LATITUDINAL GRADIENT ANALYSIS OF LOCAL SITE FACTORS INFLUENCING GROWTH IN THREE BOREAL TREE SPECIES

BY

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Abstract

Boreal tree species are affected by a range of factors including the climate and local site components ranging from nutrient availability to soil quality. It is important to understand what factors play a role in affecting tree growth in order to predict the effects a changing climate will have on tree species. Three common boreal tree species: *Larix laricina*, *Picea mariana* and *Picea glauca* were sampled along latitudinal gradients in northern and western Labrador to better understand how variations in local site factors like foliar nitrogen concentrations and rooting depth affect the radial growth of these species. It was hypothesized that there would be decreased levels of foliar nitrogen and lower growth at more northern sites, while radial growth at the southern sites would be more affected by the local site factors. Although no latitudinal trends were found in this study for any of the species, there was a functional group response observed in terms of the species relationships between foliar nitrogen concentrations and radial growth. *Larix laricina*, a deciduous conifer displayed increased growth with increased levels of nitrogen which is representative of the performance based growth strategy of this species. *Picea mariana* and *Picea glauca* are both evergreen conifers. These two species displayed conservative growth strategies with no response and a very weak response, respectively, in terms of their growth rates with foliar nitrogen concentrations. Rooting depth and tree height were also found to be contributing factors in association with radial growth for *Picea glauca*. The lack of any latitudinal growth responses in relation to the measured variables of this study makes it difficult to predict future growth trends in relation to global climate change, but it does provide an initial understanding of the different factors which could play a role in affecting growth.

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Table of Contents

List of Tables

List of Figures

Introduction

The climate is changing, and in some areas of the world the changes are more drastic than in others (Meehl *et al*. 2007). It is in the northern latitudes of the planet that the effects of climate change are expected to be most pronounced (Serreze *et al*. 2000). During the twentieth century alone the temperature increased over 0.6°C in this region (Houghton *et* al. 2001). The boreal forest is located within this northern geographic range from 45 to 70° north of the equator (Larsen 1980). The diversity of species assemblages found throughout the boreal range are simplistic, and the most common coniferous genera include spruce (*Picea*), fir (*Abies*), pine (*Pinus*), and larch (*Larix*) (Soja *et al*. 2007). Plant species found in the boreal region are limited by a range of biotic and abiotic interactions including soil moisture, nutrient availability, and insect infestations. In addition, substantial climatic variation exists throughout the region including variations in temperature and precipitation patterns (Bonan and Shugart 1989). These conditions along with other local and global factors interact to affect the growth of plant species in the boreal region, but how future climatic shifts will alter the growth regimes of these common species remains poorly understood.

Labrador is in the north-eastern region of Canada surrounded by the Labrador Sea to the east and by the province of Quebec to the south and west. Labrador is one of the few boreal forest regions in Canada with limited human interference on the landscape, and it is 60% covered in forest (Roberts *et al*. 2006). The tree species in Labrador are similar to other boreal locations, but they vary latitudinally with black spruce (*Picea mariana*) being most commonly found in the landscape up to 57°N latitude, while in the more northern regions up to 60°N there is a shift to white spruce (*Picea glauca*) dominating the landscape (Ryan 1978). This variation is due to both a mix of physiological characteristics of the individual species and local site characteristics which determine the type of species that can survive and dominate in an area.

Factors influencing boreal tree growth across latitudinal gradients

Latitudinal gradients provide a good theoretical framework to study the effects of changing resources and climatic effects on plant growth across a region. Gradients can be useful in predicting future effects of changing climate or nutrient availability on plants from one latitudinal site based on what plants at another site from higher or lower latitudes are doing in response to these same factors. Generally, there is an increase in species richness the closer in latitude to the equator one is (Allen *et al*. 1991). This same effect is found for elevation differences where more complex species richness is found at moderate to low elevations versus low species richness at higher elevations (Allen *et al*. 1991). Growth conditions around the equator are more consistent than the conditions plants encounter as their growth expands towards the southern and northern poles. Temperature and precipitation are relatively consistent on an annual basis in more tropical areas, while in the northern latitudes of the planet temperature and precipitation can fluctuate on a large scale. Other studies also show that diversity decreases with increasing latitude and that this is related to temperature differences (Qian and Ricklefs 2007; Qian 2008).

With increasing latitude, plants encounter a range of changes in climatic conditions as well as biotic and abiotic conditions that affect their growth. Increasing latitude causes a decline in temperature which is one of the main factors limiting the expansion and growth of trees. Increasing latitude lengthens the period of frost cover and shortens the time period of the frost-free growing season. Trees require a certain amount of heat in order to undertake growth each year. The latitudinal limits for tree growth are associated with the 10°C isotherm during the month of July, beyond this there is not a long enough period of heat to sustain the annual growth of tree species (Bryson 1966). Temperature affects many biological processes including germination, photosynthesis, and radial and apical growth (Schenk 1996). Apical growth or tree height can be negatively affected by the harsh conditions found in more northern locations, as taller trees are more exposed to winds (Gamache and Payette 2004). By being exposed, damage can occur to foliar tissue which may have negative effects later on for photosynthesis and growth, but if trees are shorter, they are better able to protect themselves with snowpack.

With the increasing temperature expected for Arctic regions, some studies have shown that this will help to release more of the trapped nutrients from the frozen soil (Robinson *et al*. 1995; Aerts 2006). The increases in temperature will allow the soil to thaw more quickly and for the soil microbes to decompose plant litter and nutrients into usable forms. Moisture is also an important factor in this whole process, as if there is not enough moisture in the soil, than the organisms responsible for the breakdown of plant litter into an inorganic form that plants can reuse will not be able to function properly. This is because the soils will dry out rapidly with the increase in temperature if there is not enough moisture input (Aerts 2006). Increases in temperature can also affect how litter is broken down both in the short- and long-term. Over short-term periods, individual microorganisms can adjust their chemistry through phenotypic responses, and in the long-term, the actual species present and breaking down the litter may change (Aerts 2006). It is possible that increasing temperatures may cause the expansion of some detritivoires into more northern latitudes and increase litter breakdown. All of these processes require a minimum amount of heat in order to function.

Plants require a period where the temperatures are suitable for growth. A good measure used for tree species in the boreal forest is the number of growing degree days which is an association with the accumulated warmth during the growing season (Prentice *et al*. 1992). Prentice *et al*. (1992) indicated that there needed to be more than 900 growing degree days at temperatures above 5° C in order for the typical coniferous species found in the boreal forest to grow. Growing degree days often defines the northern limits of growth for many tree species (Sykes *et al*. 1996), and is related to the energetic requirements needed in order for trees to complete their lifecycle. There are changes both throughout the day and seasonally in the amount of heat available to plants which ultimately determines the growing season. With diurnal variation, the rotation of the earth causes changes in the hours of light and dark with temperature changes slightly lagging behind light changes (Larcher 1980). Seasonal variation also creates changes in the amount of light available to plants especially along latitudinal gradients. At higher latitudes the length of day and night change throughout the course of the year, so that during the summer there is more sunlight and heat available to plants for a longer time period than in the winter (Larcher 1980). The growing season in higher latitudes is defined by both the temperatures experienced which allow physiological processes to take place, as well as the level of energy received in these areas that help support the physiological processes (Larsen 1989). The amount of incoming energy is one of the large reasons why tree lines exist along latitudinal gradients, as Larsen (1989) indicates that there is a strong correlation between incoming radiation received throughout the year and the forest borders.

Permafrost is another factor influencing tree growth across latitudinal gradients, as higher latitudes have more permafrost. At lower latitudes in the boreal forest the permafrost can be discontinuous, but with increasing latitude the permanently frozen ground becomes continuous, extending to depths of hundreds of metres (Larsen 1980). Permafrost impedes the warming of soils during the growing season and keeps the ground temperature around roots below a favourable level for the absorption of water and nutrients (Larsen 1989). The low temperatures in the soil also impede decomposition. Each summer a small active layer thaws on the surface which is where the trees are able to gather nutrients and water while the microorganisms help to slowly decompose litter into forms usable by the trees (Larsen 1980). The permafrost may impede water drainage due to the frozen soils, but if there is enough length to the warming season certain species of trees including *Picea mariana* and *Picea glauca* are able to grow in the shallow active layer (Crawford 2008).

Nutrient gradients also play a large role in tree species distribution and growth throughout changing latitudes. The nutrients available to species growing at higher latitudes can be difficult to access, as they are contained within frozen and gravelly soils. There are large quantities of nutrients present in the boreal soils, however, access to the nutrients is difficult because of low temperatures which keep the soils frozen much of the year and either very high or very low moisture content within the soil which can limit microbial activity (Robinson 2002). With an increase in latitude, the type of species present to break down soil litter often differs with fewer decomposers found at higher latitudes than lower ones, which is one reason there is such a slow breakdown of litter into available nutrient forms (Aerts *et al*. 2006).There are also issues with low input rates of nutrients in Arctic and boreal systems. The cycling rate of nutrients in these systems is the lowest of any ecosystem (Körner 2003). Plants tend to have a higher level of nutrient reabsorption from senescing foliage particularly phosphorous and nitrogen at higher latitudes as Oleksyn *et al*. (2003) found with Scots pine, than at lower latitudes in order to maintain growth. With an increase in latitude, it generally becomes cooler and temperature is shown to have a dampening effect on the breakdown of organic material and movement of nutrients throughout the soils (Körner 2003; Reich and Oleksyn 2004). Plants must be able to cope with the stress accompanied with growing at higher latitudes, and many studies have shown that there are differences in growth characteristics between plants at southern latitudes versus more northern latitudes (Kollmann and Bañuelos 2004; Dorrepaal *et al*. 2005).

A limiting resource: nitrogen

Nitrogen is a limiting factor to plant growth in the boreal system, and boreal soils typically have a high level of nitrogen contained in organic or inorganic forms. Much of the nitrogen is contained in the soil due to its slow rate of mineralization into a form that plants can easily take up from the frozen soils (Robinson 2002). It has been found that ammonium is the predominant form of inorganic nitrogen available to plants in the Arctic soils (Robinson 2002). Nadelhoffer (1991) also found that with increased soil temperature another inorganic form of nitrogen (nitrate) is found sometimes at higher levels than ammonium. It has been mentioned that deciduous areas of the boreal forest have faster nutrient turnover and nitrogen accessibility than coniferous forested areas (Jerabkova *et* al. 2006). Jerabkova *et al*. (2006) also found that areas of deciduous forest in the boreal had higher levels of ammonium and soluble inorganic nitrogen as compared to the coniferous areas, which is likely due to the faster decomposition rates of deciduous plant litter. A study by Henry and Jefferies (2002) illustrated that plants are able to directly take up organic forms of nitrogen such as amino acids in order for plants to attain the needed amounts of nitrogen. A study by Kielland (1994) also found that arctic species use organic forms of nitrogen including some amino acids in order to satisfy the annual nitrogen requirements. Deciduous species in particular had higher uptake rates of the amino acid forms compared to evergreen species (Kielland 1994). Nitrogen is important to plants, as it is the main component in many physiological functions. Nitrogen is used to build DNA and RNA, as well as being a part of different enzymes and proteins, and it is used for photosynthesis, although in coniferous species a higher proportion is found to be allocated to cell wall proteins (Takashima *et al*. 2004).

It is important for tree species to reabsorb as much of the nitrogen as possible from their needles when they are shed in order to allow for new growth under nitrogen limited regimes (Hikosaka 2005). It has been shown that nitrogen concentrations differ along a latitudinal gradient, with plant leaf litter from more northern sites having lower nitrogen concentrations than those from more southern latitudes (Dorrepaal *et al*. 2005). In contrast, Reich *et al*. (1996a) found that European populations of Scot pine trees had higher levels of needle nitrogen at increased latitudes as compared to more southern latitude trees of the same species, likely a compensation for the low levels of soil nitrogen available and for the cooler temperatures found at higher latitude sites. Variation in nitrogen availability can happen within individual sites and between sites along a latitudinal gradient and, as such, can be looked at as a local site variable. The amount of nitrogen present at a site depends on a range of factors including temperature, soil composition, latitude, and the depth of the organic layer, but can vary substantially across small spatial scales as a consequence of a range of biotic factors.

