaf nitrogen content in *Pinus radiata* (Sheriff *et al* 1986) and *Ulmus americana* L. (Reich *et al* 1989) and non-stomatal limitations have been shown to be greater than stomatal limitations in plants grown with low levels of available nitrogen and subject to drought (Reich *et al.* 1989). Stomatal conductance in black spruce was also correlated with leaf nitrogen again suggesting non-stomatal limitation.

The increase seen in net assimilation and residual conductance of the tamarack seedlings with increasing foliar phosphorous concentration suggests there may have been a phosphorous limitation as well. This is similar to the results of Mugasha *et al.* (1993), who found that fertilization of tamarack, growing in peatlands, with P-K increased foliar P levels and increased needle mass, which they suggested was attributable to a phosphorous limitation prior to fertilization. The decrease in net assimilation and residual conductance of black spruce seedlings as foliar phosphorous increased, indicates that they were not limited by foliar phosphorous.

Gas Exchange and Microhabitat

Similar to foliar nitrogen concentration, the values of net assimilation, water use efficiency, and mesophyll conductance were affected by the availability of nitrate and ammonium. As previously discussed the availability of nitrogen impacts on foliar nitrogen levels, and foliar nitrogen affects net assimilation, water use efficiency, and mesophyll conductance in both species. So the impact of nitrogen availability on gas exchange is brokered through their effect on foliar nutrients. As shown for foliar nitrogen, the gas exchange variables were positively correlated with nitrate availability for black spruce, while those for tamarack were positively correlated with ammonium availability. This again could indicate a difference in preference for the form of nitrogen uptake, or differential abilities in uptake of different forms of nitrogen between species.

The higher growth rates (relative, and average annual growth rates) in black spruce on warmer microsites is consistent with results of other studies. Low soil temperatures have been found to reduce shoot growth in Douglas-fir seedlings (Lopushinsky and Kaufman 1984), white spruce (Brand 1990) and also a variety of other vascular plant species (Anderson and McNaughton 1973). This may be the result of the impact cold soils have on gas exchange. Low soil temperatures have been found to reduce stomatal conductance, transpiration, and net photosynthesis (Turner and Jarvis 1974; Day *et al.* 1991; Day *et al.* 1990; Kramer 1942; Lawrence and Oechel 1983). This in turn may lead to reduction in growth rate, and may explain some of the variability in growth found within even aged peatland black spruce (Lieffers 1986; Groot and Horton 1994; Yin 1992). Variation in growth of both black spruce and tamarack may also be attributable to

variation in net assimilation resulting from variation in microhabitat. Microhabitat impacted gas exchange both through its effect on foliar nutrients and also directly. Ultimately variations in net assimilation are expected to lead to variations in growth rate (Brand 1990, Lamhamedi and Bernier 1994).

Conclusion

This work established that there are microhabitats that are relevant to peatland trees and that do affect their performance. These microhabitats are not discrete, but rather consist of interconnected gradients of resources and environmental conditions. Black spruce and tamarack grow on the same range of these gradients and conditions, and do not show niche separation in relation to microhabitat. It is possible that black spruce and tamarack have differential uptake abilities or preferences for different nitrogen forms (NH_4^+ for tamarack and NO_3^- for black spruce). This may indicate niche partitioning of available nitrogen, and it also may explain the presence of a deciduous conifer (tamarack) in a nutrient poor environment.

Previous studies of tree seedling response to microhabitat variation have focused on seedling growth (Kuuluvainen 1993; Adams 1974; Messier and Kimmins 1992), while in this study I also quantified the response of foliar nutrients and gas exchange to microhabitat variation. Microhabitat variation was correlated with foliar nutrient concentration in both species, and foliar nutrients, in turn, were correlated with gas exchange. The variation in gas exchange may, in turn, result in some of the variation in growth rates that has been observed within even aged peatland stands (Yin 1992). In

addition, black spruce growth rates were also correlated with soil temperature which, due to the range of soil temperature found along the hummock to hollow gradient, could also help explain the variance in black spruce growth in peatlands.

Further research is needed to examine the affinity of black spruce and tamarack for different forms of nitrogen, to determine whether there are differences and whether any differences are due to the soil conditions or to species preferences. These questions could be answered with both controlled environment and *in situ* studies, in a variety of soil conditions (anaerobic vs. aerobic soil conditions; warm vs. cold soils). Controlled environment studies on the influence of nitrogen source, and also of soil conditions on foliar nutrients, gas exchange, and nitrogen metabolism may also be useful. Additional work also needs to be done on how far into the life of the tree it is affected by microhabitat variations, and when do variations in microhabitat cease to be of importance. This study did not examine the impacts of variation in microhabitat on root growth. An examination of the variation in root biomass and fine root production along microhabitat gradients, though difficult to do in a field setting, would be extremely informative.

LITERATURE CITED

Adams, S.N. 1974. Some relations between forest litter and growth of sitka spruce on poorly drained soils. J. Appl. Ecol. **11**: 761-765.

Anderson, J.E., and McNaughton, S.J. 1973. Effects of low soil temperature on transpiration, photosynthesis, leaf relative water content, and growth among elevationally diverse plant populations. Ecology **54**: 1220-1233.

Andrus, R.E., Wagner, D.J., and Titus, J. E. 1983. Vertical zonation of *Sphagnum* mosses along hummock-hollow gradients. Can. J. Bot. **61**: 3128-3139.

Beatty, S.W. 1984. Influence of microtopography and canopy species on spatial patterns of forest understory plants. Ecology **65**: 1406-1419.

Bell, G., Lechowicz, M.J., and Schoen, D.J. 1991. The ecology and genetics of fitness in forest plants. III. Environmental variance in natural populations of *Impatiens pallida*. J. Ecol. **79**: 697-713.

Bernard, J.M., Seischab, F.K., and Gauch, H.G., Jr. 1983. Gradient analysis of the vegetation of the Byron-Bergen swamp, a rich fen in western New York. Vegetatio **53**: 85-91.

Binkley, D., and Matson, P. 1983. Ion exchange resin bag method for assessing forest soil nitrogen availability. Soil Sci. Soc. Am. J. **47**: 1050-1052.

Bloom, A.J. 1985. Wild and cultivated barleys show similar affinities for mineral nitrogen. Oecologia **65**: 555-557.

