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Influence of seedbed, light environment, and elevated night temperature on growth and carbon allocation in pitch pine (*Pinus rigida*) and jack pine (*Pinus banksiana*) seedlings

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Abstract

Jack pine (*Pinus banksiana* Lamb.) and pitch pine (*Pinus rigida* Mill.) are two autecologically similar species that occupy generally disjunct ranges in eastern North America. Jack pine is boreal in distribution, while pitch pine occurs at temperate latitudes. The two species co-occur in a small number of stands along a 'tension-zone' that traverses central Maine. These populations provide an opportunity for studying differences between boreal and temperate species in their adaptation to climatic factors.

As seedling establishment and early growth are key life-stages governing tree distribution, we experimentally evaluated the influence of seedbed light environment and substrate on the success and early growth of these species. Under similar environments, first-year jack pine seedlings allocated relatively more biomass to roots and pitch pine more to foliage. This might provide pitch pine with an adaptive advantage when soil moisture was not limiting and an advantage to jack pine if substantial moisture stress occurred. Complex ontogenetic shifts in these allocation patterns occurred over second and third years of growth, which resulted in an equalization of interspecific differences in shoot–root ratios by the end of the third growing season. Night temperatures of 4–5 °C above ambient reduced growth of jack pine seedlings, while that of pitch pine was unaffected. However, foliar respiration and respiratory response to temperature were not significantly different between species and did not explain observed differences in temperature response.

Keywords: Ontogeny; Distribution; Climate change; Photosynthesis; Respiration

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1. Introduction

The natural range of a species (or ecotype of a species) is determined by complex interactions of the physiological attributes of that species and the environment in which it establishes, grows, and eventually reproduces. Within that range, occurrence at any particular site is further determined by the supply of viable seed, the availability of suitable sites for germination of seed and establishment of seedlings (safe-sites), and the ability of the seedlings to compete with co-occurring plants for necessary resources.

The limited co-occurrence in eastern Maine of two usually allopatric (geographically separate) *Pinus* species that occupy similar niches provides an opportunity for studying how these processes might differ for boreal-adapted and temperate-adapted species. The temperate pitch pine (*Pinus rigida* Mill.) and the boreal jack pine (*Pinus banksiana* Lamb.) are shade-intolerant and typically occupy similar edaphic habitats, growing on dry sites in sandy, gravelly, or thin soils (Little and Garrett, 1990; Rudolph and Laidly, 1990). At present, the southern range limit of jack pine coincides with the northern limit for pitch pine along a narrow zone that crosses central Maine. This ‘tension zone’ also defines the southern or northern limits of numerous other plant species (McMahon, 1990). Conkey et al. (1995) have described sympatric (geographically intermixed) populations of the two pine species at this coincident range limit in and around Acadia National Park (ANP) on Mount Desert Island, Maine. In these populations, Conkey et al. (1995) found that mature trees of both species showed good growth and no signs of species-specific stress. We have shown that neither freeze-tolerance nor reproductive efforts are limiting for either species where their populations overlap at ANP (Greenwood et al., 2002). However, the two species differ in their seed germination trajectories with respect to temperature, with jack pine germinating faster at relatively lower temperatures. This may provide an early growth advantage to jack pine when soil temperatures are low (Greenwood et al., 2002).

Environment may also play a selective role at seedling-establishment and early growth stages, when susceptibility to environmental stresses is at a maximum (Kozlowski and Pallardy, 1997). Our surveys of available seedbeds in ANP stands where both species were co-occurring and regenerating identified safe-sites for germination in both high-light (full sunlight) and low-light (partial shade) environments. Within these energy environments we identified two common surface substrates: a fine organic duff that resembles ground peatmoss and a moderately course granitic sand. Transect counts of regenerating seedlings indicated the presence of regeneration pulses that were asynchronous between these species (Greenwood et al., 2002). However, low numbers of seedlings surviving from any particular cohort precluded explicit analysis of interspecific differences in seedbed preference. To investigate the influence of seedbed on germination and early growth, we established an experiment evaluating the roles of light environment and substrate type on these processes.

Our study also offered the possibility of evaluating differences between these boreal and temperate *Pinus* species in their carbon allocation patterns in response to similar environmental conditions. Functions describing growth responses to environment are usually key components of models used to predict species range limits under changing climate scenarios (Bonan and Sirois, 1992). Numerous studies have demonstrated that changes in temperature are correlated with altered patterns of carbon partitioning and associated patterns of growth and development (Farrar and Williams, 1991; Callaway et al., 1994; Laurence et al., 1994; Pell et al., 1994; Wang et al., 1995; Maherali and DeLucia, 2001).

Ryan (1991), Amthor (1994), Carey et al. (1997) and others have suggested that climatic warming results in increased allocation of photosynthetically fixed carbon to maintenance respiration (R_m), the respiratory costs resulting from physiological functions not directly related to plant growth. R_m is strongly temperature-dependent and generally shows an exponential relationship with temperature over the range of growing season temperatures in temperate forests (Thornley, 1970; Amthor, 1989). Amthor (1989) estimated that temperate plant species expend approximately 50% of their fixed carbon in respiration, and Ryan (1991) proposed that R_m (including ion uptake) accounts for approximately 75% of respiratory carbon allocation. The temperature dependence of R_m suggests that this proportion may increase with rising global temperatures. Such increases in R_m

would have additive effects on plant growth by decreasing the pool of available carbon and increasing the carbon storage required to supply respiratory carbon when photosynthetic production is low.

