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

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Abstract

One-year old seedlings of 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.) were subject to seven soil temperatures (5, 10, 15, 20, 25, 30 and 35 °C) for 4 months. All aspen seedlings, about 40% of jack pine, 20% of white spruce and black spruce survived the 35 °C treatment. The seedlings were harvested at the end of the fourth month to determine biomass and biomass allocation. It was found that soil temperature, species and interactions between soil temperature and species significantly affected root biomass, foliage biomass, stem biomass and total mass of the seedling. The relationship between biomass and soil temperature was modeled using third-order polynomials. The model showed that the optimum soil temperature for total biomass was 22.4, 19.4, 16.0 and 13.7 °C, respectively, for jack pine, aspen, black spruce and white spruce. The optimum soil temperature was higher for leaf than for root in jack pine, aspen and black spruce, but the trend was the opposite for white spruce. Among the species, aspen was the most sensitive to soil temperature: the maximum total biomass for aspen was about 7 times of the minimum value while the corresponding values were only 2.2, 2.4 and 2.3 times, respectively, for black spruce, jack pine and white spruce. Soil temperature did not significantly affect the shoot/root (S/R) ratio, root mass ratio (RMR), leaf mass ratio (LMR), or stem mass ratio (SMR) ($P > 0.05$) with the exception of black spruce which had much higher S/R ratios at low (5 °C) and high (30 °C) soil temperatures. There were significant differences between species in all the above ratios ($P < 0.05$). Aspen and white spruce had the smallest S/R ratio but highest RMR while black spruce had the highest S/R but lowest RMR. Jack pine had the highest LMR but lowest SMR while aspen had the smallest LMR but highest SMR. Both LMR and SMR were significantly higher for black spruce than for white spruce.
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1. Introduction

The study of plant responses to temperature has been a recurring focus for botanical research during the past several decades (Long and Woodward, 1988). It has now become even more topical as scientists attempt to predict vegetation responses to global climate change and increasing atmospheric CO_2 concentration (Hillier et al., 1994). At the current rate of increase (ca. 1.8% per annum), the atmospheric CO_2 concentration will reach 500–700 ppm from the current 350 ppm by the end of the 21st century (Eamus

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and Javis, 1989; Eamus, 1992). Such increase in CO_2 and other greenhouse gases (CH_4 and N_2O) can lead to an increase of 1.5–4.5 °C in the mean global surface temperature by year 2100 (Houghton et al., 1990). The greatest warming will likely occur in the boreal and subarctic regions (IPCC, 1995). Such warming can have profound impact on soil temperatures in these regions.

The boreal forest is one of the earth's largest terrestrial biomes, covering 11% of the earth's terrestrial surface (Bonan and Shugart, 1989) and contains about 800 Pg carbon (Apps et al., 1993). The potential impact of climate change on the structure and function of Canadian boreal forests is thus of great importance to the global carbon balance (Peng and Apps, 1998). Soil temperature is one of the most important factors controlling the physiological activity and growth of plants (Long and Woodward, 1988) and the distribution and function of the boreal forest (Bonan and Shugart, 1989; Bonan, 1992). Soil temperature can influence plant physiological activities directly and indirectly through its impact on the absorption of water and nutrients (Long and Woodward, 1988). Soil temperature also influences the rate of organic decomposition and thus nutrient availability to plants, which in turn influences the physiological activities and growth (Moore, 1981, 1984; Schlentner and Van Cleve, 1985; Van Cleve and Yarie, 1986). Thus a better understanding of the responses of boreal trees to changes in soil temperature can be critical for understanding the response of boreal forests to global climate change. Understanding the differences between species in their response to changes in soil temperature is particularly important for predicting possible changes in the species composition of boreal forests. Although there are extensive studies on the effects of soil temperature on plant physiology and growth (Davidson, 1969; Lopushinsky and Kaufmann, 1984; Wilson, 1988; Lopushinsky and Max, 1990; Camm and Harper, 1991; Larigauderie et al., 1991; Vapaavuori et al., 1991; Landhausser et al., 1996; Landhausser and Lieffers, 1998; Maherali and Delucia, 2000), the differences between major boreal tree species in response to a wide range of soil temperatures are still not well understood. This study investigated the responses of biomass production and allocation in seedlings of four boreal tree species to a wide range of soil temperatures (5–35 °C).

