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Radiation and soil temperature interactions on the growth and physiology of eastern white pine (*Pinus strobus* L.) seedlings

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Abstract

A greenhouse experiment was set up during one growing season to test the hypothesis that soil temperature controls a significant part of the light response of eastern white pine (*Pinus strobus* L.) seedlings that is observed in the field. The experimental design was a three by three factorial split-plot design, with three levels of light availability: 10%, 40% and 80% of full light; and three levels of soil temperature: 16 °C, 21 °C, and 26 °C in the soil at midday. The results show significant interactions between light and soil temperature factors on several variables (gas exchange, root growth, leaf-mass ratio and leaf–mass per unit area), but not on shoot dry mass. These interactions indicate that, in the field, a significant proportion of the light response of young eastern white pine could result from changes in soil temperature, especially under conditions of limiting water availability. Our results suggest that soil temperature must be taken explicitly into account as a driving variable when relating the growth of young eastern white pine to photosynthetic radiation.

Introduction

Soil temperature is a strong determinant of both root and shoot growth of plants (Bowen, 1991; Kaspar and Bland, 1992; Nielsen, 1974; Nobel, 1999). Under natural conditions, increases in soil temperature are often due to increased radiation, and frequently result in increased nitrogen mineralization and nutrient availability (Munson et al., 1993; Nambiar et al., 1979; Stoneman and Dell, 1993). Such interactions tend to hide the impact of soil temperature itself as a controlling variable on shoot and root growth of plants.

Aside from its impact on soil microbial processes and nutrient turnover, soil temperature may influence plant growth through at least two means. First, root metabolic activity increases with soil temperature, with two consequences: increased cell division – resulting in higher root growth – and intensification of growth hormone synthesis, mainly cytokinins, gibberellins and abscisic acid (Bowen, 1991; Lyr and Garbe, 1995; Spollen et al., 2000). Secondly, higher soil temperatures increase root water absorption, through a decrease in soil water viscosity and an increase in both root permeability and hydraulic conductivity (Bowen, 1991; Dodd et al., 2000; Kramer, 1983). Soil temperature is known to induce specific aboveground plant responses, including changes in leaf and shoot morphology (Stoneman and Dell, 1993), and in stomatal conductance and photosynthesis (Day et al., 1991; Dodd et al., 2000; King et al., 1999). Soil temperature also influences photosynthesis through plant water status (Burdett, 1990; Nambiar et al., 1979), but may also influence stomatal conductance and other aboveground responses through its effects on hormonal signals and root sink-strength (Bowen, 1991;

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Dodd et al., 2000; Lyr and Garbe, 1995; Meinzer, 1993). Under natural conditions, both root and aboveground response to soil temperature will depend on the species and on site factors (such as soil characteristics and co-occurring vegetation).

In forestry, soil temperature can be modified by manipulations of surface soil which either mix horizons, remove the organic horizon, or create mounds (Bassman, 1989; Brand and Janas, 1988; Örlander et al., 1998). For example, scarification, which mixes surface organic and mineral horizons, is generally thought to improve seedling survival by promoting root growth, and thus improving water and nutrient absorption (Andersen et al., 1986; Burdett, 1990; Nambiar et al., 1979; Stupendick and Shepherd, 1979). Several studies have demonstrated increased shoot and root growth of seedlings as a result of increased soil temperature following scarification (Bassman, 1989; Brand and Janas, 1988), or planting in warmer microsites (Balisky and Burton, 1997; Roy et al., 1999).

Both eastern white pine (*Pinus strobus* L.) seedlings (Brand and Janas, 1988) and saplings (Boucher et al., 1998) have shown increased growth following scarification and consequent increase in soil temperature. However, in these latter studies, the simultaneous effects of other environmental factors (such as light availability) prevented the determination of soil temperature effects on growth increment. Since eastern white pine is often found on sandy or shallow soils (Wendel and Smith, 1990), prone to warming as light availability increases, we wanted to test the hypothesis that a significant part of the light response of eastern white pine seedlings was due in fact to a change in soil temperature.