Plants native to higher latitudes or altitudes may exhibit a greater increase in R_m with increasing temperature than their counterparts from lower latitudes. This has been demonstrated in northern and southern ecotypes of species as well as pairs of allopatric species that occupy ecologically similar niches (e.g., Mooney and Bilings, 1961; Mooney, 1963; Lechowicz et al., 1980; Friend and Woodward, 1990; Miroslavov and Kravkina, 1991). In many of these comparisons, species or ecotypes from different climates exhibit different degrees of response to experimentally warmer temperatures, with the species or ecotypes associated with the cooler climate showing a greater absolute increase in its allocation to R_m (Larigauderie and Körner, 1995). Following this hypothesis, carbon allocation to R_m should show greater sensitivity to increased temperatures in the boreal jack pine compared with temperate pitch pine. Unless other mechanisms compensate for increased R_m allocation, it would be expected that growth of pitch pine seedlings relative to jack pine should be enhanced if ambient temperatures increased at their common range limit.

In this paper, we draw on the results of a number of inter-related experiments to evaluate the influence of substrate type, light environment, and night temperature on the carbon physiology and growth of a temperate and a boreal pine species that occupy similar ecological niches. Responses to these environmental variables afford inferences between carbon allocation strategies and seedling success.

2. Materials and methods

2.1. Seed source and growing conditions

Seed collected from natural stands in ANP (44°21′N, 68°13′W), was stored at 4 °C, and, prior to sowing, treated for 12 h in a 3% hydrogen peroxide solution followed by moist stratification at 4 °C for one month. We used Ray Leach cells (200 ml; Stuewe & Sons, Inc., Corvallis, OR, USA) for germination and first-year seedling growth. Seedlings were grown in Orono, ME, USA (44°21′N, 68°13′W), in a medium of peat, sand, and vermiculite (2:1:1, v/v/v), containing Osmocote 18–6–12 (N–P–K) (Scott-Sierra, Milpitas, CA, USA) at a rate of 4 kg m^{-3}. We maintained soil water near field capacity by manual watering. In all experiments, we monitored air and soil (3 cm-depth) temperatures with calibrated type-T thermocouples (Omega, Meridian, CT, USA) and incident quantum flux with Li-Cor Model 190 quantum sensors (Li-Cor, Lincoln, NE, USA), connected to Campbell CR-10 and CR10x dataloggers with multiplexers (Campbell Scientific, Logan, UT, USA).

We made biomass determinations after autumn budset (late October). Careful repeated washings were used to remove potting media from roots, which were separated from shoots at the root collar, and needles were separated from woody components after drying to constant mass in a 70 °C oven.

2.2. Seedbed experiment

In this experiment we tested the effects of two light environments and two substrates (peat and sand) on growth and allocation. The high-light treatment provided the energy environment of full sunlight, while the low-light treatment (60% interception shadecloth) simulated the light environment under a partial overstory. These energy environments and substrates represent the most common seedbed conditions available for establishment in the pitch and jack pine stands at ANP (Greenwood et al., 2002). For the seedbed substrate treatments, we filled cells with 9–10 cm of peat-sand-vermiculite growing medium, which was overlaid with 1 cm layer of either sand (Agway Grower's Grit) or sifted peat moss. We covered the sowed seeds with a second 1 cm layer of either sand or peat. Planted tubes were placed in trays of 96 cells equally divided between species and substrates, and we assigned 10 trays to each of three replicate pairs of light environments (30 trays total). This experiment and germination responses are further described in Greenwood et al. (2002).

In October 1997, we recorded stem height and root collar diameter for all seedlings, and selected a random subset of 60 seedlings (30 of each species) per treatment combination (240 seedlings) for harvest and biomass determinations. We measured specific leaf area (SLA) for a subset of 36 jack pine and 36 pitch

Table 1
Allometric models used to determine seedling biomass at the beginning of the elevated night-temperature experiment

Species	Attribute	Regression model	r^2	$P > F$
Pitch pine	Total biomass	$\ln y = 1.936 + 0.476(\ln d^2h)$	0.67	<0.0001
	Shoot biomass	$\ln y = 1.615 + 0.504(\ln d^2h)$	0.71	<0.0001
	Root biomass	$\ln y = 1.760 + 1.782(\ln d^2h)$	0.57	0.001
Jack pine	Total biomass	$\ln y = 2.254 + 0.322(\ln d^2h)$	0.36	0.01
	Shoot biomass	$\ln y = 1.887 + 0.330(\ln d^2h)$	0.34	0.01
	Root biomass	$\ln y = 1.080 + 0.295(\ln d^2h)$	0.27	0.02

pine seedlings by scanning needles on a calibrated flatbed scanner prior to drying and measuring projected needle area with WinNeedle, Version 4.0 (Régent Instruments, Inc., Quebec, Canada). Needles were dried at 65 °C for 72 h and weighed on an analytical balance.

