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Growing season temperatures limit growth of loblolly pine (*Pinus taeda* L.) seedlings across a wide geographic transect

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Abstract We grew potted loblolly pine (*Pinus taeda* L.) seedlings from a single provenance under well watered and fertilized conditions at four locations along a 610 km north–south transect that spanned most of the species range to examine how differences in the above-ground environment would affect growth rate, biomass partitioning and gas exchange characteristics. Across the transect there was an 8.7°C difference in average growing season temperature, and temperature proved to be the key environmental factor controlling growth rate. Biomass growth was strongly correlated with differences in mean growing season temperature ($R^2 = 0.97$) and temperature sum ($R^2 = 0.92$), but not with differences in mean daily photosynthetic photon flux density or mean daily vapor pressure deficit. Biomass partitioning between root and shoot was unchanged across sites. There was substantial thermal acclimation of leaf respiration, but not photosynthesis. In mid-summer, leaf respiration rates measured at 25°C ranged from 0.2 μmol m^{-2} s^{-1} in seedlings from the warmest location to 1.1 μmol m^{-2} s^{-1} in seedlings from the coolest site. The greatest biomass growth occurred near the middle of the range, indicating that temperatures were sub- and supra-optimal at the northern and southern ends on the range, respectively. However, in the middle of the range, there was an 18% decrease in biomass increment between two sites, corresponding to 1.4°C increase in mean growing season temperature. This suggests that thermal acclimation was insufficient to compensate for this relatively small increase in temperature.

Keywords Loblolly pine · Thermal acclimation · Net photosynthesis · Dark respiration

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Introduction

Climate simulations predict that temperatures in this century will increase by approximately 2°C in the southeastern United States (Meehl et al. 2007). Most biological processes determining net biomass accumulation are temperature dependent, including photosynthesis and respiration (Hellmers 1962). Yet factors such as the ability of a species to acclimate physiologically to different temperature regimes, changes in the length of the growing season and increased potential for high temperature stress complicate predictions of how warmer conditions will affect tree growth.

Many studies of the effect of temperature on tree growth have reported that higher temperatures increase tree growth. Height growth of a population of genotypes of *Pinus sylvestris* (L.) planted in genetic trials throughout Europe was greatest in sites in the southern (warmest) locations, and least in the colder northern sites (Reich and Oleksyn 2008). The annual biomass increment of mature moist tropical evergreen forests growing on different sites with mean annual temperatures ranging from 10 to 27°C

was substantially greater in warmer sites than cooler sites (Raich et al. 2006). Most experimental warming studies using tree species also report an increase in growth in elevated temperatures. For example, temperature increases of 2 and 4°C over ambient increased biomass growth of *Fagus sylvatica* (L.) saplings (Overdieck et al. 2007). Diameter growth of *Pinus sylvestris* was enhanced by elevated temperatures (Peltola et al. 2002). Increasing temperature 4°C significantly increased biomass growth in both *Pinus sylvestris* and *Picea abies* seedlings (Sallas et al. 2003). However, some experimental warming studies have reported no effect of elevated temperature on growth. A 3.5°C increase in temperature over ambient had almost no effect on biomass growth of *Pseudotsuga menziesii* (Mirb. Franco) seedlings (Olszyk et al. 2003). Similarly, a 3 to 5°C increase in air temperature had no effect on diameter growth of trees in a *Pinus sylvestris–Betula pubescens* (Ehrh.) forest in southern Norway (Rasmussen et al. 2002). There have also been observations of decreased growth in response to experimental warming. In a year that was warmer than normal, seedlings of *Acer rubrum* (L.) and *A. saccharum* (Marsh.) exposed to ambient+4°C had substantially less biomass growth than in the ambient treatment (Norby et al. 2000).

A longer growing season as well as thermal acclimation may explain increases in growth under warmer conditions. Thermal acclimation is a reversible, physiological change that enables optimum functioning of plants under different temperature regimes (Atkin and Tjoelker 2003). Thermal acclimation of respiration, which reduces the loss of carbon at higher temperatures and increases metabolic activity at lower temperatures, has been commonly observed in trees (Rook 1969; Paembonan et al. 1991; Teskey and Will 1999; Bolstad et al. 2003; Lee et al. 2005; Ow et al. 2008; Tjoelker et al. 2008). Thermal acclimation of photosynthesis causes a shift in the temperature optimum that enhances carbon gain. Some tree species exhibit this acclimation (Battaglia et al. 1996; Gunderson et al. 2000; Mäkelä et al. 2004), but others do not (Ow et al. 2008; Warren 2008).