Another issue with regaining nutrients, specifically nitrogen from soils, is paludification. The process of paludification is the build up of the forest floor into very thick layers of sphagnum with slow decomposition that may eventually turn into peatlands (Crawford *et al*. 2003). Labrador is an area where paludification often occurs. Litter decomposition is quite slow in these soils due to the moisture content which remains frozen or very cold throughout the year. *Sphagnum* spp. also acts to slow the decomposition through increased soil acidity, and by changes in the moisture and temperature regimes which negatively affect decomposers in the soils (Turetsky 2003). The *Sphagnum* spp. also affects decomposition in boreal soils due to its rapid growth and biomass accumulation which is resistant to decomposition (Turetsky 2003).

The growth of plants, particularly trees, is affected by paludified soils. *Picea mariana* and *Larix* are both capable of growing on bog and peatlands, as, in the boreal forest, this terrain remains frozen throughout much of the year (Crawford *et al*. 2003). Issues arise during spring when the soil begins to thaw and there is an influx of water into the system which can be harmful to these species' growth. When the summer season commences, the soil is more aerated in the top-most layer of the organic matter providing good growing conditions to *Larix* and *Picea mariana* (Roy *et* al. 1999; Crawford *et al*. 2003). Paludified soils also cause problems along a latitudinal gradient, as trees are able to grow in paludified soils as long as they are in their temperature range, but they are unable to reproduce due to the peat growth at more northern latitudes (Crawford *et al*. 2003).

Plant strategies for nutrients

Tree species are able to use different strategies to survive in the harsh conditions of the northern boreal forest. Many coniferous species retain their needles throughout a period of years. This differs depending on the species. *Larix* trees drop their needles each year and must grow new ones. Some common boreal tree species like *Picea glauca* and *Picea mariana* are able to retain their needles for almost twice as long when at higher elevations or latitude compared to their lower latitudinal counterparts (Ewers and Schmid 1981; Reich *et al*. 1996b). Ewers and Schmid (1981) found that the average needle retention in bristlecone pine is between 2 to 15 years depending on climatic variables. A study done on *Picea mariana* in the boreal forest found that the length of needle retention varied from 5 to 7 years in southerly areas to 30 years at high latitudes (Lamhamedi and Bernier 1994). Reich *et al*. (1996b) explained that the difference seen in needle retention time is a phenotypic response to low temperatures and nutrients, as well as to a shorter growing period. Li *et al*. (2006) also found that leaf longevity of coniferous trees at higher latitudes and elevations is dependent on nutrient resource availability and abiotic stressors. Körner (1998) illustrated that a longer retention of needles occurs with a lower soil temperature because lower soil temperatures may harm the function of roots for taking up nitrogen. For this reason it becomes more practical to extend the leaf longevity of needles to retain the nitrogen. Körner (1989) explained that having longer needle retention time in some higher altitude tree species may actually increase the levels of some nutrient concentrations including nitrogen. By having higher nutrient levels in older needles, it helps to support higher metabolic levels than would be normally found in the same aged needles of similar species. Körner (1989) explained that the growth of the needles from higher altitudes occurred in such a way that the nutrient concentration was comparatively high to those same species from lower altitudes.

Other local site factors affecting growth

Irradiance levels are another big factor influencing the growth of individual trees. Light levels vary greatly along the latitudinal gradient from the equator, to areas where 24 hours of darkness occur above the Arctic Circle. Plants receive their photosynthetic radiation through direct radiation, so the degree of solar elevation can play a large role in determining growth (Kuuluvainen 1992). Kuuluvainen (1992) found that the shape of a tree’s canopy may determine the amount and consistency of photosynthetic radiation the plant receives. There is a latitudinal difference found in relation to crown shape and solar elevation, with more northern latitudes having narrower crowns to attain more even solar radiation throughout the day, and more southern latitudes having broader crowns to intercept more radiation when the sun is at its peak strength at noon (Kuuluvainen 1992).

Rooting depth is another factor that plants growing in the boreal range must adapt to. Roots are an important part of plant growth, as they transport water and nutrients to the rest of the plant. The soil in the boreal region is completely frozen much of the season with only a very shallow layer thawing during the spring and summer growing season. This does not provide much depth for the roots to expand downwards and gather nutrients. A study by Schenk and Jackson (2002) found that the rooting depth of vegetation in the boreal forest region depended on its latitudinal location and was correlated to such factors as length of growing season, precipitation, and the depth of the organic layer. All of these factors interact to influence how much of the soil thaws and to what depth. Schenk and Jackson (2002) also found that the depth of the rooting layer increased with a longer and warmer growing period, while the rooting depth decreased at higher latitudes and areas where the organic layer was deeper. This is to be expected, as higher latitudes have cooler temperatures throughout a longer period of the year, and the organic layer can act as insulation shielding the soil from incoming solar radiation and any thaw action.

Functional group responses to resource availability

The different coniferous tree species in the boreal forest can be considered part of two functional groups: evergreen conifers and deciduous conifers. Each of these functional groups has different adaptations and responses to varying levels of resource availability. Evergreen conifers are able to retain their needles throughout the year. By doing this, they do not have to acquire as many new nutrients each year in order to produce new foliage; however, they do have to initially invest a lot of energy and resources into constructing needles that can withstand the harsh conditions in the boreal forest for a number of years (Aerts 1995). This includes producing needles with a lot lignin to ensure they can withstand the icy winds during the winter and insects during the summer (Chabot and Hicks 1982). Deciduous conifers drop their needles each year and must grow new ones. This growth strategy is less conservative than the growth strategy of evergreen conifers, as these tree types need to be able to access resources each year in order to grow new foliage. This can be difficult, as many nutrients are trapped or slowly released due to low soil temperatures, mineralization and decomposition rates (Gower and Richards 1990). It is expected that an evergreen conifer growth strategy would be better suited to northern climates where nutrients are limited due to temperature and decomposition rates (Chabot and Hicks 1982), however deciduous conifers are found in northern areas and are able to grow. It may be beneficial to deciduous conifers to drop their needles each year, as by doing this they invest less energy and resources into constructing their foliar tissue (Gower and Richards 1990). Also, with less structural material found in the needles of deciduous evergreens, the plant litter on the ground can be broken down more quickly by soil decomposers, which leads to increased nutrient availability in deciduous areas of the forest (Aerts 1995; Jerabkova *et* al. 2006). This deciduous growth strategy may also be beneficial in more northern climates like the boreal forest as less damage can be done to the trees or their foliage from icy winds and snow (Gower and Richards 1990), and there is less respiratory cost to these trees during the dark periods in the winter season (Hansen *et al*. 1996). The evergreen strategy is also beneficial to plants growing in the more northern areas of the boreal forest as they are able to commence photosynthesis earlier in the season and finish later due to the retention of their needles (Givnish 2002).

There are tradeoffs in terms of needle use patterns between deciduous and evergreen conifers, but there are also differences in how these functional groups respond to nutrient availability. *Picea mariana* and *Picea glauca* are both evergreen conifers, and they have both been found to be good at reabsorbing nutrients when senescing their older needles, however *Larix laricina,* a deciduous conifer, has been found to be approximately 20% better at nutrient reabsorption than its sympatric evergreens (Gower and Richards 1990). Deciduous conifers are able to more easily attain nutrients from the soils as compared to the evergreen species, due in part to the plant litter of deciduous species being able to be more easily decomposed (Jerabkova *et al*. 2006). There are differences between the two functional groups in how they respond to water availability. In general, deciduous conifers like *Larix laricina* are able to use increased water availability better than evergreen conifers in terms of favouring increased growth (Montague and Givnish 1996), as water is used less efficiently by this species (Gower and Richards 1990). Evergreen conifers including *Pinus contorta* have been found to have higher nutrient use efficiencies than deciduous conifers like *Larix*, which also increases along a latitudinal gradient towards more northern sites for *Pinus* (Kloeppel *et al*. 2000). Studies have also shown that evergreen conifers have longer-lived roots than deciduous species, which further contributes to nutrient conservation (Aerts 1995).

Objectives

The main objective of this research project is to better understand how variations in local site factors, affect the radial growth of three common boreal tree species: *Larix laricina*, *Picea mariana* and *Picea glauca* along a latitudinal gradient in western and northern Labrador. The individual tree factors measured at each site that will be investigated include the available rooting depth, foliar nitrogen concentrations, radial growth, and tree height. It is hypothesized that at more northern locations there will be less foliar nitrogen present in plant tissues and decreased rooting depth available to the trees which will lead to a decrease in the radial growth exhibited by the trees. It is also expected that there will be decreased height shown at the more northern locations in association with the decreased growth due to the harsher conditions experienced at northern latitudes. At more southern sites, it is hypothesized that local site factors will be more influential in affecting the growth of the tree species, as increased rooting depth and increased concentrations of foliar nitrogen are expected to be found and associated with increases in radial growth and tree height due to more amenable growth conditions. I will test these predictions by examining the effects of foliar nitrogen, rooting depth and tree height on radial growth at sites along a latitudinal gradient.

This is important in order to understand the effects that climate change will have on nutrients and tree growth in the boreal forest in the future. By understanding how trees are currently responding to variations in climate and nutrients along a latitudinal gradient, we will gain insight into the factors that are limiting the radial growth of trees at higher latitudes. It also allows a better understanding of whether there are any differences in the factors that are limiting radial growth of tree species at lower latitudes as compared to higher latitudes. This may help to predict what type of responses trees will show to increases in temperature and potential increases in nutrient availability in the future, as well as which species may be the better competitors in the boreal forest.

Study Area

Four sites in Western Labrador and six sites in Northern Labrador were sampled from 52°N to 57°N (Figure 1). The sites in Western Labrador were accessed via floatplanes landing on lakes, while the Northern Labrador sites were sampled via float planes landing in fjords and coastal inlets which were surrounded by steep cliffs and/or small mountains. The sites sampled in northern Labrador were mainly at sea level. In Western Labrador, the mean elevation of the sites ranged from 480m to 650m (Table 1). The vegetation differs across Labrador with the southern and western portions of Labrador covered in subarctic forest and subarctic tundra while the northern sites are mainly alpine tundra and arctic tundra (Government of Newfoundland and Labrador 2009). White spruce is the dominant tree species throughout the northern areas of Labrador, while black spruce and eastern larch dominate throughout the southern and interior portions (Payette 2007). The major disturbances in this region are fire and insect outbreaks. The growing degree days for plants in Labrador ranges between 480 to 1010 based on above 5°C rates (Environment Canada 2009).

Study Species

The three species looked at in this study include black spruce (*Picea mariana* (Mill.) BSP), white spruce (*Picea glauca* (Moench) Voss), and eastern larch (*Larix laricina* (Du Roi) K. Koch). All three species are found throughout the Northeast United States and most of Canada especially in the boreal forest (Farrar 2000). *Picea mariana* is found growing on a variety of sites but mainly on wet and poorly-drained sites in either pure stands or intermixed with *Larix* and in more northern areas with *Picea glauca*, *Abies balsamea*, and *Populus tremuloides* (Farrar 2000). Ninemets and Valladares (2006) indicates that *Picea mariana* is a shade-tolerant species having an index of 4.08 ± 0.18 on a scale of 1 to 5, with 5 being most tolerant (Table 2). It is a slow-growing and relatively short-lived species reaching its maturity between 150 and 200 years old (Preston and Braham 2002). *Picea mariana* reproduces well on moist sites and especially after fire has swept through an area (Preston and Braham 2002).

Picea glauca grows on a wide range of soils and in an extensive variety of climates, and it is often found with *Populus tremuloides*, *Picea mariana*, and *Abies balsamea* (Farrar 2000). This species is a highly shade-tolerant species with a score of 4.15 ± 0.17, as illustrated in Table 2 (Ninemets and Valladares 2006). It grows well and is often found at the arctic tree line. *Picea glauca* reaches its maturity between 250 and 300 years of age and is a slow-growing species but slightly faster than *Picea mariana* (Preston and Braham 2002).

Larix laricina is often found growing on sites that are poorly-drained and cold including sphagnum bogs and muskeg and is usually intermixed with *Picea marina* and sometimes with *Thuja occidentalis* in more southern sites (Farrar 2000, Preston and Braham 2002). The *Larix* genus in general performs best on moist sites that are well-drained and in areas with high light availability, as the species is very intolerant of shade and usually reaches maturity between 150 and 180 years (Preston and Braham 2002). Ninemets and Valladares (2006) indicate that *Larix laricina* has a shade tolerance of 0.98 ± 0.09 indicating that the species is very intolerant of shade (Table 2).