Materials and methods

Experimental design and control of soil temperatures

The experiment was performed in an open-sided polyethylene greenhouse (about 80% light transmission) at Université Laval, Québec City, Canada (46°82'N, 71°22'W). The greenhouse was open on all sides (approx. 1.5 m high openings on the longest sides and almost fully open on both ends) allowing good aeration. On May 22, 1998 (day of year (DOY) 142), 2-year old eastern white pine (*Pinus strobus* L.) seedlings (Province of Quebec conventional containerized seedlings, root plug volume of 110 cm^3) were planted in sand beds. Based on a 20 seedling sample, the seedling size and mass prior to planting were as follows (averages with standard deviations): Total height = 12 ± 2 cm; Total dry mass = 4.0 ± 0.9 g; Root dry mass = 1.6 ± 0.5 g; Leaf–mass ratio = 0.71 ± 0.06.

The sand beds were 1.6 m × 3.3 m × 0.25 m open boxes filled with 22 cm of silica sand. Each sand bed was subjected to one of three light regimes through the use of neutral shade cloths: 10% of full light (low light level or LL), 40% of full light (medium light level or ML), and 80% of full light (high light level or HL, no shade cloth used). Dividers were placed within each sand bed to create three separate compartments (subplots). Each compartment in a given sand bed was subjected to one of three soil temperature regimes that was achieved through day-time heating or cooling of the soil through the use of cold or hot water piped in rubber hoses buried 20 cm below the soil surface. These treatments targeted mid-day peak temperature at 10 cm in the soil of: 16 °C for the low soil temperature (LST), 21 °C for the moderate soil temperature (MST), and 26 °C for the high soil temperature (HST). Compartments subjected to the low (16 °C) and moderate (21 °C) soil temperature treatments required refrigeration in order to obtain the desired midday soil temperatures, while those subjected to the high (26 °C) soil temperature treatment required heating. To let soil cool naturally during the night, the HST thermostat was connected to a timer set to shut off the thermostat at dusk and reopen at dawn (respectively around 7 PM and 5 AM EST). Soil temperature levels were chosen according to extreme values measured under natural conditions in a typical eastern white pine site (Boucher et al., 1998). The sides of each compartment were isolated with polystyrene. Holes were drilled in the bottom to allow for drainage and in the sides for the passage of the hose.

Prior to planting, the soil in each compartment was covered with layers of air-bubbled aluminium foil (Thermofoil®, Cie-Nergy Inc., Charlesbourg, Qc, Canada) between two plastic sheets, to prevent radiative heating of the soil and evaporation from the soil surface. Under ML and HL levels, there were two layers of insulating foil for the LST and MST treatments, and one layer for the HST treatment. Under LL level, there was one layer of foil for the LST and MST treatments, and no foil for the HST treatment (plastic sheets only). These combinations were selected to provide the least possible difference in soil temperature between the three light levels for each soil temperature level. Two 10 cm crossed cuts in the insulating material provided a watering opening for each planted seedling while maintaining insulation at the stem base.

Of the 24 seedlings planted in each compartment, 16 were buffer seedlings (planted 15 cm from the border of the compartment) and 8 were experimental seedlings (25 cm spacing). Seedlings were under experimental conditions one week after planting, so that the experimental period lasted 105 days, from May 29 (DOY 149) to September 10 (DOY 253) 1998.

Experimental conditions

All desired midday soil temperature levels were reached within the first week after planting and then monitored on a daily basis using hand-held soil thermometers for the first 63 days (DOY 149 – 211). Starting on DOY 211, soil temperature and photosynthetic-photon flux density (PPFD) were recorded hourly on a datalogger. Nine thermistors, one for each subplot compartment in one block (3 light levels × 3 soil temperature levels), were planted approximately 10 cm deep in the soil beside a seedling root plug of each subplot. A tenth sheltered thermistor was used to measure greenhouse air temperature at seedling height. Only data recorded with the datalogger are shown (Figure 1).

PPFD was monitored with one reference quantum sensor (model LI-190SB, LI-COR, Inc., Lincoln, NE, USA) placed in the middle of the experimental setup at seedling height in an HL sand bed. PPFD under LL and ML conditions was measured at seedling height on one day using two quantum sensors (one under HL and, simultaneously, one under LL or ML) and two hand-held light meters (model LI-250, LI-COR, Inc., Lincoln, NE, USA). The one day measurement series (6 measures per light level; two measurements in the morning, two at noon, and two in the afternoon) resulted in the following percentages relative to HL: LL = 12 ± 2%, ML = 51 ± 4%. Considering the approx. 80% light transmission of the polyethylene greenhouse, the following percentages were attributed to the light levels relative to full light conditions: LL = 10%, ML = 40%, and HL = 80%.