2. Materials and methods

2.1. Plant materials

The experiment was performed on 1-year-old seedlings of black spruce (*Picea mariana* (Mill.) B.S.P.), white spruce (*Picea glauca* (Moench) Voss), jack pine (*Pinus banksiana* Lamb.) and trembling aspen (*Populus tremuloides* Michx.). All the seedlings were dormant when the experiment was initiated.

2.2. Experimental design

The experiment was a split-plot design with two greenhouses, seven soil temperatures and four species. Each greenhouse contained a complete replication of seven soil temperatures (5, 10, 15, 20, 25, 30 and 35 °C). Each soil temperature was controlled using a separate soil temperature control system. The soil temperature control system consists of a large box (112 cm wide, 196 cm long and 16 cm deep) with eight rows of containers (13.5 cm tall, 11 cm top diameter and 9.5 cm bottom diameter) fixed to the bottom. There were 14 containers in each row. Each species was randomly assigned to two rows in each temperature. The soil temperature was controlled by circulating temperature-controlled water in the space between containers. Each container had a hole at the bottom so that excess irrigation water or fertilizer solution could drain freely out of the system (see Cheng et al., 2000 for details). The systems were insulated to minimize the effect of soil temperature on air temperature. The location of each soil temperature within the greenhouse was assigned randomly. Soil and air temperatures were monitored continuously using an SCXI-MS100 temperature system (National Instruments, Austin, TX) and a Pentium computer. The daily average soil temperature was generally within ±0.41 °C of the set value (see Cheng et al., 2000 for more details).

2.3. Environmental conditions in the greenhouse

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

was 16 h or longer during the entire duration of the experiment (4 months). The natural light was supplemented using high pressure sodium lamps on cloudy or short days. The growing medium was a mixture of peat moss and vermiculite (50/50 v/v). Seedlings were watered to saturation every 2 days with 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, 0.003 ppm Mo (Landis et al., 1989). The electrical conductivity of the growing medium during the experiment was 1.3 mS/cm, within the range (<2.2 mS/cm) recommended by Landis et al. (1989). Soil pH was about 5.9 throughout the experiment.

2.4. Biomass measurements

Five seedlings were selected randomly from each row and harvested at the end of the fifth month. The samples were oven-dried at 70 °C for 48 h. The dry mass of foliage, roots and stems were measured separately on an analytic balance.

2.5. Data analysis

The data were analyzed using analysis of variance (ANOVA). The original data were subjected to log-transformation to satisfy the assumptions of ANOVA. ANOVA was conducted using SAS statistics package

(SAS Institute, Cary, NC). The data from the 35 °C treatment was excluded from the analysis because of the high mortality that occurred at this soil temperature. Multiple comparisons were conducted to identify species that were significantly different from each other when ANOVA showed a significant species effect.

The relationship between soil temperature and biomass was modeled using third-order polynomials (see Table 1 for parameters). The first derivative of the 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 within the range of the data. The second root was ignored. The second derivative of the model was used as an indicator of sensitivity to soil temperature.

3. Results

3.1. Biomass

Soil temperature significantly affected the total seedling biomass and the biomass of leaf, stem and root ($P < 0.05$, Table 2). However, the effect on leaf biomass was only marginally significant ($F = 4.57 < F_{0.05} = 5.05$). The total biomass and component biomass generally increased with increasing soil temperature and then decreased as the soil temperature

Table 1
Relationships between biomass and soil temperature for 2-year old trees[a]

| 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

| | 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

[a] Model: $Y = a_0 + a_1 T + a_2 T^2 + a_3 T^3$.