2.3. Response to elevated temperatures

We used 2-year-old seedlings from the seedbed experiment to experimentally test the hypothesis that a species adapted to a temperate climate will exhibit relatively greater growth response to atmospheric warming than its boreal counterpart. We approached this by growing seedlings in both ambient and elevated nighttime temperature environments while maintaining common daytime conditions. Increased night temperatures were selected as (1) these could be experimentally maintained while not interfering with the natural light regime, and (2) climate change models for northeastern North America predict greater increases in night compared to daytime temperatures (Karl et al., 1993). In a collateral experiment, we established Q_{10} values for the temperature response of foliar respiration to test the hypothesis that boreal species will have greater losses to R_m with increasing temperature.

We repotted unharvested seedlings from the 1997 experiment into 5 l containers and maintained them in a shade house (40% interception shadecloth) through the 1998 growing season. Prior to the 1999 growing season, we recorded height and diameter at root collar and repotted the 3-year-old seedlings into 25 l pots. To estimate initial biomass for relative growth rate (RGR) determinations, we harvested 40 seedlings, 20 per species, and developed allometric relationships between stem volume and biomass components using linear regression. Equations were of the form

$$\ln y = a + b(\ln d^2 h) \tag{1}$$

where y is the biomass component (total, shoot, or root) being evaluated, d the stem diameter just above root collar, and h the height of the main stem (Table 1).

In May 1999, we randomly assigned two jack pine and two pitch pine seedlings to each of 12 groups (four seedlings per group) arranged in three blocks. Within groups, we rotated seedlings monthly to minimize positional shading effects. We randomly allocated six groups to the elevated night temperature treatment. For these treatments, we placed boxes (cubes of 1.2 m per side) of foil-faced foamboard (4.8 cm thickness) over the groups to be warmed, covering treated seedlings with a box each night at dusk, and removing boxes before sunrise from 1 June to mid-September 1999. For nights when supplemental heating was needed to maintain a target temperature differential of 4–5 °C above ambient, we programmed a Campbell CR10X datalogger to turn on a 50 W light bulb in a light-tight enclosure. During the day, all seedlings were exposed to ambient conditions.

Upon completion of treatments we measured the stem height and stem diameter at the root collar of all seedlings, removed 50–75 current year needles from each of the 48 seedlings to calculate SLA for each individual, and harvested all seedlings for component biomass determinations, calculating species averages within each unit.

2.4. Gas exchange measurements

We measured gas exchange on trees being used for the elevated night temperature experiment with an open-system LI-6400 infrared gas analyzer (LI-COR, Inc., Lincoln, NE). In August 1999, we randomly selected four trees per species from each temperature treatment (16 seedlings) for measurement of photosynthetic rates of current-year foliage. Photosynthesis was measured during morning hours at full sunlight (2000 μmol m^{-2} s^{-1} PPFD) and a 'shade-simulation' value of 25% full-sunlight (500 μmol m^{-2} s^{-1} PPFD). A LI-6400-02B light source provided illumination, and we equilibrated seedlings to the cuvette light intensity for 5–7 min before taking measurements. We determined leaf areas with WinSeedle, Version 4.5A (Régent Instruments, Inc., Quebec, Canada).

We developed Q_{10} relationships (Eq. (2)) for foliar maintenance respiration (R_m) by measuring four separate sets of six seedlings from each species at temperatures of 15, 20, 25, 30, and 35 °C. For each set of seedlings and temperature, we determined R_m on three separate days (3 reps). Before measurements, we maintained trees in the dark at measurement temperature for at least one hour. We recorded a set of four respiration measurements at 30 s intervals for a single current-year foliage sample from each seedling. We determined projected leaf area of samples as previously described, and converted from an area to a mass basis using seedling-specific SLA.

We calculated Q_{10} for respiration for a set of seedlings that had been measured at both 20 and 35 °C. Values were derived from the equation

$$Q_{10} = \left(\frac{k_2}{k_1}\right)^{10/(T_2-T_1)} \tag{2}$$

where k_1 is the respiration rate at 20 °C (T_1) and k_2 the respiration rate at 35 °C (T_2) (Salisbury and Ross, 1992).

2.5. Statistical analysis

All analyses were performed using SAS Version 6.12 (SAS Institute, Inc., Cary, NC, USA). For each analysis of variance (ANOVA), we tested the assumption that error terms are randomly, independently, and normally distributed using the Shapiro–Wilk statistic and the assumption of variance homogeneity with a Levine's Test (Steel et al., 1997). When necessary, we log-transformed data to meet the assumptions of ANOVA.

In the seedbed experiment, we analyzed growth data with a nested ANOVA. The main effects were species, light, germination substrate, and the nested effect of block within light. Analyses were performed on tray-level means by species and substrate type. We analyzed data from the elevated night temperature experiment with a three-factor ANOVA (species, treatment, and block). We tested for differences in photosynthetic rates using ANOVA, species differences in SLA using a two-factor ANOVA (species and treatment), and analyzed respiration data with a three-factor ANOVA (species, treatment, block). To obtain normal distributions of residuals, we performed the ANOVAs of gas exchange data after square-root transformations.