Materials and Methods

Field protocol

Increment cores were collected from the sampled species: *Picea mariana*, *Picea glauca*, and *Larix laricina* at ten sites scattered across Labrador (Figure 1). Sites were selected in the western portion of Labrador according to their placement along a latitudinal gradient from 52 to 55°N and in northern Labrador according to the location of available trees. At each site 20 trees were sampled taking two cores from opposite sides of the tree at breast height (1.3 metres) from living dominant or co-dominant trees using a 5.1mm Swedish increment borer and following standard dendrochronology techniques (Stokes and Smiley 1968).

Individual tree measurements were also taken for all the *Picea mariana* and *Picea glauca* trees. These include the diameter at breast height (DBH), the individual tree height measured with a clinometer, the rooting depth around each tree which was measured by taking three or four depth probe measurements around the rooting system within 30cm distance from the trunk and averaging these values. These measurements were not completed for *Larix laricina* due to limitations in the amount of time available for sampling protocol at each site, so the individual tree measurements were only completed on one tree species at each site.

Needle samples were obtained from the sampled species by clipping branches on opposite sides of the individual trees to get a more representative canopy sample. Any new growth was removed from the canopy clippings so that discrepancies in nitrogen content due to the rapid growth found in new needles was accounted for. This is because there are usually higher levels of nitrogen found in new needles as compared to older needles (Perry 1995). The needle samples were stored in sealed Ziploc bags with a small bit of water for a maximum of six hours until they could be dried.

Dendrochronology lab analysis

All core samples were transported back to the Mount Allison Dendrochronology Lab where individual cores were glued into slotted mounting boards and sanded flat to a high polish using successive grades of sand paper from 80 grit to 600 grit. This allowed the cellular structures to be highly visible in order to allow for an accurate measurement of ring widths by identifying ring boundaries. The annual ring widths of each core were measured to the nearest 0.001mm using a 63X light microscope coupled to a Velmex stage measuring system. Tree-ring width chronologies for each sampled site were constructed and checked for signal homogeneity using the program COFECHA (Holmes 1986). After the site chronologies were established, they were single detrended using first a negative exponential curve or a linear regression curve depending on the fit in order to standardize the curves. If the first two modes could not be applied, a 50 year cubic smoothing spline was used in order to remove age and growth related anomalies through the program ARSTAN (Cook and Holmes 1986). Figure 2 and 3 illustrate two cores from the most northern site (site 1 in Figure 1) with the top graph in each figure either having a negative exponential curve applied to the raw measurements (Figure 2) or a 50 year cubic smoothing spline (Figure 3). The bottom graph in Figures 2 and 3 shows the new indexed growth after the equation has been fit to the measurements to produce standardized measurements. Standardized radial growth measurements were used as this removes the effects of endogenous stand disturbances like age related effects; specifically it evens out the high levels of growth seen in early years and low levels of growth seen in later years (Holmes 1986). Standardized growth measurements were also used in this study in order to produce measurements that were normally distributed. The last three years of standardized growth were obtained from the standardized measurements for each core and averaged to create one number in order to compare to the nitrogen values and the other local site factors collected at each site including rooting depth and tree height.

Nitrogen analysis

Foliar nitrogen concentrations were measured for the three tree species, as foliar nitrogen has been found to correlate strongly to available soil nitrogen (Walters and Reich 1997; Garten 1993, Hobbie and Gough 2002). Needle samples from *Picea mariana*, *Picea glauca*, and *Larix laricina* were removed from Ziploc storage bags upon return from field sampling and all the needles were cut away from the twigs. Any needles that were brown or yellow were removed from the sample. Approximately 60 needles from the two branches on each tree were placed into small paper envelopes and allowed to dry for four days in a dehydrator at approximately 65°C. They were then stored in sealed bags with silica beads to avoid water uptake from the air. Upon return from the field, needle analysis was undertaken in Mount Allison University`s Elemental Analysis Lab. Needles from each tree were ground to a powder using a mortar and pestle and stored in small plastic capsules. Approximately 20-30 mg of sample was weighed into small tin boats using a Mettler Toledo MX5 electronic scale. Samples were then combusted in order to obtain the total percent nitrogen of each sample using an Elementar Vario EL III elemental analyser.

Statistical analysis

Each tree species was analyzed separately as the two species with the individual tree measurements (*Picea mariana* and *Picea glauca*) were both located in different areas and not at similar latitudes, and, although the *Picea mariana* and *Larix laricina* sites were located along the same latitudinal gradient, *Larix laricina* did not have the individual tree measurements to compare with those of *Picea mariana*. The program R (R v. 2.1; The R Foundation for Statistical Computing, Vienna, Austria) was used to analyze all data.

A) Latitudinal effects on local site factors and growth

An ANOVA was used to analyze the effects of site on growth, percent nitrogen, rooting depth and tree height for *Picea mariana* and *Picea glauca*, while only growth and percent nitrogen were included in the models analyzed for *Larix laricina*. For the ANOVA analyses on *Larix laricina*, site was considered the independent variable, while growth or percent nitrogen were the dependent variables. A Tukey multiple comparison of the means was used as a post-hoc test for both growth and percent nitrogen. The ANOVA for *Picea mariana* also had site as the independent variable, while the dependent variables included growth, percent nitrogen, rooting depth or tree height. For this data set tree height had to be log-transformed to meet assumptions of normality. Tukey multiple comparison of the means were undertaken on all the *Picea mariana* variables except percent nitrogen as there were no significant effects found between site and percent nitrogen. ANOVA was also used for the *Picea glauca* data with site as the independent variable and growth, percent nitrogen, rooting depth or tree height as the dependent variables. Percent nitrogen, rooting depth and tree height had to be log-transformed to meet the normality assumptions. All the measured variables for *Picea glauca* had Tukey multiple comparison of the means post-hoc tests run on them.

Four data points were removed from the statistical analysis of tree height for *Picea mariana* for any trees over 18 metres at the four sites, and three data points were removed from the statistical analysis of tree height for the *Picea glauca* sites by removing data points for any trees over 20 metres, as there were no trees this tall at any of the sites. These tall trees were removed from the analysis, as measurement errors occurred while using the clinometers to determine the tree height at each site. The errors occurred due to not being able to attain a distance of 5 metres from the base of the tree to provide a good length for calculations of the height. The trees were also growing on a slope which impacted the angle measured in the clinometers when measuring the tree height.

B) Linear regression analysis

The relationship between percent nitrogen and radial growth for *Larix laricina, Picea mariana* and *Picea glauca* was modelled by running a linear regression analysis for each species with percent nitrogen as the independent variable and radial growth as the dependent variable. The nitrogen data were log-transformed for *Larix laricina* in order to make the relationship linear.

C) Multiple regression analysis

A multiple regression analysis was undertaken on the sites at which *Picea mariana* and *Picea glauca* were sampled to infer which independent variables of the different factors measured at each site were having the largest effect on radial growth. The dependent variable for both *Picea mariana* and *Picea glauca* was radial growth. The independent variables for the *Picea mariana* and *Picea glauca* regression analysis were site, percent nitrogen, rooting depth and tree height. Stepwise regression with Akaike Information Criteria selection was used to choose the best fit model. Site was found to explain the most variation for *Picea mariana,* while site, rooting depth and tree height explained the maximum variation for *Picea glauca*.

Results

Larix laricina

An ANOVA was used to determine the role that latitude, characterized as site, has on both the average standardized growth and percent nitrogen from the three sites sampled in western Labrador. The sites were arranged along a latitudinal gradient from 52° N to 53° N and again at 55° N. The 54° N site did not have any *Larix* present. The ANOVA indicated that significant site differences existed in the average standardized growth ($p < 0.0001$; Figure 4A). Results from the analysis also indicated that there was a highly significant effect of site on needle nitrogen concentration ($p < 0.0001$; Figure 4B). The most northern site in Western Labrador (Site 7 in Figure 4) illustrates both significantly lower nitrogen concentrations and growth as compared to the other more southern sites. A linear regression analysis indicated that there was a significant relationship between percent nitrogen and radial growth ($p < 0.0001$; Figure 5), with an increase in the percent of foliar nitrogen relating to an increase in radial growth rates.

Picea mariana

The four *Picea mariana* sites in western Labrador were sampled from 52 to 55° N. An ANOVA was used to determine the role that latitude, represented as site, plays in predicting the percent nitrogen, growth, average soil depth, and tree height. The results indicated that radial growth varied significantly with site ($p = 0.0198$; Figure 6A), shown at the four *Picea mariana* sites. Specifically, the most northern site (site 8) illustrated higher radial growth than the two most southerly sites. ANOVA results also indicated that no site differences existed for foliar nitrogen concentration ($p = 0.1667$; Figure 6B). There was no relationship found between percent nitrogen and radial growth for *Picea mariana* after performing a linear regression analysis on the data (Figure 7).

Significant differences in tree height existed among sites ($p = 0.0008$; Figure 8A). Figure 8A illustrated that the most northern site (site 7) from the four western sites had much shorter trees in comparison to the other three more southern sites. ANOVA results also indicated that the average soil depth differed across the four sites ($p < 0.0001$; Figure 8B). Figure 8B graphically represents the average soil depth seen at the four sites and illustrates that the second most southern site (site 9) had much shallower rooting depths than the other three sites.

A multiple regression analysis on the *Picea mariana* variables only retained site in the selected model. None of the local site factors including average soil depth, percent nitrogen or height were significant predictors of radial growth (Table 3). The regression analysis indicated that the effect of site in the model is only explaining about 15% of the variation ($R^2 = 0.1461$).

Picea glauca

ANOVA was used to determine the role that the following variables played in relation to latitude: percent nitrogen, growth, average soil depth, and tree height. The results indicated that there is a highly significant effect of site on the average standardized growth for the six sites ($p < 0.0001$; Figure 9A). Post-hoc analysis indicated that site 6, the most southern site in northern Labrador and site 2, the second most northern site, had significantly lower radial growth than site 1, the most northern site. ANOVA results also indicated that site had a significant effect on the percent nitrogen found at the six sites ($p = 0.0328$; Figure 9B). Post-hoc analysis revealed that trees at site 5 had significantly higher foliar nitrogen than at site 2, but that none of the other sites differed. Results from a linear regression analysis indicated that there is a slightly significant relationship between percent nitrogen and radial growth for *Picea glauca* ($p = 0.092$; Figure 10).

There was a significant effect of site on tree height, as indicated by the ANOVA results ($p < 0.0001$; Figure 11A). Figure 11A illustrates that the most northern site (site 1) had trees that were significantly taller than trees at sites 2, 4 and 5. ANOVA results also indicated that there was a highly significant effect from site on average soil depth ($p < 0.0001$; Figure 11B). Sites 1 and 6, the most northern and southern sites, had similar soil depths, and they both had significantly deeper soils than sites 2,3,4, and 5.

The multiple regression analysis completed on *Picea glauca* illustrates that site is having a highly significant effect on growth ($p < 0.0001$), while average soil depth and tree height both have significant effects on growth ($p = 0.008$, $p = 0.002$ respectively) as displayed in Table 4. The model predicted about 33% of the variation seen ($R^2 = 0.3328$), and the regression analysis indicated that there is a negative relationship with radial growth for both average soil depth and tree height (Table 4).

Discussion

The findings of this study indicate that there are individual site responses occurring in reaction to measured local site factors rather than distinctive latitudinal trends. There was also a functional group response for radial growth shown by the three species. This functional group response is seen when looking at the results of percent nitrogen compared to the average standardized growth exhibited by each species. *Picea mariana* shows no relationship between percent nitrogen and radial growth (Figure 7). *Picea glauca* shows very little response in its growth to foliar nitrogen (Figure 10), while radial growth in *Larix laricina* illustrates a significant response to percent nitrogen (Figure 5). Latitude had varying effects on species growth, but overall showed no distinctive trends for any of the species. None of the measured site factors displayed any latitudinal trends in their effect on radial growth. At each site, individual responses were found in relation to the measured local site factors. Radial growth for *Picea mariana* was found to have no relationship with foliar nitrogen concentrations, and there was no significant response of rooting depth or tree height. *Picea glauca*, on the other hand, did show a slight relationship between radial growth and foliar nitrogen and there was a significant, although negative, response of rooting depth and tree height on radial growth. The tree species used in this study fall under two functional groups: deciduous conifers and evergreen conifers. These two functional groups can have different responses to nutrient availabilities and other local site factors.