Water and nutrients were applied together, every 2 – 3 weeks. Soil moisture was monitored with a hand-held soil hygrometer, and was maintained close to field capacity throughout the experiment. Fertilization (20:20:20 N:P:K, complete solution, at 1.0 g dm^{-3} of water) was done through the openings in the insulating material at the base of the stem of each seedling. Because of inherent variation in transpiration rates, the volumes of fertilizer solution given varied according to light levels (regardless of the soil temperature treatment). Total application volumes were of about 2.0 dm^3 per seedling under LL, 2.5 dm^3 under ML, and 3.0 dm^3 under HL for the treatment period. In all cases, the resulting nutrient concentrations of the soil solution provided high nutrient availability, according to Province of Québec nursery standards for eastern white pine (M. Lamhamedi, pers. comm.).

Seedling morphology and biomass

At the end of the experimental period (September 14, DOY 257), five seedlings per subplot were carefully extracted from the sand for measurement of morphological variables and their root systems were washed. Total length of the stem, apical shoot length and hypocotyl diameter were measured. Seedlings were then separated into five parts: Apical shoot foliage, current-year branch foliage, remaining foliage, aboveground wood (stem and branches) and total root system. Five fascicles from the apical shoot of each seedling were kept for total surface area determination using the volume displacement method and Johnson's (1984) calculations for eastern white pine needles. The same fascicles were later oven dried (48 h at 65 °C) to determine leaf dry mass per unit fresh leaf area (LMA). All parts of each seedling were oven dried to obtain dry masses.

Three ratios were calculated from the dry mass measurements. Leaf–mass ratio (LMR) is the ratio of leaf dry mass to the total aboveground dry mass. Leaf-mass per unit leaf area (LMA) is the ratio of leaf dry mass to its surface area (g m^{-2}). Root–shoot dry mass ratio (R/S) was also calculated.

Seedling physiology

One experimental seedling per subplot was randomly chosen for measurements of gas exchange and water potential. Gas exchange measurements were made in the morning (between 10h00 and 12h20 EST) and again in the afternoon (between 14h00 and 15h50 EST) of August 5 (DOY 217) using a portable photosynthesis system (model LI-6200, LI-COR, Inc., Lincoln, NE, USA) with a 0.25-dm^3 cuvette. Measurements were made at light saturation (PPFD > 1200 μmol m^{-2} s^{-1}) with a halogen lamp installed approx. 20 cm over the cuvette, and using two detached fascicles (Edwards, 1989) from the apical shoot of each selected seedling. Once detached, fascicles were put into a plastic bag with a wet towel, and