3. Results

3.1. Seedbed effects

Shaded treatment blocks showed a mean integrated value of photosynthetically active radiation (PAR, λ =400–700 nm) over the course of the 1997 growing season (71 days) of 1466 mol m^{-2}, while the high-light treatments accumulated a mean of 2380 mol m^{-2}. This difference in radiation regimes resulted in a mean midday air temperature differential of approximately 5 °C. Nighttime air temperatures were within 1 °C, with the shaded plots slightly warmer on clear nights. The intensity of solar radiation interacting with substrate resulted in a range of mean daytime soil temperatures of 27–34 °C, with the high-light + sand (HS) environment exhibiting the highest temperatures and the low-light + peat (LP) treatment the lowest (Fig. 1). We believe that the order of treatments by daytime temperatures reflects the potential moisture stress due to the direct relationship between temperature and evaporative demand.

For both species, growth (dry mass) was greatest in the high-light + peat (HP) treatment, while seedlings grown in the HS treatment exhibited the lowest growth (Table 2). Allocation to foliage was consistent across treatments, except for the reduction in the HS treatment, as was seedling basal (root collar) caliper. Allocation to stemwood was greater in both low-light environments. Consistent with this pattern, relative

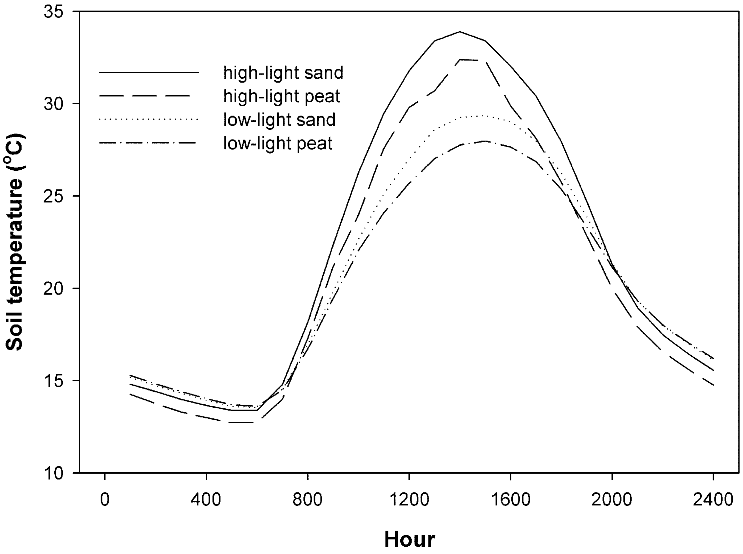

Fig. 1. Mean hourly soil temperatures during the 1997 growing season for the seedbed environment experiment. Temperatures were sampled every 60 s at a depth of approximately 3 cm with type-T thermocouples.

allocation to foliage and stemwood was also repeated within light-environments with wood/foliage ratios ($g\ g^{-1} \pm$ S.E.) of 0.41 ± 0.03 (LP) and 0.43 ± 0.01 (LS) in the shaded treatments, and 0.36 ± 0.02 in both-full sun treatments despite the reduced growth of the HS seedlings. Environmental influences were not apparent in proportional biomass allocation to foliage (needle-weight-ratio; NWR).

At the end of the growing season, total growth (dry mass) was not significantly different between species (Table 3). However, pitch pine showed greater shoot biomass than jack pine ($P < 0.01$), primarily due to greater foliage mass. In contrast, jack pine showed greater allocation to roots, resulting in pitch pine having a significantly greater S:R than jack pine ($P < 0.01$). The tendency for pitch pine to allocate relatively more biomass to aboveground components compared to jack pine was also reflected in foliage area-to-root mass ratios (FARM) and needle weight ratio (NWR, the ratio of needle biomass to total biomass). Although pitch pine allocated greater resources to foliage, projected needle areas for

Table 2
Seedbed environment effects on growth and allocation patterns for both species

Attribute	Environmental treatment			
	Low-light peat substrate	Low-light sand substrate	High-light peat substrate	High-light sand substrate
Total biomass (g)	1.09 ± 0.05 bc	1.20 ± 0.04 ab	1.27 ± 0.05 a	0.95 ± 0.05 c
Shoot biomass (g)	0.62 ± 0.03 a	0.67 ± 0.03 a	0.65 ± 0.04 a	0.47 ± 0.03 b
Root biomass (g)	0.47 ± 0.02 b	0.53 ± 0.02 b	0.62 ± 0.02 a	0.48 ± 0.03 b
Stem wood (g)	0.18 ± 0.01 ab	0.20 ± 0.01 a	0.17 ± 0.01 b	0.12 ± 0.01 c
Foliage (g)	0.44 ± 0.02 a	0.47 ± 0.02 a	0.47 ± 0.03 a	0.34 ± 0.02 b
Shoot height (cm)	7.3 ± 0.25 a	7.5 ± 0.26 a	6.08 ± 0.25 b	5.24 ± 0.20 b
Basal caliper (mm)	2.18 ± 0.05 a	2.20 ± 0.05 a	2.26 ± 0.05 a	1.96 ± 0.06 b
NWR ($g\ g^{-1}$)	0.40 ± 0.16 a	0.39 ± 0.01 a	0.37 ± 0.01 a	0.38 ± 0.02 a

High-light treatments were under full sunlight and low-light filtered by 60%-interception shade cloth. All seedlings were grown in a peat-sand-vermiculite growth media with time-release fertilizer, topped with 2 cm of either sifted peat (peat substrate) or quartz grit (sand substrate). Data are seedling means ± standard error. Needle weight ratio (NWR) is the ratio of needle to total biomass. Letters indicate row-wise Tukey's HSD groupings ($\alpha = 0.05$).