In the warm temperate zone of the southeastern USA where this study takes place, the growing season lengthens from the northern to the southern portion of the range, but the length and duration of high temperature periods (>35°C) in the summer also increase. These temperatures are supra-optimal for carbon gain of loblolly pine (Teskey and Will 1999). In this study, we grew loblolly pine seedlings at four sites along a north–south (N–S) gradient from North Carolina to Florida for one growing season (March to November) in pots that were well watered and well fertilized. The 610 km distance between sites represented an 8.7°C difference in mean growing season temperature. The main objective of the study was to investigate the degree to which growing season temperatures or other above-ground environmental factors controlled growth across a N–S transect of sites when soil nutrients and water were not limiting. We hypothesized that growth would increase from the coolest to the warmest sites because warmer conditions throughout the growing season would increase the rate of growth and that respiratory thermal acclimation would minimize the effect of high temperatures on maintenance respiration rates in summer.

Materials and methods

Plant material and growth conditions

In January 2004, 120 one-year-old, bare root, open-pollinated loblolly pine seedlings were planted in 7.6 l pots filled with Fafard Professional Potting Mix (Conrad Fafard Inc., Agawam, MA). The seedlings, from a mixed seed-source representing the upper coastal plain provenance, were acquired from the Plum Creek Timber Company nursery in Jesup, GA. The planted seedlings were kept in an unheated greenhouse in Athens, GA that generally mimicked outside ambient conditions. The seedlings were maintained in a well watered condition and fertilized once a week using an NPK-with-micronutrient mix (Miracle-Grow, Scott's Miracle-Grow Products Inc., Marysville, OH) and chelated Fe (Hi-Yield Chemical Company, Bonham, TX).

In early March, 34 randomly selected seedlings were placed in each of four sites along a 610 km N–S transect across the interior range of loblolly pine in the Southeastern United States: Coweeta, NC (35.0°N, 83.3°W, 643 m elevation); Athens, GA (33.9°N, 83.4°W, 229 m elevation); Macon, GA (32.8°N, 83.6°W, 116 m elevation); and Gainesville, FL (29.7°N 82.3°W, 54 m elevation). Coweeta, NC, our northernmost and coolest site, is situated just north of the northern native range limit of loblolly pine, while Gainesville, FL, our southernmost and warmest site, is situated near the southern range limit. The experimental plots were located in full sun. Seedlings were placed 0.75 m apart on landscape fabric to control weeds and the pots were stabilized with wooden stakes.

In order to provide optimum levels of water and nutrients, each seedling was supplied with 0.63 l of water and a dilute nutrient solution (MiracleGrow) three times each day using a drip irrigation system (The Toro Co., Bloomington, MN) and irrigation timer (Model 7001, Dig Irrigation Corps., Vista, CA). In order to prevent root mortality due to high soil temperatures, each pot was wrapped with reflective insulation (Reflectix Inc., Markleville, IN) and the irrigation system delivered water to the seedlings three

times during the middle of the day, at 1100, 1400 and 1600 hours. Soil temperatures were monitored with iButton temperature chips (Dallas Semiconductor, Dallas, TX) randomly placed in five pots at each site. The iButtons recorded soil temperature every 30 min for the duration of the experiment. Since soil temperatures at the four sites never exceeded 30°C (data not shown), temperature related root mortality was unlikely.

At each site throughout the experiment, temperature and relative humidity were recorded 1 m above ground every 15 min using a Hobo sensor/datalogger (Hobo Pro, Onset Computer Corp., Bourne, MA) placed in a solar radiation shield. Photosynthetic photon flux density (PPFD) was measured with quantum sensors (Model LI-190, Li-Cor Inc., Lincoln, NE) on site at Coweeta and Athens and recorded using dataloggers (Model 21X, Campbell Scientific Inc., Logan, UT). PPFD data for the Macon site were from the Jeffersonville, GA weather station located 32 km from the site. For the Gainesville site, PPFD data were averaged from the Alachua, Citra, and Putnam Hall, FL weather stations located between 20 and 40 km from the site (Florida Automated Weather Network, http://fawn.ifas.ufl.edu).

