Effects of soil temperature on ecophysiological traits in seedlings of four boreal tree species

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Abstract

One-year-old seedlings of black spruce (*Picea Mariana* (Mill.) B.S.P.), white spruce (*Picea glauca* (Moench) Voss.), jack pine (*Pinus banksiana* Lamb.) and aspen (*Populus tremuloides* Michx.) were exposed to 5, 10, 15, 20, 25, 30 and 35 °C soil temperatures for 4 months. The rate of net photosynthesis (A), stomatal conductance, mid-day xylem water potential, the internal to ambient CO_2 concentration ratio (C_i/C_a), and specific leaf area (SLA) were evaluated 3 months after the initiation of the treatments. The responses of the above variables generally showed a bell-shaped curve except the C_i/C_a ratio. The relationships between soil temperature and the ecophysiological variables (except C_i/C_a) were modeled using third-order polynomials. The models suggest that jack pine generally had the highest optimal soil temperature among the four species, followed sequentially by black spruce, trembling aspen and white spruce. Aspen was generally more sensitive to low soil temperatures than the conifers while black spruce was more sensitive to high soil temperatures than other species. Jack pine and trembling aspen generally showed different response patterns than black and white spruce. The photosynthesis in aspen and jack pine was progressively less limited by stomatal conductance (relative to mesophyll limitation) as soil temperature increased from 5 to 35 °C whereas in the spruces, stomatal conductance was the least limiting to photosynthesis at moderate soil temperatures (10–15 °C for white spruce, 15–20 °C for black spruce). The xylem water potential of jack pine and aspen was more sensitive to low soil temperatures while that of the spruces was more sensitive to high soil temperatures. The specific leaf area of jack pine and aspen showed large variations with changes in soil temperature while that of the spruces was relatively constant throughout the range of soil temperatures. Most of the conifer seedlings in the 35 °C soil temperature treatment died at the end of the experiment while all aspen seedlings survived.

1. Introduction

Soil temperature is one of the most important environmental factors in the boreal forests (Bonan and Shugart, 1989). Soil temperature can directly affect physiological processes and traits of trees, such as stomatal conductance, transpiration, nutrient re-translocation, carbon dioxide uptake (Lawrence and Oechel, 1983; Delucia, 1987; Day et al., 1989, 1991; Harper and Camm, 1993; DeLucia et al., 1991; Land-haausser et al., 1996), the maximum capacity of carboxylation and electron transport of photosynthesis (Cai and Dang, 2002), leaf resistance to heat (Chai-sompongpan et al., 1990), carbon/biomass allocation

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(Pereira, 1990; DeLucia et al., 1992), and growth (Heninger and White, 1974; Lopushinsky and Max, 1990). Soil temperature also influences plant physiological processes indirectly, such as through its effects on nutrient availability, nutrient absorption and growth (Anderson and McNaughton, 1973; McGill and Cole, 1981; Camm and Harper, 1991).

Because of the large area that the boreal forest occupies, there are large variations in soil temperature, ranging from cold in wetlands to warm in south facing slopes and newly burned sites (Bonan and Shugart, 1989; OMNR, 1997). Even within the same site, soil temperature varies with micro-topographics, for instance, the soil temperature at mounds is generally higher than at lower spots. Soil temperature also varies diurnally and seasonally. Soil temperature can be modified through silvicultural measures, for example, site preparation can increase soil temperature by as much as 10 °C (Dobbs and McMinn, 1973; Orlander et al., 1990). We exposed 1-year-old seedlings of four boreal tree species (*Picea Mariana* (Mill.) B.S.P., *Picea glauca* (Moench) Voss., *Pinus banksiana* Lamb. and *Populus tremuloides* Michx.) to a wide range of soil temperatures (5–35 °C), encompassing the soil temperature conditions in boreal forest sites during the growing season. We have reported the soil temperature effects on biomass production and allocation (Peng and Dang, 2003) and some key parameters of a coupled photosynthesis-stomatal conductance model (Cai and Dang, 2002) earlier. This paper reports the results on foliar gas exchanges, the relative limitations of stomata and mesophyll to photosynthesis, xylem water potential, and the specific leaf area (SLA). The specific leaf area is an important morphological trait affecting photosynthesis.