Boerner, R.E.J., and Koslowsky, S.D. 1989. Microsite variation in soil chemistry and nitrogen mineralization in a beech-maple forest. Soil Biol. Biochem. **21**: 795-801.

Bonan, G.B., and Shugart, H.H. 1989. Environmental factors and ecological processes in boreal forests. Annu. Rev. Ecol. Syst. **20**: 1-28.

Brand, D.G. 1990. Growth analysis of responses by planted white pine and white spruce to changes in soil temperature, fertility, and brush competition. Forest Ecol. and Mgmt. **30**: 125-138.

Bubier, J.L., Moore, T.R., and Roulet, N.T. 1993. Methane emissions from wetlands in the midboreal region of northern Ontario, Canada. Ecology **74**: 2240-2254.

Bubier, J., Costello, A., Moore, T.R., Roulet, N.T., and Savage, K. 1993. Microtopography and methane flux in boreal peatlands, northern Ontario, Canada. Can. J. Bot. **71**: 1056-1063.

Caemmerer, S., von, and Farquhar, G.D. 1981. Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. Planta **153**: 376-387.

Carnell, R., and Anderson, M.A. 1986. A technique for extensive field measurement of soil anaerobism by rusting of steel rods. Forestry **59**: 129-140.

Chabot, B.F., and Hicks, D.J. 1982. The ecology of leaf life spans. Ann. Rev. Ecol. Syst. **13**: 229-259.

Chapin, F.S. III, Bloom, A.J., Field, C.B., and Waring, R.H. 1987. Plant responses to multiple environmental factors. Bioscience **37**: 49-57.

Collins, S.L. 1990. Habitat relationships and survivorship of tree seedlings in hemlock-hardwood forest. Can J. Bot. **68:** 790-797.

Collins, S.L., and Good, R.E. 1987. The seedling regeneration niche: habitat structure of tree seedlings in an oak-pine forest. Oikos **48**: 89-98.

Conlin, T.S.S., and Lieffers, V.J. 1993. Anaerobic and aerobic CO_2 efflux rates from boreal forest conifer roots at low temperatures. Can. J. For. Res. **23**: 767-771.

Dang, Q.L., Lieffers, V.J., Rothwell, R.L., and Macdonald S.E. 1991. Diurnal variation and interrelations of ecophysiological parameters in three peatland woody species under different weather and soil moisture conditions. Oecologia **88**: 317-324.

Day, T.A., and DeLucia, E.H., Smith, W.K. 1990. Effect of soil temperature on stem sap flow, shoot gas exchange and water potential of *Picea engelmannii* (Parry) during snowmelt. Oecologia **84**: 474-481.

Day, T.A., Heckathorn, S.A., and DeLucia, E.H. 1991. Limitations of photosynthesis in *Pinus taeda* L. (loblolly pine) at low soil temperatures. Plant Physiol. **96**: 1246-1254.

Delcourt, H.R., Delcourt, P.A., and Thompson, Webb III. 1983. Dynamic plant ecology: The spectrum of vegetational change in space and time. Quartenary Science Review **1**: 153-175.

Delucia, E.H. 1986. Effect of low root temperature on net photosynthesis, stomatal conductance and carbohydrate concentration in Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) seedlings. Tree Phys. **2**: 143-154.

DeLucia, E.H., and Smith, W.K. 1987. Air and soil temperature limitations on photosynthesis in Engelmann spruce during summer. Can. J. For. Res. **17**: 527-533.

Evans, J.R. 1989. Photosynthesis and nitrogen relationships in leaves of C_3 plants. Oecologia **78**: 9-19.

Greenway, K.J., Macdonald, S.E., and Lieffers, V.J. 1992. Is long-lived foliage in *Picea mariana* an adaptation to nutrient-poor conditions? Oecologia **91**: 184-191.

Groot, A., and Horton, B.J. 1994. Age and size structure of natural and second-growth peatland *Picea mariana* stands. Can. J. For. Res. **24**: 225-233.

Grubb, P.J. 1977. The maintenance of species-richness in plant communities: The importance of the regeneration niche. Biol. Rev. **52**: 107-145.

Hartgerink, A.P., and Bazzaz, F.A. 1984. Seedling-scale environmental heterogeneity influences individual fitness and population structure. Ecology **65**: 198-206.

Hollinger, D.Y. 1992. Leaf and simulated whole-canopy photosynthesis in two co-occurring tree species. Ecology **73**: 1-14.

Jeglum, J.K. 1974. Relative influence of moisture-aeration and nutrients on vegtation and black spruce growth in northern Ontario. Can. J. For. Res. **4**: 114-126.

Johnson, L.C., and Damman, A.W.H. 1991. Species-controlled *Sphagnum* decay on a south Swedish raised bog. Oikos **61**: 234-252.

Jones, H.G. 1985. Partitioning stomatal and non-stomatal limitations to photosynthesis. Plant Cell Environ. **8**: 95-104.

Karlin, E.F., and Bliss, L.C. 1984. Variation in substrate chemistry along microtopographical and water-chemistry gradients in peatlands. Can. J. Bot. **62**: 142-153.

Knapp, A.K., and Smith, W.K. 1982. Factors influencing understory seedling establishment of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) in southeast Wyoming. Can. J. Bot. **60**: 2753-2761.

Kozlowski, T.T. 1982. Water supply and tree growth. Part II. Flooding. For. Abstr. **43**: 145-161.

Kozlowski, T.T. 1986. Soil aeration and growth of forest trees. Scand. J. For. Res. 1: 113-123.

Kramer, P.J. 1942. Species differences with respect to water absorption at low soil te[illegible]res. Amer. J. Botany **29**: 828-833.

Kuuluvainen, T., Hokkanen, T. J., Jarvinen, E., and Pukkala, T. 1993. Factors related to seedling growth in a boreal Scots pine stand: a spatial analysis of a vegetation-soil system. Can. J. For. Res. **23**: 2101-2109.

Lamhamedi, M.S., and Bernier, P.Y. 1994. Ecophysiology and field performance of black spruce (*Picea mariana*): A review. Ann. Sci. For. **51**: 529-551.

Latham, R.E. 1992. Co-occurring tree species change rank in seedling performance with resources varied experimentally. Ecology 73: 2129-2144.