Growth measurements

Height and diameter of the seedlings were measured monthly from April through October using a meter stick and calipers (VWR International, Westchester, PA). Unfortunately, height and diameter measurements were not completed at the Gainesville site during the later part of the growing season. Therefore, those measurements are reported only from the Coweeta, Athens and Macon sites. At the end of the experiment in November, all seedlings were harvested and individual seedling biomass was determined by separating seedlings into needles, stems and coarse roots, oven drying at 60°C for 1 week, verifying they had reached a constant mass and weighing each component using a precision balance (GT4800, Ohaus Corp., Pine Hurst, NJ).

Net photosynthetic measurements

Over the period from mid-September to mid-October, a randomly selected group of 10 seedlings was moved from each site into a growth chamber (GC36, Environmental Growth Chambers, Chagrin Falls, OH) at the University of Georgia in Athens, GA. Seedlings were measured one site at a time, and all measurements were performed in the same growth chamber. Measurements were made on fully expanded fascicles from the current growing season and all measurements were completed within 3 days.

Measurement of net photosynthesis (A_{max}) was made at three temperatures, 15, 25 and 35°C, under saturating PPFD and low vapor pressure deficits (VPDs). Growth chamber PPFD was 700 μmol m^{-2} s^{-1} at the top of the seedlings. Net photosynthesis was measured in the growth chamber with a portable photosynthesis system (LI-6400, Li-Cor Inc., Lincoln, NE). The cuvette temperature was set to the growth chamber measurement temperature, 15, 25 or 35°C. Relative humidity was set to keep the cuvette VPD between 0.8 and 1.4 kPa, as in the growth chamber. Cuvette CO_2 concentration was maintained at 370 μmol mol^{-1} and PPFD of 1,600 μmol m^{-2} s^{-1}. Seedlings were exposed to each temperature for a minimum of 1 h before measurement to allow the seedlings to equilibrate. Before and after the A_{max} measurements, the growth chamber was maintained at a constant temperature equal to the mean temperature at each site the week before measurements. This was 17.1°C for Coweeta, 19.7°C for Athens, 21.1°C for Macon and 23.7°C for Gainesville. Foliage dark respiration (R_d) at 15, 25 and 35°C was measured in the laboratory using a temperature-controlled cuvette designed for R_d measurements (Teskey 1997).

Respiration measurements

Using the same seedlings from the A_{max} measurements, fully expanded fascicles of needles from the current growing season were placed in a 0.25 l cuvette with thermoelectric temperature control (Thermoelectric Cooling America Corp., Chicago, IL) connected to a CO_2/H_2O analyzer (LI-7000, Li-Cor Inc., Lincoln, NE). Compressed gas cylinders of CO_2 in air served as the source gas entering the cuvette at a rate of 0.5 l min^{-1} controlled by a mass flow controller (FMA 5870, Omega Engineering Inc., Stamford, CT). The gas was first passed through a dew-point generator (LI-610, Li-Cor Inc., Lincoln, NE) before entering the cuvette so that the dew point remained lower than the cuvette temperature, preventing condensation and maintaining a constant VPD at each measurement temperature. The foliage was exposed to the measurement temperature for a minimum of 1 h prior to measurement to allow them to equilibrate.

Data analysis

We calculated the cumulative temperature sum, mean growing season temperature, mean daily VPD and mean daily PPFD of each site. To examine the effect of environmental factors ranging from supra- to sub-optimal for growth across the four sites on biomass accumulation, we calculated the absolute difference in each factor using the site of the highest mean biomass accumulation (Athens) as the baseline. The cumulative daily temperature sum, mean

growing season temperature, mean daily VPD and mean daily PPFD of the Gainesville, Macon, and Coweeta sites were calculated as the absolute difference from the Athens site value. Linear regression was used to determine the degree of correlation with mean growing season biomass accumulation.

Analysis of variance was used to determine differences in A_{max} and R_d temperature response among sites. Biomass, height and diameter data were also analyzed using analysis of variance. Mean separation tests on significant differences ($P \leq 0.05$) were conducted using the Holm–Sidak test. An allometric analysis of biomass was made to determine if there were differences in root and shoot biomass partitioning among sites following procedures in Bongarten and Teskey (1987).