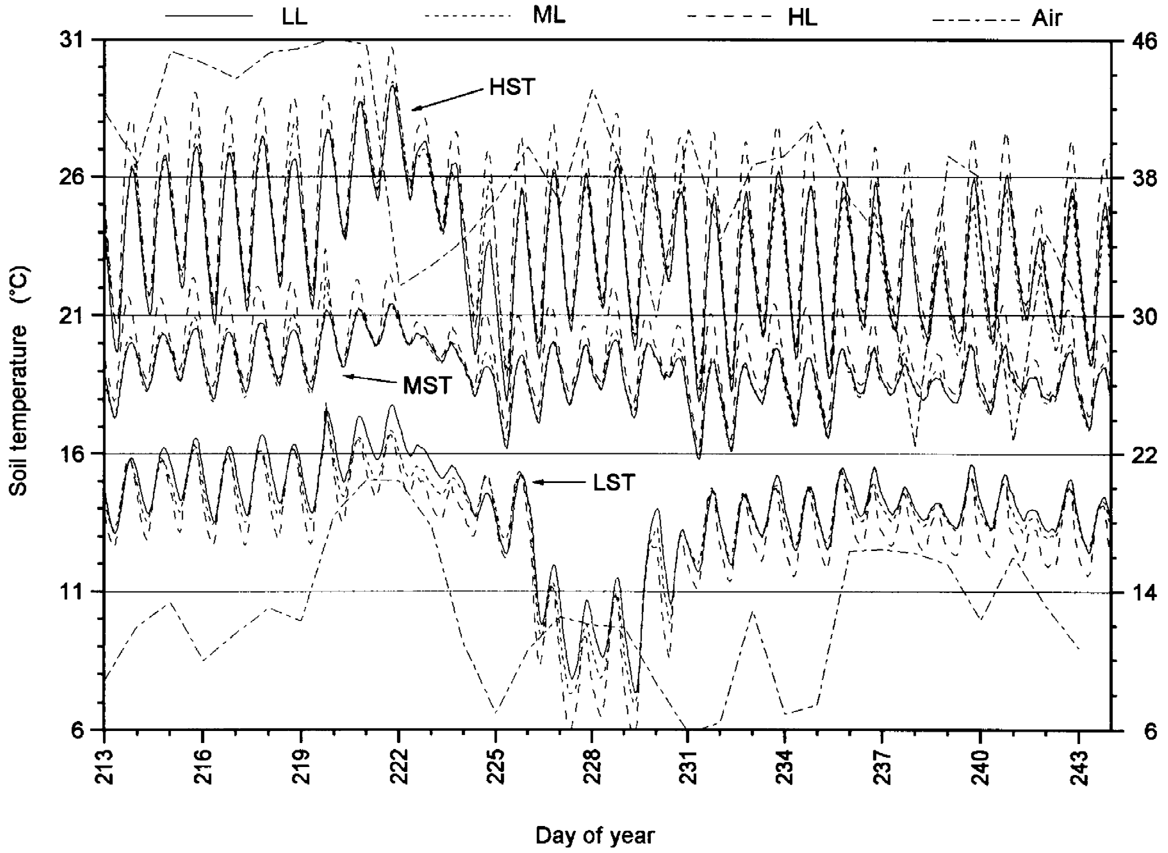

Figure 1. Hourly soil temperatures in the different combinations of light and soil temperature treatments during the month of August 1998. Daily minimum and maximum air temperature are also shown. Abreviations: LL = low light; ML = medium light; HL = high light; LST = low soil temperature; MST = moderate soil temperature; HST = high soil temperature.

rapidly brought out of the greenhouse to measure gas exchange under cooler and uniform conditions. Air temperature and relative humidity inside the cuvette during measurements were, respectively, 31 ± 2 °C and 36 ± 5% in the morning, and 34 ± 1 °C and 20 ± 2% in the afternoon. The same fascicles were oven dried (48 h at 65 °C) to obtain leaf dry mass. Subsamples of 5 fascicles per seedling were kept for determination of total surface area using the method previously mentioned. After dry mass determination, LMA was calculated for each seedling used for gas exchange measurements. Gas exchange data were then recalculated with actual leaf surface area.

Shoot water potential was measured in the afternoon of August 6 (DOY 218) using a pressure chamber (PMS Instruments, Corvallis, OR, USA). Apical shoots used for gas exchange measurements were sampled by block within a few minutes and put in a cooler filled with ice and water. Measurements were completed within 30 min of sampling. The measurement dates for gas exchange and water potential were chosen to assess treatment impact on well developed and acclimated current-year needles, just prior to water and fertilizer application.

At the end of the experiment, foliage from the apical shoot of 5 seedlings per subplot was collected for leaf nitrogen determination. Oven dried leaf material was ground (0.42 mm), and 0.2 g subsamples were used to determine total nitrogen by the Kjeldahl method (Bremner and Mulvaney, 1982).

Statistical analyses

The experimental design was a three by three factorial split-plot design in three complete blocks (for a total of nine sand beds). The main plots were the three sand beds; one of three light regimes was randomly assigned to each bed. Within each main plot were three subplots (compartments); one of three soil temperature treatments was randomly assigned to each

Table 1. Average midday (14h00–15h00 EST) soil temperatures (standard deviations in parentheses) during the beginning of August (DOY 213–226) at 10 cm depth for the different treatments

	Light levels			
	LL (10%)	ML (40%)	HL (80%)	Average
LST (16 °C)	15.7 (1.5)	15.4 (1.4)	15.4 (1.4)	**15.5 (1.4)**
MST (21 °C)	20.2 (0.6)	20.4 (0.6)	21.7 (0.7)	**20.8 (0.9)**
HST (26 °C)	26.2 (1.4)	26.2 (1.3)	28.1 (1.1)	**26.9 (1.5)**

