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Effects of soil temperature on growth and biomass allocation in four boreal tree species

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ABSTRACT

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Trembling aspen (*Populus tremuloides* Michx.), black spruce (*Picea mariana* (Mill.) B.S.P.), white spruce (*Picea glauca* (Moench) Voss), and jack pine (*Pinus banksiana* Lamb.) seedlings were subject to seven soil temperature treatments 5, 10, 15, 20, 25, 30 and 35°C. At the beginning and end of the experiment, the height and diameter of all seedlings were measured. Ten seedlings from each treatment combination were harvested at the end of the experiment for the determination of biomass allocation. It was found that soil temperature, species and interaction of soil temperature and species had significant effects on biomass and relative growth rate (RGR) of diameter. The relationship between each parameter and soil temperature was modeled using a 3rd order polynomial function. The model showed that the optimum soil temperatures were 19.4°C, 17.3°C, 15.3°C and 21.8°C, respectively, for aspen, black spruce, white spruce and jack pine. The biomass variables showed nonlinear responses to changes in soil temperatures between 5°C and 30°C in all tree species. All the aspen seedlings, about 40 percent of jack pine, 20percent of white spruce and black spruce seedlings survived the 35°C treatment during the experiment. Among the species, aspen had the largest response in total biomass and biomass of different components to soil temperatures. The maximum total biomass for aspen was about 7 times the minimum value, the corresponding values for black spruce, jack pine and white spruce were 2.2, 2.4 and 2.3 times, respectively. The total biomass and biomass of different organs at soil temperature 5°C were smaller than those at temperature 30°C for aspen, black spruce and jack pine. The results were reversed for white spruce. The total biomass at 5°C was 14.3 percent of the value at the optimum soil temperature for aspen, the corresponding values for black spruce, jack pine and white spruce were 45 percent, 42 percent and 42 percent, respectively. Soil temperature did not significantly affect leaf to root ratio, shoot to root ratio, shoot mass to total mass ratio (SMR), leaf mass to total mass ratio (LMR), or stem mass to total mass ratio (SMR). But there were significant differences between species in all the above ratios and different species responded differently to soil temperature treatments. The relative growth rate (RGR) also varied with species. Soil temperature did not affect RGR in jack pine and white spruce. The RGR of black spruce was sensitive to soil temperatures over the whole range while RGR of aspen was only sensitive to soil temperature below 15°C.

Table of Contents

LIST OF TABLES

LIST OF FIGURES

ACKNOWLEDGMENTS

Introduction

During the past several decades, studies of plant responses to temperature have provided a recurring focus for botanical research (Long and Woodward 1988). However, now it is perhaps more topical than ever as attempts are made to predict vegetation responses to global climate change and increase in atmospheric CO_2 concentration (Hillier et al. 1994). Atmospheric CO_2 concentration has been increasing at approximately 1.8 percent per annum. In other words, atmospheric CO_2 concentration will increase from the current level of approximately 350 ppm to 500-700 ppm by the end of the 21st century (Eamus and Jarvis 1989, Eamus 1992). It is anticipated that global mean surface temperature will increase 1.5°C to 4.5°C by year 2100 (with regional, seasonal, and diurnal heterogeneity) if the current rate of anthropogenic emission of greenhouse gases (principally CO_2, CH_4 and N_2O) continues (Houghton et al.1990). Scientists anticipate that the greatest warming will occur in the boreal and subarctic regions (IPCC 1995). The global warming will likely accelerate CO_2 release from terrestrial ecosystems because of the positive effect of increased temperature on decomposition (Jenkinson et al. 1991).

The boreal forest is one of the earth's largest terrestrial biomes, extending over 14.7 million km^2 (11 percent of the earth's terrestrial surface) (Bonan and Shugart 1989). These forests contain about 800 Pg C in biomass, detritus, soil, and peat pools (Apps et al. 1993). The Canadian boreal forest covers about 2.5 million km^2 (about 17 percent of the world's boreal forest) and stores about 200 Pg C (Apps et al. 1993). The boreal forest may play an important role in the global C cycle and climate. The potential impact of climate change on

both structure and function of Canadian boreal forest ecosystems is thus of great interest and concern (Peng and Apps 1998).

Soil temperature is one of the most important factors controlling the distribution and function of the boreal forests (Bonan and Shugart 1989), and physiological activity and growth of plants (Long and Woodward 1988). Soil temperature can directly influence the rate of biochemical reactions in various metabolic processes and indirectly through its impact on the absorption of water and nutrients (Long and Woodward 1988). Increasing soil temperature from global climatic change could have major impacts on nutrient cycling of boreal forests (Jenkinson et al. 1991, Raich and Schlesinger 1992) through its influence on soil microbial activity (Insam et al. 1989, Nadelhoffer et al. 1991, Ellert and Bettany 1992, Tate et al. 1993, Houghton et al. 1998). Generally, root permeability and growth are higher at higher soil temperatures (Kramer 1942, Nambiar et al. 1979, Lawrence and Oechel 1983a, Tryon and Chapin 1983, Lopushinsky and Max 1990, Camm and Harper 1991, Vapaavuori et al. 1991). Root growth tends to increase with increasing temperature until an optimum is reached above which root growth will be reduced (Brar et al. 1970, Cooper 1973, Dougherty and Morikawa 1980, Lopushinsky and Kaufmann 1984, Glinski and Lipiec 1990). Cold soil temperature has been shown to reduce photosynthesis and transpiration (Linder 1972, Anderson and McNaughton 1973, Delucia 1986, Landhäausser et al.1996). At root temperatures below 10°C, stomatal conductance and transpiraton decline sharply (Kramer 1940 and 1942, Harvraneck 1972, Kaufmann 1975, Running and Reid 1980, Smith 1985). Net photosynthesis also declined in response to cold soil temperature (Babalola et al. 1968).

Low soil temperature reduces dry matter production and height growth in trees (Dougherty and Morikawa 1980, Lopushinsky and Kaufmann 1984). Plant biomass increases with increasing soil temperature (Cooper and Thornly 1976, Gosselin and Trudel 1986, Landhäausser *et al.* 1996). The reduction in biomass and growth at low soil temperature is attributed to 1) low nutrient availability because of slow rates of decomposition in cold soils (Moore 1981, 1984, Schlentner and Van Cleve 1985, Van Cleve and Yarie 1986), 2) slow nutrient uptake (Bhat 1982, Cumbus and Nye 1985, Chapin *et al.* 1986), and 3) slow nutrient cycling (Brown 1970, Pastor and Post 1988, Zak *et al.* 1993). In contrast, shoot/root ratio generally increases with increasing soil temperature (Davidson 1969, Larigauderie *et al.* 1991, Wilson 1988, Thornley 1972) because of the greater inhibition of low soil temperatures on leaf and shoot growth (Landhäausser and Lieffers 1998). However, a decrease in shoot/root ratio with increasing soil temperatures has also been observed for some species, such as *Phaseolus vulgaris* (Brouwer 1964), maize (*Zea mays* L.) (Grobberlaar 1963), *Ceanothus greggi* (Larigauderie *et al.* 1991) and *Andropogon gerardii* Vitman (Delucia *et al.* 1992). The low soil temperature inhibition of carbohydrate translocation from shoot to roots (Marowitch *et al.* 1986) may contribute to the high shoot/root ratios in cold soil. Relative growth rate is generally increases with increasing soil temperature (Gosselin and Trudel 1986, Martin *et al.* 1989, Maherali and Delucia 2000).

Aspen (*Populus tremuloides* Michx.), black spruce (*Picea mariana* (Mill) B.S.P.), jack pine (*Pinus banksiana* Lamb), and white spruce (*Picea glauca* (Moench) Voss.) are four economically important and ecologically) tree species in the boreal forest. Understanding the response of these species to soil temperature change can be an important aspect in understanding the response of boreal forests to global climate change. Although there are

many studies on soil temperature effects, relationships between soil temperature and the growth and development of boreal tree species are still poorly understood. The present study investigates the impact of soil temperature on biomass, biomass allocation and relative growth rate of the four boreal tree species. The hypotheses tested include (1) soil temperatures significantly influence dry matter accumulation of the four species, and (2) the pioneer tree species (aspen and jack pine) and mid-succession species (spruces) respond differently to soil temperature.

Literature review

Soil temperature and growth

Research indicates that the mean annual soil temperature for the boreal forest ranges from approximately 5 °C to < 8 °C and that the mean summer soil temperature ranges from approximately 15 ° to < 18 °C (ECORC, 2001). Soil temperature has been recognized as an important factor affecting plant growth (Sutton 1969, Walker 1969). Soil temperature affects the growth of roots and shoots of many tree seedlings (Barney 1951, Hellmers 1963, Heninger and White 1974). Soil temperature influences the initiation, branching, orientation and the turnover rate of root systems (Lopushinsky and Kaufmann 1984, Kaspar and Bland 1992). It also affects root morphology and permeability (Kramer 1942), and water and nutrient uptake (Tryon and Chapin 1983, Grossnickle and Black 1985, Andersen *et al.* 1986, Pritchard *et al.*1990, Tindall *et al.*1990).

Soil temperature is a major factor controlling root growth in trees. It is one of the factors affecting the water status and root growth of newly planted conifer seedlings in the spring and early summer (Lippu and Puttonen 1991). Low soil temperatures reduce root growth of coniferous species (Stone and Schubert 1959, Nambiar et al. 1979, Grossnickle and Reid 1983, Tyron and Chapin 1983, Grossnickle and Black 1985). Soil temperature lower than 3°C consistently causes a reduction in root growth (Husted and Lavender 1989). Low root temperature can also lead to root mortality (Arndt 1937). In general, root growth tends to increase with increasing temperature until an optimum is reached above which root growth is reduced (Arndt 1937, Brar *et al.* 1970, Pearson *et al.* 1970, Cooper 1973). The optimum soil

temperature for the root growth of white spruce (*Picea glauca* (Moench) Voss.) was 19°C (Heninger and White 1974). McMichael and Quisenberry (1993) observed that the optimum temperature for root growth was between 28 and 35°C in cotton (*Gossypium hirsutum* L.) and between 23 and 25°C in sunflower (*Helianthus annuns*). Root growth for white and black spruce seedlings was higher at a soil temperature of 22°C than at 10°C (Grossnickle and Black 1985). Black spruce seedlings have maximum root growth at day-night temperatures of 21-19°C (Odlum and Ng 1995). Root growth was greatest in Sitka spruce (*Picea sitchensis*) under a 25-20°C day-night soil temperature regime (Binder et al. 1990). Barney (1951) reported that root growth of loblolly pine (*Pinus taeda*) increased with increasing soil temperature from 5 to 25°C but decreased with further increases to 35°C. Lopushinsky and Max (1990) found that root growth in Douglas fir (*Pseudotssuga menziesii* (Mirb.) Franco), Pacific silver fir (*Abies amabilis* (Dougl.) Forbes), noble fir (*Abies procera* Rehd.), lodgepole pine (*Pinus cortorta* Dougl. Ex Loud) increased rapidly with soil temperature above 10°C and attained maximum at 20°C. At 30°C, no root growth occurred in Douglas fir, Pacific silver fir, noble fir and other firs while root growth in lodgepole pine was 30 to 39 percent of maximum. Vapaavuori *et al.* (1991) found that root growth of both Scotch pine (*Pinus sylvestris* L.) and Norway spruce was completely inhibited at root temperatures of 5 and 8°C, but increased almost exponentially as root temperatures increased. Several studies have shown that a soil temperature near 20°C promotes rapid root growth in seedlings of western conifers (Nambiar *et al.* 1979, Tryon and Chapin 1983, Ritchie 1985). Tryon and Chapin (1983) pointed out that because of low soil temperature (1-10°C) and low nutrient availability at some taiga sites, it is likely that below ground processes such as root growth exert a major influence over tree growth and distribution.