Results

The mean growing season temperatures were 17.6, 22.5, 23.9 and 26.3°C for the Coweeta, Athens, Macon and Gainesville sites, respectively, which provided a maximum difference in mean growing season temperature of 8.7°C (Table 1). Between adjacent sites, the temperature differences ranged from 1.4°C between Athens and Macon, 2.4°C between Macon and Gainesville and 4.9°C between Coweeta and Athens. Mean daily VPD for the growing season was highest in Athens, but similar and relatively low across sites, ranging from 0.39 to 0.47 kPa. Mean daily PPFD was also similar, ranging from a minimum of 38.12 to a maximum of 44.96 moles day^{-1} at Coweeta and Macon, respectively.

A strong linear relationship was found between mean seedling biomass and the absolute difference in mean growing season temperature ($P = 0.01$, adj. $r^2 = 0.97$, mean biomass $= 300.73 - 30.53x$) (Fig. 1a). The relationship was also as strong between mean seedling biomass and the absolute difference in daily temperature sum ($P = 0.02$, adj. $r^2 = 0.92$, mean biomass $= 299.23 - 1.35x$) (Fig. 1b). There were no significant relationships between either mean seedling biomass and the absolute difference in mean daily VPD ($P = 0.72$) or mean seedling biomass and the absolute difference in mean daily PPFD ($P = 0.15$) (Fig. 1c, d).

Mean height growth did not differ among sites for 7 out of 8 months measured and mean total height was not significantly different across the sites at the end of the growing season (Gainesville site not recorded; Fig. 2a). In contrast, mean seedling diameter growth was significantly different among sites for the final 6 of 8 months measured (Fig. 2b). Diameter growth began sooner at the Athens and Macon sites, which were warmer, than at Coweeta. From June onward, the seedlings grown at Coweeta had the smallest diameter growth. The seedlings grown at Athens had significantly larger diameter growth than the seedlings grown at Macon beginning in September. The differences in diameter growth at the end of the growing season paralleled the differences in accumulated biomass among these sites.

Many significant differences existed among the four sites in mean root, shoot and leaf biomass (Fig. 3). At the end of 8 months of treatment, the seedlings grown at Athens had significantly higher mean shoot and leaf biomass than those grown at Coweeta, Macon or Gainesville. The seedlings grown at Athens and Macon had significantly larger root biomass than the seedlings grown at Coweeta or Gainesville. There were no significant differences in root, shoot or leaf biomass between Coweeta and Gainesville, the coolest and warmest sites.

Allometric analyses of component tissue biomass from all seedlings and sites showed no significant differences in the slopes of the relationship between total biomass and either root or shoot biomass when calculated separately for each of the four sites. This demonstrated that carbon partitioning among needles, stems and roots within the seedlings did not differ across the four sites (Fig. 4).

As expected A_{max} changed with measurement temperature (Fig. 5). The highest mean A_{max} was at 25°C and the lowest was at 35°C. There were no significant differences in mean A_{max} among seedlings from the four sites at any of the three measurement temperatures, indicating there had been no acclimation to the different site temperature regimes.

Leaf R_d increased with increasing measurement temperature; however, the rate of R_d differed significantly across the four sites (Fig. 6). The seedlings grown at Gainesville, which had the highest mean growing season temperature, exhibited significantly lower R_d at all three measurement temperatures than the seedlings grown at the other three sites. Conversely, the seedlings grown at Coweeta, with the lowest mean growing season temperature, exhibited significantly higher leaf R_d than seedlings from Gainesville when measured at 15°C, and significantly

Table 1 Mean growing season temperature, mean daily vapor pressure deficit (VPD) and mean daily photosynthetic photon flux density (PPFD) for Coweeta, NC, Athens, GA, Macon, GA and Gainesville, FL during the study

Location	Growing season temperature (°C)	Mean daily VPD (kPa)	Mean daily PPFD (mole day^{-1})
Coweeta	17.6	0.45	38.12
Athens	22.5	0.47	42.20
Macon	23.9	0.39	44.96
Gainesville	26.3	0.40	39.11