compartment. There was therefore a total of 27 experimental units (3 blocks × 3 sand beds × 3 compartments). Analysis of variance (ANOVA) was performed on all measured variables and calculated ratios using the GLM procedure of the SAS software (version 6.12, SAS Institute, Inc., Cary, NC, USA). Specific within-treatment comparisons were performed by orthogonal contrasts (Steel and Torrie, 1980). Two contrasts were made when there was a significant light effect and two contrasts when a significant soil temperature effect was observed: (1) linear effect of light and/or soil temperature, (2) quadratic effect of light and/or soil temperature. Four contrasts were made when there was a significant interaction between light and soil temperature. Comparisons were LST (16 °C) versus MST (21 °C) levels, and MST (21 °C) versus HST (26 °C) levels, for both the linear and quadratic effects of the light factor: (1) Light linear LST vs MST, (2) Light quadratic LST vs MST, (3) Light linear MST vs HST, (4) Light quadratic MST vs HST. Homogeneity of variance of all data was verified by visual evaluation of residual plots (Devore and Peck, 1994). No transformation was necessary.

Inherent problems with ratios result in the violation of fundamental ANOVA postulates (Bauce et al., 1994; Lison, 1958). Ratios were therefore corrected prior to ANOVA using the adjusted ratio method of Bauce et al. (1994).

Results and discussion

Experimental conditions

Soil temperature measurements indicate that the target soil temperature levels were obtained, with little difference between light levels within each soil temperature level (Figure 1 and Table 1). Since both natural cooling of the soil during the night and incident sunlight were used in the experiment, daily environmental fluctuations were of greater amplitude under HST and HL in terms of soil temperature and PPFD (Figure 1, PPFD not shown), as for natural conditions under high light (Bazzaz and Carlson, 1982; Pearcy and Sims, 1994). The 4 day drop in soil temperature in LST subplots shown in Figure 1 (DOY 226 – 229) was due to a temporary failure of a solenoid valve.

Foliar nitrogen concentrations were not affected by the treatments (Table 2), as expected under conditions of non-limiting nutrient supply. Mean values of foliar nitrogen concentrations on an area and dry mass basis at the end of the experiment were 0.85 g m^{-2} and 19.5 mg g^{-1}, respectively. These values are high compared to values obtained in other studies of eastern white pine seedlings (Brand and Janas, 1988; Elliott and Vose, 1993). Midday shoot water potential was unaffected by soil temperature treatments, but readings were significantly reduced by increasing light levels (Table 2), with values going from −0.93 MPa under LL treatment, to −1.13 MPa under the HL treatment. However, these values are high compared to those reported in other studies of eastern white pine under natural conditions (Boucher et al., 1995, 1998; Elliott and Vose, 1993, 1994). Since shoot water potential was measured during a warm period, just 1 day prior to rewatering, comparison with other studies suggests that water availability was high for the duration of the experiment. Mean height growth increments measured in this study (data not shown) were substantially higher than those with white pine seedlings of comparable initial size after one growing season under natural conditions (133% vs 107%; Burgess and Wetzel, 2000).

Aboveground response

Total shoot dry mass was strongly affected by light levels, as anticipated, but not affected by soil temperature (Table 2). However, the treatments had a small but significant effect on the allocation of aboveground biomass to foliage. Increased light decreased the proportion of aboveground biomass in leaves (LMR) by 5%, while higher soil temperatures increased LMR by 2% (Table 2 and Figure 2A, B). High LMR in low light increases light capture per unit wood mass and, hence, decreases respiratory losses, especially in high-shade or mid-shade tolerant species like eastern white pine (Givnish, 1988; Pearcy and Sims, 1994; Walters et al., 1993). Data regarding the impact of soil temperature on aboveground dry mass