Table 2
ANOVA for soil temperature effects on biomass production in 2-year old black spruce, white spruce, jack pine and trembling aspen[a]

Source	Root			Leaf			Stem		
	MS	MS ratio	$F_{0.05}$	MS	MS ratio	$F_{0.05}$	MS	MS ratio	$F_{0.05}$
T	14.77	9.72	5.05[*]	8.60	4.57	5.05	6.67	10.76	5.05[*]
S	86.65	46.34	9.28[*]	11.18	159.71	9.28[*]	79.39	441.06	9.28[*]
T × S	3.24	2.42	2.40[*]	3.58	3.44	2.40[*]	3.66	3.45	2.40[*]
	Total			S/R			SMR		
T	9.12	6.86	5.05[*]	2.06	2.61	5.05	0.27	2.08	5.05
S	45.98	183.92	9.28[*]	15.38	9.73	9.28[*]	4.67	35.92	9.28[*]
T × S	2.83	2.67	2.40[*]	0.58	1.32	2.40	0.08	1.60	2.40
	RMR			LMR					
T	1.30	2.50	5.05	0.58	2.42	5.05			
S	9.26	12.18	9.28[*]	16.81	29.49	9.28[*]			
T × S	0.39	1.50	2.40	0.15	2.14	2.40			

[a] T: soil temperature; G: greenhouse; S: species; RMR: root mass ratio; LMR: leaf mass ratio; SMR: stem mass ratio.
[*] Significant at $\alpha = 0.05$.

increased further (Fig. 1). The optimal soil temperature varied with organs and species. For aspen, jack pine and black spruce, the optimal soil temperature for leaf was higher than that for stem or root. In white spruce, in contrast, the optimal soil temperature for root was higher than that for foliage and stem (Table 3). Among the four species, jack pine generally had the highest and aspen had the second highest optimal soil temperatures (Table 3). The optimal soil temperatures in white spruce were generally lower than those for black spruce (Table 3 and Fig. 1). In general, aspen was more sensitive to soil temperature than were the conifers while the differences in sensitivity were small among the conifers (Fig. 2).

The total biomass and component biomass were significantly different among species (Table 2). Aspen produced significantly greater amount of total and

Table 3
Optimum soil temperatures (°C) for biomass production of 2-year old trees

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
Average	19.8	16.3	22.3	13.5

component biomass than did the conifers (Fig. 1). However, the differences between conifers varied with organs (Fig. 1). White spruce and black spruce produced a greater amount of total biomass than jack pine while there was no significant difference between the two spruces ($P > 0.05$, Fig. 1D). White spruce had the highest while jack pine had the lowest root biomass among the conifers (Fig. 1A). Black spruce had significantly higher leaf biomass than white spruce while there was no significant difference in leaf biomass between jack pine and the spruces (Fig. 1B). Black spruce had the highest stem biomass and jack pine had the smallest stem biomass among the conifers (Fig. 1C).

There were also significant interactions between species and soil temperature (Table 2 and Fig. 1). For instance, jack pine had lower root mass than the spruces at intermediate soil temperatures (between 10 and 25 °C), but had similar root mass to the spruces at other soil temperatures (Fig. 1A). The stem and total biomass of black spruce were smaller than those of white spruce at soil temperatures below 10 °C. At higher soil temperatures, however, black spruce had greater stem and total biomass than white spruce (Fig. 1C and D). White spruce had a higher stem biomass than jack pine at all testing soil temperatures. White spruce also had higher total biomass than jack pine at soil temperatures below 20 °C but the trend was the opposite at 30 °C soil temperature (Fig. 1D).
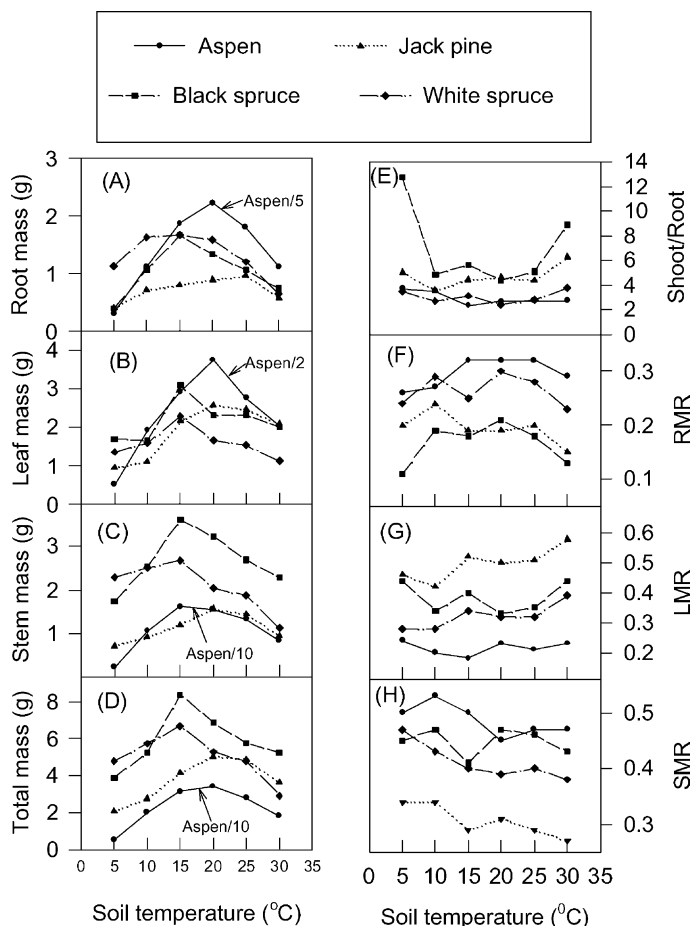
Fig. 1. Biomass and biomass allocation of 2-year old trees grown at different soil temperatures. RMR: root mass ratio; LMR: leaf mass ratio; SMR: stem mass ratio. Aspen/5, aspen/2 and aspen/10 indicate that the values for aspen were divided by 5, 2 and 10, respectively, to fit all the species into the same graph.