Lawrence, W.T., and Oechel, W.C. 1983. Effects of soil temperature on carbon exchange of taiga seedlings. II. Photosynthesis, respiration, and conductance. Can. J. For. Res. **13**: 850-859.

Lechowicz, M.J., and Bell, G. 1991. The ecology and genetics of fitness in forest plants. II. Microspatial heterogeneity of the edaphic environment. J. Ecol. **79**: 687-696.

Lechowicz, M.J., Schoen, D.J., and Bell, G. 1988. Environmental correlates of habitat distribution and fitness components in *Impatiens capensis* and *Impatiens pallida*. J. Ecol. **76**: 1043-1054.

Lieffers, V.J., and Rothwell, R.L. 1986. Effects of depth of water table and substrate temperature on root and top growth of *Picea mariana* and *Larix laricina* seedlings. Can. J. For. Res. **16**: 1201-1206.

Lieffers, V.J., and Rothwell, R.L. 1987. Rooting of peatland black spruce and tamarack in relation to depth of water table. Can. J. Bot. **65**: 817-821.

Lieffers, V.J. 1986. Stand structure, variability in growth and intraspecific competition in a peatland stand of black spruce *Picea mariana*. Holarctic Ecology **9**: 58-64.

Lindholm, T., and Markulla, I. 1984. Moisture conditions in hummocks and hollows in virgin and drained sites on the raised bog Laaviosuo, southern Finland. Ann. Bot. Fennici. **21**: 241-255.

Lopushinsky, W., and Kaufmann, M.R. 1984. Effects of cold soil on water relations and spring growth of Douglas-fir seedlings. Forest Sci. **30**: 628-634.

Lowther, J.R. 1980. Use of a single sulphuric acid-hydrogen peroxide digest for analysis of *Pinus radiata* needles. Commun. Soil Sci. Plant Anal. **11**: 175-188.

Macdonald, S.E., and Lieffers, V.J. 1990. Photsynthesis, water relations, and foliar nitrogen of *Picea mariana* and *Larix laricina* from drained and undrained peatlands. Can. J. For. Res. **20**: 995-1000.

Malmer, N. 1986. Vegetational gradients in relation to environmental conditions in northwestern European mires. Can. J. Bot. **64**: 375-383.

Mead, D.A. 1978. Comparative height growth of eastern larch and black spruce in northwestern Ontario. For. Chron. **54**: 296-297.

Messier, C., and Kimmins, J. P. 1992. Growth of western red cedar seedlings in relation to microtopography, forest floor nutrient status, and fireweed and salal on clear-cut sites in coastal British Columbia. Can. J. For. Res. **22**: 273-278.

Montague, T.G., and Givnish, T.J. 1996. Distribution of black spruce vs. eastern larch along peatland gradients: relationship to relative stature, growth rate, and shade tolerance. Can. J. Bot. in press.

Moore, T.R. 1989. Growth and net production of *Sphagnum* at five fen sites, subarctic eastern Canada. Can. J. Bot. **67**: 1203-1207.

Mugasha, A.G., Pluth, D.J., and Hillman, G.R. 1993. Foliar responses of tamarack and black spruce to drainage and fertilization of a minerotrophic peatland. Can. J. For. Res. **23**: 166-180.

Oaks, A., and Hirel, B. 1985. Nitrogen metabolism in roots. Ann. Rev. Plant Physiol. **36**: 345-365.

Ohlson, M., and Zackrisson, O. 1992. Tree establishment and microhabitat relationships in north Swedish peatlands. Can. J. For. Res. **22**: 1869-1877.

Oswald, B.P., and Neuenschwander, L.F. 1993. Microsite variability and safe site description for western larch germination and establishment. Bulletin of the Torrey Bot. Club **120**: 148-156.

Pate, J.S. 1981. Patterns of nitrogen metabolism in higher plants and their ecological significance. *In* J.A. Lee, S. McNeill, and I.H. Rorison *eds*. Nitrogen as an Ecological Factor. The 22nd Symposium of the British Ecological Society. Oxford, England, 1981. pp 225-255.

Payandeh, B. 1973. Analysis of forest drainage experiment and microhabitat relationships in north Swedish peatlands. Can. J. For. Res. **22**: 1869-1877.

Raven, J.A., and Smith, F.A. 1976. Nitrogen assimilation and transport in vascular land plants in relation to intracellular pH regulation. New Phytol. **76**: 415-431.

Reich, P.B., Walters, M.B., and Tabone, T.J. 1989. Response of *Ulmus americana* seedlings to varying nitrogen and water status II. Water and nitrogen use efficiency in photosynthesis. Tree Physiol. **5**: 173-184.

Ruel, J.C., Loustau, D., and Pineau, M. 1988. Relations entre la microtopographie, les caracteristiques de la couverture morte et la repartition des essences dans une erabliere a Bouleau jaune. Can. J. For. Res. **18**: 1196-1202.

Sheriff, D.W., Nambiar, E.K.S., and Fife, D.N. 1986. Relationships between nutrient status, carbon assimilation and water use efficiency in *Pinus radiata* (D. Don) needles. Tree Physiology **2**: 73-88.

Small, E. 1972a. Photosynthetic rates in relation to nitrogen recycling as an adaptation to nutrient deficiency in peat bog plants. Can J. Bot. **50**: 2227-2233.

Small, E. 1972b. Ecological significance of four critical elements in plants of raised sphagnum peat bogs. Ecology **53**: 498-502.

St. Hilaire, L.M., and Leopold, D.J. 1995. Conifer seedling distribution in relation to microsite conditions in a central New York forested minerotrophic peatland. Can. J. For. Res. **25**: 261-269.

Steel, R.G.D., and Torrie, J.H. 1980. Principles and Procedures of Statistics. A Biometrical Approach. 2nd Ed. McGraw-Hill Publishing Co., Toronto, Ont., Canada. 633pp.

Swanson, L.E., and Rothwell, R.L. 1989. Substrate freeze-thaw in a drained Alberta fen. Can. J. For. Res **19**: 1024-1029.

Swanson, L.E., and Rothwell, R.L. 1986. Thawing of ground frost on a drained and undrained boreal wetland site. Amer. Water Res. Assoc. **July**: 231-236.

Tabachnick, B.G., and Fidell, L.S. 1989. Using Multivariate Statistics. 2nd Edition HarperCollins Publishers, Inc., New York, New York, U.S.A. 255pp.