Table 3
Interspecific differences (mean ± 1 S.E.) for first-year pitch pine and jack pine seedlings

Attribute	Pitch pine	Jack pine
Total biomass	1.13 ± 0.03	1.13 ± 0.03
Shoot biomass*	0.64 ± 0.02	0.57 ± 0.02
Root biomass*	0.49 ± 0.02	0.56 ± 0.02
Stem wood biomass	0.18 ± 0.01	0.17 ± 0.01
Needle biomass*	0.47 ± 0.02	0.40 ± 0.01
Shoot height*	7.02 ± 0.18	6.15 ± 0.16
Stem diameter	2.16 ± 0.04	2.16 ± 0.04
S:R*	1.46 ± 0.06	1.06 ± 0.03
SLA*	60.5 ± 1.0	67.8 ± 1.1
Seedling PNA	28.3 ± 1.0	27.1 ± 0.9
FARM*	65.0 ± 2.6	50.5 ± 1.6
NWR*	0.42 ± 0.01	0.36 ± 0.01

Biomass data are expressed in g, height in cm, diameter in mm, specific leaf area (SLA) and foliar-area-to-leaf-mass ratio (FARM) in $cm^2 g^{-1}$, and other ratios in $g g^{-1}$ (NWR = needle weight ratio, foliar mass/total biomass; PNA = projected needle area).

* Significant differences between the species ($P \leq 0.05$).

seedlings of both species were not significantly different due to a higher specific leaf area (SLA) for jack pine (Table 3). Allocation to stem growth on a biomass basis did not differ significantly between species. However, pitch pine seedlings were significantly taller than jack pine ($P < 0.01$).

The absolute values of growth components (total, shoot, foliar, and root biomass) exhibited no significant species × treatment differences. Nevertheless, species × treatment effects were apparent in relative allocation patterns. FARM and S:R ratios were significantly lower for both species in the high-light compared to low-light treatments (Fig. 2). The decreases in FARM and S:R were far more dramatic for pitch pine than jack pine ($P = 0.04$ and 0.03 for species × treatment interaction effects, respectively).

3.2. Elevated night-temperatures

At the end of their third growing season, absolute biomass of all components (total, shoot, root, foliage, and stem-wood) showed no significant species, treatment, or interactive effects. Relative growth rates (RGR) were greater for jack pine seedlings, which were smaller than pitch pine at the start of the season (Fig. 3a). This effect was significant across treatments ($P < 0.01$), and these differences held true for both aboveground ($P = 0.02$) and below ground ($P < 0.01$) growth components (Fig. 3b and c). By the end of the fourth growing season, S:R which had been greater for pitch pine during early seedling growth (Table 3), was not significantly different between species. However, FARM and NWR displayed significant species effects ($P = 0.02$ and 0.03, respectively), with pitch pine still exhibiting greater allocation to foliage relative to roots than

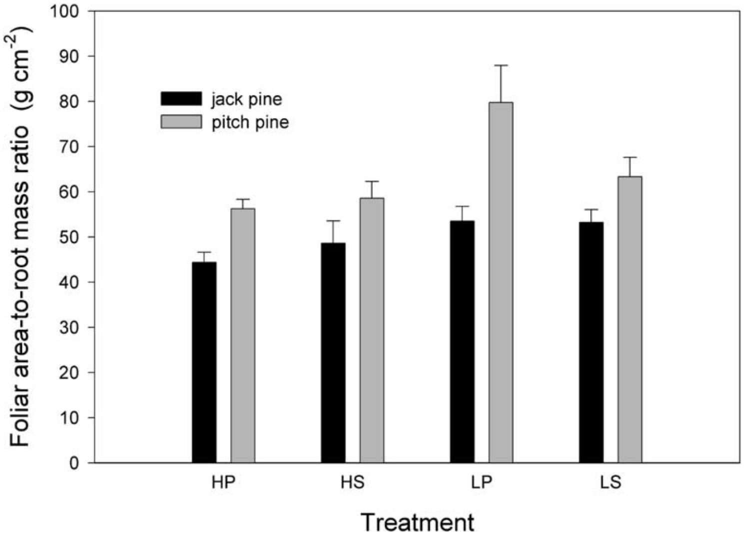

Fig. 2. Foliage area-to-root mass ratios of first-year jack pine and pitch pine seedlings grown in four simulated microsites: high-light, peat substrate (HP), high-light, sand substrate (HS), low-light peat substrate (LP) and low-light, sand substrate (LS). Bars indicate one standard error.