Fig. 1 Relationship between mean total seedling biomass and climatic conditions during the study at Coweeta, NC, Athens, GA, Macon, GA and Gainesville, FL. Climate means for each site were subtracted as absolute differences from the Athens, GA site mean (the site with the highest biomass accumulation). Regression lines were presented when statistically significant at $P \leq 0.05$. **a** Absolute difference in mean growing season (GS) temperature. Linear regression, $P = 0.01$, $r^2 = 0.97$, mean biomass $= 300.73 - 30.53x$. **b** Absolute difference in mean daily temperature sum. Linear regression, $P = 0.02$, $r^2 = 0.92$, mean biomass $= 299.23 - 1.35x$. **c** Absolute difference in mean daily vapor pressure deficit (VPD): $P = 0.72$. **d** Absolute difference in mean daily photosynthetic photon flux density (PPFD): $P = 0.15$
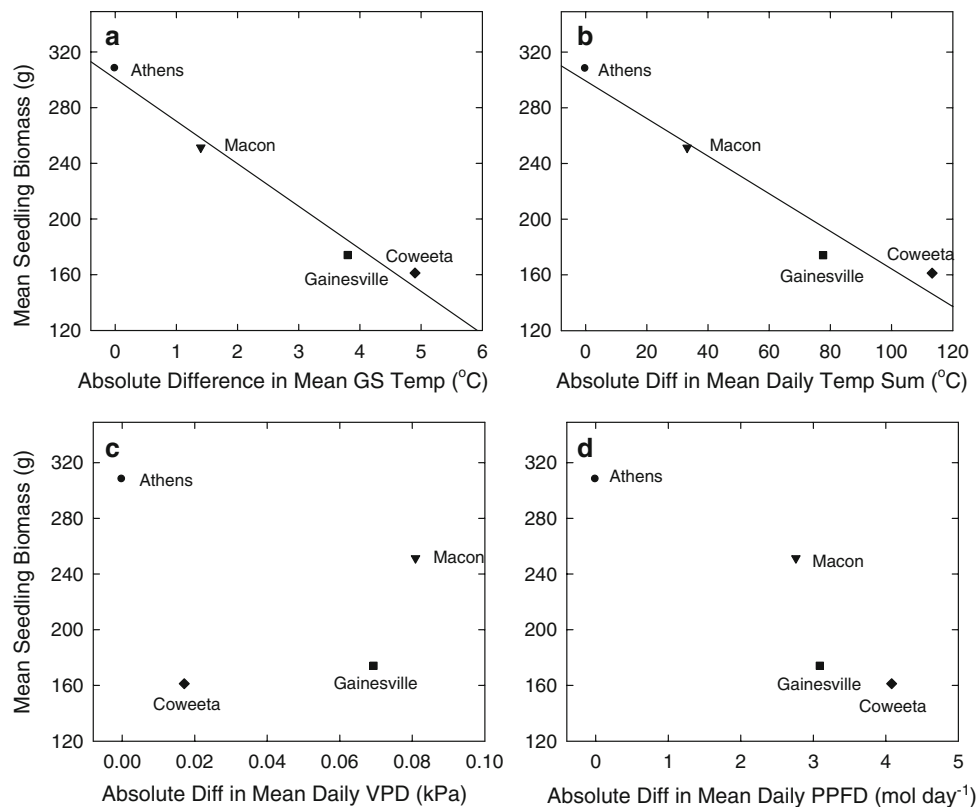

higher R_d than seedlings from all of the other sites at 25 and 35°C. There was no difference in R_d at the three temperatures between seedlings from the Athens and Macon sites. At 25°C, R_d ranged from 1.1 µmol m^{-2} s^{-1} in seedlings grown at the coolest site to 0.2 µmol m^{-2} s^{-1} in seedlings from the warmest site, i.e., an 82% decrease. The Q_{10} was also higher in seedlings from Coweeta (1.8) than Gainesville (1.3). These patterns indicated that this species was capable of substantial thermal acclimation of leaf respiration.