Tarnocai, C. 1984. Peat resources of Canada. Natl. Res. Counc. Can., Ottawa, Ont., Canada. Publ. 24140. 17pp.

Tilton, D.L. 1977. Seasonal growth and foliar nutrients of *Larix laricina* in three wetland ecosystems. Can. J. Bot. **55**: 1291-1298.

Turner, N.C., and Jarvis, P.G. 1974. Photosynthesis in sitka spruce (*Picea sitchensis* (Bong.) Carr.) IV. Response to soil temperature. J. Appl. Ecol. **12**: 561-576.

Tyrrell, L.E., and Boerner, R.E.J. 1987. *Larix laricina* and *Picea mariana*: relationships among leaf life-span, foliar nutrient patterns, nutrient conservation, and growth efficiency. Can. J. Bot. **65**: 1570-1577.

Vitt, D.H. 1990. Growth and production dynamics of boreal mosses over climatic, chemical and topographic gradients. Bot. J. Lin. Soc. **104**: 35-59

Vitt, D.H., Bayley, S.E., and Tai-Long, J. 1995. Seasonal variation in water chemistry over a bog-rich fen gradient in Continental Western Canada. Can. J. Fish. Aquat. Sci. **52**: 587-606.

Vitt, D.H., Crum, H., and Snider, J.A. 1975. The vertical zonation of *Sphagnum* species in hummock-hollow complexes in northern Michigan. Mich. Bot. **14**: 190-200.

Yin, F.Y. 1992. Msc. Thesis, University of Alberta.

Zaerr, J.B. 1983. Short-term flooding and net photosynthesis in seedlings of three conifers. Forest Sci. **29**: 71-78.

Zoltai, S.C. 1988. Wetland Environments and Classification. *In* Wetlands of Canada. Ecological Classification Series, No. 24. National Wetlands Working Group, Canada Committee on Ecological Land Classification. Ottawa. pp. 1-23

APPENDIX A

DATA SUMMARY

Table A1. Microhabitat characteristics for all black spruce and tamarack seedlings.

Species	#	Micro Positon	NO3 Avail.	NH4 Avail.	PO4 Avail.	pH	Avg Temp Rank	Aeration Depth	Water Table Depth	Avg Soil Temp
BS	2	19	1.39	11.95	2.76	6.79	92.2	4.8	18.73	7.79
BS	3	14.7	3.07	5.2	1.68	6.85	76.8	-0.8	11.13	9.06
BS	4	17.1	1.59	3.73	1.54	7.52	90.4	7.5	22.20	7.99
BS	5	11.4	1.35	5.41	1.07	7.65	91.6	4.8	28.70	8.05
BS	7	16.1	0.75	3.24	1.34	6.82	94.8	7.8	23.93	7.99
BS	9	15.5	0.87	8.89	2.78	7.24	97	5.9	17.37	7.89
BS	10	35.3	1.17	3.71	0.36	6.95	77.6	25.6	35.73	9.06
BS	13	3.6	0.87	10.14	2.3	5.74	114.8	10.2	26.50	5.21
BS	15	11.2	0.91	6.98	0.49	7.28	65.2	9.2	21.90	9.77
BS	17	29.2	1.17	4.05	0.99	7.1	119	10.8	30.70	3.39
BS	25	43.7	0.83	4.09	2.59	7.41	3	32.8	44.17	15.03
BS	29	34.8	0.63	7.02	2.29	4.54	11.6	29.6	37.50	13.41
BS	30	30.3	0.85	1.68	0.35	7.08	8.2	16.4	44.67	13.71
BS	31	43.6	1.05	9.29	0.74	6.41	82.8	29.9	39.03	8.65
BS	32	31.5	1.19	2.88	0.38	6.84	38.2	21.2	24.37	11.44
BS	33	36	1.22	3.17	0.29	5.03	18.8	23.9	45.87	12.80
BS	39	22.9	1.38	4.84	1.31	6.81	53.8	6	10.93	10.32
BS	41	21.7	1.37	5.57	1.21	5.65	59	12.9	26.87	10.07
BS	42	8.3	1.4	2.08	2.03	6.55	37.4	-4.8	15.57	11.39
BS	44	7.8	1.04	11.15	1.27	6.75	36.2	19.6	23.13	11.44
BS	45	6.5	1.36	6.18	4.58	4.85	93.4	1.3	5.53	7.99
BS	46	20.6	1.3	10.03	0.7	6.93	25.6	10.6	23.77	12.09
BS	47	27	0.94	6.68	0.33	6.36	42.2	13.1	39.67	11.13
BS	50	30.9	0.84	6.09	1.92	6.42	56	28.1	29.47	10.32
BS	51	18.3	1	2.34	2.15	4.17	30.8	12	32.10	11.79
BS	52	20.2	1.09	3.63	1.48	6.92	48	12.8	29.20	10.68
BS	53	9.8	0.95	6.62	1.43	7.34	81	2.7	23.47	8.91
BS	54	19.6	0.94	2.36	0.74	4.51	40.6	20.1	28.77	11.18
BS	55	18.5	0.96	2.05	0.96	7.18	57.6	16.8	26.13	10.22
BS	56	26.2	1.54	6.97	0.72	6.83	39.2	23.1	26.97	11.59
BS	57	26.2	3.09	8.53	0.82	6.96	48.4	16.2	25.03	10.73
BS	58	30.7	1.54	5.42	0.57	7.04	100.4	16.6	28.37	7.64
BS	61	41.6	2.89	2.82	1.61	7.77	78	3.4	38.53	9.16
BS	63	38.1	1.41	2.7	0.4	3.22	27.4	25.4	55.83	11.99
BS	64	21.6	1.48	7.8	0.41	6.03	43.6	13.2	36.27	11.03
BS	65	40.4	0.52	1.97	0.9	7.21	7.2	21.4	46.33	14.52
BS	67	32.2	0.93	1.63	0.31	7.05	9	22.5	41.70	13.66
BS	68	25.5	1.12	5.6	0.84	7.52	17	19.8	30.80	12.90
BS	69	39.3	1.85	8.9	1.33	4.99	52.8	31	35.20	10.52
BS	70	23.3	1.35	4.09	0.32	7.7	96	8.8	20.10	7.13
BS	71	24.8	1.38	2.09	0.39	6.77	83.8	12.6	42.23	8.65
BS	72	35.7	1	2.55	0.28	7.25	98.8	30.3	39.37	4.66
BS	73	13.7	1.15	11.35	1.21	6.95	108.2	7	15.67	6.88
BS	74	31.5	1.36	7.5	0.33	5.49	44.6	18	34.07	10.93
BS	75	12	0.44	2.96	1.08	7.17	90.4	0	7.73	8.25
BS	80	20.5	1.21	5.78	0.74	7.3	106.6	3.5	19.03	7.13
BS	81	18.2	1.02	3.14	0.64	7.59	116	9.2	17.67	4.81
BS	82	21.2	1.23	4.35	0.56	7.47	101.2	21.3	26.37	7.49
BS	83	39.1	1.13	3.73	0.27	7.28	24	10.3	44.67	12.25
BS	86	27.1	1.2	5.01	1.04	7.48	95.4	13.9	22.37	7.89
BS	87	23.1	1.05	5.4	0.3	7.1	25.8	10.4	44.43	12.04
BS	88	21	1.48	8.86	3.13	6.4	91.4	3.4	12.20	8.15
BS	94	26.2	1.02	5.09	0.78	6.56	98.6	13.3	25.17	7.74
BS	98	21.7	1.26	3.52	0.76	6.75	111.4	16.2	29.77	6.12
BS	99	28.2	0.97	2.96	0.3	7.43	22.4	30.4	38.20	12.40