Species responses to foliar nitrogen concentrations and local site factors

Larix laricina

Larix laricina illustrates a strong relationship between percent foliar nitrogen and radial growth, as is seen in Figure 5. Figure 4 also illustrates that the most northern site in western

Labrador (site 7) had much lower percent nitrogen values for its foliage, as well as substantially lower growth rates. This could indicate a latitudinal trend in growth rates and percent nitrogen; however, with only three sites it is difficult to determine whether the one more northern site has lower growth due to individual site differences or if it is due to latitudinal location. It is also important to note that site 7 had considerably younger trees as compared to site 10 (Table 1). This may indicate that the relationship between percent nitrogen and growth could be an effect of stand age at this site, although site 9 did have similar aged trees as site 7, making it difficult to determine whether a latitudinal trend is being expressed. Ninemets (2002) indicated that there is no trend between foliar nitrogen concentrations and tree age for *Picea* and *Pinus*, but that net assimilation rates decreased with increasing age. This indicates that age may have an effect on the radial growth in terms of how the nitrogen is being used by the tree to produce biomass. Tree age may also affect radial growth, as Carrer and Urbinati found that radial growth in older *Larix* trees is more affected by the climate (2004). In general there is a site specific response occurring in how percent nitrogen is affecting radial growth. The percent nitrogen results from this study for *Larix laricina* are comparable to results from another study examining foliar nitrogen content in boreal trees (Ryan 1995). The study by Ryan (1995) found foliar nitrogen concentrations around 2.1% for *Larix* trees sampled at similar latitudes as the trees in this study but in western Canada.

Picea mariana

Picea mariana did not illustrate as much of a response in terms of percent nitrogen in its foliage across sites (Figure 6A). There was a slight response of growth to site, with site 8 having higher radial growth rates as compared to the more northern site 7 and more southern sites 9 and 10 (Figure 6B). There were no latitudinal trends found in the *Picea mariana* results. These increased growth rates may be due to this site having the oldest trees sampled in western Labrador, and therefore an older stand age. Stand age can affect many things including soil quality which may lead to increased growth (Lamarche 2004). Bond *et* al. (2007) found that apical growth is not affected by the age of the tree for *Picea*, while Carrer and Urbinati (2004) found that the radial growth of *Larix* and *Pinus* are more affected by climate with increasing age. Carrer and Urbinati (2004) indicate that with increasing tree age, changes in radial growth are better explained by climate variance. These findings may help explain why site 8 is showing increased growth rates compared to the other sites, as potentially this site experienced better climatic conditions during the growing season which allowed for increased growth rates.

Two of the local site factors measured for *Picea mariana,* average rooting depth and tree height were both significantly influenced by site, but overall site was found to be the only good predictor of growth. This species is quite conservative and slow growing, as it reaches maturity around 200 years (Farrar 2000). *Picea mariana* is also a shade tolerant species, as Ninemets and Valladares (2006) indicated that it has a tolerance of 4.08 ± 0.18 on a scale of 1-5 with 5 being the most tolerant (Table 2). This may help explain why the species is quite unresponsive to resource availability variation, as the results found here show that local site factors including average rooting depth and percent nitrogen do not play a large role in affecting the growth of *Picea mariana*. The foliar nitrogen concentrations measured in the *Picea mariana* trees from this study have similar concentrations as the concentrations measured in the same species by Ryan (1995). Ryan (1995) found that the average foliar nitrogen concentration in the *Picea mariana* needles sampled at similar latitudes in western Canada was 0.6%.

Picea glauca

Picea glauca illustrated an intermediate response between *Larix laricina* and *Picea mariana* in terms of radial growth rates in response to foliar nitrogen concentrations, with slight increases in growth rates associated with increased percent nitrogen (Figure 10). There was a significant relationship between percent nitrogen and site, as well as between average standardized growth and site (Figures 9A and 9B). No latitudinal trends were expressed in the results, as there were no clear gradient occurring with either increases or decreases in growth relating to the percent nitrogen and site position, rather individual site differences were occurring. The foliar nitrogen concentrations for *Picea glauca* were similar to concentrations found in a study by Ryan (1995) for comparable boreal forest species. Ryan (1995) found that *Picea mariana* had nitrogen concentrations around 0.6% and *Picea engelmannii* had concentrations around 0.9%. These species are closely related to *Picea glauca* and similar in their growth and resource usage strategies (Preston and Braham 2002).

There were some interesting results with *Picea glauca* when analyzing the responses of rooting depth and tree height to site. There were no latitudinal trends expressed in these data, as no clear gradients were established between site and either rooting depth or tree height. In both the rooting depth and tree height analyses, sites 1 and 6, the most northern and southern sites from northern Labrador, showed similar responses in terms of the average tree height per site and the average rooting depth. This is interesting, as it would be expected that the more northern sites would have shallower rooting depths and tree heights in response to colder temperatures and harsher conditions (Gower and Richards 1990). Sites 1 and 6, along with site 5 had similar aged trees which were older than the other three sites, indicating that stand age may be affecting the species response to local site factors like rooting depth and soil nutrient availability (Lamarche

2004). Site 5 is significantly different from sites 1 and 6 and this is likely due to individual site characteristics, as these trees were sampled at tree line and have many climatic and site variables impacting their growth.

Another interesting result with *Picea glauca* was the negative relationship found between growth and tree height from a multiple regression analysis. These results indicate that there is increased radial growth with decreased tree height. The *Picea glauca* trees sampled in this study were located at tree line, and, as such, they are exposed to harsh conditions from cold temperatures and icy winds (Crawford 2008). Trees that are shorter are better protected by snowpack during the winter season which helps lessen the damage icy winds can cause on foliage and desiccation issues (Crawford 2008). Hadley and Smith (1989) indicate that conifers growing at the tree line lose protective wax coatings on their needles due to the severe abrasion from ice particles in the wind. In order to protect their foliage, a shorter stature may be advantageous in these more northern sites.

The results found in this study suggest that *Picea glauca* may not be as conservative a species as *Picea mariana*, although it is hard to determine whether the results seen with *Picea mariana* are due to there not being at a broad enough latitudinal gradient to see the effects latitude and local site factors may play on its growth. However, *Picea glauca* still illustrates the conservative strategies found in *Picea mariana*. Ninemets and Valladares (2006) indicate that *Picea glauca* is slightly more shade tolerant than *Picea mariana* at 4.15 ± 0.17 on a scale from 1 to 5 with 5 being the most shade tolerant. *Picea glauca*'s shade tolerance can also help explain the slow growth found in this species, similar to that of *Picea mariana*, as it reaches maturity around 200 years (Farrar, 2000).

Functional group responses

Deciduous conifer: *Larix laricina*

Larix laricina falls under the deciduous conifers, as it loses its needles each year. This may be representative of the performance strategy of this species as fast growing. Farrar (2000) indicates that *Larix* reaches maturity earlier than the two evergreen conifers *Picea mariana* and *Picea glauca*, by about 50 years (Table 2). With quicker growth, *Larix* may use a less conservative strategy for resource use than the slower growing evergreen conifers with which it co-occurs. There is a high cost associated with being deciduous, mainly in the loss of needles each year. By being less conservative, *Larix* must be able to acquire extra nutrients in order to sustain its more rapid growth or have physiological mechanisms that allow its survival in an area normally dominated by evergreen conifers. The nutrient availability in boreal soils is quite low due to a combination of interactions between low soil temperatures, mineralization rates, decomposition rates, and root function (Gower and Richards 1990). Each year, *Larix* must grow a new set of needles that can undergo photosynthesis and gas exchange which is costly in both carbon and nitrogen, whereas evergreen species like *Picea mariana* and *Picea glauca* are able to retain their needles for many years, sometimes up to 30 years (Lamhamedi and Bernier 1994). Gower and Richards (1990) indicate that *Larix* has up to twice the photosynthetic capacity in its needles as compared to the retained needles on evergreen conifers. There are tradeoffs between retaining needles and having decreased photosynthetic capacity versus growing new needles each year and having increased photosynthetic capabicity which includes carbon assimilation in order to build new needles (Gower and Richards 1990). Evergreen species must invest much more energy and carbon into creating desiccation proof needles to survive the harsh winter conditions, while it may be advantageous to deciduous conifers to construct a cheap needle that can be disposed of easily (Gower and Richards 1990). Wright *et al*. (2004) suggest that longer lived needles should be tougher and more durable and better able to survive the harsh conditions found in the northern boreal forest. However, these longer-lived needles have lower investments in nitrogen and lower photosynthetic capacity (Kloeppel *et al*. 2000). With higher nitrogen concentrations in the needles, there is an increased responsiveness in terms of growth in *Larix* suggesting that this species has higher performance strategies and is more physiologically plastic (Ryan 1995; Wright *et al*. 2004). *Larix* has also been found to have a much larger specific leaf area, including thinner, less dense leaves, as compared to sympatric evergreen conifers (Gower and Richards 1990). *Larix* is a shade intolerant genus that requires areas of open light with little shading from neighbours (Ninemets and Valladares 2006). The large open areas *Larix* is found in the boreal may also be part of the reason it is able to grow more quickly than its sympatric evergreen conifers. The deciduous strategy of *Larix* is also beneficial during the winter season, as evergreen needles can be damaged and killed from ice abrasion and desiccation and have increased respiratory costs, while *Larix* manages to avoid this by dropping all of its needles (Gower and Richards 1990, Hansen *et al*. 1996).

Evergreen conifers: *Picea mariana* and *Picea glauca*

The conservative strategies associated with evergreen conifers include maintaining their needles for a long period of time and investing a lot of energy into needle construction, partially in terms of carbon, a necessary component of lignin. High lignin content increases the toughness of the leaf, ensuring that they can withstand a number of years in harsh elements (Chabot and Hicks 1982). There are also lower nitrogen concentrations in evergreen needles due to the increased levels of supporting tissue in the needles which causes evergreen needles to have a lower photosynthetic capacity as compared to deciduous conifers (Chabot and Hicks 1982, Wright *et al*. 2004). This strategy of maintaining needles for a longer period of time allows the trees to compensate for the decrease in photosynthesis by having to allocate less energy into creating new needles each year. Also, by retaining their needles throughout the year, evergreens can be photosynthetically active for longer periods of time than their deciduous counterparts by being active earlier in the season and later in the fall (Givnish 2002). Wright *et al*. (2004) indicated that increased leaf lifespan may not be representative of the best ecological response, as leaves with lower leaf mass per area have increases in photosynthetic capacity. Wright *et al*. (2004) also indicated that a faster turnover in tissue may allow more flexibility in response to differences in light and soil resources, however the time that the needles are displayed for helps to make up for this

Nutrient use efficiency between functional groups

Larix, a deciduous conifer, has been found to use nitrogen as efficiently as sympatric evergreen species like *Picea mariana* (Gower and Richards 1990). Initially, *Larix* has much higher levels of nitrogen in its foliage as compared to sympatric evergreen conifers, with concentrations being upwards of 25-49% greater than the evergreen nitrogen concentrations (Gower and Richards 1990). This indicates that *Larix* has increased benefits of higher nitrogen concentrations in terms of enhanced photosynthetic capacity and carbon assimilation (Wright *et al*. 2004; Reich *et al*. 1998). *Larix* is also much better at reabsorbing nitrogen from senescing tissues by relocating almost 20% more than their sympatric evergreens (Gower and Richards 1990). This is important in order for the deciduous conifer strategy to work for *Larix*, as there are very low amounts of nitrogen available in the frozen boreal soils. By being able to conserve and recycle the nitrogen in their needles despite dropping them each year, *Larix* trees are able to produce new needles each year that allow for their high photosynthetic capacity (Gower and

Richards 1990). In the long-run deciduous conifers like *Larix* lose more nutrients, as all the carbon in each needle is lost when they are dropped (Gower and Richards 1990). Evergreen conifers on the other hand hold onto their needles for many years, and leaf lifespan has been found to be a good predictor for nutrient use efficiency (Yin 1994)

Picea mariana and *Picea glauca* are both evergreen conifers. These species need to be more conservative in their nutrient use strategies, as they are not able to retrieve as much nitrogen from senescing tissues as deciduous species like *Larix laricina* (Gower and Richards 1990). Evergreen species are able to retrieve some nitrogen from older needles on the trees and reallocate this to newer needles of higher productivity (Chabot and Hicks 1982). It is also harder for these species to attain nutrients from the soils, as the breakdown of leaf litter is much slower under evergreen conifers due to the high levels of lignins and structural materials found in the coarse needles (Jerabkova *et al*. 2006). Jerabkova *et al*. (2006) indicated that areas in the boreal forest where deciduous trees are found have higher levels of soluble inorganic nitrogen like ammonium available to be used as compared to evergreen stands. This may be one of the reasons why evergreens are still using a conservative strategy in needle life span, due to the difficulty in attaining nutrients to construct new needles. Evergreen species should be favoured in areas of low soil nutrients as there is much leaching of nutrients including nitrogen from soils (Givnish 2002). Givnish (2002) explains that evergreen needles which are retained longer and need fewer nutrients for construction and maintenance are beneficial to trees growing on nutrient poor soils, since the nutrients may be hard to attain in order to produce a full set of new needles each year. Evergreen strategies are also favourable at higher latitudes where the growing season is shorter, as they are able to commence water uptake and photosynthesis earlier than deciduous species which must grow new needles (Givnish 2002). This is representative of the species sampled in this study, as only the evergreen species *Picea glauca* was present at higher latitudes.