In northern forests, soil temperature strongly affects performance of tree species (Tryon and Chapin 1983). Low soil temperatures were thought to be limiting to plant growth and strongly influence tree distribution (Viereck 1979). Under cold soil conditions, sucker initiation in aspen was limited (Zasada and Schier 1973, Johansson and Lundh 1988, Lavertu et al.1994). Changes in soil temperature resulted in changes in root growth, water uptake, oxygen supply, mineral nutrition, root morphology, and metabolism in many plant species (Cooper 1973, Abbas Al-Ani et al. 1983). Low soil temperature adversely affectes the initiation, elongation, branching and morphology of new roots. For example, the process of initiation and elongation were greatly retarded below a critical root temperature between 11 and 14°C in Monterey pine (Pinus radiata D. Don) seedlings (Nambiar et al. 1979). Nambiar et al. (1979) found that soil temperature greatly affected the initiation of new root lateral primordial as well as the elongation, branching, diameter, weight and morphology of the root system in Monterey pine Tryon and Chapin (1983) reported that roots penetrated to a greater depth in warm sites compared to cold ones.

Root elongation in several boreal forest tree species is promoted by an increase in soil temperature (Lawrence and Oechel 1983a, Tryon and Chapin 1983). Root elongation for both white and black spruce seedlings increased from 0.5 mm day^{-1} to a high of 1.5-2.0 mm day^{-1} as soil temperature (at 10 cm) increased from 2 to 12°C (Tryon and Chapin 1983). These authors also found that root elongation of greenhouse-grown tree seedlings increased with increasing root temperature in six Alaskan taiga species: black spruce, white spruce, aspen, balsam poplar (P. balsamifera), white birch (Betula papyrifera), and tamarack (Larix laricina). Among these spruces, warm-adapted aspen was most sensitive to soil temperature changes. Root elongation in aspen was slower in fine roots compared to large roots. In black

spruce, fine roots were less temperature sensitive than large roots. Roots formed at lower temperatures were thicker and less branchy than those formed at higher soil temperatures (Brouwer and Hoagland 1964). Root length per unit of dry weight was about 30 percent shorter when grown at 15°C than at 20 to 35°C in *Eucalyptus marginata* (Jarrah) in the greenhouse (Stoneman and Dell 1993). Camm and Harper (1991) found that white spruce produced 11 to 30 percent less long-roots (length >10 mm) at 3 or 7°C soil temperature than at 11°C. Abbas Al-Ani and Hay (1983) found similar results on branching and morphology of new roots. The processes of initiation and elongation are markedly retarded when soil temperature was below a critical value (11 and 14°C respectively). Cooper (1973) has started that root diameter in tomato plants generally decreased as temperature increased with a temperature optimum of 25°C. Abbas Al-Ani and Hay (1983), however, observed that soil temperatures from 5 to 25°C had only small effects on diameters of individual roots.

Low soil temperatures inhibit leaf and shoot growth (Landhäausser and Lieffers 1998). Soil warming significantly enhanced relative diameter growth of woody plants, especially shrubs, but *Vaccinium corymbosum* (a shrub species) showed reduced leaf sizes under soil heating (Farnsworth *et al.* 1995). Leaf expansion of maize seedlings was very sensitive to low soil temperature, which could be reduced by insulating the basal meristems near the chilled substrate (Watts 1972, Engels and Marschner 1990). Rook and Hobbs (1976) reported that leaf growth was restricted at low soil temperatures but there was no reduction in shoot extension. But Lopushinsky and Max (1990) found that maximum shoot growth also occured at 20°C in Douglas fir, pacific silver fir, noble fir, lodgepole pine and ponderosa pine. Heninger and White (1974) also found that the best shoot and total seedlings growth in white spruce and jack pine occurred at 19°C and 27°C, respectively. In ponderosa pine, height

growth of seedlings from a high-elevation province was unaffected by cold soil, but height growth of low-elevation seedlings was reduced. These authors recommended that root temperature should be maintained at 20°C for most species, and possibly higher (23-25°C) for low-elevation sources of ponderosa pine.

Soil temperature and physiological processes

Soil temperatures directly influence ecophysiological processes (Lopushinsky and Kaufmann 1984). The beginning and the end of growing season are closely related to soil thawing and freezing (Ryden and Kostov 1980). Cold soil temperatures have been shown to reduce photosynthesis in several coniferous species (Babalola *et al.* 1968, Havranek 1972, Linder 1972, Wesselius and Brouwer 1972, Anderson and McNaughton 1973). Landhäausser *et al.* (1996) found that net assimilation rate in black spruce increased from 1.2 μmol m^{-2}s^{-1} to 6.5 μmol m^{-2} s^{-1} when soil temperature increased from 3 to 10°C but did not increase with further increase of soil temperature to 15°C.

Soil temperature influences the photosynthesis (p_n) and stomatal conductance (g_s) of the tree species. Seedling net photosynthesis (p_n) and stomatal conductance (g_s) showed significant interactions between soil temperature and storage duration treatments in white spruce (Harper and Camm 1993). Soil temperature did not affect seedling g_s or p_n although the degree and extent of storage duration effects were depended on soil temperature. Babalola *et al.* (1968) found that photosynthesis of Monterey pine decreased at soil temperatures below 10°C, and p_n in Engelmann spruce (*Picea engelmannii* Parry ex Engelm) declined sharply when soil temperature below 8°C. However, Day *et al.* (1990) observed that p_n in young Engelmann spruce trees were greater for the trees in the cold soils (<3.5°C) than for trees in

the warm soils until about 15.00 hours. Delucia (1987) reported that root temperature between 10 and 20°C had no effect on p_n of Engelmann spruce, but p_n and g_s declined sharply as soil temperature decreased below 8°C: p_n and g_s decreased to 50 and 34 percent of the values at 20°C respectively after 7 days at a root temperature of 0.7°C. Neilson *et al.* (1972) showed that p_n was positive at soil temperatures between –5°C and 30°C with the maximum rate occurring between 15 and 20 °C.

Leaf conductance to water vapor was not significantly affected by root temperature. Low g_s at low root temperatures has been attributed to a decline in shoot water potential or other hydraulic and/or hormonal signals, and low g_s may result in stomatal limitations to photosynthesis (Benzioni and Dunstone 1988, Smith and Dale 1988, Day *et al.* 1991). Both leaf dark respiration and g_s were reduced by the 5°C soil-temperature treatment at 15°C air temperatures in seedlings of aspen (*Populus tremuloides* Michx), balsam poplar (*Populus balsamifera* L.) and paper birch (*Betula papyrifera* Marsh), from interior Alaska (Lawrence and Oechel 1983a, b).

Plant metabolisms are directly affected by low soil temperatures. In the last decade a number of reviews (Berry and Bjorkman 1980, Guy 1990) have been published on the subject. Several important physical factors that may influence photosynthesis have been found to change dramatically along the natural elevation range occupied by Engelmann spruce (Smith and Geller 1979). Also in the first growing season increasing soil temperature from 5 to 15°C improved the net photosynthetic rate (p_n) of white pine and white spruce (Brand 1990). Delucia (1987) suggested that a threshold soil temperature of approximately 8°C resulted in sharp decline in g_s and p_n in Engelmann spruce (*Picea engelmannii* Parry). Turner and Jarvis (1975) worked with root temperature of –8°C to 20°C on *Picea sitchensis* (Bong.) Carr.

suggested that the decrease in p_n and g_s in response to cold soil temperature was partially a result of physiological state of the seedlings: a marked decrease in p_n and g_s occurred at -1 ^{0}C in cold hardened and at 1^0C in unhardened seedlings. Soil temperatures above these levels had little effect on g_s and p_n. They suggested that these effects resulted from changes in root permeability resulting from acclimation to cold temperatures.

It is widely recognized that low soil temperature reduces transpiration (Kramer 1949). The magnitude of reduction varies with species, being greater in species that normally grow in warm soils than in those in cold soils (Kramer 1942, Kozlowski 1943). Kaufmann (1975) pointed out that transpiration rate would decrease if soil temperature became low enough to reduce stomatal opening. Therefore, the magnitude of the effect of root temperature on transpiration depends upon the degree to which stomata conductance is affected by leaf water potential. Babalola et al. (1968) found that the transpiration rate of Monterey pine seedlings in moist soil at 10°C was 27 percent of the rate at 26.7°C. Lopushinsky and Kaufmann (1984) reported that the transpiration of Douglas fir increased with increasing soil temperature and maximum rate occurred at 34°C. Meinzer et al. (1997) concluded that the reason for reduction of total plant transpiration with low soil temperature was the reduction of the leaf area.

Soil temperature also affects plant phenology. Cold soil may lead to delays in the timing of bud flush (Lavender et al. 1973, Sorensen and Campbell 1978). Lavender et al. (1973) suggested that low soil temperature (5°C) played a major role in regulating the timing of bud flush. However, Timmis and Worrall (1974) observed no differences in flushing dates between cold and warm rooted plants. Hulbert (1988) reported that an increase in soil temperature from 16.1 to 20.0°C (10 cm depth) in the field caused a 34 percent increase in the number of flowering stables for Andropogon gerardii.

Soil temperature and water uptake

It has been known at least since the time of Hales in the 18th century that low soil temperatures reduce water uptake by plants (Kramer 1942, 1949). Kramer found that when soil was near freezing, water uptake by seedlings of several pine species native to the eastern United States was only 14 to 38 percent of the rate that occurred at 25°C. Kaufmann (1975) documented that at soil temperatures of 0 to 5°C, xylem pressure potential decreased to as low as –20.4 bars as a result of decreased water uptake, even though soil moisture was adequate. In cold soil the viscosity of water increased and permeability of cytoplasmic membranes of roots to water decreased (Lopushinsky and Kaufmann 1984). Grossnickle and Black (1985) reported that jack pine and white spruce seedlings at low soil temperatures showed greater initial water stress than seedlings at higher soil temperatures.