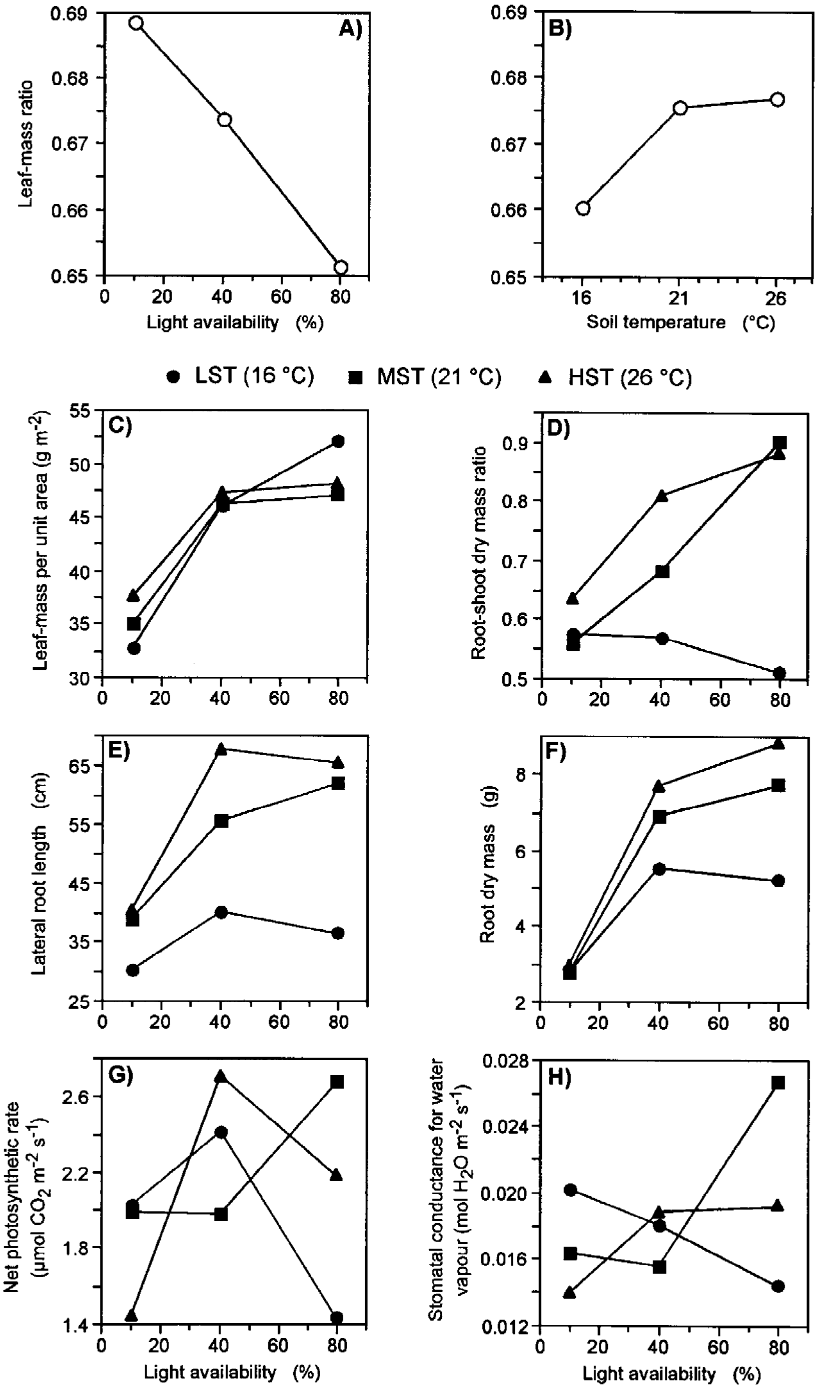

Figure 2. Light availability and soil temperature effects on (A and B) leaf-mass ratio (LMR), (C) leaf-mass per unit area (LMA), (D) root–shoot dry mass ratio (R/S), (E) lateral root length, (F) root dry mass, (G) morning light saturated net photosynthetic rate on area basis (A_{area}), and (H) afternoon stomatal conductance for water vapour (g_{wv}) of the white pine seedlings. Each point represents the mean of 3 blocks and 5 samples (n=15) in all graphics, except in graphics G and H where there was no sample (n=3). Ratios presented are adjusted ratios (A, B, C and D).

Table 2. Summary of ANOVA (*P*-values for *F*-test and mean square of errors) for midday shoot water potential (Ψ_s), leaf nitrogen on area basis (N_{area}), net photosynthetic rate on area basis (A_{area})†, stomatal conductance for water vapour (g_{wv})†, lateral root length (L.r.l.), root dry mass (DM_{roots}), shoot dry mass (DM_{shoot}), root-shoot dry mass ratio (R/S), leaf-mass ratio (LMR), and leaf-mass per unit leaf area (LMA) variables and ratios. All data are from the mid September sampling, except Ψ_s, A_{area}, and g_{wv} that were measured in early August. Ratios are adjusted ratios. Llin and Lquad = linear and quadratic effects of the light factor; MSE = mean square of error. Significant ($P<0.05$) effects are in bold