Conclusions

The findings of this thesis do not support the initial hypotheses of higher latitudes being more limited in nitrogen and having lower radial growth rates, or that tree's growth rates at the southern sites will be more affected by variations in local site factors. There were no latitudinal trends expressed in foliar nitrogen concentrations, radial growth, average rooting depth or tree height in this study. This is likely due to the latitudinal gradients used in this study not being broad enough to encompass large shifts in climate and resource availability. There were, however, functional group responses expressed in terms of the relationship between foliar nitrogen concentrations and radial growth. The deciduous conifer *Larix laricina* illustrated higher growth rates with increases in percent nitrogen, representative of the performance-based growth strategy of this species. *Picea mariana* and *Picea glauca*, both evergreen conifers displayed conservative growth strategies. *Picea mariana* had no response in growth to increases in foliar nitrogen concentration, while *Picea glauca* showed a weak response of higher radial growth with increased nitrogen levels. This study indicates that tree species growth strategies have important effects on how resources are used and responses to resource availability will be very species-specific. The lack of predictability of growth responses across these gradients and at the northern limits does not bode well for our predictive ability with respect to global change.

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Table 1: Study site information for the six sites from Northern Labrador and four sites from Western Labrador. Sites are listed from most northern to southern. Climate data obtained from the Environment Canada Canadian climate normals page. The standard deviation for the average yearly temperature of Nain is 1.4°C, Schefferville is 1.2°C, and Wabush Lake is 1.1°C. Initials under average tree age are: *Pg* – *Picea glauca*, *Pm* – *Picea mariana*, and *Ll* – *Larix laricina*. Growing Degree Days (GDD) at each study site are approximated from the nearest climate station.

Site	Site	Latitude	Elevation (m)	Grid	Weather	GDD	Average Yearly	Average Tree
Number		Longitude		Zone	Station	(above 5°C)	Temperature (°C)	Age
1	Tasiuyak Lake	57° 15' 47.1" N	14 ± 5	20V	Nain	488.3	-3	151 (*Pg*)
		62° 11' 24.5" W						
2	Kingurtik Lake	56° 46' 26.6" N	3 ± 6	20V	Nain	488.3	-3	118 (*Pg*)
		62° 32' 11.5" W						
3	Tasisuak Lake	56° 38' 52.4" N	0 ± 5	20V	Nain	488.3	-3	110 (*Pg*)
		62° 57' 50.6" W						
4	Anaktalik Lake	56° 29' 35.5" N	21 ± 5	20V	Nain	488.3	-3	111 (*Pg*)
		62° 41' 19.0" W						
5	Diane Lake	56° 20' 46.1" N	340 ± 5	20V	Nain	488.3	-3	149 (*Pg*)
		62° 42' 05.5" W						
6	Cabot Lake	56° 08' 53.6" N	48 ± 7	20V	Nain	488.3	-3	131 (*Pg*)
		62° 37' 51.0" W						
7	Indian Lake	55° 01' 08.4" N	489 ± 6	19U	Schefferville	615.9	-5.3	39 (*Pm*)
		66° 00' 24.6" W						60 (*Ll*)
8	Sims Lake	54° 01' 17.3" N	484 ± 5	20U	Schefferville	615.9	-5.3	136 (*Pm*)
		65° 58' 35.4" W						
9	Ritchie Lake	53° 00' 16.2" N	566 ± 7	20U	Wabush Lake	786.5	-3.5	62 (*Pm*)
		65° 59' 56.8" W						51 (*Ll*)
10	Angie Lake	52° 01' 24.9" N	644 ± 5	20U	Wabush Lake	786.5	-3.5	109 (*Pm*)
		65° 56' 52.7" W						103 (*Ll*)

Table 2: Study species and physiological growth tolerances. Shade, drought and water-log tolerance are on a scale of 1-5 with 5 being the most tolerant from Ninemets and Valladares (2006). Leaf characteristics obtained from Farrar (2000).

Common Name	Scientific Name	Shade Tolerance	Drought Tolerance	Water-log Tolerance	Average Age of Maturity	Leaf Characteristics
Eastern Larch	*Larix laricina* (Du Roi) K. Koch	0.98 ± 0.09	2	3	150	flattened, 2-5 cm long, 15-60 per tuft
White Spruce	*Picea glauca* (Moench) Voss	4.15 ± 0.17	2.88	1.02	200	straight, stiff, 15-22 mm long, pointed tip
Black Spruce	*Picea mariana* (Mill.) BSP	4.08 ± 0.18	2	2	200	straight, 8-15 mm long, blunt-pointed, dense along twig

Table 3: Multiple regression analysis values for *Picea mariana* from four sites in western Labrador.

Variable	Standard Error	DF	R^2	F - value	p - value
site	0.2259	62	0.1461	3.536	0.0197

Table 4: Multiple regression analysis values for *Picea glauca* from six sites in northern Labrador. Model degrees of freedom were 102, model $R^2 = 0.3228$ and the model p-value < 0.0001.

Variable	Estimate	Standard Error	DF	F - value
site	1.427	0.138	5	6.25
average soil depth	-0.006	0.003	1	7.32
height	-0.021	0.006	1	10.03

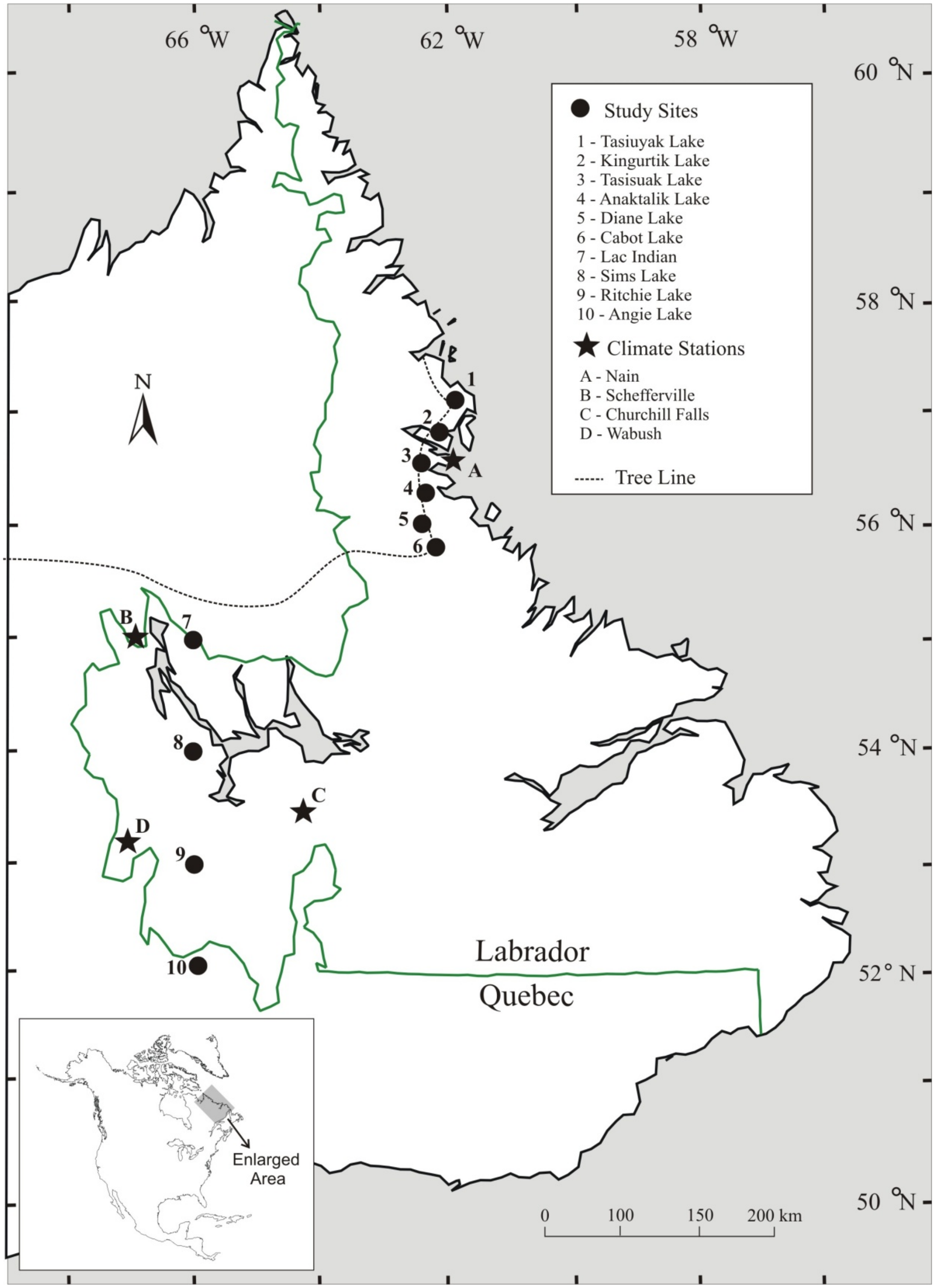

Figure 1: Map of Labrador illustrating the locations of the six sites sampled in northern Labrador and the four sites sampled in western Labrador. The closest climate stations are indicated with a star, and the approximate position of the tree line throughout Labrador in relation to the sites is indicated with a dashed line

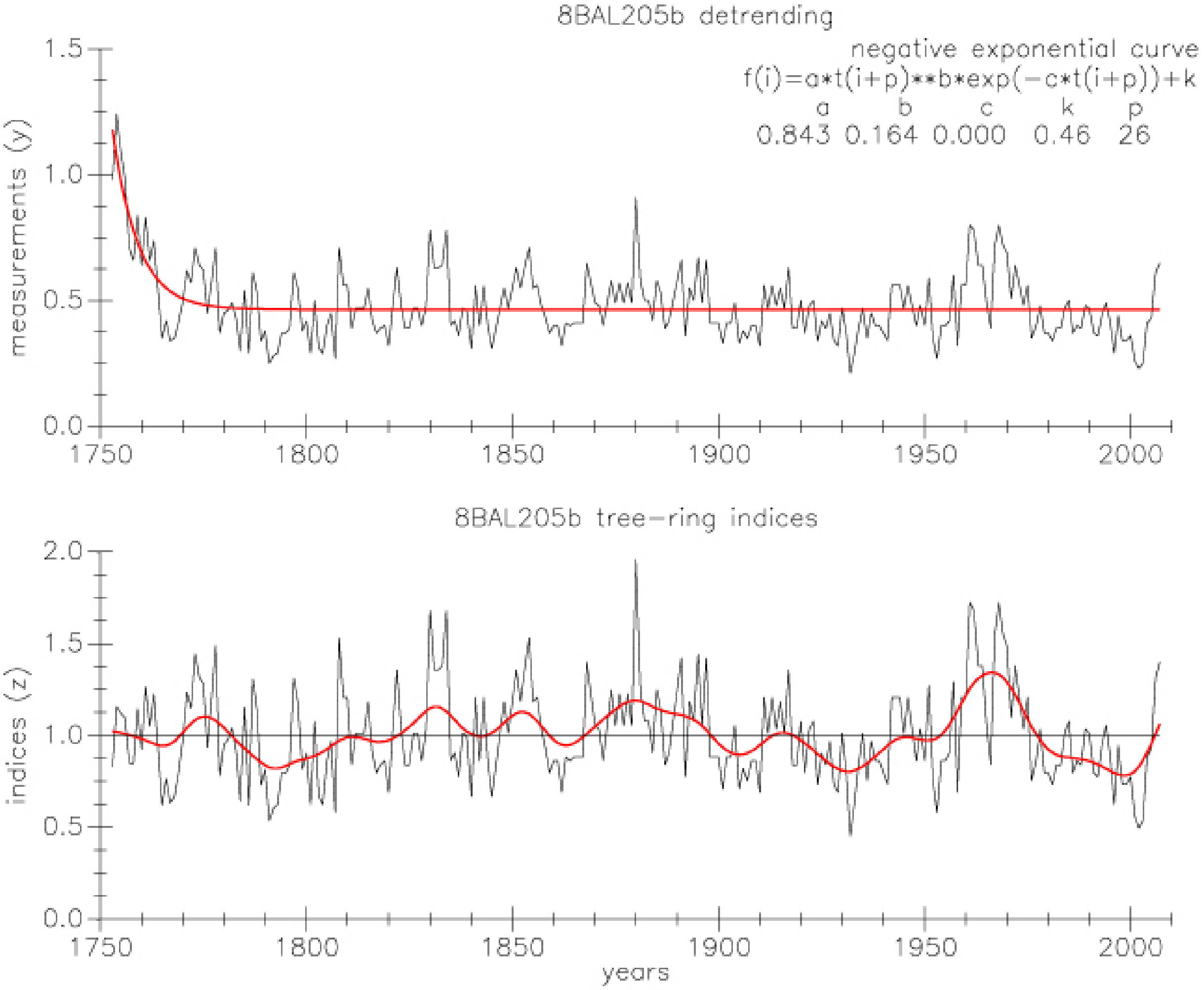

Figure 2: Core sample from Tasiuyak Lake illustrating the raw measurements in the top image (thin wavy black line) and the standardized measurements in the bottom image (thin wavy black line), using a negative exponential curve (top thick black line). Measurements were standardized using the program ARSTAN to remove age-related variation in the growth. The bottom graph shows the standardized measurements with anything over 1.0 indicating above average growth and anything below 1.0 indicating below average growth.