Table A1 continued

Species	#	Micro Positon	NO3 Avail.	NH4 Avail.	PO4 Avail.	pH	Avg Temp Rank	Aeration Depth	Water Table Depth	Avg Soil Temp
BS	101	16.4	0.78	3.12	2.29	7.49	63	10.4	17.37	9.87
T	3	24.9	1.55	4.26	1.68	4.9	38.2	13.7	26.70	11.39
T	4	23.6	1.18	3.18	1.36	6.98	81	15.5	36.07	8.91
T	5	33	0.59	7.82	1.22	5.19	54.8	35	43.70	10.47
T	7	28.5	0.96	2.92	1.61	3.21	36.6	34	40.80	11.54
T	10	22.3	1.2	2.84	1.14	7.34	97.8	13.4	20.70	7.84
T	13	48.5	0.8	3.98	0.92	3.38	31.6	37.8	41.47	11.74
T	15	8.4	1.43	2.38	2.27	7.03	85.6	-2.2	11.50	8.50
T	16	26.1	1.47	2.91	0.91	7.03	6	16.8	39.90	14.47
T	17	14.3	0.72	4.09	3.65	6.42	112.2	4.8	18.40	5.72
T	19	16.7	1.14	7.25	1.52	7.33	47.6	20.3	18.30	10.73
T	21	24.1	1.07	4.84	1.06	6.94	62.8	25.9	25.97	9.87
T	22	37.5	0.72	4.51	1.22	4.55	25.7	25	44.33	12.19
T	23	4.8	0.93	2.57	1.87	6.5	104	-3	7.87	7.13
T	27	33.3	1.15	3.29	1.18	3.23	9.8	20.3	50.70	13.61
T	29	10.6	0.91	7.55	1.87	6.94	86.8	8.3	10.97	8.60
T	30	16	2.36	5.31	2.91	6.89	61	-0.5	5.93	10.02
T	31	27.9	1.41	8.75	2.43	6.51	16.4	11.4	27.23	12.95
T	33	22	1.35	3.67	1.38	6.95	42.8	8.4	27.33	11.03
T	35	14.4	1.18	7.57	8.72	6.96	56.2	-1.9	9.43	10.27
T	36	15.1	2.2	5.15	1.97	6.96	8.2	15.4	21.97	14.42
T	38	13.6	2.11	4.2	5.26	6.63	80	6.6	5.50	8.95
T	39	21.7	0.92	4.6	0.99	7.57	6.8	11.5	25.60	14.47
T	41	14.2	1.77	12.62	4.73	7.68	14.2	8.9	13.93	13.36
T	42	24.8	1.13	9.62	0.77	7.11	38.4	2.1	22.57	11.33
T	44	27.6	0.53	10.55	2.44	7.59	17.4	15.1	23.90	12.85
T	45	24.4	0.91	5.17	0.55	7.03	57.6	9 3	16.63	10.12
T	46	10.2	0.91	19.91	5.4	6.45	71.2	-0.3	7.20	9.46
T	47	25.3	1.23	3.25	0.48	6.06	30	29.6	21.90	11.79
T	51	24.4	0.69	3.74	1.29	4.89	14.6	24.1	33.83	13.00
T	52	20.9	1.41	9.49	0.99	5.27	43.6	18.9	27.97	10.95
T	53	5.6	0.73	12.65	1.65	6.37	34.8	-1.4	27.37	11.49
T	54	16.1	0.96	4.52	1.57	53	40.6	9	31.90	11.18
T	61	28.7	1.17	8.3	0.48	7.18	74.8	20	28.80	9.46
T	62	16.5	1.05	1.64	0.66	6.86	85.4	3.5	29.00	8.60
T	63	38.1	1.6	3.37	0.38	3.66	20.6	22.8	50.90	12.70
T	65	38.1	0.93	3.17	0.47	6.91	31.8	30.2	38.10	11.84
T	66	23	1.44	2.17	0.46	6.97	60	18.2	27.83	10.17
T	67	64.2	1.52	6.89	1.52	7.09	71.4	7	60.60	9.46
T	69	44.1	1.34	4.92	0.5	7.59	63.6	29.3	41.33	9.87
T	72	31.6	0.76	4.22	0.61	7.92	62.2	15.6	30.67	9.92
T	73	34.8	0.9	8.74	0.44	7.16	7.8	16.5	37.07	13.97
T	76	35	1.3	2.91	0.74	7.37	83.2	16.3	23.37	8.91
T	77	30.7	1.66	5.25	0.42	5.42	18.2	14.9	36.93	12.75
T	79	42.7	1.33	4.1	0.55	7.19	26.8	34.8	44.17	12.19
T	80	14.1	1.16	3.78	0.4	7.5	64.8	11.1	33.50	9.82
T	81	12	1.51	2.51	1.08	6.31	95.6	4.6	6.63	7.84
T	83	31.7	1.28	6.68	0.39	7.42	59.4	24.2	27.70	10.17
T	84	33.2	1.55	5.4	0.35	6.31	28.6	33	41.57	11.89
T	87	43.4	1.28	7.17	0.35	6.98	62	38.7	37.77	9.77
T	88	22.6	1.33	4.6	0.32	5.52	69.8	22.9	36.10	9.51
T	89	18.8	0.73	3.39	0.48	7.22	110.6	17.2	26.80	5.97
T	90	25.5	1.34	6.57	0.4	6.8	108.8	26	26.37	5.46
T	91	20.3	0.88	5.97	1.43	6.6	117.8	19.3	29.57	4.15
T	92	28.6	1.27	4.64	0.48	7.56	79.6	35	31.37	9.01
T	93	37.8	1.17	2.56	1.07	3.88	83.6	26.3	45.87	8.50
T	94	13	1.73	7.52	1.27	6.39	81.6	10.2	19.73	8.91