Low soil temperatures also decreased biological activity of plants by restricting water uptake due to increased root resistance and water viscosity (Kaufmann 1975, Lawrence and Oechel 1983a and 1983b, Lopushinsky and Kaufmann 1984, Goldstein et al. 1985, Wolff et al. 1977). Kaufmann (1977) found that root resistance of Monterey pine seedlings increased at about 12°C and became more limiting for water absorption at lower temperatures. Running and Reid (1980) also found that root resistance to water was 67 percent of total plant resistance at 7 °C and 93 percent at 0°C soil temperature and root in lodgepole pine seedlings. Teskey (1982) found that root resistance in seedlings of Pacific silver fir was less affected by low root temperature than that in several other Pacific Northwest conifers. He concluded that root resistance was unaffected by decreasing soil temperature until about 2°C at which it increased rapidly with further decrease in soil temperature. When soil temperature was below 1.5°C, stomata closed. Although water absorption and xylem water pressure potential

decreased in response to low soil temperature, moisture stress did not reach lethal limits (Lopushinsky and Kaufmann 1984). The water potential of Douglas fir seedlings decreased to -2 Mpa at the soil temperature of 1.3 ^{0}C (Lopushinsky and Kaufmann 1984). Doring (1935) measured the change in rate of water absorption in 57 species when the plants were transferred from 20°C growing solution to 0 $-$ 2°C growing solution. The changes ranged from a 7 percent increase in water uptake to a decrease of 79%, with the majority of the species showing marked reductions. Similar results led Kramer (1940) to conclude, "low soil temperature is the most important environmental factor affecting the rate of water absorption." Other researchers (Unger and Danielson 1967) also suggested that growth reduction at low soil temperatures might be due to an influence on the water status of the plant. But Nielsen and Humphries (1966) pointed out that it would be an over simplification to attribute the reduction in growth entirely to reduced water uptake.

Soil temperature and nutrient uptake

Low soil temperatures reduce nutrient uptake (Chapin 1974, Bhat 1982, Cumbus and Nye 1985) and nutrient cycling in the forest (Jenkinson et al. 1991, Raich and Schlesinger 1992). The nutrient uptake is reduced when aspen plants are moved into chilled soil conditions (Chapin et al. 1986). Warming soil temperature has been shown to increase N-mineralization and increase N-availability (Peterjohn et al. 1994). The low uptake is attributed to the low nutrient availability and slow root activity under low soil temperature. The presence of permafrost restricts the rooting zone of trees and the amount of nutrients available for uptake. Slow rates of decomposition in cold soils result in low nutrient availability as nutrients are tied up in the forest floor (Tamm 1953, Siren 1955, Weetman 1962, Brown 1970,

Tyrtikov 1973, Moore 1980, 1981, 1984, Van Cleve *et al.* 1983a, b, Van Cleve and Yarie

1986). In interior Alaska, forest floor decomposition is directly correlated to soil temperature

(Flanagan and Van Cleve 1977, 1983, Fox and Van Cleve 1983, Schlentner and Van Cleve

1985, Van Cleve and Yarie 1986). Since the rates of organic matter decomposition and

mineralization have a positive relationship with soil temperature, the rate of soil nitrogen

cycling within natural ecosystems can be enhanced by increasing soil temperature (Pastor and

Post 1988, Zak *et al.* 1993). Soil temperature is influenced by the thickness of organic soil

(Viereck 1970a) and vegetation, such as *Calamagrostis. canadensis* (Hogg and Lieffers 1991).

Soil temperature and carbon cycling

Carbon is assimilated by plant through photosynthesis and is lost through respiration

process, which represents the dynamic exchange of carbon between the terrestrial ecosystem

and the atmosphere. Warmer soils may stimulate microbial activity and increase

decomposition rates (Van Cleve *et al.* 1990), which will lead to greater carbon loss from the

soil. Schlesinger and Mitchell (1987) reported that the increase of soil temperature caused an

exponential respiratory loss of carbon. Bonan and Van Cleve (1992) pointed out that boreal

forests contain large quantities of carbon in the soil, prompting concerns that climatic

warming may stimulate decomposition and accentuate increasing atmospheric CO_2

concentration. In black spruce, white spruce, and paper birch forests, decomposition increased

with the soil warming caused by a $5^{\circ}C$ increase in air temperature (Bonan and Van Cleve

1992).

Soil temperature and biomass

Low soil temperature delays the onset of root and shoot growth and reduces dry matter production and height growth in conifers (Dougherty and Morikawa 1980, Lopushinsky and Kaufmann 1984). Plant growth increases as soil temperature increases up to an optimum and then decreases as temperature continues to increase (McMichael and Burke 1998). The optimum soil temperature for root, shoot and total seedling biomass was 19°C and 27°C for white spruce and jack pine, respectively (Heninger and White 1974). Landhäausser and Lieffers (1998) reported that the root dry weight on aspen doubled from an average of 4.9 g at 6°C to 8.4 g at 12°C and almost tripled to 11.3 g at 20°C. Stoneman and Dell (1993) reported that total plant growth and shoot growth of *Eucalyptus marginata* (Jarrah) seedlings in greenhouse were maximal at a soil temperature of 30°C, but root growth had a slightly lower temperature optimum such that the root/shoot ratio was highest at 20°C.

Soil temperature significantly affects the biomass and components of the plants. Brand (1990) documented that height, basal area, total biomass and biomass allocation increased markedly with increasing soil temperatures in both white spruce and black spruce. Landhäausser *et al.* (1996) reported that the mean biomass increased 30 percent when soil temperature increased from 3 to 15°C. The root biomass and root/shoot ratio also increased. Cooper and Thornly (1976) showed that as root temperature increased the fraction of the total plant dry matter accumulated in tomato fruits decreased significantly. There are also some evidences for genetic variability occurring with a species in the response of plant dry mass to changes in soil temperature (Quisenberry *et al.* 1981, McMichael and Quisenberry 1986, Brar *et al.* 1990). Several studies have reported a decrease in root/shoot ratio with increasing soil temperature from 5 to greater than 25°C. This is thought to be due to higher soil temperature

having a greater positive effect on shoot growth than on root growth (Davidson 1969, Wilson 1988, Larigauderie *et al.* 1991).

Soil temperature affected the biomass allocations. Davidson (1969) and Thornley's model (1972) postulated that shoot/root should increase with increasing soil temperature because higher temperature would increase rates of root function. Landhäausser and Lieffers (1998) also reported that the shoot/root ratio of the seedlings was lower at the low soil temperature (6°C) than at the warm soil temperatures (12 and 20°C) on trembling aspen. The effect of temperature on shoot/root ratio is through its influence on resource acquisition and allocation. However, some other studies (Grobbelaar 1963, Brouwer 1964, Larigauderie *et al.* 1991) found the opposite trend, *i.e.*, shoot/root ratio increased with decreasing soil temperature from 5 to 25°C. Camm and Harper (1991) reported that white spruce seedlings planted in cold soil (3°C) developed a higher shoot/root ratio than seedlings in warm soil (11°C), because the higher soil temperature caused more carbohydrate allocation to shoots relative to roots (Marowitch *et al.* 1986). Landhäausser *et al.* (1996) also found that the greatest increase in net assimilation rate occurred at soil temperatures between 3 − 10°C and root mass and shoot/root ratio decreased with increasing soil temperature from 3 to 15 °C in black spruce. In contrast, the shoot/root ratio was unaffected by soil temperatures on ponderosa pine (Maherali and DeLucia 2000) and Martin *et al.* (1989) also found that temperature did not affect shoot/root ratios of holly (Il *ex attenuate cv. East Palatka*) and elm (*Ulmus parvifolia cv. Drake*). Soil temperature had no effect on leaf area ratio (the ratio of leaf area to total biomass). However, dry weights of shoots and roots in holly, and roots in elm, decreased quadratically, shoots of elm decreased linearly with increased soil temperature. Gosselin and Trudel (1986) observed that increasing root zone temperature from 12 to 36°C

increased shoot dry mass as well as overall productivity of 6 —week old pepper (*Capsicum annuum* L.) plants. They also showed that an increase in root temperatures partially offset the negative effect of low night air temperatures (8 to 24 °C) on leaf dry mass and area.

RGR was positively affected by an increase in soil temperature. The change in growth was not directly related to photosynthetic rate (p_n) changes in carbon partitioning and foliage morphology. (Brand 1990). Maherali and DeLucia (2000) and Martin *et al.* (1989) also found that total biomass at the end of the experiment and relative growth rate (RGR) were maximum in soil temperatures of 25°C and decreased at higher and lower temperatures. Thus the effect of soil temperature on RGR was primarily through its influence on net assimilation rate. Therefore, if soils warm appreciably in response to global change it is possible this will be accompanied by reduced allocation of biomass to roots, representing reduced carbon inputs belowground. The relevant finding is that trembling aspen will not alter biomass allocation in response to soil warming (King *et al.* 1999).

Materials and Methods

Plant Materials

The experiment was performed on one-year-old seedlings of black spruce, white spruce, jack pine and trembling aspen. The coniferous seedlings were obtained from the A and R Container Tree Seeding Nursery in Dorion, Ontario. The aspen seedlings were grown from seeds in the Lakehead University greenhouse. The aspen seed was from a single provenance that consisted of 5 wind - pollinated families. All the seedlings were dormant when the experiment was initiated.

Experimental design

My experiment was carried out in two greenhouses on the Lakehead University campus. The treatment structure was 7 × 4 factorial. The controlled factors were soil temperature with 7 levels, 5, 10,15, 20,25, 30 and 35 °C, and species with 4 levels, aspen, jack pine, black spruce and white spruce. The experiment was executed in a split-spilt-plot design (refer to Fig. 1). The whole plots were the two greenhouses (complete blocks). The sub plots were specially-constructed water baths that allowed soil temperature to be controlled at predetermined levels (Cheng *et al.* 2000). The sub-sub plots were rows of pots that were submerged in the water baths. Each water bath contained 8 rows of pots: each row contained 14 pots. Seedlings of the 4 subject species were assigned at random to 2 rows of pots within each water bath.