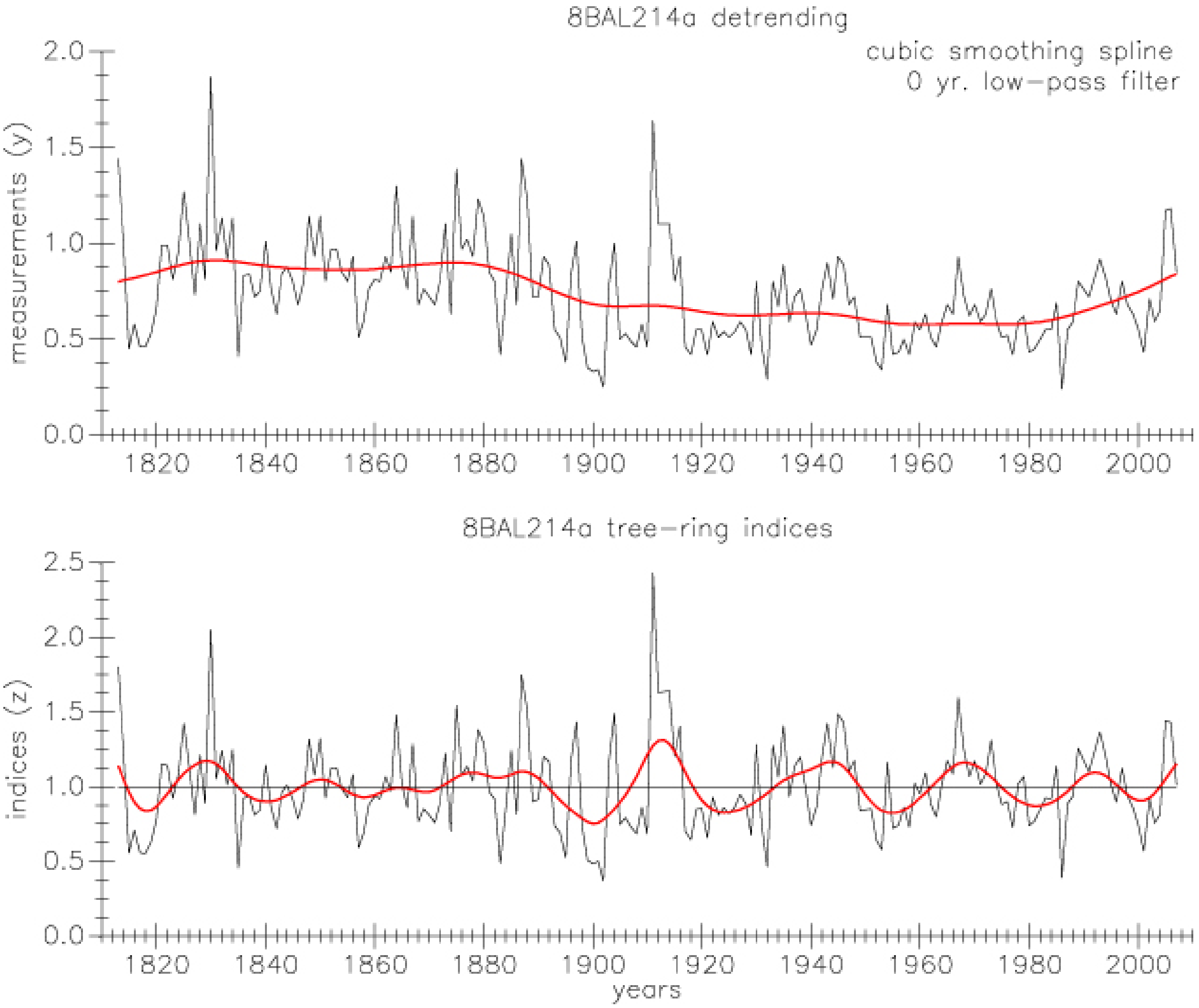

Figure 3: Tasiuyak Lake core sample illustrating the raw measurements in the top image (black line) and the standardized measurements in the bottom image (black line) after having a 50 year cubic smoothing spline applied (top red line). Measurements were standardized using the program ARSTAN to remove age-related variation in the growth. The bottom graph shows the standardized measurements with anything over 1.0 indicating above average growth and anything below 1.0 indicating below average growth.

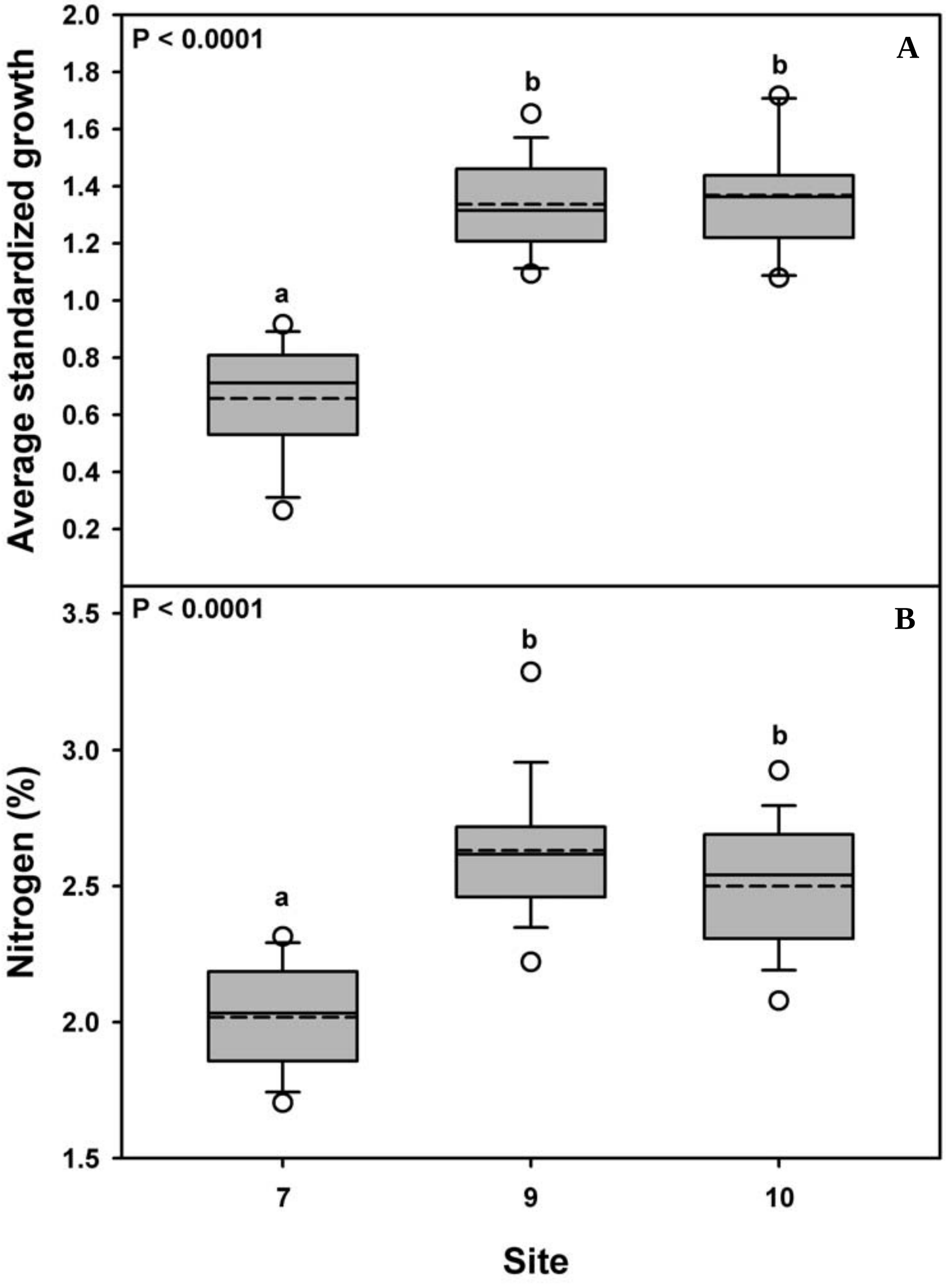

Figure 4: Box and whisker plots for average standardized growth (A) and percent nitrogen (B) of *Larix laricina* from three sites in western Labrador. Sites are numbered according to site placement from north to south which can be found in Figure 1. Box plots contain site median values (solid line) and mean values (dashed line). Data were analyzed using an ANOVA, with p-values displayed indicating the significance level of the relationship between site and the measured variable. Lowercase letters indicate significant differences between sites at α = 0.05 level.

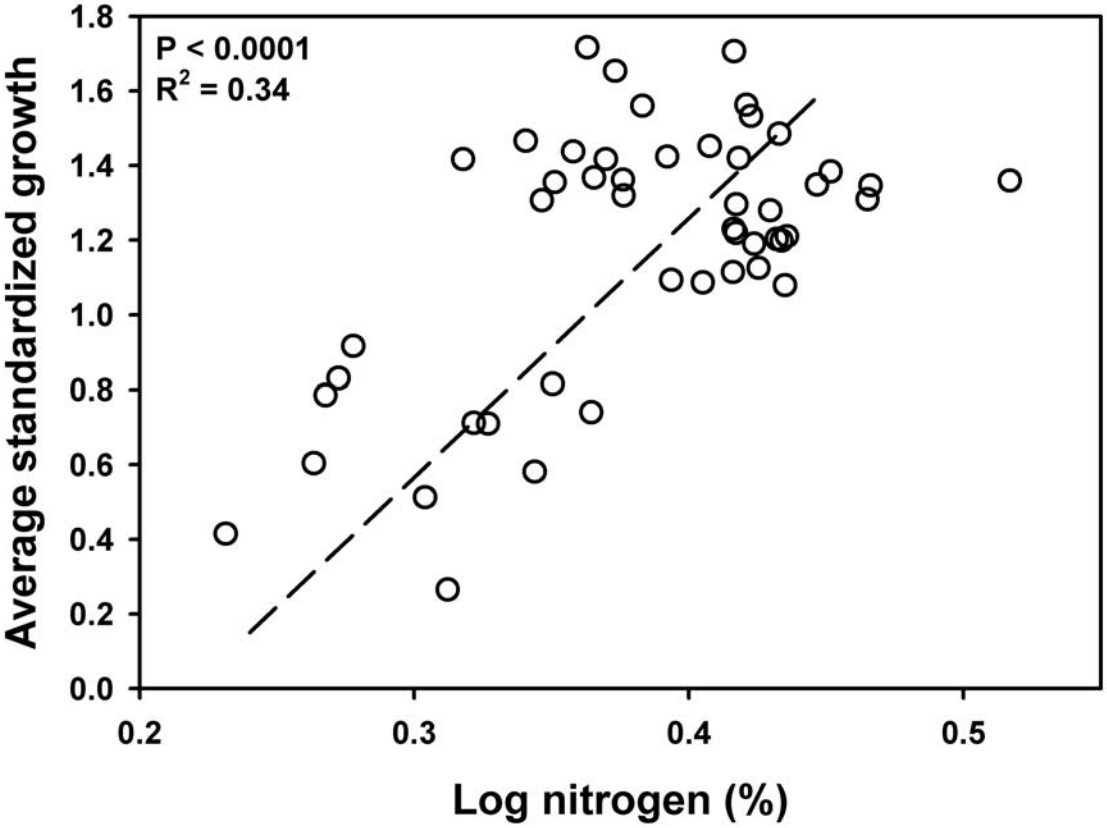

Figure 5: Scatter plot of the relationship between percent nitrogen and the average standardized growth for *Larix laricina*. Data were analyzed using a simple linear regression, with percent nitrogen data being log-transformed to make the data linear. The dotted line represents the best fit line for this data.