Note: Micro-position, aeration and water table depth are in cm above water table; nutrient availabilities are in µg/g of resin; soil temp is in degrees C.

Table A2. Foliar nutrient concentration, height growth, and age for each black spruce and tamarack seedling.

Species	#	Tot%N	Tot%P	Tot%K	Leader	Height	Age	RGR	Avg Growth
BS	2	0.829	0.099	0.486	6.1	68.6	13	8.89	5.28
BS	3	0.914	0.091	0.510	4.4	76.6	15	5.74	5.11
BS	4	0.756	0.062	0.480	2.4	37.6	11	6.38	3.42
BS	5	0.673	0.071	0.430	4.7	41.2	8	11.41	5.15
BS	7	0.629	0.104	0.466	2.7	32.2	9	8.39	3.58
BS	9	0.710	0.058	0.456	2.9	42.6	11	6.81	3.87
BS	10	0.722	0.051	0.359	4.9	51.3	16	9.55	3.21
BS	12	0.528	0.072	0.273	3.5		14		
BS	13	0.619	0.058	0.377	6.9	47.7	11	14.47	4.34
BS	15	7.123	0.545	0.310	3.2	55.2	13	5.80	4.25
BS	17	0.575	0.078	0.489	2.2	42.5	17	5.18	2.50
BS	23	0.740	0.107	0.454	3.9	26.5	9	14.72	2.94
BS	25	0.730	0.104	0.490	3.2	50.2	10	6.37	5.02
BS	27	0.816	0.127	0.645	4.6		10		
BS	29	0.785	0.100	0.507	5.6	60.7	17	9.23	3.57
BS	30	0.721	0.097	0.599	8.8	65.9	13	13.35	5.07
BS	31	0.671	0.139	0.500	1.8	42.8	11	4.21	3.89
BS	32	0.615	0.129	0.596	4.5	44	11	10.23	4.00
BS	33	0.654	0.098	0.535	4.7	52	9	9.04	5.78
BS	39	0.786	0.113	0.552	2.4	41	16	5.85	2.56
BS	41	0.631	0.111	0.528	2.7	51.1	17	5.28	3.01
BS	42	0.714	0.105	0.547	8.4	74.5	17	11.28	4.38
BS	44	0.534	0.093	0.373	1.7	38.7	11	4.39	3.52
BS	45	0.661	0.125	0.442	2.9	51.8	14	5.60	3.70
BS	46	0.816	0.100	0.494	6.8	63	11	10.79	5.73
BS	47	0.605	0.091	0.481	6.7	59.2	15	11.32	3.95
BS	50	0.468	0.067	0.276	2.3	36.5	16	6.30	2.28
BS	51	0.594	0.098	0.487	7.1	86	12	8.26	7.17
BS	52	0.725	0.120	0.435	3.6	37.2	11	9.68	3.38
BS	53	0.723	0.134	0.521	4.2	50.9	11	8.25	4.63
BS	54	0.798	0.104	0.470	5.7	44.2	13	12.90	3.40
BS	55	0.958	0.122	0.535	10.9	70	11	15.57	6.36
BS	56	0.924	0.094	0.382	6.5	47.3	9	13.74	5.26
BS	57	0.930	0.093	0.521	4.5	49	11	9.18	4.45
BS	58	0.721	0.103	0.462	4.8	58	13	8.28	4.46
BS	59	0.941	0.091	0.406	10.4	63.7	12	16.33	5.31
BS	61	0.698	0.109	0.433	2.8	48.7	15	5.75	3.25
BS	63	0.843	0.086	0.546	16	100	12	16.00	8.33
BS	64	0.852	0.118	0.538	9.7	67.6	9	14.35	7.51
BS	65	0.687	0.109	0.509	7.4	59.1	11	12.52	5.37
BS	67	0.905	0.118	0.423	8.6	66.8	12	12.87	5.57
BS	68	0.791	0.096	0.480	10.1	75	15	13.47	5.00
BS	69	0.721	0.067	0.402	4.7	53.6	11	8.77	4.87
BS	70	0.821	0.069	0.457	4.8	61.1	13	7.86	4.70
BS	71	0.648	0.074	0.417	5.3	56.4	8	9.40	7.05
BS	72	0.642	0.078	0.513	5.2	51.1	13	10.18	3.93
BS	73	0.702	0.094	0.422	4.6	44.8	11	10.27	4.07
BS	74	0.798	0.089	0.428	3	39.3	11	7.63	3.57
BS	75	0.650	0.074	0.372	2.4	32	13	7.50	2.46
BS	80	0.710	0.069	0.521	2	41.2	18	4.85	2.29
BS	81	0.863	0.086	0.459	4.7	59.1	17	7.95	3.48
BS	82	0.906	0.082	0.454	3.5	47.6	11	7.35	4.33
BS	83	0.693	0.088	0.450	3.8	48	14	7.92	3.43
BS	86	0.736	0.060	0.363	2.8	35	13	8.00	2.69
BS	87	0.827	0.083	0.546	7.3	75.8	11	9.63	6.89
BS	88	0.809	0.101	0.528	5.9	43.4	12	13.59	3.62
BS	94	0.680	0.051	0.364	2.2	29.3	16	7.51	1.83
BS	98	0.699	0.068	0.441	4.5	48.7	12	9.24	4.06
BS	99	0.635	0.063	0.352	4.4	68.1	15	6.46	4.54