Greenhouse (I)
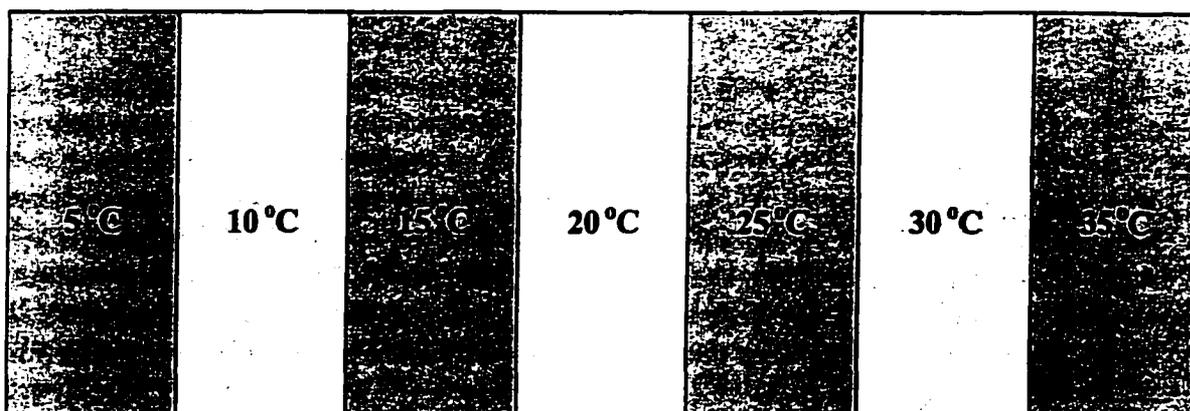
Greenhouse (II)
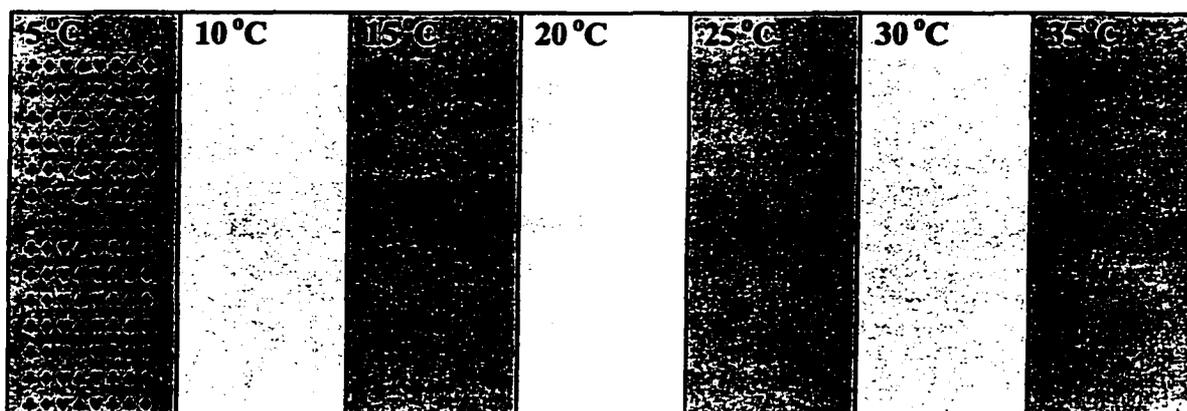
Figure 1. Map of the split-split plot experimental design: Greenhouses (whole plots) were complete blocks of the soil temperature-by-species experiment. Each greenhouse contained 7 temperature controlled water baths (sub plots). Each water bath contained 8 rows of pots (sub sub plots). Each species was assigned at random to 2 rows of pots per water bath.

Growing requirements

The day and night temperatures in the greenhouses were controlled at 22.5 ± 0.6 and 14.3 ± 0.3 (S.E.) °C, respectively. The daytime temperature fluctuated more than night temperature and was generally above the set point on sunny days. High-pressure sodium

lamps were used to extend the natural photoperiod to 16 hours in the early part of the experiment when the natural day length was less than 16 hours.

The growing medium was a mixture of peat moss and vermiculite (50/50 volume/volume). Seedlings were watered to saturation every two days using a fertilization solution of 126 ppm N, 44 ppm P, 83 ppm K, 40 ppm Mg, 52 ppm S, 30 ppm Ca, 2.5 ppm Fe, 0.67 ppm Mn, 0.4 ppm Zn, 0.3 ppm Cu, 0.12 ppm B, and 0.003 ppm Mo. The fertilization solution was formulated according to Landis *et al.* (1989).

The experiment was started on 6 February 1999 and continued for 4 months. At the end of each month, the salinity and pH of the growing medium solution were measured using an AGRITEST pH & ES/TDS meter that was manufactured buy HANNA Instruments, Portugal. The largest value of electrical conductivity (EC) was 1.3 mS/cm, which is within the range (<2.2 mS/cm) recommended by Landis *et al.* (1989). Soil pH was about 5.9 throughout the experiment.

We saw no difference between the soil volume at the end of the experiment compared to the beginning of the experiment. However, exact measurements pertaining to either soil settling or change in moisture content of soil were not conducted.

Growth and biomass measurements

The height and diameter at the root collar of all seedlings were measured at the beginning and end of the experiment. Height growth and root collar diameter growth were calculated from these measurements.

At the end of the experiment, I was supposed to draw a random sample of 5 seedlings for each species from each of the 2 rows of seedlings within each temperature treatment.

Instead, I drew a single random sample of 10 seedlings from each species from 28 seedlings (2 rows per species times 14 potted seedlings per row) available in each temperature treatment. As a result, two sources of variance became confound, namely, a) experimental error (between rows within species, temperatures, and greenhouses) and b) experimental error (between seedlings within rows, species, temperature, and greenhouse. This error had consequences that are explained below.

Each sampled seedling was divided into foliage, stem, and root components. All leaves of sampled seedlings were removed, and roots were cut from the seedlings. All samples of components were oven-dried at 70°C for 48 hours for the determination of biomass. The dry mass of foliage, roots and stems were measured separately on an analytical balance.

Data analysis

The data were analyzed using analysis of variance (ANOVA). The linear model for my experiment is

$$Y_{ijklm} = \mu + G_i + \sigma'_{(i)} + T_j + GT_{ij} + \sigma''_{(ij)} + S_k + GS_{ik} + ST_{jk} +$$

$$GST_{ijk} + \varepsilon_{(ijk)l} + \rho_{(ijkl)m}, \qquad\qquad\qquad \text{Eq. 1}$$

$$i = 1, 2 \qquad j = 1, 2, 3, ..., 7 \qquad k = 1, 2, 3, 4 \qquad l = 1, 2 \qquad m = 1, 2, ..., t^1$$

where

Y_{ijklm} = the measured response of the mth seedling in the lth row in the kth species in the jth temperature treatment in the ith greenhouse

μ = the overall mean

G_i = the random effect of the ith greenhouse

$\delta_{(i)}'$ = the restriction error[2] due to the first split in the design

T_j = the fixed effect of the jth soil temperature

GT_{ij} = the mixed interaction effect of the ith greenhouse with the jth temperature

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[1] The number of trees per row, t in indices specifications above, was intended to be 5 but, due to an error in the sample design, it may have been anything from 0 to 10 in practice.

[2] For more on restriction errors, see Anderson and McLean (1974).

$\delta_{(ij)}$" = the restriction error[1] due to the second split in the design

S_k = the fixed effect of the kth species

GS_{ik} = mixed interaction effect of the ith greenhouse with the kth species

TS_{jk} = the fixed interaction effect of the j_{th} soil temperature with the k_{th} species

GTS_{ijk} = the mixed interaction effect of the ith greenhouse with the jth soil temperature and the kth species

$\varepsilon_{(ijk)l}$ = the random effect of the lth row within species, temperatures, and greenhouses (This is the source of experimental error.)

$\rho_{(ijkl)m}$ = the random effect of the mth seedling within rows, species, temperatures, and greenhouses (This is the source of sampling error.)

The expected mean squares associated with Eq. 1 are presented in Table 1. The tests of hypotheses that follow from the expected mean squares are presented in Table 2.

ANOVA residuals were examined for normality and homogeneity of variance to ensure that the ANOVA assumptions were met. In order for the assumptions to be met, the log transformation was applied to the biomass data and the square root transformation was applied to the relative growth rate data.

Data from the 35°C soil temperature treatment were not included in the analysis due to high seedling mortality at this temperature.

The relationships between soil temperature and the growth and biomass variables were modeled using third-order polynomials. The first derivative of this model was used to estimate the optimum soil temperature. This was done by setting the first derivative equal to zero and solving for the root that fell within the range of the data. The second root was ignored.

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[1] For more on restriction errors, see Anderson and McLean (1974).

Table 1. Expected mean squares.

Source	df	Expected Mean Square
G_i	1	$\sigma^2 + 5\sigma^2_\varepsilon + 40\,\sigma_{\delta\cdot\cdot}^2 + 240\,\sigma_{\delta\cdot}^2 + 240\,\sigma_G^2$
$\delta_{(i)}$'	0	$\sigma^2 + 5\sigma^2_\varepsilon + 40\,\sigma_{\delta\cdot\cdot}^2 + 240\,\sigma_{\delta\cdot}^2$
T_j	5	$\sigma^2 + 5\sigma^2_\varepsilon + 40\,\sigma_{\delta\cdot\cdot}^2 + 40\,\sigma_{GT}^2 + 80\,\Phi(T)$
GT_{ij}	5	$\sigma^2 + 5\sigma^2_\varepsilon + 40\,\sigma_{\delta\cdot\cdot}^2 + 40\,\sigma_{GT}^2$
$\delta_{(ij)}$''	0	$\sigma^2 + 5\sigma^2_\varepsilon + 40\,\sigma_{\delta\cdot\cdot}^2$
S_k	3	$\sigma^2 + 5\sigma^2_\varepsilon + 60\,\sigma_{GS}^2 + 120\,\Phi(S)$
GS_{ik}	3	$\sigma^2 + 5\sigma^2_\varepsilon + 60\,\sigma_{GS}^2$
TS_{jk}	15	$\sigma^2 + 5\sigma^2_\varepsilon + 10\,\sigma_{GTS}^2 + 20\,\Phi(TS)$
GTS_{ijk}	15	$\sigma^2 + 5\sigma^2_\varepsilon + 10\,\sigma_{GTS}^2$
$\varepsilon_{(ijk)l}$	48	$\sigma^2 + 5\sigma^2_\varepsilon$
$\rho_{(ijkl)m}$	384	σ^2

Table 2. Tests of hypotheses as indicated by the expected mean squares presented in Table 1.

Hypothesis	Test statistic	Reference F-distribution
$\sigma_G^2 = 0$	No test – no estimate of MS(δ')	n/a
$\sigma_{\delta\cdot}^2 = 0$	No test – no estimate of MS(δ')	n/a
$\Phi(T) = 0$	MS(T)/MS(GT)	F(5, 5)
$\sigma_{GT}^2 = 0$	No test – no estimate of MS(δ'')	n/a
$\sigma_{\delta\cdot\cdot}^2 = 0$	No test – no estimate of MS(δ'')	n/a
$\Phi(S) = 0$	MS(S)/MS(GS)	F(3, 3)
$\sigma_{GS}^2 = 0$	No test – no estimate of MS(ε)	n/a
$\Phi(TS) = 0$	MS(TS)/MS(GTS)	F(15, 15)
$\sigma_{GTS}^2 = 0$	No test – no estimate of MS(ε)	n/a
$\sigma_\varepsilon^2 = 0$	No test – no estimate of MS(ρ)	n/a

Results

Biomass

With are exception soil temperature, species, and the soil temperature - species interaction had significant effects on root biomass, leaf biomass, stem biomass and total biomass. In the case of leaf biomass, the effect of temperature was not significant (Table 3).