3.2. Biomass allocation

Soil temperature did not have significant effects on the shoot/root (S/R) ratio, root mass ratio (RMR), leaf mass ratio (LMR), or stem mass ratio (SMR) (Table 2). There were also no significant interactions between species and soil temperature (Table 2). However, despite that ANOVA did not show any statistic significance, black spruce clearly had much greater shoot to root ratio and lower RMR at high (30 °C) and low (5 °C) than at other soil temperatures (Fig. 1E and F).

There were significant differences between species in all the above ratios ($P < 0.05$). Aspen and white spruce had the smallest shoot to root ratio but highest RMR while black spruce had the highest S/R but lowest RMR (Fig. 1E). Jack pine had the highest LMR but lowest SMR while aspen had the smallest LMR but highest SMR (Fig. 1G and H). Both LMR and SMR were significantly higher for black spruce than white spruce (Fig. 1G and H).

4. Discussion

4.1. Biomass

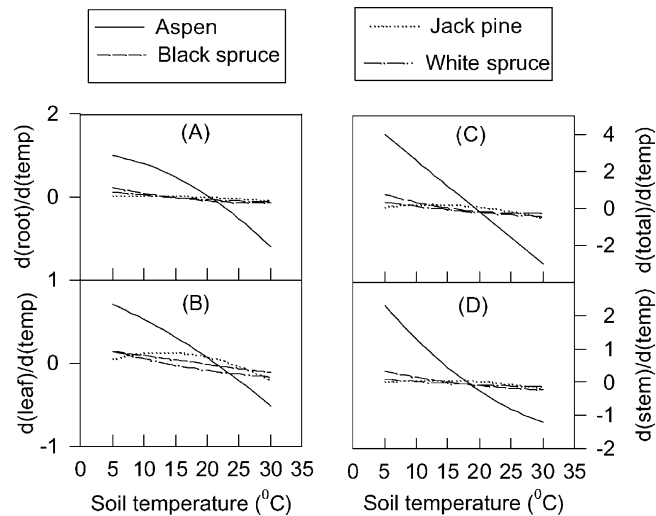The root, leaf, stem and total seedling biomass of the four boreal tree species showed a parabolic

Fig. 2. Second-order derivative of biomass–soil temperature relationship models for 2-year old trees grown at different soil temperatures. The values indicate the sensitivity of each biomass component to soil temperature.

response to soil temperatures between 5 and 30 °C. This response pattern is in agreement with the theoretical pattern proposed by McMicheal and Burke (1998) and the reported response for other tree species, e.g., Douglas-fir, Pacific silver fir, noble fir, Lodgepole pine and Ponderosa pine (Lopushinsky and Max, 1990). This pattern is probably related to the low soil temperature limitation on water and nutrient uptake (Chapin et al., 1986; Orlander et al., 1990) and high temperature limitation on oxygen uptake by roots (Garzoli, 1988).