2. Materials and methods

2.1. Plant materials

One-year-old seedlings of black spruce (*P. Mariana* (Mill.) B.S.P.), white spruce (*Picea glauce* (Moench) Voss.), jack pine (*P. banksiana* Lamb.) and Aspen (*P. tremuloides* Michx.) were used for the experiment. The conifer seedlings were obtained from A&R Container Tree Seedling Nursery (Dorion, Ontario). Aspen seedlings were grown from seeds in the Lakehead University Greenhouse and cold hardened at the end of the fourth month by exposing them to 15/5 °C at daytime/night temperatures and 8 h-photoperiod. All the seedlings were dormant when the soil temperature treatments were initiated.

2.2. Experimental design

The experiment was a split-plot design with two greenhouses, seven soil temperatures and four species. Each greenhouse contained seven-soil temperatures: 5, 10, 15, 20, 25, 30 and 35 °C. 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 to facilitate the free drainage of irrigation water and fertilizer solution (Cheng et al., 2000). The systems were insulated to minimize the effect of soil temperature on air temperature. The location of each soil temperature within each greenhouse was assigned randomly. Soil and air temperatures were monitored continuously using an SCXI-MS100 temperature system (National Instruments Co., Austin, TX, USA) and a Pentium computer. The daily average soil temperature was generally within ±0.41 °C of the set value (Cheng et al., 2000).

2.3. Growing conditions

The average day and night temperatures in the greenhouses were 22.5 ± 0.6 and 14.3 ± 0.3 (S.E.M.) °C, respectively. However, the daytime temperature fluctuated more than night temperature and was generally above the setpoint on sunny days. High-pressure sodium lamps were used to extend the natural photoperiod to 16 h in the early part of the experiment.

The growing medium was a mixture of peat-moss and vermiculite (50/50 (v/v)). Seedlings were watered and fertilized to saturation every 2 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, 0.003 ppm Mo. The salinity and pH of the growing medium solution were measured at the end of each month using an AGRITEST pH and EC/TDS meter (HANNA Instruments, Portugal). The largest value of electrical conductivity (EC) was 1.3 mS cm^{-1}, which is within the range (<2.2 mS cm^{-1}) recommended by Landis et al. (1989). The pH of the growing medium solution was about 5.9.

2.4. Measurements of ecophysiological traits

At the beginning of the third month of the experiment, two seedlings of each species were randomly selected from each row in each soil temperature for the measurement of foliar gas exchange and mid-day xylem water potential (ψ). The gas exchange was measured using a PP-Systems CIRAS-1 gas exchange system and Parkinson Leaf chambers with automatic environment control (PP-Systems, Haverhill, MA, USA). The measurements were taken at $22 \pm 0.1\,^{\circ}\text{C}$ air temperature, 360 ± 10 ppm CO_2, $800\,\mu$ mol m^{-2} s^{-1} photosynthetically active radiation, and 13.5 ± 0.22 mbar water vapor pressure. The xylem water potential was measured using a Scholander pressure chamber (PMS Instruments Co., Corvallis, OR, USA). Projected leaf area for conifers was measured using a Regent WinSeedle system (Regent Instruments Inc., Quebec City, Quebec, Canada). All the above measurements were made on the current year foliage. After the leaf area measurement, the foliage was dried at $70\,^{\circ}\text{C}$ for 48 h for determining the dry mass and specific leaf area. All gas exchange parameters were calculated according to Farquhar et al., 1980.

2.5. Data analysis

The data were analyzed using analysis of variance (ANOVA). The effect of soil temperature was tested against the interaction between soil temperature and greenhouse. Species effect and all interactions were tested against the experimental error. All dependent variables were graphically examined using probability plots for the normality of distribution and using scatter plots for the homogeneity of variance. All the data satisfied the above two assumptions for ANOVA. The analyses were conducted using SAS statistics package (SAS Institute Inc., Cary, NC, USA).