Source of variation	Df	Ψ_s	N_{area}	A_{area}	g_{wv}	L.r.l.	DM_{roots}	DM_{shoots}	R/S	LMR	LMA
Block	2	0.267	0.431	0.073	0.325	0.007	0.051	0.100	0.055	0.302	0.605
Light	2	**0.017**	0.081	0.115	0.270	<0.001	<0.001	<**0.001**	0.187	**0.028**	0.002
Main plot MSE	4	0.0065	0.0199	0.1722	1.5 E-5	24.665	4.5258	0.7852	0.1200	0.0015	50.384
Soil temperature	2	0.167	0.384	0.457	0.521	<0.001	<0.001	0.739	0.001	**0.039**	0.348
Soil temp. ∗ Light	4	0.989	0.609	**0.014**	**0.044**	**0.043**	**0.018**	0.258	<**0.001**	0.106	**0.041**
Contrasts											
Llin 16 °C vs 21 °C	1			**0.016**	**0.008**	**0.022**	**0.010**		<**0.001**		**0.013**
Lquad 16 °C vs 21 °C	1			0.042	0.230	0.906	0.758		0.404		0.711
Llin 21 °C vs 26 °C	1			0.922	0.266	0.873	0.326		0.107		0.606
Lquad 21 °C vs 26 °C	1			**0.012**	0.095	0.105	0.783		0.067		0.710
Subplot MSE	12	0.0071	0.0107	0.1802	2.0 E-5	151.56	2.6334	1.7815	0.0095	0.0008	24.537
MS sampling error	108					63.378	1.9666	2.3242	0.0203	0.0015	13.493

†Afternoon A_{area} and morning g_{wv} not significant.

partitioning are rare. Stoneman and Dell (1993) measured increased aboveground biomass allocation due to higher soil temperature in *Eucalyptus marginata* (Jarrah) seedlings. Indirect evidence can also be found in Bassman (1989); values of LMR in *Picea engelmannii* × *glauca* seedlings were higher in warmer mounds than in cooler control plots (up to approx. 5 °C difference at 12 cm depth). Increased soil temperatures would enhance water and nutrient uptake and thus favour the production of foliage. The opposing impacts of photosynthetic radiation and soil temperature on LMR suggest a possible tradeoff in the plant, between sun/shade acclimation at the leaf level, and root-shoot relationships influencing carbon allocation in aboveground parts (Dodd et al., 2000; Givnish, 1988; Grime, 1994; Lyr and Garbe, 1995; Pearcy and Valladares, 1999).

Light and soil temperature also influenced leaf mass per unit area (LMA). Increased light produced greater LMA, an expected result since LMA is known to be a good integrator of light availability (Chabot et al., 1979; Ellsworth and Reich, 1992; Pearcy and Sims, 1994). However, soil temperature interacted strongly with light levels (Table 2), with the increase in LMA with light levels being more pronounced under cold soil treatment than under either moderate or warm soil treatment (Figure 2C). Under natural conditions, higher soil temperatures normally accompany high light availability, but water absorption is hindered in cool soils (Bowen, 1991; Kramer, 1983). Our results suggest a possible role of drought tolerance response in the increase in LMA with increasing light availability, but other root factors may be involved (Abrams and Mostoller, 1995; Muraoka et al., 2000; Pearcy and Sims, 1994).

Root response

Root growth increased significantly with both increasing light availability and soil temperatures. Increase in root length due to increased light went from 21% under LST, to 59% under MST (Table 2 and Figure 2E). Similarly, root dry mass increased 87% under LST compared to 178% under MST (Table 2 and Figure 2F). This increase was not simply the result of biomass reallocation toward roots, since allometric regressions revealed that aboveground dry mass increased with increasing root dry mass under all light levels (results not shown). It is, therefore, apparent that roots benefited from enhanced photosynthate production when soil temperature increased. The influence of increased soil temperature on plant root growth is well known. Direct impacts include increased cell divisions and higher root permeability and hydraulic conductivity. Indirect impacts influencing root growth are higher water and nutrient absorption, intensification of growth hormones synthesis, and positive feedbacks from aboveground growth through sink-source relationships (Bowen, 1991; Dodd et al., 2000; Grime, 1994; Lyr and Garbe, 1995; Mooney and Winner, 1991). In the present study, maximum increase in root growth was observed at a soil temperature of 21 °C, but we also observed a trend of increasing root growth at soil temperatures above 21 °C, as noted for *Quercus robur* L. in Lyr and Garbe (1995). King et al. (1999) showed that root biomass increase in *Populus tremuloides* Michaux due to higher soil temperature occurred only under high N availability, which was the case in the present study.