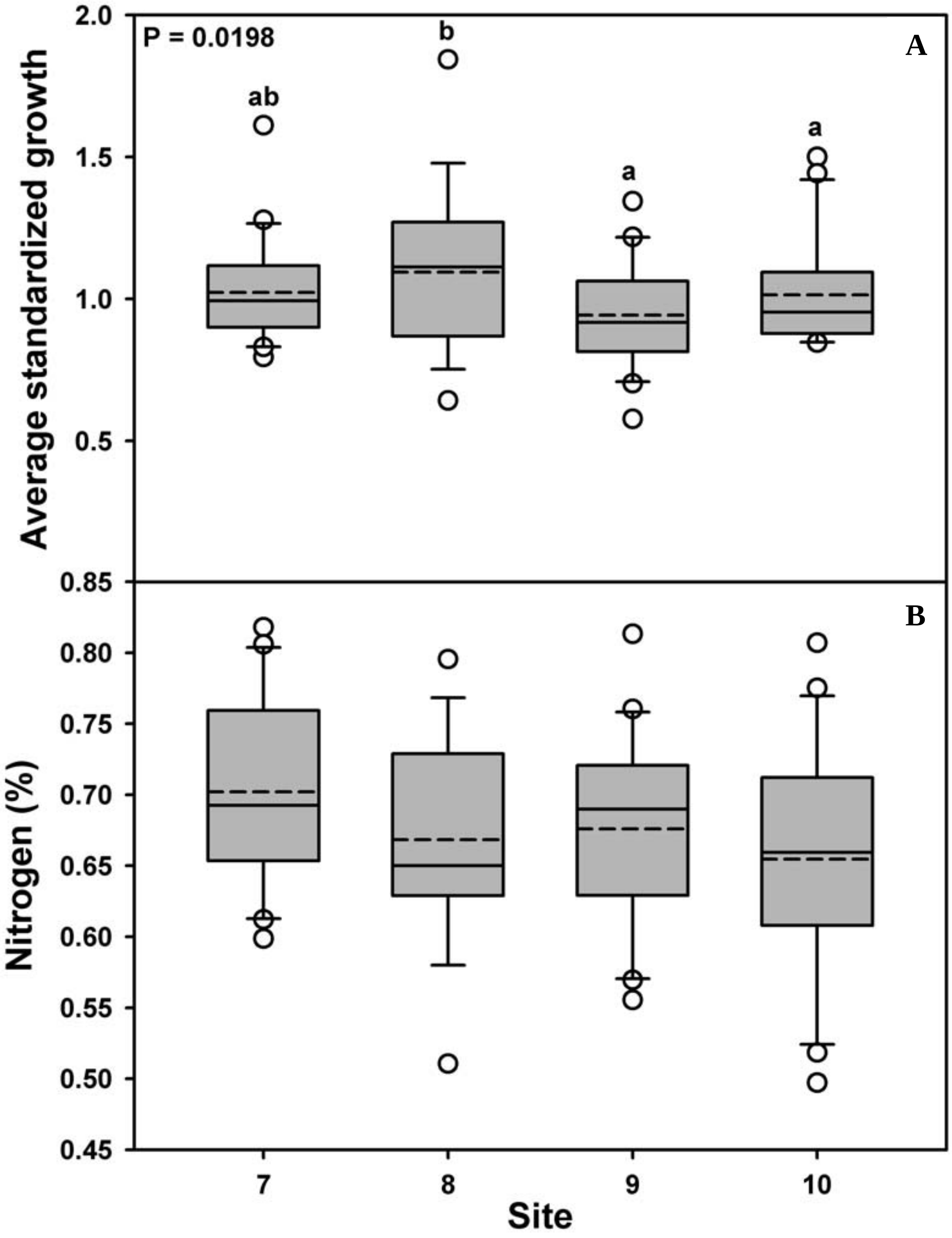

Figure 6: Box and whisker plots for the average standardized growth (A) and percent nitrogen (B) from four sites in Western Labrador sampled containing *Picea mariana*. Numbering for the sites corresponds to the placement from north to south in Figure 1. The site median is shown with a solid line and the mean is shown using a dashed line within the box plots. Data were analyzed using an ANOVA, with displayed p-values indicating the significance level of the relationship between site and the measured variable. Model df = 3, error df = 62 for the average standardized growth. Lowercase letters indicate significant differences between sites at α = 0.05 level.

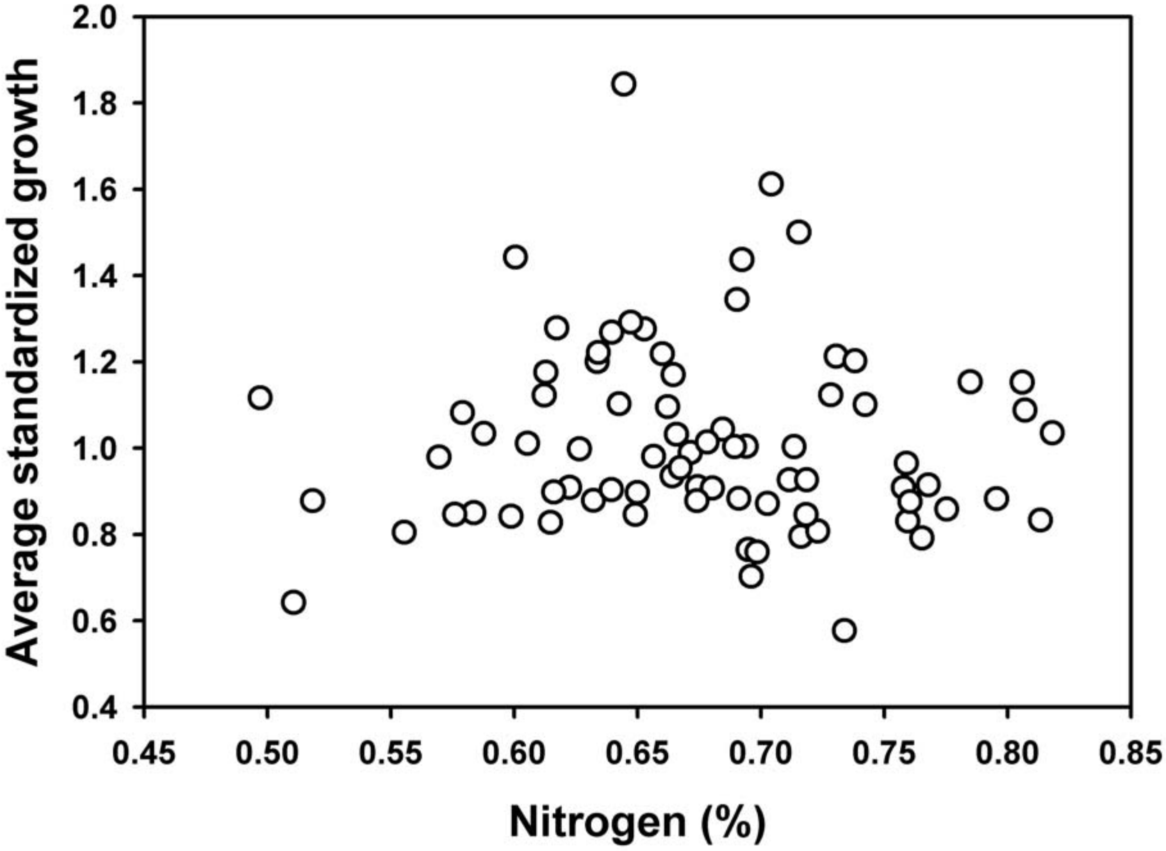

Figure 7: Scatterplot of the relationship between percent nitrogen and the average standardized growth for *Picea mariana*. Data were analyzed using a simple linear regression. No relationship was found.

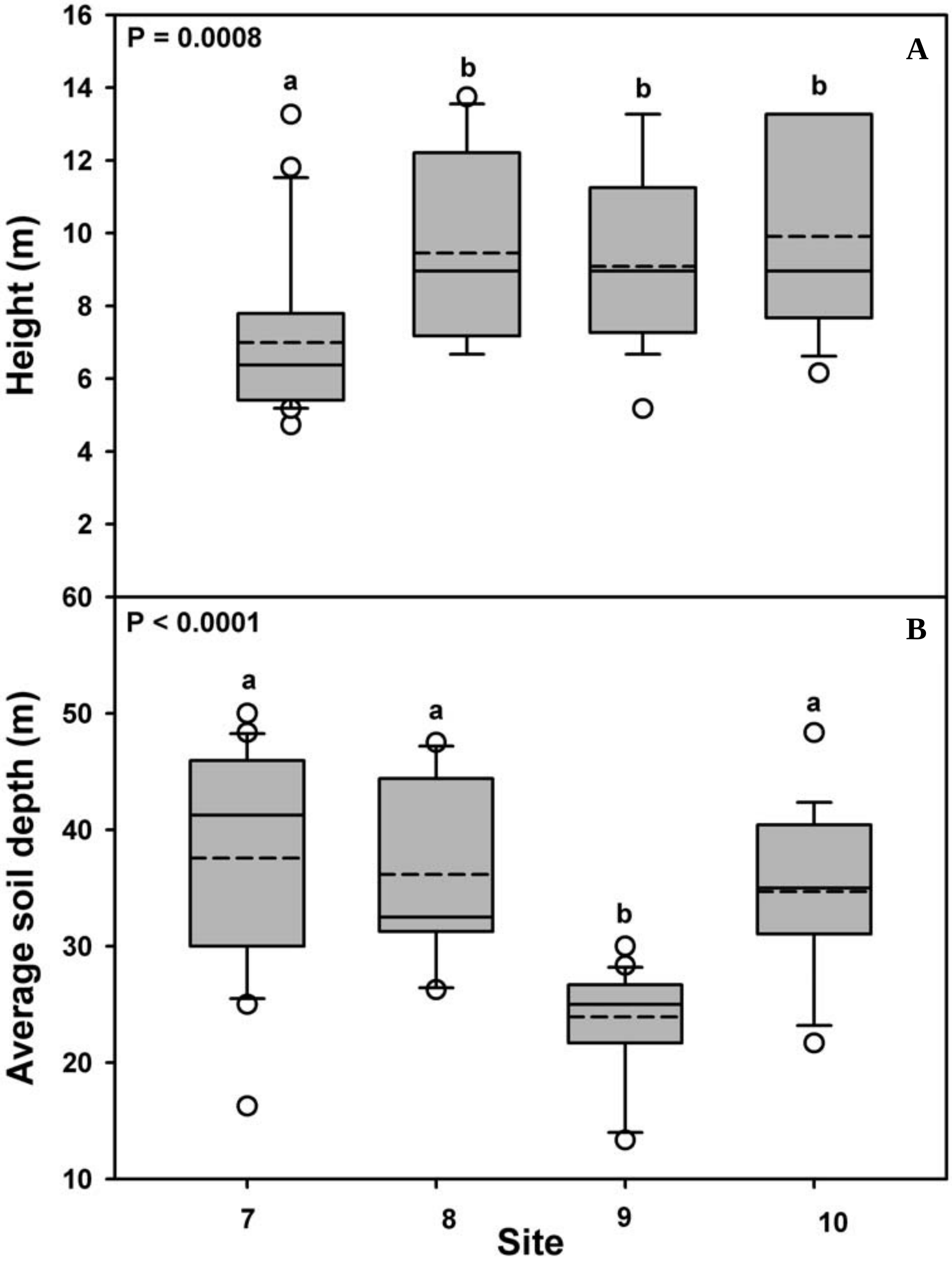

Figure 8: Box and whisker plots of average height (A) and average soil depth (B) for four *Picea mariana* sites in western Labrador. Site numbering corresponds to the north to south placement indicated in Figure 1. The site median is shown with a solid line and the mean is indicated by the dashed line through the box plots. Data were analyzed using an ANOVA, with displayed p-values indicating the significance level of the relationship between site and the measured variable. Lowercase letters indicate significant differences between sites at $\alpha = 0.05$ level.