Third-order polynomials were used to model the relationships between soil temperature and ecophysiological variables (model parameters are provided in Table 1). The first derivative function of the models was used to express the sensitivity of each ecophysiological variable to soil temperature. The soil temperature at which the first derivative has a value of zero is defined as the optimal temperature.

3. Results

3.1. Net photosynthesis (A)

Soil temperature significantly affected the rate of net photosynthesis (A) in all species (Table 2). The rate initially increased with increasing soil temperature and then decreased with further increase in soil temperature (Fig. 1a). The optimum soil temperature for A derived from the model (Table 1) varied with tree species: 20.0 °C for aspen, 20.9 °C for white spruce, 22.0 °C for black spruce and 25.4 °C for jack pine (Table 3, Figs. 1a and 2a).

Aspen was the most sensitive to low soil temperatures among all four species while the three conifers were similar in their responses to low temperatures (Fig. 2a). Black spruce was the most sensitive to high soil temperature, followed sequentially by jack pine, white spruce and aspen (Fig. 2a). Aspen had the lowest rate of photosynthesis at 5 °C soil temperature but the highest A at other soil temperatures except 30 °C at which jack pine had the highest A. Black spruce generally had a higher A than white spruce at all soil temperatures except 35 °C (Fig. 1a).

Within the same species, the sensitivity of A varied with soil temperature (Fig. 2a). The conifers were more sensitive to high temperatures, particularly black spruce and jack pine. Aspen, in contrast, was more sensitive low temperatures (Fig. 2a).

3.2. Stomatal conductance (g_s)

Soil temperature significantly affected g_s (Table 2), with g_s initially increased with increasing soil temperature and then decreased with further increases in soil temperature (Fig. 1b). The optimum soil temperatures for g_s were 20.5 °C for aspen, 17.7 °C for white spruce, 24.3 °C for black spruce and 27.3 °C for jack

Table 1
Regression coefficients and the coefficient of determination for relationships between ecophysiological traits and soil temperature

Species	Variable	b_0	b_1	b_2	b_3	r^2
Aspen	A	−1.341	1.359	−0.046	0.000403	0.98
	g_s	−112.571	48.817	−1.880	0.022444	0.94
	ψ	1.681	−0.097	0.004	−0.000042	0.97
	SLA	82.941	11.377	−0.189	−0.001398	0.91
White spruce	A	6.071	−0.217	0.025	−0.000636	0.98
	g_s	−13.883	31.512	−1.063	0.006495	0.91
	ψ	1.701	−0.138	0.006	−0.000073	0.96
	SLA	44.330	1.375	−0.0003	−0.000667	0.99
Black spruce	A	8.187	−0.596	0.063	−0.001490	0.98
	g_s	203.274	−24.643	2.897	−0.065479	0.95
	ψ	1.298	−0.058	0.001	0.000008	0.94
	SLA	80.238	−2.928	0.333	−0.006838	0.84
Jack pine	A	6.473	−0.652	0.074	−0.001604	0.90
	g_s	81.749	2.237	0.368	−0.011783	0.95
	ψ	1.185	−0.039	0.001	−0.000004	0.93
	SLA	28.933	1.984	0.236	−0.007470	0.90

Model: $Y = b_0 + b_1 T_{soil} + b_2 T_{soil}^2 + b_3 T_{soil}^3$, where "$Y$" is an ecophysiological trait, T_{soil} is soil temperature, and b_0 to b_3 are regression coefficients. All the regressions are significantly at 95% confidence level. *Note*: A, rate of net CO_2 assimilation; g_s, stomatal conductance; ψ, mid-day xylem water potential; SLA, specific leaf area; r^2, correlation coefficient.

pine (Figs. 1b and 2b, Table 3). As with A, g_s of aspen was the most sensitive to low temperatures while black spruce was the most sensitive to high soil temperatures among all the species (Fig. 2b).