Discussion

Mean growing season temperature had a very large effect on seedling biomass accumulation in this study. Total biomass accumulation was highest at the Athens site, and it was 18% less at the Macon site, 43% less at the Gainesville site and 48% less at the Coweeta site. Mean growing season temperatures were highly correlated ($R^2 = 0.97$) with biomass accumulation in this study. Seedling growth was not correlated with PPFD or VPD, perhaps because the differences in PPFD and VPD across this 610 km transect were relatively small. Athens had a mean growing season temperature of 22.5°C. A decrease in mean growing season temperature relative to the Athens site of 4.9°C (Coweeta) or an increase of 3.8°C (Gainesville) produced very

substantial reductions in biomass growth. The Coweeta and Gainesville sites, which were near the northern and southern edges of the species native range, were clearly sub- and supra-optimal for growth of this upper coastal plain provenance of loblolly pine. Carbon partitioning did not change across the four sites, so the causes of these growth differences were most likely related to the net accumulation of carbon, i.e., the balance between rates of net photosynthesis and total plant respiration. Hawkins et al. (1999) also found that temperature did not affect carbon allocation in *Pseudotsuga menziesii* and *Abies amabilis* seedlings grown at 10 and 20°C.
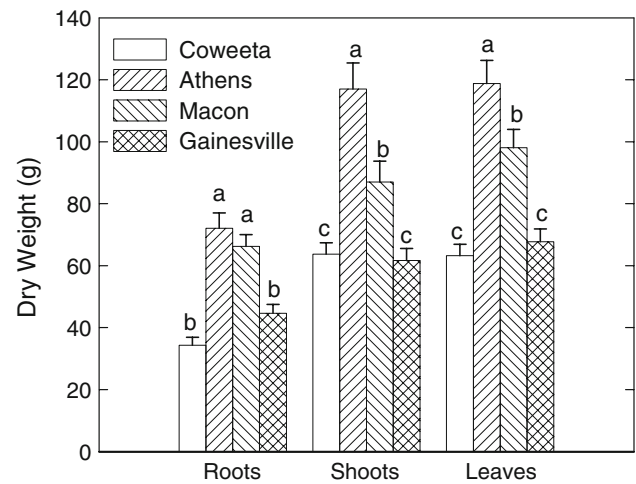
The provenance used in this study was from the middle of the loblolly pine range. The amount of growth reduction at the northern and southern sites might have differed if genotypes from those locales had been selected. Significant genotype × temperature interactions have been reported for *Pinus sylvestris* families (Sonesson and Eriksson 2000). However, results from loblolly pine family plantings in different geographic locations have shown that there is little change in the ranking of the relative growth performance of most, but not all, loblolly pine families in different environments (McKeand et al. 1997). A similar result was found when *P. banksiana* families were exposed to either ambient or elevated CO_2 and temperature (Cantin et al. 1997). This indicates that some genotypes adapted to warmer or cooler conditions will have different
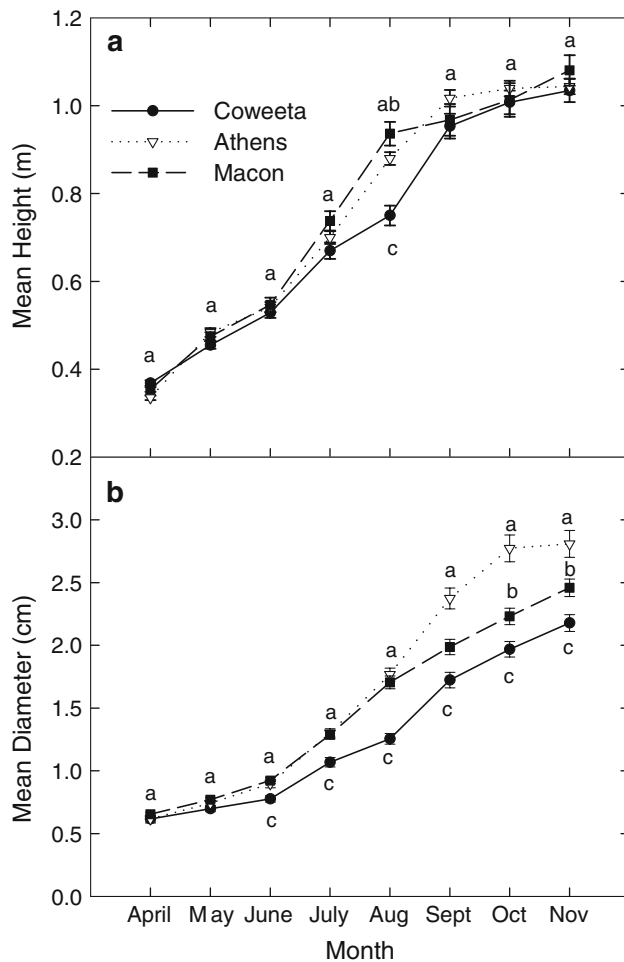
Fig. 2 Mean height (**a**) and diameter (**b**) measured monthly on seedlings grown from April to November at Coweeta, NC, Athens, GA and Macon, GA. *Different letters* indicate statistically significant differences among sites for that month ($P \leq 0.05$). *Error bars* represent ±1 standard error of the mean (SEM)