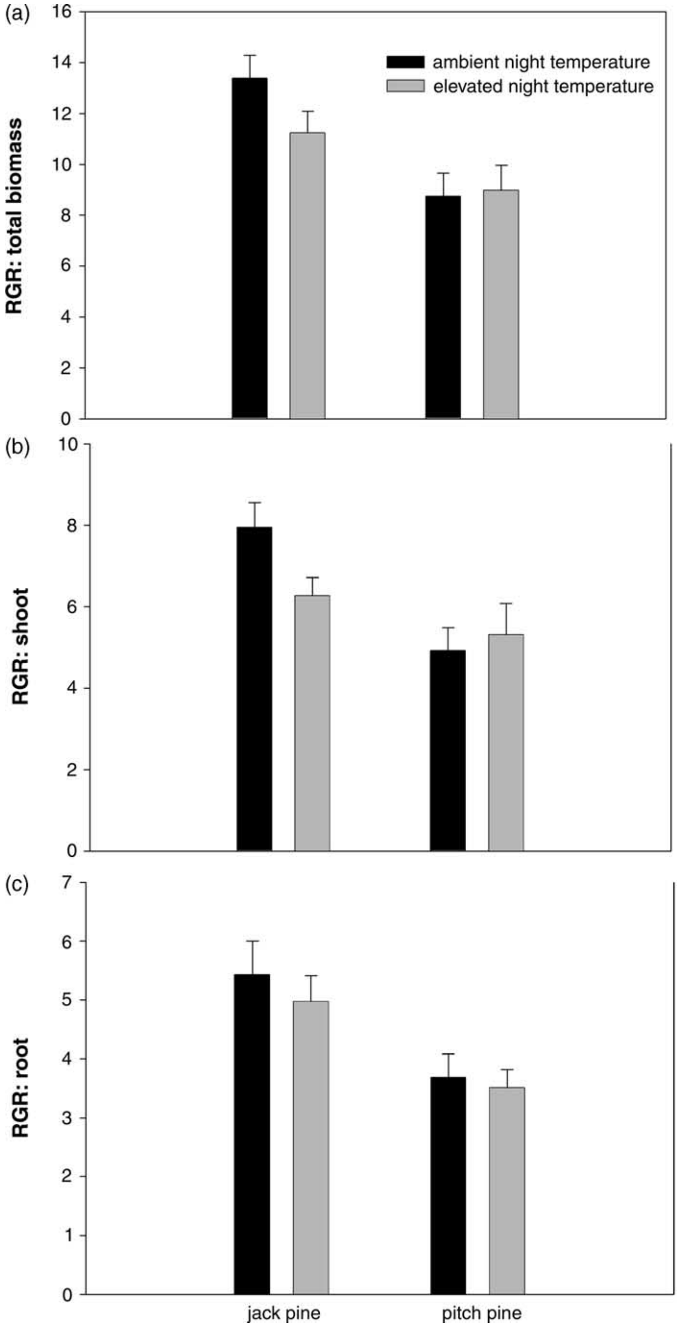

Fig. 3. Relative growth rates (g g total biomass^{-1} year^{-1}) for total biomass (a), shoot (b) and root (c) components of 3-year-old jack and pitch pine seedlings after one growing season at ambient and elevated (+4–5 °C) nighttime temperatures. Bars indicate one standard error.

Table 4
Photosynthetic rates for seedling pitch and jack pine foliage at light intensities representing full sunlight and partial canopy establishment sites ($n = 8$ seedlings species^{-1}, mean ± 1 S.E.)

Species	PPFD (μmol m^{-2} s^{-1})	Net assimilation (μmol m^{-2} s^{-1})
Pitch pine	500	13.3 ± 1.2
	2000	22.0 ± 1.7
Jack pine	500	12.1 ± 1.2
	2000	19.4 ± 1.6

Differences between species were non-significant at $\alpha = 0.05$.

jack pine. Thus, the equalization of R:S was principally due to jack pine increasing relative allocation to stem growth.

In this experiment, species × treatment effects indicated a relative inhibition of shoot growth for jack pine in the warm-night treatment, while that of pitch pine did not differ between treatments. Analysis of RGR showed significant species × treatment effects for shoot biomass ($P = 0.05$), but not root ($P = 0.72$), or total ($P = 0.21$) biomass (Fig. 3). The S:R of jack pine declined under the warm-night treatment and that of pitch pine remaining unchanged ($P > F$ of 0.08 for species × treatment effects). Both FARM and NWR exhibited no species × treatment effects ($P = 0.18$ and 0.46, respectively).

During the third growing season, current-year foliage of both species showed greatly reduced SLA compared to that of first-year seedlings. This is consistent with patterns of decreasing SLA with tree age that has been described for other conifers where the most rapid rates of change occur during juvenile life-stages (Day et al., 2001). Although, differences in SLA between species were small with jack pine at 42.9 ± 0.8 cm^2 g^{-1} and pitch pine at 40.3 ± 0.6 cm^2 g^{-1} differences were significant at $P < 0.001$, due to low variation in leaf morphology.

Table 5
Q_{10} values for pitch and jack pine foliage over the temperature range of 15–35 °C

Species	Q_{10} foliar respiration	
	Mass basis	Area basis
Jack pine	1.67 ± 0.15	1.84 ± 0.10
Pitch pine	1.80 ± 0.12	1.79 ± 0.11

Values (mean ± standard error) were calculated on both mass and area bases.