3.3. C_i/C_a ratio

The two pioneer species, jack pine and trembling aspen, showed a different pattern of response to soil temperature than the spruces. The internal to ambient CO_2 concentration ratio in jack pine and aspen generally increased as the soil temperature increased from 5 to 35 °C (Fig. 1c). In the spruces, however, the C_i/C_a ratio increased as soil temperature increased from 5 to 15 °C, decreased as soil temperature increased from 15 to 25 °C (black spruce) or 30 °C (white spruce), and increased again as soil temperature increased further (Fig. 1c).

3.4. Mid-day xylem water potential (Ψ)

Soil temperature significantly affected Ψ (Table 2, Fig. 1d). Ψ generally became less negative with increasing soil temperature below optimum and then

Table 2
Analysis of variance for soil temperature effects on net photosynthesis (A), stomatal conductance (g_s), mid-day xylem water potential (ψ), and specific leaf area (SLA)

Source	Degree of freedom		MS (A)	F	MS (g_s)	F	MS (Ψ)	F	MS (SLA)	F	$F_{0.05}$
	d.f._1	d.f._2									
T	6	6	139.3	15.6[*]	134861.7	6.2[*]	0.6	6.0[*]	12385.8	7.1[*]	4.28
S	3	56	103.9	14.4[*]	169758.6	12.7[*]	0.8	8.0[*]	607420.4	989.9[*]	2.78
$S \times T$	18	56	20.8	2.7[*]	487415.1	36.5[*]	2.5	25.0[*]	25961.3	42.3[*]	1.80
Error	56		7.6		13350.5		0.1		613.6		

Note: T, soil temperature; S, species; error, experimental error.
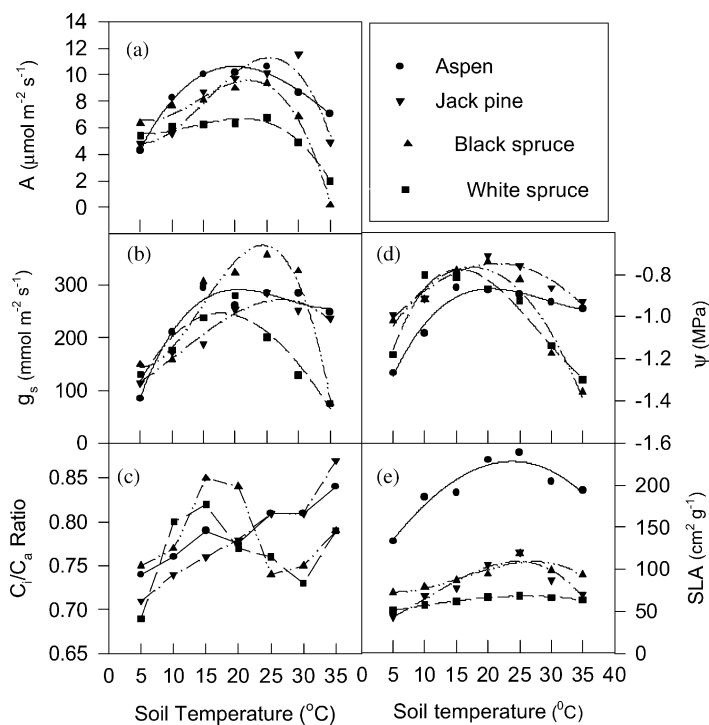[*] Significant at 95%.

Fig. 1. Soil temperature effects on: (a) net photosynthesis (A); (b) stomatal conductance (g_s); (c) internal to ambient CO_2 concentration ratio (C_i/C_a); (d) mid-day xylem water potential (ψ); and (e) specific leaf area (SLA) in trembling aspen, white spruce, black spruce and jack pine. Lines represent modeled values (see Table 1 for model parameters). The C_i/C_a ratio was not modeled.

became more negative with further increase in soil temperature beyond the optimum (Fig. 1e). The models showed that the optimum soil temperature (i.e. when Ψ was the least negative) was 21.0 °C for aspen, 15.4 °C for white spruce, 17.6 °C for black spruce and 21.0 °C for jack pine (Figs. 1d and 2c, Table 3).