Table A2 continued

Species	#	Tot%N	Tot%P	Tot%K	Leader	Height	Age	RGR	Avg Growth
BS	101	0.824	0.098	0.494	3.1	39.7	12	7.81	3.31
T	3	1.265	0.185	0.470	2.9	30.9	11	9.39	2.81
T	4	1.330	0.148	0.520	7.6	48.7	9	15.61	5.41
T	5	1.320	0.129	0.384	4.2	41.3	14	10.17	2.95
T	7	1.256	0.138	0.402	9.7	74	16	13.11	4.63
T	9	1.235	0.125	0.356	2.3	63.9	13	3.60	4.92
T	10	1.331	0.124	0.385	2.5	58.2	14	4.30	4.16
T	13	1.245	0.164	0.417	1	38.3	14	2.61	2.74
T	15	1.242	0.119	0.574	2.5	62.3	13	4.01	4.79
T	16	1.037	0.128	0.425	5.5	76.1	15	7.23	5.07
T	17	1.052	0.112	0.351	2.5	81.5	11	3.07	7.41
T	19	1.102	0.135	0.357	1.5	53.8	11	2.79	4.89
T	21	1.311	0.156	0.456	4.1	53.6	12	7.65	4.47
T	22	1.255	0.117	0.493	3.9	60.7	13	6.43	4.67
T	23	1.276	0.156	0.423	3	80.9	12	3.71	6.74
T	27	1.396	0.158	0.513	3.5	69	15	5.07	4.60
T	29	1.321	0.122	0.422	6.1	61.9	11	9.85	5.63
T	30	1.120	0.104	0.354	4.3	50.5	9	8.51	5.61
T	31	1.208	0.146	0.464	6.5	68.6	13	9.48	5.28
T	33	1.200	0.164	0.337	7.5	66.4	16	11.30	4.15
T	35	1.107	0.111	0.353	6.9	59.1	16	11.68	3.69
T	36	1.435	0.137	0.367	3.4	65	17	5.23	3.82
T	38	1.213	0.146	0.389	4.5	63.2	11	7.12	5.75
T	39	1.400	0.198	0.421	2.5	47.1	10	5.31	4.71
T	41	1.208	0.159	0.373	3.8	58.6	16	6.48	3.66
T	42	1.284	0.144	0.373	10.7	65.9	10	16.24	6.59
T	44	1.203	0.210	0.530	4.4	70.8	15	6.21	4.72
T	45	1.121	0.129	0.365	4.7	66.1	11	7.11	6.01
T	46	1.221	0.120	0.379	4.4	70.1	13	6.28	5.39
T	47	1.270	0.191	0.441	3.8	60.9	16	6.24	3.81
T	50	1.074	0.106	0.522	3.4		10		
T	51	1.361	0.228	0.574	7.5	83.9	16	8.94	5.24
T	52	1.478	0.198	0.548	3.4		15		
T	53	1.369	0.201	0.557	6.1		12		
T	54	1.105	0.140	0.478	5.1	71.5	12	7.13	5.96
T	57	1.387	0.164	0.424	7.5	64.1	11	11.70	5.83
T	61	1.203	0.097	0.382	4.7	55	11	8.55	5.00
T	62	1.212	0.158	0.390	7	84.8	15	8.25	5.65
T	63	1.372	0.108	0.495	15.8	98.4	12	16.06	8.20
T	65	1.014	0.098	0.563	2.6	94.2	15	2.76	6.28
T	66	1.098	0.100	0.503	5.8	83.5	15	6.95	5.57
T	67	1.208	0.140	0.418	3.4	54	15	6.30	3.60
T	69	1.144	0.105	0.360	4.5	58.4	14	7.71	4.17
T	71	1.173	0.100	0.462	3.6	75.2	11	4.79	6.84
T	72	1.304	0.105	0.383	4.6	81.3	21	5.66	3.87
T	73	1.255	0.141	0.441	0.8	65.7	13	1.22	5.05
T	76	1.112	0.109	0.389	1.4	41.3	13	3.39	3.18
T	77	1.273	0.113	0.491	4.5	64.8	13	6.94	4.98
T	79	1.240	0.121	0.470	2.1	61.8	10	3.40	6.18
T	80	1.494	0.092	0.431	6.7	67.1	13	9.99	5.16
T	81	1.290	0.077	0.371	1.4	41.1	17	3.41	2.42
T	83	1.367	0.110	0.525	4.4	48.8	13	9.02	3.75
T	84	1.599	0.127	0.587	7	104.1	19	6.72	5.48
T	87	1.531	0.140	0.530	3.5	55	19	6.36	2.89
T	88	1.552	0.115	0.531	4.5	51.8	15	8.69	3.45
T	89	1.431	0.102	0.485	8	51	16	15.69	3.19
T	90	1.661	0.129	0.425	4	63	14	6.35	4.50
T	91	1.593	0.109	0.425	3.2	54.2	16	5.90	3.39
T	92	1.225	0.124	0.360	7	58.4	13	11.99	4.49
T	93	1.350	0.148	0.433	7.4	68.8	14	10.76	4.91
T	94	1.529	0.126	0.400	3.7	67.7	13	5.47	5.21

Tot %N, %P, and %K are % of dry weight; leader and height are in cm; avg growth is in cm/year.

Table A3. Mean gas exchange values for each black spruce and tamarack seedling.