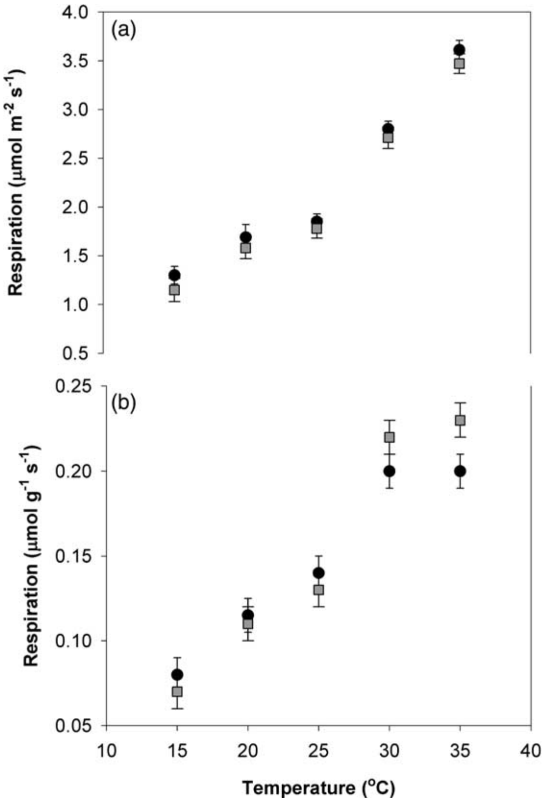

Fig. 4. Response of foliar respiration air temperature for dark-adapted jack and pitch pine seedlings on a projected needle area basis (a) and mass basis (b). Bars indicate one standard error.

3.3. Gas exchange

Although photosynthetic rates were slightly higher for pitch pine than for jack pine (Table 4), those differences were not statistically significant. Similarly, respiration rates, calculated on either mass or area bases (Fig. 4) and respiratory Q_{10} values (Table 5) were not different.

4. Discussion

4.1. Influence of seedbed environment on establishment and early growth

Mortality of germinants during the first growing season showed no trends related to environment or species. However, environmental variation in growth, indicative of sublethal stress levels, and carbon allocation patterns provide insight into broader questions related to their distribution. As would be expected, these shade-intolerant species maximized growth under full sunlight. For both species, the high-light peat-substrate (HP) treatment provided the best growing conditions with maximum biomass accumulation (Table 2).

Nevertheless, the high-light sand-substrate (HS) seedlings exhibited lower growth rates than the partial sunlight treatments. Apparently, sub-lethal environmental stresses related to the HS substrate more than offset the advantage of higher light intensities. Differential nutrient availability due to substrate type was unlikely a limiting factor. Considering the soil volume of the growth cells, the peat or sand overlays represented only approximately 20% of the available soil volume. In addition, growth rates between substrate types in the low-light treatments was not significantly different, with the sand substrate seedlings slightly outperforming those growing in the peat overlay. It is possible that a small increase in moisture retention ability in the peat-topped cells provided seedlings with a critical additional supply of moisture in the high-light treatments where both surface evaporation and transpirational demand would be greatest. When dried, the peat layer could have provided a barrier to evaporation from the underlying soil. Additionally, the greater volumetric water content of peat provided enhanced evaporative cooling. In support of this possibility, we found midday temperature maxima were several degrees lower in peat-topped than sand-topped tubes, despite the comparatively higher albedo of the lighter colored sand (Fig. 1).

The low growth rates in the HS seedlings were due to decreased growth of foliage, stem and roots compared to HP seedlings, indicating an overall inhibition of carbon availability and not variability in allocation patterns. The overall lower growth rate of the HS seedlings may have resulted from the combined effects of decreased integrated gas exchange as stomates closed earlier in the day due to plant water stress and increased losses of fixed carbon to R_m resulting from higher air and soil temperatures. A top coating of duff over mineral soil may be an important component of safe-sites for establishment of these species in the harsh, bedrock-dominated localities where both occur at their respective range limits in Maine. At the Cadillac Mountain site (where both species are regenerating), Greenwood et al. (2002) found most surviving germinants were located where several cm of mineral soil was overlain by 1–2 cm of organic duff. However, as soil temperature and moisture were not measured in that study, explicit comparison with these results was not possible.

In contrast the exceptional growth of the HP seedlings was primarily due to greater root growth of pitch pine seedlings. The consistently lower S:R and FARM of jack pine would presumably impart an advantage when a high probability of moisture stress existed during the first year of seedling development (Schulze, 1984). In contrast, the greater plasticity in FARM found in pitch pine (Fig. 2) would maximize growth potentials by concentrating investment of resources in photosynthetic area (Cornelissen et al., 1996; Poorter and Remkes, 1990). This strategy would be most effective when levels of moisture stress are relatively consistent during seedling establishment and early growth. The risk in this strategy is seedling damage or mortality when stochastic exposure to moisture stress occurs with insufficient time to modify FARM in response to changing conditions. Elliot et al. (1999) reported extensive mortality of pitch pine seedlings due to atypical growing season drought in North Carolina. It is not known how commonly such events limit regeneration of pitch pine. However, this observation is consistent with the finding of Greenwood et al. (2002) that jack pine seedlings are more likely to occur on shallower soils than pitch pine at the ANP study site, and with their conclusion that a cool, dry climate favors the establishment of jack pine while warmer, moister conditions favor pitch pine regeneration. In this scenario, when water is not limiting pitch pine would be favored by its greater investment in photosynthetic area during subsequent growing seasons, both in competition with jack pine and in its competitive response to other co-occurring vegetation. The greater stem height growth of pitch pine would also impart a theoretical advantage in interspecific competition.