Root-shoot allocation

Observations of root–shoot ratio (R/S) response indicate that in cool soils, both root dry mass and aboveground dry mass increased almost equally following an increase in photosynthetic radiation, with a slight 11% decrease in response to light under LST (Table 2, Figure 2D). However, in warmer soils, root dry mass increased substantially, while shoot dry mass increased only slightly, resulting in a R/S increase of 61% in response to light under MST (Table 2, Figure 2D). Increased R/S under enhanced photosynthetic radiation is a general response in plant species, and reflects higher transpiration demands (Grime, 1994; Pearcy and Sims, 1994). High initial R/S of containerized seedlings before planting has not been found to improve acclimation to site conditions (Bernier et al., 1995). However, once planted or after germination, development of a higher R/S in warmer soils could increase drought avoidance and survival (Burdett, 1990; Nambiar et al., 1979; Örlander et al., 1998). The R/S response observed in the current experiment supports previous observations of a positive long-term impact of scarification/higher soil temperature on root growth of conifer seedlings (Bassman, 1989; Boucher et al., 1998; Brand and Janas, 1988; Örlander et al., 1998). It is, therefore, apparent that increasing soil temperature could affect above-ground growth by improving root growth and water uptake of seedlings. The conditions of high soil water and nutrient availability imposed in this experiment did not permit this effect to manifest itself.

Gas exchange response

Gas exchange measurements support the observation of an interaction between light levels and soil temperatures observed in plant growth. Values of A_{area} and g_{wv} increased with increasing photosynthetic radiation, but only in warmer soils. In low soil temperature, A_{area} actually decreased by 30% in response to increased light (Table 2 and Figure 2G). The increased photosynthetic rates with increasing soil temperature did translate into significantly higher total seedling biomass (results not shown), but nearly all the increase went to root biomass, suggesting a higher root sink strength for photosynthates (Farrar, 1999). Values of g_{wv} increased with increased light only under MST (Table 2 and Figure 2H). King et al. (1999) also measured higher photosynthetic rates with increased soil temperature in *Populus tremuloides* Michaux plants. The intermediate values of both A_{area} and $g_{wv,}$ measured in seedlings in HST subplots under HL, compared to seedlings in MST subplots (Figure 2G, H), could be the consequence of an acclimation of these seedlings to environmental fluctuations of greater amplitude (Bazzaz and Carlson, 1982; Pearcy and Sims, 1994). As for measurements under cold soil temperatures, reduced root permeability or increased water viscosity – viscosity of pure water increases by 28% from 26 to 16 °C (Nobel, 1999) – might have resulted in a drop in both A_{area} and g_{wv} under the highest light regime. When soil temperatures are low, control of water loss under high light availability is also crucial, since root permeability and hydraulic conductivity are reduced, and for the same soil water content, water is more strongly retained due to higher viscosity (Bowen, 1991; Dodd et al., 2000; Kramer, 1983).

Conclusions

Reports of positive and unambiguous links between root growth – or other factors related to increased soil temperature – and aboveground traits of seedlings are few (Dodd et al., 2000; King et al., 1999; Lyr and Garbe, 1995; Stoneman and Dell, 1993; Vapaavuori et al., 1992). There is some indirect evidence of aboveground response of young plants to increased soil temperature following site preparation, but interactions with soil water, light availability, and/or soil nutrients are always confounded with soil temperature (Baliski and Burton, 1997; Bassman, 1989; Boucher et al., 1998; Brand and Janas, 1988). Our study is unique in the control of the interaction between light availability and soil temperature, and shows clearly that the efficiency with which light captured by the shoot is transformed into shoot growth is controlled in part by soil temperature. Although the exact mechanisms for such control were not investigated here, it is clear that soil temperature as a signal can only be perceived by the shoots through its action on root functions. Such functions include the absorption of water and nutrients, and the generation of hormonal signals. Our results were obtained after only one growing season and may not reflect long term acclimation to environmental conditions. They suggest, however, that in the field, expected light response after canopy release of seedlings cannot be properly evaluated unless the dynamics of soil temperature are properly accounted for.

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