For all the species, root biomass, foliage biomass, stem biomass and total biomass increased with increasing soil temperature and then decreased as the soil temperature increased further (Figure 2). However, the optimal soil temperature varied by organ and species.

The optimum soil temperature for root biomass was: 20.5°C for aspen, 14.7°C for black spruce, 21.1°C for jack pine and 14.8°C for white spruce (Table 4 and Figure 2A). The optimum soil temperature for leaf biomass derived from the model was 21.3°C for aspen, 18.9°C for black spruce, 23.7°C for jack pine, and 13.5°C for white spruce (Table 4 and Figure 2B). The optimum soil temperature for stem biomass was 18.1°C for aspen, 15.4 °C for black spruce, 22.0°C for jack pine, and 11.9°C for white spruce (Table 4 and Figure 2C). The optimum soil temperatures for the total biomass was 19.4°C for aspen, 16.0°C for black spruce, 22.4°C for jack pine, and 13.7°C for white spruce (Table 4 and Figure 2D). In general, aspen was more sensitive to changes in soil temperature than were the conifers (Figure 3). In addition, the change of growth rate of biomass components in aspen was different at different soil temperatures. The change of growth rate of biomass components decreased with increasing soil temperatures. This means that the change of growth rate of biomass component at the lower temperature is higher than that at the higher temperature.

Table 3. Analysis of variance for the effect of soil temperature on biomass (g).

Source	df	ROOT MS	MS-ratio	F-critical	LEAF MS	MS-ratio	F-critical	STEM MS	MS-ratio	F-critical
Greenhouse	1	22.20	No test		6.23	No test		14.32	No test	
δ'	0	No test	No test			No test			No test	
T	5	14.77	9.85	5.05 *	8.60	4.57	5.05	6.67	10.77	5.05 *
G*T	5	1..52	No test		1.88	no test		0.62	no test	
δ''	0	No test	No test			No test			No test	
S	3	86.65	46.34	9.28 *	11.18	159.71	9.28 *	79.39	441.06	9.28 *
G*S	3	1.87	No test		0.07	No test		0.18	No test	
T*S	15	3.24	2.42	2.40 *	3.58	3.44	2.40 *	3.66	3.45	2.40 *
G*T*S	15	1.34	No test		1.04	No test		1.06	No test	
EXP.Error	48	No est.	No test		0.37	No test		0.36	No test	
Samp. Error	384	No est.								
Corr Total	479									

Source	df	TOTAL MS	MS-ratio	F-critical	Leaf/Root MS	MS-ratio	F-critical	Shoot/Root MS	MS-ratio	F-critical
Greenhouse	1	13.64	No test		4.91	No test		2.25	No test	
δ'	0	No test	No test		No test	No test		No test	No test	
T	5	9.12	6.85	5.05 *	2.80	2.19	5.05	2.06	2.61	5.05
G*T	5	1.33	no test		1.28	no test		0.79	no test	
δ''	0	No test	No test		No test	No test			No test	
S	3	45.98.1	183.92	9.28 *	44.93	17.41	9.28 *	15.38	9.73	9.28 *
G*S	3	0.25	No test		2.58	No test		1.58	No test	
T*S	15	2.83	2.67	2.40 *	0.89	1.78	2.40	0.58	1.32	2.40
G*T*S	15	1.06	No test		0.50	No test		0.44	No test	
EXP.Error	48	No est.	No test		0.37	No test		0.36	No test	
Samp. Error	384	No est.								
Corr Total	479									

Source	df	RMR MS	MS-ratio	F-critical	LMR MS	MS-ratio	F-critical	SMR MS	MS-ratio	F-critical
Greenhouse	1	1.00	No test		1.47	No test		0.01	No test	
δ'	0	No test	No test		No test	No test		No test	No test	
T	5	1.30	2.50	5.05 *	0.58	2.42	5.05	0.27	2.08	5.05
G*T	5	0.52	no test		0.24	no test		0.13	no test	
δ''	0	No test	No test		No test	No test		No test	No test	
S	3	9.26	12.18	9.28 *	16.81	29.49	9.28 *	4.67	35.92	9.28 *
G*S	3	0.76	No test		0.57	No test		0.13	No test	
T*S	15	0.39	1.50	2.40	0.15	2.14	2.40	0.08	1.60	2.40
G*T*S	15	0.26	No test		0.07	No test		0.05	No test	
EXP.Error	48	No est.	No test		0.37	No test		0.36	No test	
Samp. Error	384	No est.								
Corr Total	479									

Note: T = temperature, G = greenhouse, S = species, EXP. Error. = Experimental error, Samp. Error = Sampling Error, Corr. Total = Corrected Total, RMR = root mass/total mass ratio, LMR = leaf mass/total mass ratio, SMR = stem mass/total mass ratio. The F-critical value is at $\alpha = 0.05$. * indicates significant effect.
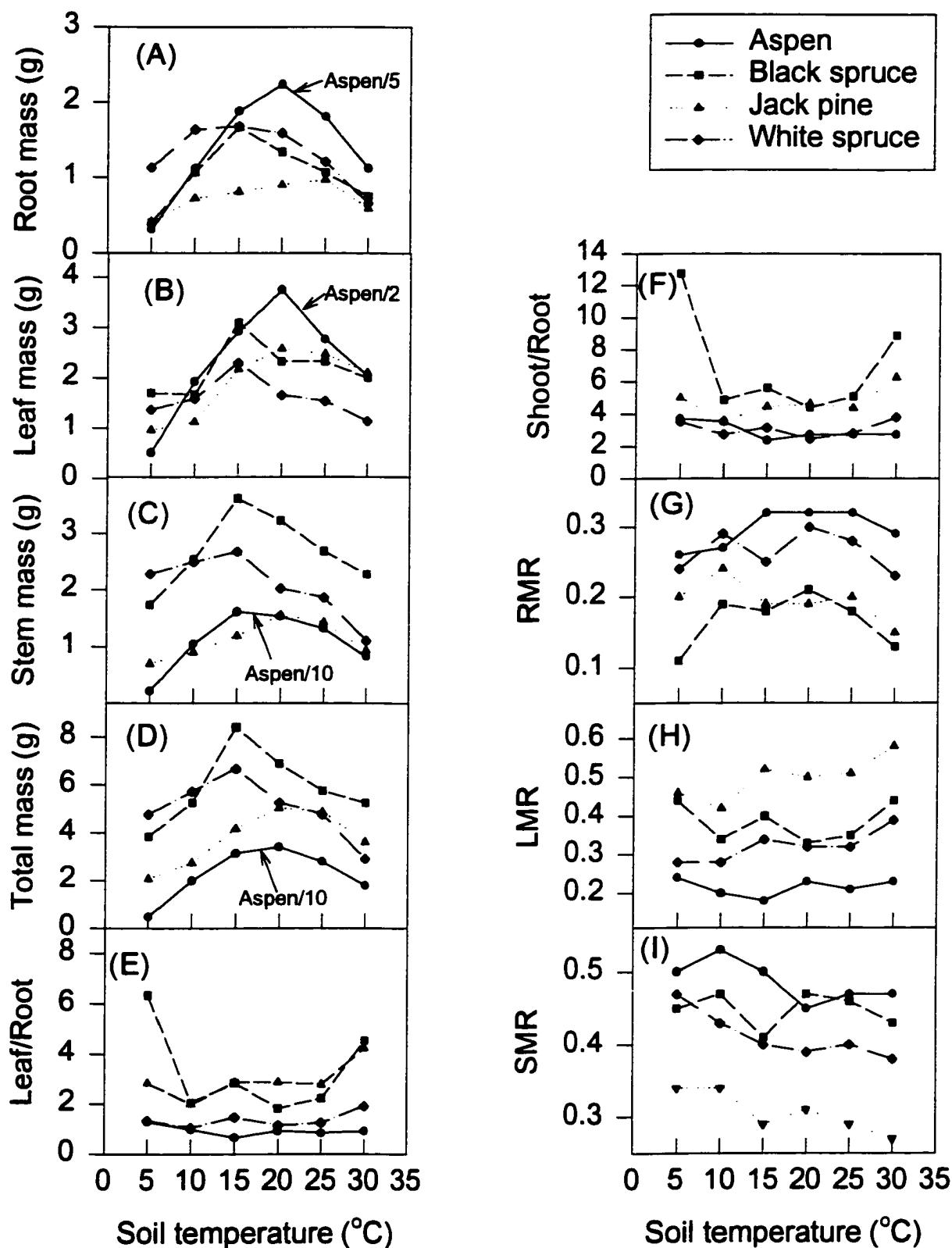
Figure 2: Soil temperature effects on biomass and biomass ratio. RMR = root mass/total mass ratio, LMR = leaf mass/total mass ratio, SMR = stem mass/total mass ratio. Aspen/5, Aspen/2 and aspen/10 indicate the values for aspen have been divided by 5, 2 and 10 respectively to fit different species into the same graph.
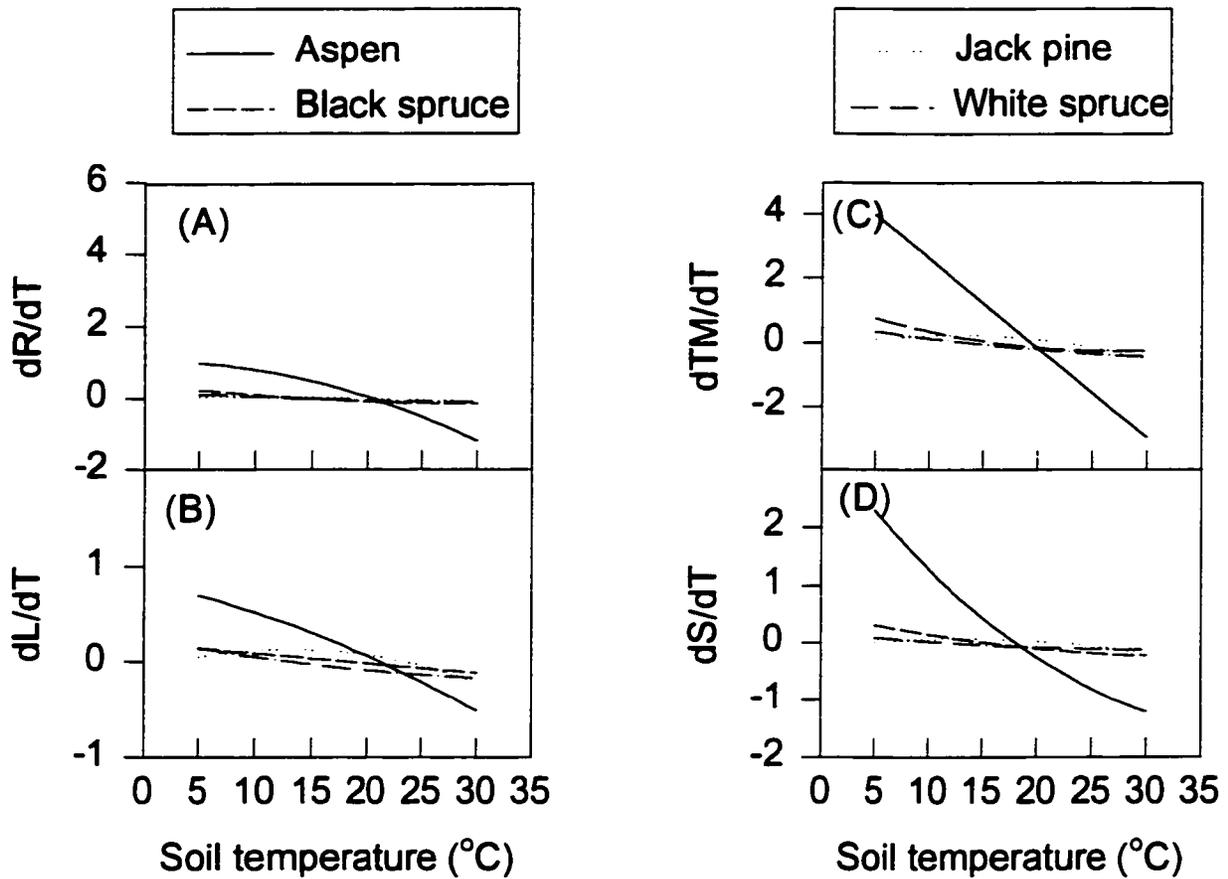
Figure 3: Sensitivity to soil temperature as described by the derivatives of biomass soil temperature relationships. R = root mass, L = leaf mass, S = stem mass, TM = total mass. Optimum soil temperatures are the temperatures at which the derivatives (dR/dT, dL/dT, dS/dT & dTm/dT) are equal to zero.