Fig. 3 Final mean component biomass of seedlings grown at Coweeta, NC, Athens, GA, Macon, GA and Gainesville, FL. *Different letters* indicate statistically significant differences among sites for each tissue type at $P \leq 0.05$. *Error bars* represent ±1 SEM
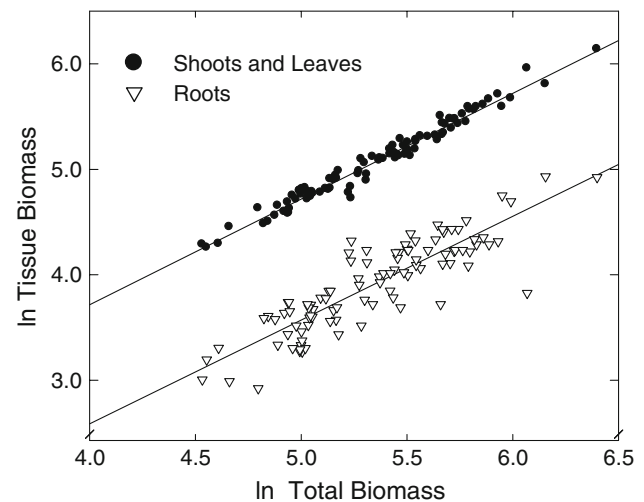
Fig. 4 Relationship between the natural log of either above-ground biomass (shoot and leaf) or root biomass and the natural log of total plant weight for all individual seedlings (data from all four sites combined)

temperature optima for photosynthesis and growth (Weston and Bauerle 2007), which in turn will shift the geographic location of their optimum growth.

It is interesting that a reduction or an increase in mean annual temperature had the same overall effect on biomass accumulation, suggesting that the temperature response curve for growth was approximately symmetric around an optimum. From the regression equation of biomass and temperature, a 1°C change in mean annual temperature from the growth optimum (which we assume was approximately the Athens site temperature) produced about a 10% change in biomass growth. In this study, increasing mean growing season temperature caused both increased (ca. Coweeta to Athens) and decreased growth (ca. Athens to Gainesville and Macon). This suggests a general conclusion: if growth temperatures are sub-optimal, increasing mean annual temperature will increase growth; if growth temperatures are supra-optimal, increasing mean annual