The xylem water potential of white spruce was the most sensitive to low soil temperatures followed by aspen, black spruce and jack pine (in decreasing

order). Black spruce was the most sensitive to high soil temperatures followed by white spruce, aspen and jack pine (Fig. 2c).

3.5. Specific leaf area

Specific leaf area was significantly affected by soil temperature and there were significant interactions between species and soil temperature (Table 2). Aspen was the most sensitive to low soil temperatures, followed by jack pine, white spruce and black spruce (Figs. 1e and 2d). Jack pine was the most sensitive to high soil temperatures, followed by aspen, black spruce and white spruce. Overall white spruce was the least sensitive to soil temperature (Fig. 2d). The soil temperatures for maximum SLA were 23.8 °C for aspen, 22.6 °C for white spruce, 27.2 °C for black spruce and 24.6 °C for jack pine (Table 3). SLA in aspen was much greater than that of conifers and SLA in jack pine and black spruce was generally greater than white spruce (Fig. 1e).

Table 3
Optimum soil temperatures for ecophysiological traits

Variable	Aspen	White spruce	Black spruce	Jack pine
A	20.0	20.9	22.0	25.4
g_s	20.5	17.7	24.3	27.3
ψ	21.0	15.4	17.6	21.0
SLA	23.8	22.6	27.2	24.6
Average	21.3	19.2	22.8	24.6

Note: A, rate of net CO_2 assimilation; g_s, stomatal conductance; ψ, mid-day xylem water potential; SLA, specific leaf area.
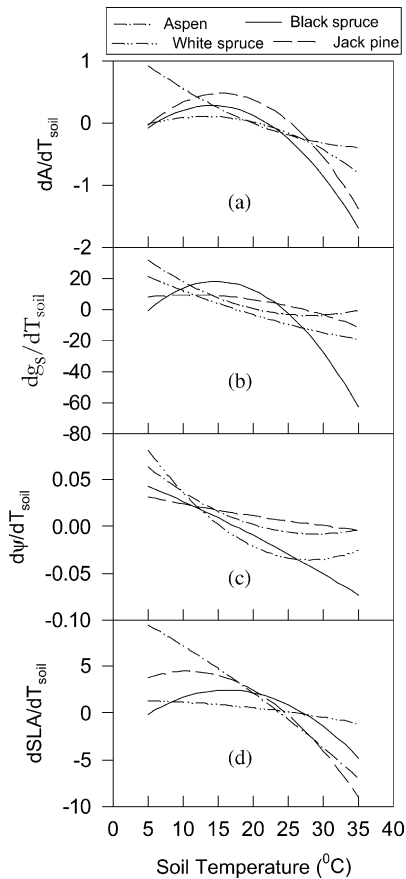
Fig. 2. First derivatives of the models presented in Fig. 1 and Table 1. Derivative values represent the rate of change in ecophysiological variables as soil temperature changes: dA/dT_{soil} = change in the rate of net CO_2 assimilation with changes in soil temperature; dg_s/dT_{soil} = change in stomatal conductance with changes in soil temperature; dψ/dT_{soil} = change in mid-day xylem water potential with changes in soil temperature; dSLA/dT_{soil} = change in specific leaf area with changes in soil temperature.