Table 4. The optimum soil temperature (°C) for biomass and relative growth rate calculated from the polynomial models.

Parameter	Aspen	Black spruce	Jack pine	White spruce
Root mass	20.5	14.7	21.1	14.8
Stem mass	18.1	15.4	22.0	11.9
Foliage mass	21.3	18.9	23.7	13.5
Total mass	19.4	16.0	22.4	13.7
RGRh	17.2	21.4	21.4	16.4
RGRd	20.0	17.2	19.9	21.7

Significant differences in biomass existed among species (Table 3). Aspen generally had greater total biomass and greater biomass of the different components than the coniferous species (Figures 2A-2D). However, there were significant interactions between species and soil temperature (Table 3). The difference between species varied with components and soil temperature (Figure 2). White spruce had greater root biomass than black spruce but black spruce had greater leaf biomass than white spruce (Figure 2A and 2B). Jack pine had the lowest root mass at soil temperatures below 25°C, and all the conifers had similar root mass at higher soil temperatures. At soil temperatures below 10°C, black spruce had smaller stem and total biomasses than white spruce, but greater than jack pine. At soil temperatures above 10°C, however, black spruce had slightly greater stem and total biomasses than both white spruce and jack pine. At all the temperature treatments, white spruce had a higher stem biomass than jack pine, and the trend was similar for total biomass at temperatures below 25°C but the pattern was reversed at higher temperatures.

Biomass allocations

Soil temperature did not have significant effect on the leaf to root ratio (Leaf/Root), leaf mass/total mass ratio (LMR), or stem mass to total mass ratio (SMR) (Table 3). But there

were significant differences between species in all the above ratios (Table 3) and different species responded differently to soil temperature treatments (species-temperature interactions in Table 3). Both Leaf/Root and Shoot/Root ratios in white spruce and aspen were relatively insensitive to changes in soil temperature (Figures 2E and 2F). Black spruce had higher Leaf/Root and Shoot/Root ratios at both high (30°C) and low (5°C) soil temperatures but the ratios remained relatively constant when soil temperature changed between 10 and 25°C (Figures 2E and 2F). Jack pine tended to have higher Shoot/Root and Leaf/Root ratios at high soil temperatures, although the magnitude of changes was very small. The Leaf/Root and Shoot/Root ratios of black spruce at 5°C soil temperature were about double the values for the other three species (Figures 2E and 2F).

The root mass to total mass ratio (RMR) of aspen, white spruce and black spruce generally showed a bell-shaped response pattern to changes in soil temperature but both spruce species diverted from this general pattern at 15°C (Figure 2G). The RMR of jack pine had a similar trend to that of spruce at 5 to 15°C of soil temperature, remained a relatively stable from 15 to 25°C and then decreased. Jack pine had a median RMR value at temperatures below15°C compared with the two spruces, then the values become more comparable to those of black spruce. Aspen generally had highest RMR values across all the soil temperatures, followed by white spruce, jack pine, and then black spruce (Figure 2G).

Leaf mass to total mass ratio (LMR) in aspen was relatively insensitive to changes in soil temperature and had lower values than the conifer species (Figure 2H). Among the conifers, the LMR values were ordered as follow: jack pine > black spruce > white spruce (Figure 2H). Jack pine and white spruce generally showed increasing LMR with increasing

soil temperatures while black spruce trended to have higher LMR at both low and high soil temperatures (Figure 2H).

The stem mass to total mass ratio (SMR) in white spruce and jack pine decreased as soil temperatures increased. The SMR in aspen increased in soil temperature from 5 to 10°C soil temperature, but decreased as soil temperature increased between 10 and 20°C, and then increased slightly as soil temperature increased further (Figure 2I). The SMR in black spruce tended to have a bell-shaped response except at 15°C where SMR was extremely low (Figure 2I). Aspen had the highest SMR values, followed by black spruce, white spruce and then jack pine (in decreasing order, Figure 2I).

Relative Growth Rate

Species and species – temperature interaction had significant effects on the relative growth rate of height (RGRh) (Table 5), but soil temperature had an insignificant effect on RGRh. The RGRh in aspen, jack pine and black spruce increased with increasing soil temperature but eventually decreased at a critical soil temperature (Figure 4A). Aspen was much more sensitive to low soil temperatures than to high temperature (Figure 4A). The RGRh of white spruce was insensitive to soil temperatures below 25°C, but showed a decline at 30°C (Figure 4A). The optimum soil temperatures for RGRh were 17.2°C for aspen, 21.4°C for black spruce, 21.4°C for Jack pine and 16.4°C for white spruce (Table 4, Figure 5A). In general, aspen had highest RGRh and jack pine and white spruce had similar and lowest RGRh among all the species. However, the differences among species were minimal at 5°C (Figure 4A).

Soil temperature, species, and species — temperature interaction all significantly affected the relative growth rate of diameter (RGRd) (Table 5). The RGRd in all the spruces increased with soil temperature below optimum and then decreased with increases in soil temperature beyond the optimum. The optimum soil temperatures for RGRd were 20.0°C for aspen and jack pine, 17.2°C for black spruce and 21.7°C for white spruce (Table 4, Figure 5B).

Table 5. Analysis of variance for the effect of soil temperature on growth.

Source	df	RGRh MS	MS-ratio	F-	RGRd MS	MS-ratio	F-critical
Greenhous	1	49.17	No test		21.64	No test	
δ′	0	No test	No test		No test	No test	
T	5	143.66	4.77	5.05	90.24	13.79	5.05 *
G*T	5	30.11	no test		6.54	no test	
δ″	0	No test	No test		No test	No teat	
S	3	1462.56	80.94	9.28 *	821.19	17.05	9.28 *
G*S	3	18.07	No test		48.16	No test	
T*S	15	55.33	3.67	2.40 *	35.76	4.12	2.40 *
G*T*S	15	15.09	No test		8.67	No test	
EXP.Error	48	No est.	No test		0.37	No test	
Samp.	384	No est.					
Corr.	479						

Note: T = temperature, G = greenhouse, S = species ratio, RGRh = relative height growth rate at the end of the 4th month, RGRd = relative diameter growth rate at the end of the 4th month.

Aspen had a much higher RGRd than the conifers (Figure 4B) and was much more sensitive to soil temperatures below 15°C than the conifers (Figure 4B). Among the conifers, black spruce and jack pine had similar RGRd, but white spruce had the lowest RGRd across the whole soil temperature range. Both spruce had the same trend across all the soil temperature treatments and the difference among spruce was that the value of black spruce was lower than white spruce over all the soil temperature treatments. The smallest value for both of spruce occurred at 30°C soil temperature (Figure 4B).
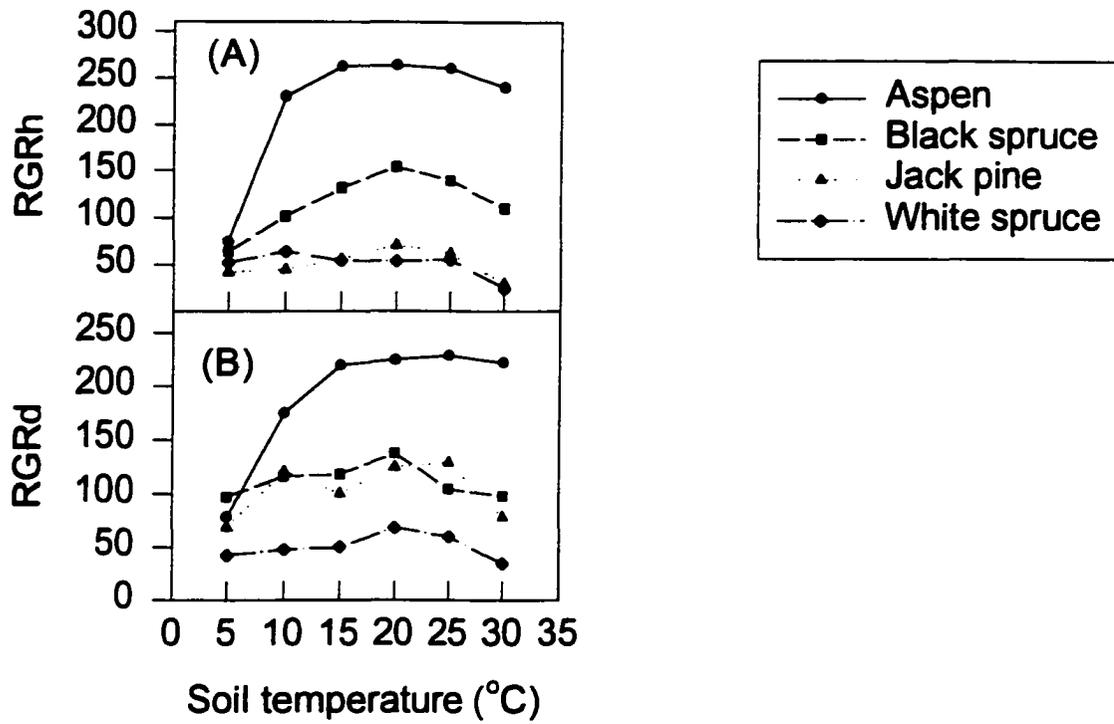
Figure 4: Soil temperature effects on seedling growth. RGRh = relative height growth rate, RGRd = relative diameter growth rate.
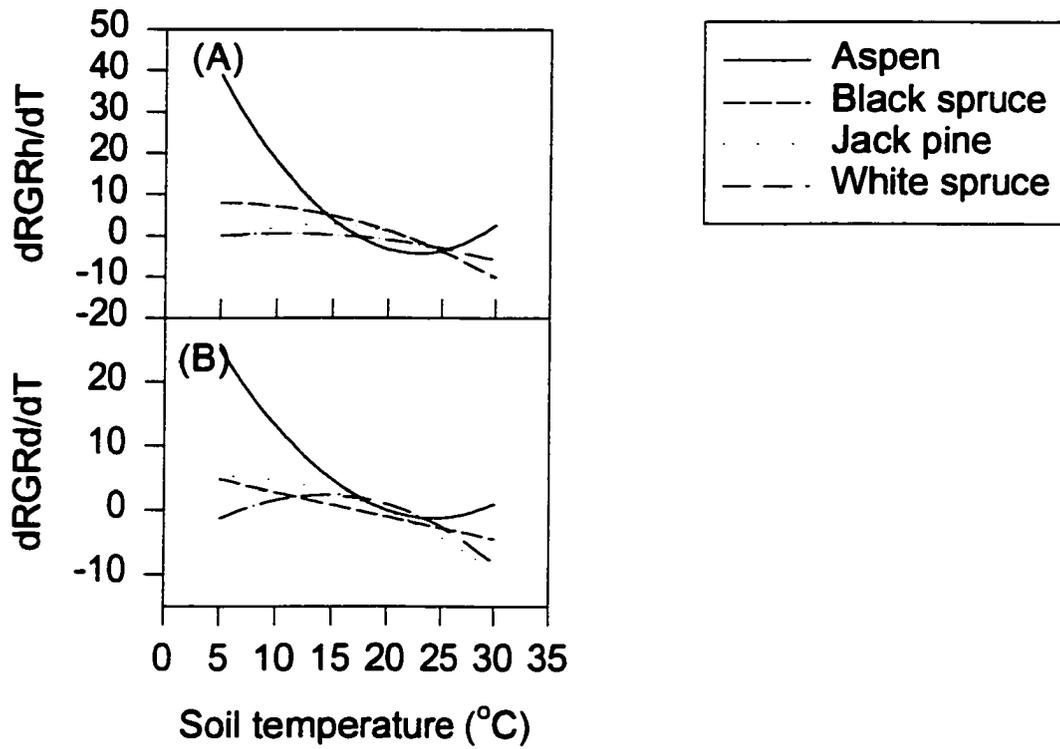
Figure 5: Sensitivity of relative growth rate in height (RGRh) and diameter (RGRd) to soil temperature as described by the derivatives of growth-soil temperature relationships.