Species	Number	E	gs	NA	WUE	gm
BS	2	0.870	76.079	2.471	2.828	7.425
BS	3	0.962	110.789	2.656	2.782	7.985
BS	4	1.196	94.548	2.426	2.067	7.318
BS	5	1.396	99.612	2.335	1.768	7.017
BS	7	1.182	74.159	1.890	1.558	5.668
BS	9	0.945	72.246	2.171	2.309	6.517
BS	10	1.479	209.034	3.310	2.493	9.920
BS	12	1.293	124.087	1.241	1.408	3.775
BS	13	1.195	102.608	2.363	2.086	7.038
BS	15	0.947	85.127	2.274	2.482	6.781
BS	17	0.748	65.272	1.632	2.340	4.827
BS	23	1.147	121.655	1.998	1.795	5.888
BS	25	1.041	74.356	1.497	1.520	4.451
BS	27	1.413	103.487	2.190	1.676	6.501
BS	29	0.974	82.836	2.257	2.326	6.710
BS	30	0.927	87.248	2.102	2.494	6.245
BS	31	1.611	75.622	2.110	1.525	6.300
BS	32	1.054	86.240	1.997	1.921	5.830
BS	33	1.300	74.670	2.218	1.837	6.533
BS	39	1.024	87.064	2.782	2.626	8.108
BS	41	1.069	84.613	2.057	2.039	6.017
BS	42	0.900	99.686	2.073	2.374	6.065
BS	44	1.075	60.535	1.834	1.790	5.462
BS	45	0.807	67.709	1.749	2.178	5.142
BS	46	1.064	111.119	2.595	2.515	7.635
BS	47	0.873	94.031	1.987	2.336	5.856
BS	50	0.796	52.569	1.565	1.960	4.586
BS	51	0.794	108.860	1.819	2.345	5.339
BS	52	1.125	133.044	2.382	2.232	6.980
BS	53	1.234	77.395	2.063	1.663	6.244
BS	54	0.965	89.973	2.365	2.558	6.911
BS	55	1.250	124.767	2.701	2.263	8.085
BS	56	1.391	118.959	2.755	2.058	8.283
BS	57	1.107	81.856	2.564	2.343	7.696
BS	58	0.815	68.302	1.997	2.521	5.967
BS	61	0.697	56.843	1.967	2.856	5.861
BS	63	0.993	135.293	2.721	2.920	8.001
BS	64	1.042	107.365	2.777	2.818	8.267
BS	65	0.748	95.367	2.194	3.084	6.482
BS	67	0.851	111.853	2.335	3.118	6.777
BS	68	0.599	109.350	1.870	3.243	5.437
BS	69	0.742	65.440	1.943	2.819	5.699
BS	70	0.911	102.783	2.101	2.493	6.126
BS	71	1.099	68.092	2.050	1.976	6.007
BS	72	1.023	70.233	1.812	1.971	5.290
BS	73	0.971	59.507	2.044	2.088	5.959
BS	74	1.249	96.074	2.579	2.081	7.548

Table A3 continued

Species	Number	E	gs	NA	WUE	gm
BS	75	0.977	73.661	1.552	1.632	4.496
BS	80	1.159	89.472	2.120	1.884	6.094
BS	81	1.103	94.516	2.268	1.993	6.638
BS	82	1.314	96.423	2.990	2.308	8.728
BS	83	0.970	73.411	1.647	1.869	4.957
BS	86	1.582	118.301	2.904	1.885	8.508
BS	87	1.099	80.872	2.295	2.238	6.893
BS	88	1.147	90.410	2.491	2.234	7.460
BS	94	1.229	88.508	2.437	2.157	7.268
BS	98	1.120	74.902	2.225	1.979	6.631
BS	99	0.753	72.525	1.760	2.326	5.244
BS	101	1.253	119.572	2.901	2.297	8.557
T	3	1.173	130.324	2.130	1.842	6.397
T	4	1.018	103.900	2.266	2.359	6.779
T	5	1.022	110.320	2.197	2.223	6.538
T	7	0.765	109.005	1.894	2.648	5.642
T	10	1.157	127.312	1.992	1.800	5.867
T	13	0.975	109.552	1.865	2.189	5.501
T	15	1.023	110.801	1.753	1.809	5.125
T	16	0.887	83.275	1.398	1.651	4.175
T	17	0.846	66.784	1.239	1.472	3.682
T	19	0.899	59.020	1.492	1.680	4.475
T	21	1.045	95.550	1.960	2.064	5.808
T	22	0.923	75.769	1.899	2.213	5.632
T	23	0.941	87.169	1.795	1.988	5.239
T	27	0.986	89.023	2.068	2.150	6.054
T	29	1.233	98.433	2.249	1.851	6.627
T	30	0.926	99.389	1.819	2.035	5.235
T	31	0.778	104.638	1.977	2.560	5.623
T	33	0.762	99.067	2.072	2.760	5.824
T	35	0.656	88.088	1.693	2.646	4.788
T	36	1.159	103.435	2.177	1.883	6.407
T	38	1.078	102.198	1.833	1.785	5.410
T	39	1.169	152.556	1.964	1.723	5.781
T	41	0.905	91.828	1.587	1.776	4.681
T	42	0.869	310.970	1.979	2.400	5.801
T	44	1.062	103.224	1.873	1.924	5.535
T	45	1.002	101.760	1.436	1.657	4.263
T	46	0.982	114.448	1.689	1.869	4.991
T	47	0.837	158.406	1.900	2.295	5.582
T	50	1.035	92.194	1.909	1.926	5.580
T	51	0.972	147.361	1.850	2.066	5.504
T	52	1.369	106.500	2.345	1.796	7.062
T	53	1.264	100.220	2.078	1.720	6.247
T	54	0.879	74.502	1.335	1.597	4.023
T	57	1.177	84.777	1.876	1.648	5.624
T	61	0.992	109.524	1.642	1.686	4.899
T	62	0.941	87.518	1.668	1.903	4.968

Table A3 continued

Species	Number	E	gs	NA	WUE	gm
T	63	0.829	93.920	1.894	2.498	5.617
T	65	0.795	87.813	1.326	1.835	3.931
T	66	0.699	101.979	1.357	2.066	3.999
T	67	0.837	74.889	1.537	1.764	4.519
T	69	0.973	91.049	1.663	1.701	4.888
T	72	0.745	121.042	1.761	2.401	5.094
T	73	1.006	159.480	1.860	1.862	5.454
T	76	0.818	58.473	1.433	1.785	4.193
T	77	0.927	102.795	1.774	1.916	5.167
T	79	1.112	89.594	1.647	1.509	4.836
T	80	0.744	92.487	1.662	2.305	4.922
T	81	0.915	60.323	1.456	1.581	4.350
T	83	0.945	104.992	1.941	2.070	5.754
T	84	1.058	104.720	2.324	2.344	6.917
T	87	0.708	131.820	1.958	2.883	5.791
T	88	0.834	88.572	2.134	2.654	6.297
T	89	0.905	101.940	2.217	2.576	6.557
T	90	0.911	78.036	2.075	2.310	6.189
T	91	0.961	62.444	1.862	2.045	5.574
T	92	0.672	98.041	1.686	2.666	4.977
T	93	0.749	92.066	1.996	2.796	5.881
T	94	0.793	87.757	2.004	2.661	5.891

Note: Units same as Table 5. Values are means of four measurements.