4. Discussion

Trembling aspen was generally more sensitive to low soil temperatures than the conifers (Figs. 1 and 2). Although all the species had smaller specific leaf area, lower rates of photosynthesis, and smaller stomatal conductance at low soil temperatures, the response was the most dramatic in trembling aspen. For instance, the photosynthesis of aspen at 5 °C soil temperature was the lowest among the four species (Fig. 1a) while it was the highest at all other soil temperatures except 30 °C. This phenomenon may have been related to differences in the stomatal control of water loss and root sensitivity to soil temperature between aspen and the conifers. Aspen is much less efficient in controlling water loss through the stomata than the conifers (Dang et al., 1997). At low soil temperatures, the uptake of water and nutrients by roots becomes difficult because of high viscosity of the soil solution and low root growth and metabolic activities (Kaufmann, 1977; Vapaavuori et al., 1992; Wan et al., 1999). Tryon and Chapin III (1983) found that the root elongation of trembling aspen was more sensitive to soil temperature than that of black spruce. Peng and Dang (2003) found that the root biomass of aspen was more sensitive to soil temperature than that of the conifers. The combination of poor root growth and water uptake, and poor stomatal control of water loss could have led to more severe moisture stress and greater decreases in photosynthesis in aspen. Indeed, the mid-day xylem water potential at low soil temperatures was more negative in aspen than in the conifers (Fig. 1d). This result is in agreement with our results on soil temperature effects on biomass production (Peng and Dang, 2003) but contradicts the finding that the quantum use efficiency of electron transport was more sensitive to soil temperature in the conifers than in aspen (Cai and Dang, 2002). However, the quantum efficiency affects the rate of CO_2 assimilation only when light is limiting. Since all the measurements in this study were conducted at a PAR (800 µmol m^{-2} s^{-1}) above the saturation point, the difference in the quantum efficiency were not manifested. Additionally, the optimal soil temperatures for photosynthesis were generally higher than those of biomass production for all four species (Table 3 and Peng and Dang, 2003). The difference may be explained by increases in root respiration with increasing soil temperature. The rate of respiration normally increases exponentially with increasing temperature and root respiration can consume 50% of the daily carbohydrate production (Lambers et al., 1998).

In contrast, black spruce was generally the most sensitive to high soil temperatures among the four species. For instance, A and g_s of black spruce showed the most dramatic decline with increases in soil temperature beyond the optimum (Figs. 1 and 2). The mortality at high temperatures was also high for black spruce: 62.5% at 30 °C and 100% at 35 °C (at the end

of the fourth month). Aspen, on the other hand, was generally the least sensitive to high soil temperatures, with a 100% survival at all soil temperatures. The results were in agreement with those of Zwiazek and Black (1988) and Peng and Dang (2003).

It is interesting to note that the optimum soil temperatures for white spruce were lower than those for black spruce. Similar differences between the two species were found for biomass production (Peng and Dang, 2003). Black spruce dominates wetland sites while white spruce grows only on upland sites. Wetlands generally have low substrate temperatures (Bonan and Shugart, 1989; Bonan, 1992). The fact that black spruce grows on cold wet sites tends to suggest that this species may have a lower optimum soil temperature than white spruce but both this study and Peng and Dang (2003) demonstrated the opposite. These results support the observation that black spruce regenerates and grows well on clearcut and burnt sites while planted white spruce on such sites often grows poorly 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) or in association with other vegetation (Zasada, 1995) where the soil temperature is lower than clearcuts or burnt sites while black spruce can regenerate after fires or clearcutting (Burns and Honkala, 1990).

The two pioneer species (aspen and jack pine) had a distinctly different pattern of relative limitations to photosynthesis by mesophyll and stomata than the spruces in response to soil temperature. The internal to ambient CO_2 concentration ratio (C_i/C_a) is an indicator for the relative limitations of stomatal resistance and non-stomatal resistance (including the diffusion resistance in the path from the sub-stomata cavity to the carboxylation site and the rate of carboxylation). When non-stomatal resistance becomes relatively more limiting to photosynthetic CO_2 assimilation than stomatal resistance, the C_i/C_a ratio will increase because the supply of CO_2 by stomata is exceeding the demand by the mesophyll. On the other hand, when stomatal resistance becomes relatively more limiting than residual resistance, the C_i/C_a will