Discussion

Biomass production

The results in this study suggest that root, leaf, stem and total seedling biomass are sensitive to changes in soil temperature in aspen, black spruce, jack pine and white spruce. The biomass variables showed nonlinear responses to changes in soil temperatures between 5°C and 30°C. This response pattern is in consistent with the general theory that plant growth increases as temperature increases up to an optimum and then decreases as temperature continues to increase (McMichael and Burke 1998). My results also agree with the findings of Lopushinsky and Max (1990) that root and shoot growth in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), Pacific silver fir (*Abies amabilis* (Dougl.) Forbes), noble fir (*Abies procera* Rehd.), lodgepole pine (*Pinus contorta* Dougl. Ex Loud) and ponderosa pine (*Pinus ponderosa* Doug. Ex Laws) increased rapidly at soil temperature above 10°C, attained maximum values at 20°C, and then decreased. Landhäausser *et al.* (1996) also reported that the root biomass showed an increase of 30 percent in paper birch, balsam poplar and black spruce species between the soil temperatures of 3 to 15°C. In general, root growth tends to increase with increasing temperature until an optimum is reached, above which root growth will decline (Brar *et al.* 1970, Pearson *et al.* 1970, Cooper 1973, Glinski and Lipiec 1990). If soil temperature deviates significantly from the optimum, the structure and function of root systems may change (Nielsen *et al.* 1960, Nielsen 1974). Low soil temperature limits the uptake of water and nutrients by roots (Chapin *et al.* 1986, Orlander *et al.* 1990) and at high root temperatures, (*e.g.,* above 25°C) oxygen uptake by roots becomes limiting (Garzoli 1988).

The biomass production of trembling aspen was more sensitive to soil temperature than the conifers (Fig. 3). For example, the root mass of aspen at 20°C (11g per tree) was 7.5 times, greater than the root mass at 5°C (1.5 g per tree). The corresponding multibles were only 4.3, 2.5 and 2.4, respectively, for black spruce, jack pine and white spruce. Landhäausser et al. (1996) have found that the biomass production of arctic deciduous species (paper birch and balsam poplar) is more sensitive to soil temperature than arctic black spruce, which indicated that mean biomass accumulation of the deciduous species was most sensitive to soil temperature than conifers. These results suggest that changes in soil temperature related to the global climate change may have a greater impact on the growth and distribution of deciduous trees than on conifers in northern forests. However, the actual effects of climate change on the growth and distribution of boreal trees may be more complex than their responses to soil temperature suggest because soil temperature may interact with other environmental variables in influencing tree growth.

The optimum soil temperature varied among species and components. My results suggest that both spruce species were more adapted to cold soil temperatures than aspen and jack pine. The optimum soil temperature for total biomass was 14°C, 16°C, 19°C and 22°C for white spruce and black spruce, aspen and jack pine, respectively. The optimum soil temperature for root growth was 15°C for both white and black spruce and 21°C for aspen and jack pine. Although these values were lower than the values reported by Heninger and White 1974 (19°C for white spruce and 27°C for jack pine), the root, shoot and total seedling biomass showed good development for both species at those temperatures. The optimal soil temperature for root growth in black spruce was also lower than the values reported by Odlum and Ng 1995 (optimum 21°C in daytime and 19°C at night for black spruce). The results for

aspen and jack pine support field observations that pioneer species are better suited to warmer soils than are spruces (mid-successional species) (Barnes and Wagner 1981, Perala 1995). The increase in root growth for 10°C increase in suboptimal soil temperature is similar to the result of Abbas Al-Ani and Hay (1983). Similar results were obtained from a field study on a black spruce where soil temperature was artificially increased by 9°C over the natural soil temperature (Van Cleve et al. 1983a). Aspen and jack pine, however, had much higher optimum soil temperatures for root growth (20.5°C and 21.1°C, respectively) than spruces. This agrees with the findings of Sutton (1980) that newly planted jack pine had higher root growth than white spruce at a soil temperature of 21°C. Grossnickle and Black (1985) found similar results for aspen from field studies. The optimum soil temperature for root growth of jack pine was similar to optimal soil temperatures for other pine species, e.g. 20 to 25°C for ponderosa pine (Stone and Schubert 1959, Larson 1967, Lopushinsky and Max 1990) and 20°C in loblolly pine (Barney 1951), while the values for spruces were similar to the value for strawberry (10-20°C) (Brouwer 1962). The leaf mass, stem mass and total biomass at a soil temperature of 5°C were smaller than those at the temperature of 30°C for aspen, black spruce, and jack pine, the result was reversed for white spruce. This may imply that warmer soil temperature was favourable to the growth of aspen, jack pine and black spruce, while white spruce preferred a colder environment. Genetic variability within the same species in the response of plant dry mass to changes in soil temperature is also reported for a number of forage legumes and cotton (Quisenberry et al. 1981, McMichael and Quisenberry 1986, Brar et al. 1990).

The optimum soil temperature for biomass production was lower for white spruce than for black spruce. This result is surprising. Black spruce generally dominates wetland areas in

the boreal forest while white spruce mainly occupies upland sites. Low land sites, particularly peatland, is characterized as having low substrate temperatures (Bonan and Shugart 1989,). The fact that black spruce can tolerate the cold wet substrates suggests that black spruce has a lower optimum soil temperature than white spruce but my results showed the opposite. However, this result is consistent with the observation that black spruce regenerates and grows well on clearcut and burnt sites while planted white spruce on clearcut sites often grows very slowly or dies during the first few years a phenomenon that is "called planting check". While it may be premature to conclude that the difference in soil temperature response is the reason for the different initial growth between the two species on clearcuts, soil temperature is likely a contributing factor. White spruce naturally regenerates under the canopy of existing forests (Burns and Honkala 1990, Lieffers and Beck 1984) or in association with other vegetation (Zasada 1995) where the soil temperature is lower than clearcuts while black spruce regenerates after fires or clearcutting (Burns and Honkala 1990).

The differences in optimum soil temperature for root and shoot growth between spruces, jack pine and aspen are probably related to the type of sites they occupy. Jack pine and aspen are pioneer species that occupy a site after a catastrophic disturbance. The spruces, on the other hand, are mid-successional species. Freshly disturbed sites, particularly burnt sites, generally have higher soil temperatures than under a forest canopy. In this study, the suitable temperature for shoot mass was 18-21°C for aspen, 15-19°C for black spruce, 22-23°C for jack pine and 12-14°C for white spruce (Table 4). My results are in contrast to the finding of Landhäausser et al. (1996) that the shoot mass in the seedlings of three arctic species (*Betula papyrifera, Populus balsamifera*, and *Picea mariana*) was not affected by soil temperatures between 3 to 15°C. Camm and Harper (1991) also reported that the shoot dry

weight of white spruce was not strongly affected by soil temperature (3 to 11°C). This discrepancy may be related to the duration of treatments. The experiments in my study lasted for 4 months. The treatment of Landhäausser *et al.* (1996) was only 55 days and Camm and Harper (1991) exposed seedlings to different soil temperatures only for 28 days.

The optimum soil temperature was lower for leaf biomass than for root biomass in white spruce but the trend was the opposite for other species. While differences in optimum soil temperature for shoot and root growth exist for other tree species, the values are generally higher for shoot growth than for root growth, e.g., the optimum soil temperature is 30°C for shoot growth and 20°C for root growth in *Eucalyptus marginata* (Jarrah) seedlings (Stoneman and Dell 1993). This difference in optimum soil temperature between leaf/shoot growth and root growth among different tree species might be associated with different seasonal growth patterns between those species. In spring, roots start growing before the leaves and stem do.