4.2. Ontogenetic growth trajectories

Patterns of carbon allocation, and their resulting allometric relationships, may exhibit dynamic changes during the early growth of seedlings that result from the interaction of genetically programmed ontogenetic trajectories and, in some species, the influence of environmental factors (Gedroc et al., 1996). In our two-species system, jack pine appeared to adhere to a predetermined pattern of above- and below-ground allocation while pitch pine appeared to move towards a resource based 'functional equilibrium' (Poorter and Nagel, 2000; Gedroc et al., 1996). Griffin et al. (1995) described a similar interspecific comparison between *P. taeda* and *P. ponderosa*, in which R:S of *P. taeda* was altered by the availability of CO_2 and N, while that of *P. ponderosa* showed little response.

Although overall growth was not significantly different at the end of the first growing season, our pitch pine seedlings showed significantly greater biomass accumulation than jack pine during their second year. Nevertheless, despite the size advantage of pitch pine seedlings after two growing seasons, by the end of the third growing season the two species again showed no differences in total biomass. S:R and height growth exhibited similarly complex ontogenetic trajectories. While pitch pine seedlings were somewhat taller than jack pine after the first and second growing seasons, jack pine also substantially outdistanced pitch pine RGR and height growth during the third growing season. These results contrast with the expectation that plants investing early in added leaf area will subsequently exhibit greater RGR (Cornelissen et al., 1996). How this apparent plateau in pitch pine growth rates integrates with the developmental strategy of this species is unclear. Some potential explanations may be ontogenetic changes in balance between aboveground and belowground allocation, investment in defensive compounds, and/or developmental phase change (transition between juvenile and reproductively mature life stages). No matter what their cause, these substantial shifts in allometry suggest that caution should be exercised in drawing conclusions from the results of short-term experiments with tree seedlings.

4.3. Response to elevated night temperature

Elevating temperature during the night decreased the RGR of jack pine while that of pitch pine remained unchanged (Fig. 3). The lack of differences in foliar respiration rates and respiratory Q_{10} values indicates that allocation to aboveground respiration did not account for these observed temperature effects. Sinks that could potentially explain the missing carbon are maintenance respiration of belowground biomass or interspecific differences in turnover of belowground components (e.g., fine roots). Reich et al. (1998) found little difference in root respiration rates among such diverse evergreen conifers as *Pinus*, *Picea*, and *Thuja*, implying that a higher turnover of fine roots is a more likely differential carbon sink. In support of this hypothesis, Steele et al. (1997) found fine root turnover to be temperature dependent in jack pine and other boreal species. Eissenstat and Yanai (1996) reported greater fine root turnover at a southern compared to a northern site for sugar maple (*Acer saccharum* Marsh.) in Michigan, again suggesting a strong correlation between temperature and fine root turnover.

As only night temperature was manipulated in this experiment, the effects of increased daytime temperature cannot be assessed. It is conceivable that increased daytime temperatures could result in compensatory increases in photosynthetic performance. However, several studies with other temperate conifers suggest that net photosynthesis either remains level or declines as temperature increases above 20 °C due to a combination of respiratory cost, changes in mesophyll resistance to CO_2 diffusion, and increased photorespiration (Day, 2000; Teskey et al., 1995). Additionally, as we previously suggested, any competitive advantage imparted to pitch pine by increased night temperatures could be tempered by increased moisture stress if the ratio of precipitation to potential evapotranspiration decreased with climatic warming.

Foliar respiration rates and respiratory Q_{10} values were within the ranges commonly reported for conifers (Sprugel et al., 1995). In this species pair, foliar respiration rates (Fig. 4) and respiratory Q_{10} values (Table 5) do not follow the pattern of higher values for species distributed at higher latitudes. It is possible that the progeny of populations growing at their common range limit exhibit similarly acclimated respiratory responses (Larigauderie and Körner, 1995). However, Lavigne (1996) and Lavigne and Ryan (1997) have shown that jack pine does not exhibit provenance or latitudinal differences in stem respiration rates, suggesting a limited potential for variation in R_m for that species. In either case, foliar

R_m and respiratory Q_{10} values would not appear to effect the competitive status of these species at their current common range limit and under predicted scenarios of climate change.

4.4. Consequence to species distribution

Traditional explanations of range limits have northern limits defined by the cold tolerance parameters of one or more lifestages of a species and the southern extent by competition for growing space (multidimensional resources) (Woodward, 1987). In models, the success of a species is often defined by parabolic or other mathematical expressions relating growth response to temperature (Bonan and Sirois, 1992). In this pair of *Pinus* species with similar autecologies and allopatric yet abutting ranges, we have found that cold tolerance, reproductive efficiency (Greenwood et al., 2002), and allocation to R_m do not appear to be responsible for current species distributions. Greater inhibition of jack pine RGR under warmer night temperatures suggests that more temperate climates and climatic warming would favor pitch pine. In turn, jack pine appears to be favored by cool spring temperatures during the germination stage (Greenwood et al., 2002).

As past climatic shifts and those predicted for the future suggest temperature and precipitation patterns change in complex manners, the influence of elevated temperatures cannot be separated from those due to changes in the availability of water and other resources. Understanding responses to climate change at a predictive level will require much additional knowledge in both qualitative and quantitative aspects. This series of studies underscores the complex nature of understanding the relationship between seedling growth patterns and response to climate change. For example, if pitch pine is provided a competitive advantage under warmer, moist conditions through greater resource investment in leaf area, the adaptive value of such an advantage might be reduced by stochastic stresses associated with increased variability in precipitation patterns.

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