decline. As soil temperature increased from 5 to 35 °C, the C_i/C_a ratio in jack pine and aspen increased almost linearly (Fig. 1c), suggesting that the non-stomatal resistance became progressively more limiting to photosynthesis relative to stomatal resistance or in other words, stomata became progressively less limiting to photosynthesis at higher soil temperatures. Such a trend was most likely resulted from the relative rates of change in the non-stomatal and stomatal resistances rather than differences in the direction of the changes, for example, a faster decline in stomatal resistance than non-stomatal resistance with increases in suboptimal soil temperature and a slower increase in stomatal resistance with increases in above-optimal soil temperature would have resulted in a continuous increase in the C_i/C_a ratio. In contrast, the C_i/C_a ratio in the spruces was the highest at moderate soil temperatures (10–15 °C for white spruce and 15–20 °C for black spruce, Fig. 1c). The reasons responsible for the different response patterns are unknown. However, it might be related to the environmental conditions in which the species naturally regenerate. The pioneer species generally regenerate on warmer sites than the spruces (Burns and Honkala, 1990). The different response patterns tend to suggest that stomata exert the least limitation to photosynthesis under the soil temperature conditions that the species naturally regenerate. This strategy can maximize the nutrient use efficiency during natural regeneration.

The xylem water potential in jack pine and trembling aspen also showed a different response pattern than that of the two spruces. The xylem water potential of jack pine and aspen was much more sensitive low soil temperatures than to high soil temperatures (Fig. 1d). In contrast, black spruce and white spruce were more sensitive to high than to low soil temperatures (Figs. 1d and 2c). Since all the seedlings in this study were well watered, the xylem water potential must have been determined by the absorbing capacity of the roots and the water loss through transpiration. The rate of transpiration is determined by the vapor pressure deficit of the air and the stomatal conductance or resistance of the leaf (when the boundary layer resistance is constant). Since the seedlings under different soil temperature treatments experienced similar vapor pressure deficit (growing in the same environment) and stomatal conductance followed similar response patterns as did the xylem water

potential (Fig. 1b and d), we conclude that the root capacity for water uptake in jack pine and trembling aspen was more sensitive to low soil temperatures while the those of black and white spruce were more sensitive to high soil temperatures. The root growth in trembling aspen was also more sensitive to low soil temperature than that of the conifers (Tryon and Chapin III, 1983; Peng and Dang, 2003).

Trembling aspen and jack pine, particularly aspen, showed much greater variation in specific leaf area than white and black spruce as soil temperature varied (Figs. 1e and 2d). In contrast, the specific leaf area of the two spruce species showed little variation with different soil temperatures (Fig. 1e). The specific leaf area is influenced by both the thickness of the leaf and the amount of carbohydrate storage in the leaf (Lambers et al., 1998). Thicker leaves and/or a greater storage of carbohydrates can lead to a smaller specific leaf area. The thickness of the leaf can be affected by various environmental factors as well as light conditions (Lambers et al., 1998; Wolfe et al., 1998). The amount of carbohydrate storage in the leaf is greatly affected by the sink strength, i.e. the rate of carbohydrate consumption by growth and respiration, particularly root respiration which can consume 50% of the daily photosynthate production (Lambers et al., 1998). Unfortunately, we have no data to separate the contributions of leaf thickness and sink strength in this study. However, the data do suggest that the specific leaf area in jack pine and trembling aspen was more plastic than that of black and white spruce.

In conclusion, this study and our previous studies suggest that silvicultural treatments that increase the root zone temperature should promote the physiological activities and growth of trembling aspen, jack pine, and black spruce if other environmental factors are not limiting. Jack pine requires the highest soil temperature for optimal growth among the four tree species. As far as soil temperature is concerned, clear-cutting, perhaps in combination with prescribed burns and/or other site preparations, should be an appropriate silvicultural system for these species. In contrast, white spruce had much lower optimal soil temperatures. Therefore, regeneration under an existing canopy, such as in the two-pass silvicultural system (Brace and Bella, 1988) or a partial cut silviculture system (Smith et al., 1997), will be the most appropriate for white spruce. When planting white spruce on an open site is desired for other seasons, trees should be planted on shaded, or partially shaded spots (such as the shady side of tree stumps or other objects) where the soil temperature is lower. The fact that growth and physiological processes have different optimal soil temperatures suggest that researchers should interpret their data with caution when only growth or physiological variables are measured.

Acknowledgements

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