Generally the root is the first organ to grow in the spring when the soil temperature is cold but the root growth will slow down or stop when the soil gets warms and shoot growth picks up speed (Oliver and Larson 1996). Our data for jack pine, aspen and black spruce are consistent with this growth pattern: the optimum soil temperature for leaf growth was higher than that for root growth. However, it may be an ecological advantage for understory trees to grow leaves first before the leaf-out of overstory trees. Dang et al. (1998) report that the understory green alder has the highest leaf nitrogen concentration and photosynthetic capacity early in the growing season while the trend is the opposite for overstory aspen trees. A differential soil temperature requirement between leaf and roots could serve as a regulatory mechanism for this growth pattern. Indeed, white spruce generally regenerates under the canopy of existing trees (Burns and Honkala 1990, Lieffers and Beck Jr. 1994) or in

association with other vegetation (Zasada 1995) and starts to grow new leaves earlier than other boreal conifers, such as black spruce. If this reversed growth trend in white spruce (between leaf and root) is true, it could be another explanation for planting check in white spruce. Planting is normally done in the spring when the soil is cold and the active growth of roots before leaf is critical for the survival and subsequent growth of the seedling. If the leaf starts to grow before roots do, the seedling may suffer drought stress and consequently have a slow or no growth during the first few years after planting. However the difference in growth patterns among those species needs to be investigated before any concrete conclusions can be drawn.

Biomass allocation

Soil temperature generally had no significant effects on the Leaf/Root and Shoot /Root ratios in the four boreal tree species. But there are some significant effects between species (Table 3). Relative to the other species, black spruce had high values at both low and high soil temperatures (Fig. 2). There are contradictory results on the influence of soil temperature on shoot/root ratio. Several studies have reported an increase in shoot/root ratio with increasing soil temperature from 5 to higher than 25°C. This is thought to be due to higher soil temperature having a greater positive effect on shoot growth than on root growth (Davidson 1969, Wilson 1988, Larigauderie et al. 1991). This is also consistent with the prediction of Thornley's model (1972) for shoot/root allocation. The explanation is that higher soil temperature causes more carbohydrate allocation to shoots relative to roots (Marowitch et al. 1986). However, my study and some other studies (Grobbelaar 1963, Brouwer 1964, Larigauderie et al. 1991) found the opposite trend, i.e., shoot/root ratio decreased with

increasing soil temperature from 5 to 25°C. Camm and Harper (1991) also reported that white spruce seedlings planted in cold soil (3°C) developed a higher shoot/root ratio than seedlings in warm soil (11°C). In the present study the relationship between biomass allocation and soil temperature seems more complex. Soil temperature did not have significant effects on the leaf to root and shoot to root ratios in aspen and white spruce (Table 3 and Figure 1E-F). However, the leaf/root and shoot/root ratios in black spruce and jack pine decreased as the soil temperature increased from 5 to 10°C, remained stable from 10 to 25°C and increased again beyond the soil temperature at 25°C. It is consistent with the finding of Landhäausser et al. (1996) that the greatest increase in net assimilation rate occurred at soil temperatures between 3 – 10°C and root biomass increased by 30 percent in black spruce seedlings when soil temperature increased from 3 to 15°C, while shoot mass was unaffected, this caused an increase in the ratios of the seedlings. The root growth of both Scotch pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies Karst*) was completely inhibited at root temperatures of 5 and 8°C, and increased almost exponentialy as root temperatures increased (Vapaavuori et al. 1991). It suggests a direct low soil temperature limitation of the growth capacity of root meristems or reductions in the extent of cell expansion (Pritchard et al. 1990). Lopushinky and Kaufmann (1984) found that low soil temperatures delayed bud burst, reduced shoot growth, and completely prevented root growth of Douglas fir. This also supported the theory that once shoot growth begins, root growth may remain at the minimum level even when the soil warms enough for rapid root elongation (Lopushinsky and Kaufmann 1984). In contrast, the ratios of leaf/root and shoot/root in aspen and white spruce in our study were unaffected by soil temperatures. Although they were consistent with the results of ponderosa pine

(Maherali and DeLucia 2000) and holly and elm by Martin *et al.* (1989), the reason for this response pattern is unknown.

The root mass to total mass ratio (RMR) showed a bell-shaped response pattern to changes in soil temperature. But the curves of the two spruce species and jack pine deviated at 15°C. These 3 species had the lowest RMR values at 15°C as the soil temperature increased from 10 to 30°C. In the sauce 3 species, leaf mass to total mass ratio appeared to have high values at 15°C. These results suggest that the allocation of carbohydrate to belowground components was the lowest at 15°C. The LMR increased with higher soil temperatures, implying soil warming enhanced the allocation of carbohydrate to the foliage. That is, leaf growth was more restricted at low soil temperatures (Rook and Hobbs 1976). Landhäausser and Lieffers (1998) reported that trembling aspen showed higher photosynthetic rate and greater allocation to aboveground structures, especially leaves, as soil temperature increased from 6 to 20°C. This in turn resulted in higher growth at high soil temperatures.

In addition, there are the different biomass allocations between the species. Aspen had the highest allocation of dry mass to root and stem and lowest to leaf. The opposite was true for jack pine. White spruce allocated more amount of dry matter to the root component than black spruce and opposite was true of the leaf component. The highest allocation of biomass production to stem occurred with aspen, followed by black spruce, then white spruce, and lastly, jack pine. This might be due to the inherent morphology and the genetic variability of black spruce and water and nutrient availability as a function of soil temperature (McMichael and Burke 1998). Biomass allocation in aspen is under strong genetic rather than environmental control (Gedroc *et al.* 1996, King *et al.* 1999).

Relative Growth Rate

The relative growth rate of height (RGRh) and diameter (RGRd) responded differently to changes in soil temperature between different species. This is in consistent to the general theory that soil temperature affects seedling growth in many tree species (Barney 1951, Hellmers 1963, Heninger and White 1974). However, the soil temperature effects on RGR for jack pine and white spruce were less than that for aspen and black spruce (Figure 3). The result is in agreement with the results for Canada blue-joint grass (*Calamagrostis canadensis*) which was found not to be strongly affected by cold soil temperatures (Landhäausser and Lieffers 1994). For most temperate and boreal conifers, little seedling growth occurs at soil temperatures below 10°C, although basic processes such as photosynthesis and respiration continue at a low rate for temperatures below 15°C. Growth steadily increases through the optimum range of 18 to 30°C. The maximum height and shoot growth occurred at a soil temperature of 20°C for most species (Lopushinsky and Max 1990). Temperatures above 30oC adversely affect growth (Kramer and Kozlowski 1979). Landis *et al.* (1992) also reported that the general response to temperature is genetic for most plants. Genetic adaptation also can influence height growth. In our study, the reason that the RGRh of black spruce and jack pine were not significantly influenced by soil temperatures is not clear. The explanation may be related to the duration of treatments. The experiments in this study lasted only 4 months, which may not be long enough to find the discrepancy of RGRd for some species. But some results were reported by the field study, which indicated that the effect of soil temperature alone on shoot development is not clear because shoot growth in conifer seedlings is controlled by both root and air temperature (Larson 1967, Lavender and Overton 1972, Stupendick and Shepherd 1979). The RGRd of black spruce was sensitive to all the

treatment soil temperatures, while RGR of aspen was only sensitive to soil temperatures below 15°C. Lopushinsky and Max 1990 found similar results for noble fir as those for aspen, *i.e.*, height growth in noble fir increased with increasing soil temperature from 5 to 15°C, and then remained relatively constant with further increase in soil temperature to 30°C. Our results on aspen were in agreement with the finding of Landhäausser and Lieffers (1998) for the same species for soil temperatures from 6 to 20°C. Cold soils are common early in the growing season in boreal forests (Lawrence and Oechel 1983a, 1983b, Tryon and Chapin 1983, Bonan 1992).

Conclusion

Soil temperature and species interaction significantly affected biomass and relative growth rate (RGR) in aspen, white spruce, black spruce and jack pine seedlings. It showed that the optimum soil temperature for total biomass, biomass components and RGR varied with tree species: 19.4°C for aspen, 17.3°C for black spruce, 15.3°C for white spruce and 21.8°C for jack pine, respectively. The biomass variables showed nonlinear responses to changes in soil temperatures between 5°C and 30°C in four tree species. The leaf mass, stem mass and total biomass at a soil temperature of 5°C were smaller than those at the temperature of 30°C for aspen, black spruce and jack pine. This may imply that warmer soil temperatures are favorable to the growth of those of three species, while white spruce preferred a colder environment.

Soil temperature did not have significant effects on biomass allocations (excepted RMR). Among the species, aspen was the most sensitive to low soil temperatures, while white spruce was sensitive to high soil temperatures. Eighty percent of both spruces and 60 percent of jack pine died at a soil temperature of 35°C. On the other hand, all aspen seedlings survived at 35°C soil temperature treatment. In my study, aspen had the largest response in total biomass and its biomass components. But the results were reversed for white spruce on total biomass and its stem biomass. The RGR also varied with species. The RGR of black spruce was sensitive to soil temperatures over the whole range while RGR of aspen was only sensitive to soil temperature below 15°C.

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Appendix A:

Regression coefficients and the coefficient of determination for relationships between biomass and RGR and soil temperature. The model is: $Y = a_0 + a_1T + a_2T^2 + a_3T^3$

Items	Aspen					Jack pine				
	a_0	a_1	a_2	a_3	r^2	a_0	a_1	a_2	a_3	r^2
Root	-3.8067	1.0760	-0.0017	-0.0008	0.9874	0.2533	0.0272	0.0022	-9E-05	0.9293
Leaf	-2.9900	0.8641	-0.0139	-0.0002	0.9599	0.9267	-0.0761	0.0158	-0.0004	0.9484
Stem	-12.1500	3.4498	-0.1226	0.0010	0.9919	0.8933	-0.0886	0.0119	-0.0003	0.989
Total	-18.9330	5.3857	-0.1379	-3E-05	0.9935	2.0867	-0.1408	0.0300	-0.0008	0.992
RGRh	-183.4200	66.9340	-3.1258	0.0457	0.9855	63.8200	-7.7595	0.7593	-0.018	0.9899
RGRd	-84.3730	42.8080	-1.7344	0.0238	0.9940	49.4200	4.8051	0.1082	-0.0077	0.6927

Items	Black spruce					White spruce				
	a_0	a_1	a_2	a_3	r^2	a_0	a_1	a_2	a_3	r^2
Root	-1.2133	0.3991	-0.018	0.0002	0.9444	0.2900	0.2131	-0.0090	8E-05	0.9947
Leaf	0.7067	0.1986	-0.0054	5E-06	0.5069	0.3133	0.2527	-0.0114	0.0001	0.7373
Stem	-0.43	0.5175	-0.0214	0.0002	0.9048	1.5967	0.1786	-0.0091	9E-05	0.9458
Total	-1.49	1.2731	-0.0566	0.0007	0.7888	2.3733	0.5962	-0.0259	0.0002	0.9383
RGRh	23.14	7.7409	0.1109	-0.0091	0.9921	57.8700	-1.3402	0.1836	-0.0058	0.8367
RGRd	67.353	7.0123	-0.2194	0.0006	0.7230	61.7430	-6.4029	0.6155	-0.0144	0.9228