The biomass production of trembling aspen was much more sensitive to soil temperature than the conifers (Fig. 2). For example, the root mass of aspen at 20 °C (11 g per tree) was 7.5 times of that at 5 °C (1.5 g per tree), but the corresponding values were only 4.3, 2.5 and 2.4, respectively, for black spruce, jack pine and white spruce. Landhausser 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. 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 what 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. The optimum soil temperature for total biomass was 14, 16, 19 and 22 °C, respectively, for white spruce, black spruce, aspen and jack pine. The values for white spruce and jack pine are lower than those reported by Heninger and White (1974) (19 and 27 °C, respectively). However, white spruce and jack pine in this study also showed good growth in root, shoot and total seedling biomass at 19 and 27 °C soil temperatures, respectively (Fig. 1). The results support field observations that pioneer species (aspen and jack pine) are more suitable for warmer soils than mid-succession species (spruces) (Barnes and Wagner, 1981; Perala, 1990). The results for black spruce is in a general agreement with the field experiment by Van Cleve et al. (1983). The optimum soil temperature for the root growth of jack pine (21.1 °C) was similar to optimal soil temperatures for other pine species, e.g., 20–25 °C for Ponderosa pine (Stone and Schubert, 1959; Larson, 1967; Lopushinsky and Max, 1990) and 20 °C in loblolly pine (Barney, 1951).

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; Bonan, 1992). The fact that black spruce can tolerate the cold wet substrates suggests that black spruce must have a lower optimum soil temperature than white spruce but our 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 (referred to as 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, 1994) 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 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. 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 warmer 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, 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 need to be investigated further before any concrete conclusions can be drawn.

Our results are in contrast to the finding of Landhausser et al. (1996) that the shoot mass in the seedlings of three arctic species (*Betula papyrifera*, *Populus balsamifera*, and *P. mariana*) was not affected by soil temperatures between 3 and 15 °C. Camm and Harper (1991) also reported that the shoot dry mass of white spruce was not strongly affected by soil temperature (3–11 °C). However, all the species in this study were affected by soil temperatures. This discrepancy in response may be related to differences in the duration of treatments and/or seed sources. Our experiment lasted for 4 months. The treatment of Landhausser et al. (1996) was only 55 days and Camm and Harper (1991) exposed seedlings to different soil temperatures only for 28 days.

4.2. Biomass allocation

Soil temperature generally had no significant effects on the biomass allocation in the four boreal tree species with the exception of black spruce at low (5 °C) and high (30 °C) soil temperatures (Fig. 1 and Table 2). There are contradictory results on the influence of soil temperature on S/R ratio in the literature. Several studies have reported an increase in S/R ratio with increasing soil temperature from 5 to over 25 °C (Davidson, 1969; Wilson, 1988; Larigauderie et al.,

1991; Landhausser et al., 1996). This response pattern is consistent with the prediction of Thornley's model (1972) for S/R allocation. However, some other studies (Grobbelaar, 1963; Brouwer, 1964; Camm and Harper, 1991; Larigauderie et al., 1991) have found the opposite trend. The discrepancies are probably attributed to differences in the differential responses of shoot and root among different tree species. For example, low soil temperatures reduce shoot growth but completely stop root growth in Douglas-fir (Lopushinsky and Kaufmann, 1984). In this study, different organs of the same species showed similar response patterns to soil temperature (but with different optimum temperatures), consequently no significant soil temperature effects on biomass ratios were detected.

There were significant differences in biomass allocation between different species. Aspen had the highest biomass allocation to root and stem but lowest to leaf. Jack pine allocated the greatest proportion of biomass to leaf but lowest proportion to stem. White spruce allocated a significantly greater proportion of biomass to roots but smaller proportion to leaf than black spruce. The difference may be related to the effectiveness of each species in controlling the balance between water uptake by roots and water loss by leaf under different internal and external moisture conditions. For example, aspen is much less effective in controlling water loss than black spruce while jack pine is more effective than black spruce (Dang et al., 1997). This conclusion is in agreement with the results of Gedroc et al. (1996) and King et al. (1999) that biomass allocation is controlled more by genetics than by the environment.

Acknowledgements

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