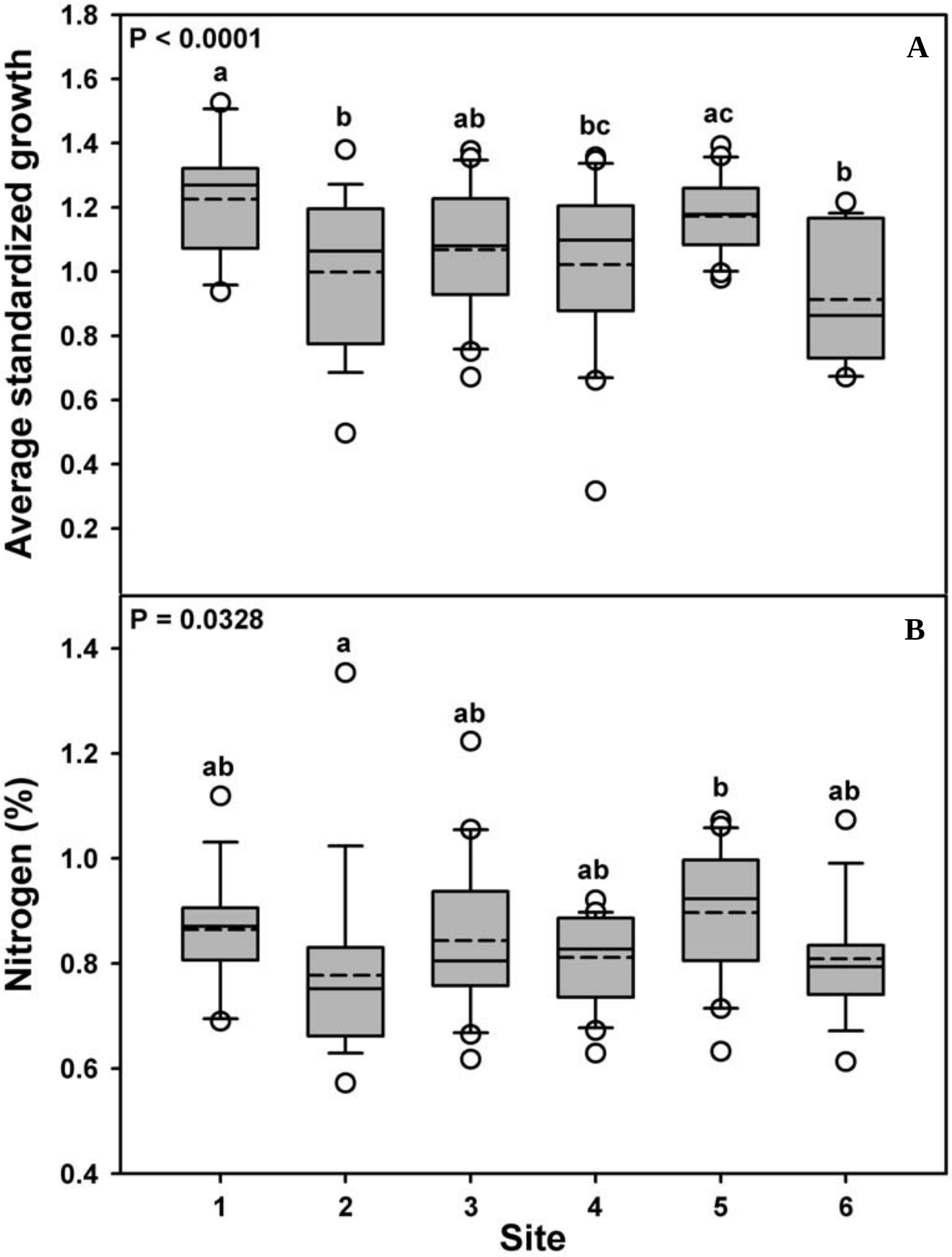

Figure 9: Box and whisker plots of average standardized growth (A) and percent nitrogen (B) for six *Picea glauca* sites in northern Labrador. Sites numbered one through six represent the order of sites from most northern to southern as shown in Figure 1. The site median is shown with a solid line and the mean is indicated by the dashed lines within the box plots. All data were analyzed using ANOVA, with displayed p-values indicating the significance level of the relationship between site and the measured variable. Lowercase letters indicate significant differences between sites at $\alpha = 0.05$ level.

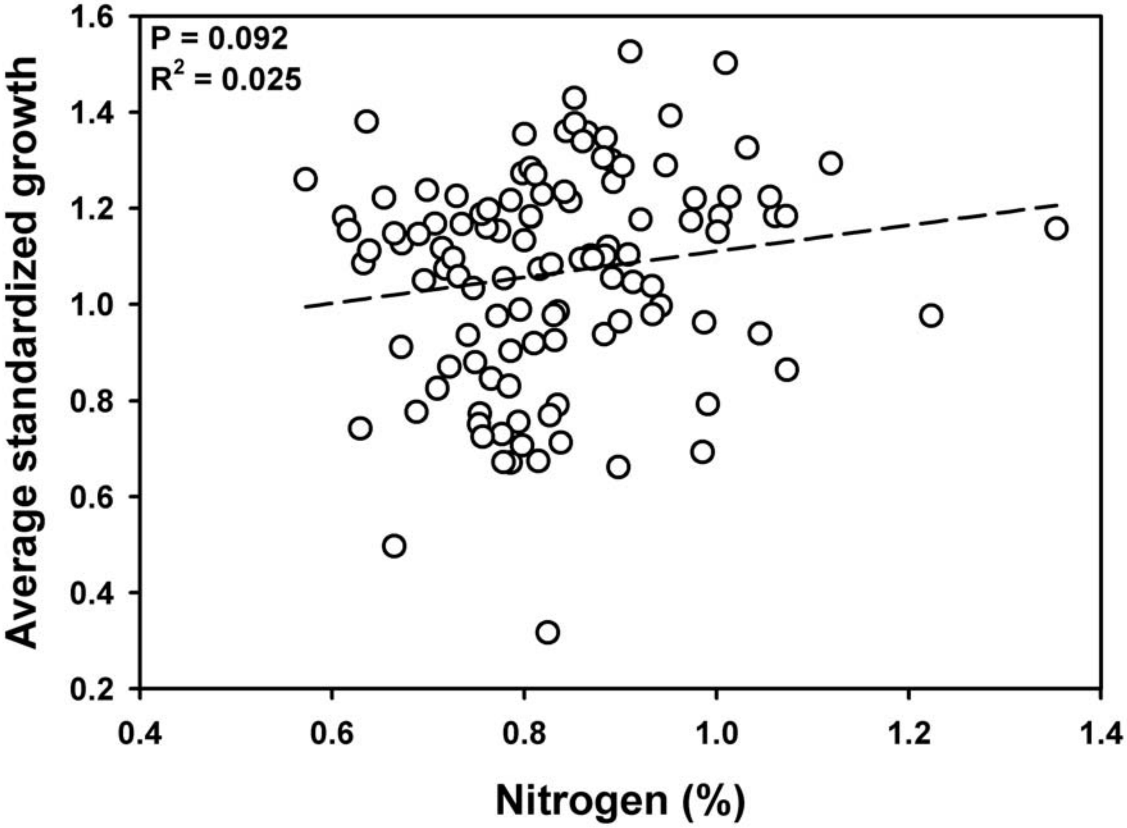

Figure 10: Scatterplot of the regression relationship between percent nitrogen and the average standardized growth for *Picea glauca*. Data were analyzed using a simple linear regression. The dotted line represents the best fit line for this data.

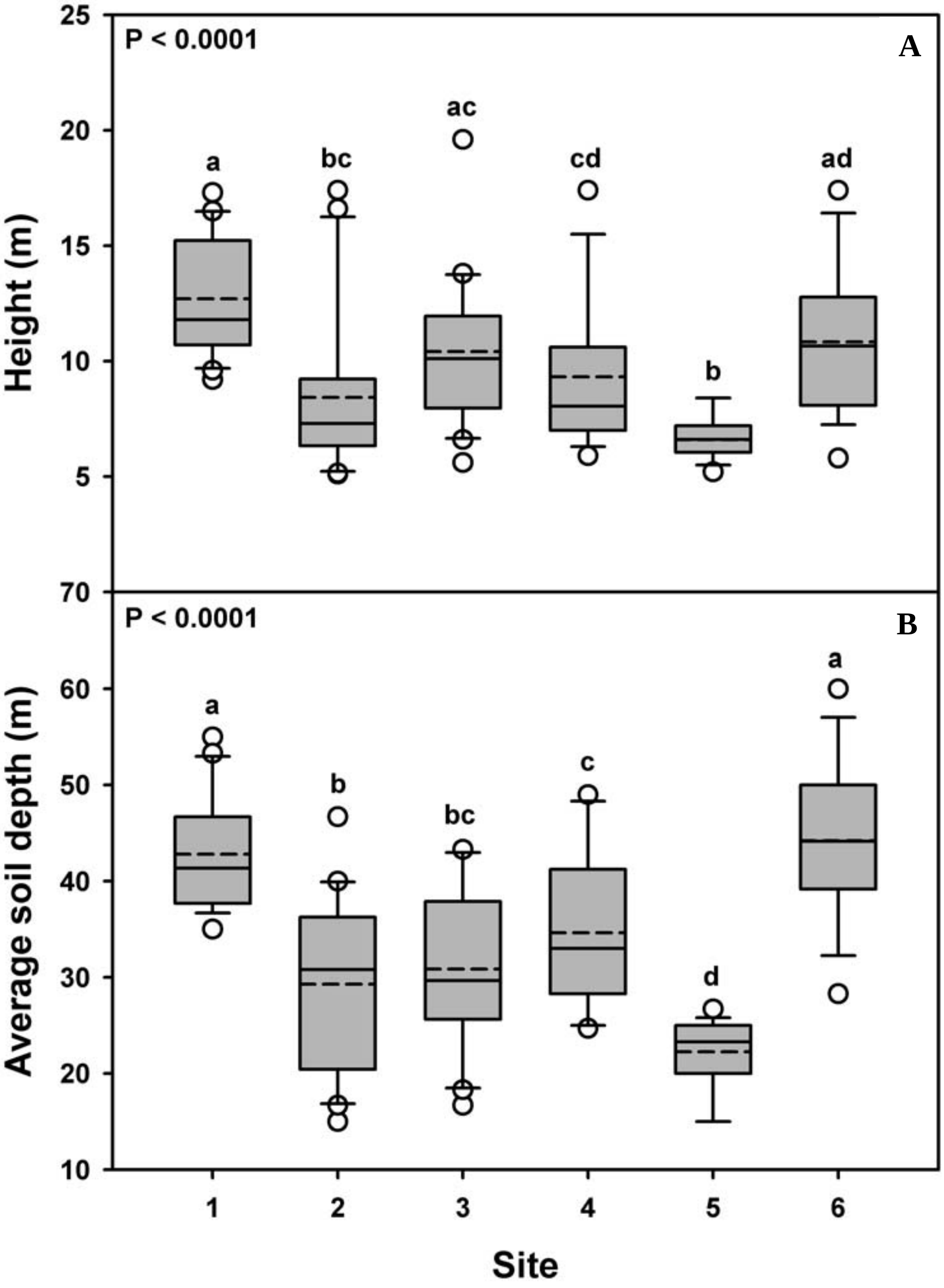

Figure 11: Box and whisker plots of height (A) and average soil depth (B) from six *Picea glauca* sites in northern Labrador. Sites are numbered according to their placement along a north to south latitudinal gradient as shown in Figure 1. The dashed line in the box plots represents the site mean and the solid line represents the median values at each site. All data were analyzed using ANOVA, with displayed p-values indicating the significance level of the relationship between site and the measured variable. Model df = 1 for average soil depth and height, error df = 102. Lowercase letters indicate significant differences between sites at α = 0.05 level.