temperature will decrease growth. Thus, studies can be expected to find either result depending on site location, species and genotype, which appears to be the case in reported studies. Warming treatments done at a range of scales and using different growth forms have had positive, negative or negligible impacts on biomass (Rustad et al. 2001). Among tree studies, increasing temperature 4°C significantly increased biomass growth in both *Pinus sylvestris* and *Picea abies* seedlings (Sallas et al. 2003), while increasing temperature 4°C reduced biomass growth in *Acer rubrum* and *A. saccharum* (Norby et al. 2000) and increasing the air temperature 3.5°C produced no change in
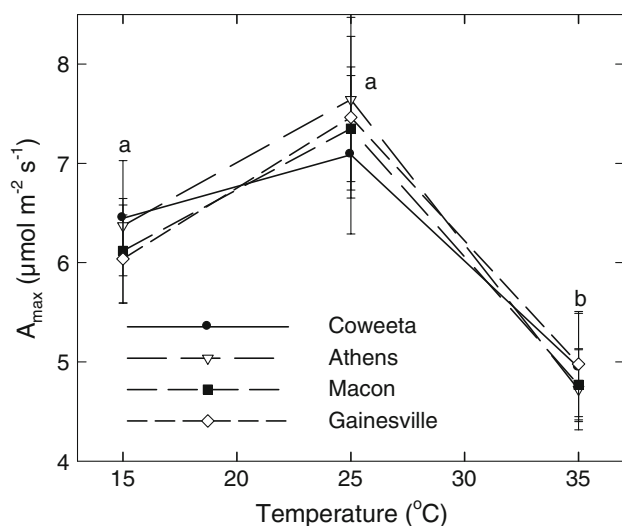
Fig. 5 Mean rate of net photosynthesis for seedlings grown at Coweeta, NC, Athens, GA, Macon, GA and Gainesville, FL measured at three temperatures. Mean photosynthetic rates were not significantly different among sites at each measurement temperature. The combined means were not significantly different at 15 and 25°C but were significantly lower at 35°C, as indicated by *different letters*. *Error bars* represent ±1 SEM
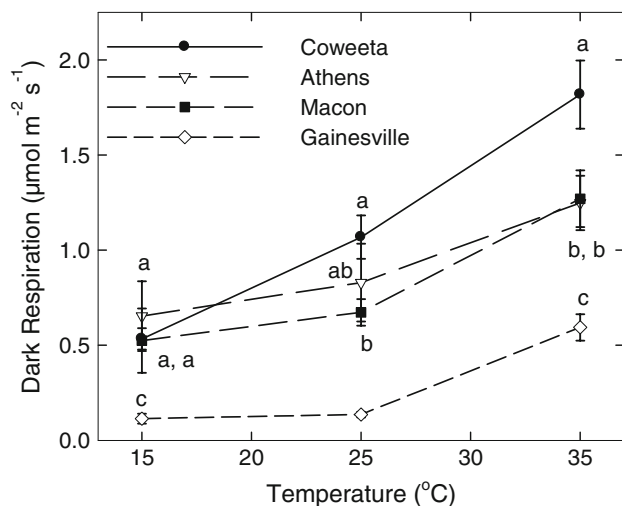
Fig. 6 Mean foliar dark respiration rates for seedlings grown at Coweeta, NC, Athens, GA, Macon, GA and Gainesville, FL measured at three temperatures. *Different letters* indicate statistically significant differences among locations at each temperature ($P \leq 0.05$). *Error bars* represent ±1 SEM

biomass compared with the ambient control in *Pseudotsuga menziesii* seedlings (Olszyk et al. 2003).

It is likely that physiological processes are affected differently by cold and heat stresses (Grace et al. 2002), so the factors contributing to the growth response at suboptimal temperatures may have been different than those at supra-optimal temperatures. At sub-optimal temperatures during the growing season, when frost damage is not a

factor, the direct control of rates of physiological and developmental processes by temperature alone is a plausible explanation for decreased growth (Juntilla and Nilsen 1993; Grace et al. 2002). In this study, the higher rate of leaf dark respiration in seedlings from Coweeta, the coolest site, appears to be evidence that the plants were acclimating to the sub-optimal temperatures by increasing maintenance respiration rates to increase the rate of physiological processes limited by temperature. At the other extreme, supra-optimal temperatures increase maintenance respiration, and decrease net photosynthesis, leading to lower overall net carbon gain at higher temperatures, as was observed in *Picea mariana* (Mill. B.S.P.) seedlings exposed to either 22/16°C or 30/24°C day/night temperatures (Way and Sage 2008) leading to carbohydrate limitations to growth (Morison and Lawlor 1999). The very low rate of leaf dark respiration in seedlings from Gainesville appears to be evidence that the plants were acclimating to the supra-optimal temperatures by decreasing maintenance respiration to maintain a more positive carbon balance.

The difference in biomass growth between the Athens and Macon sites is also of interest because the mean growing season temperature difference was only 1.4°C and yet there was an 18% difference in total biomass between the two sites. Even though the seedlings were clearly capable of thermal acclimation of respiration, this was only apparent when compared across a wide temperature range. There were no statistically significant differences in thermal acclimation between the Athens and Macon site seedlings. PPFD and VPD were more favorable for growth at the Macon site; mean daily PPFD was slightly higher and mean daily VPD was slightly lower than at the Athens site. This suggests that higher temperature, and perhaps greater temperature extremes, rather than some other environmental factor was responsible for the decreased growth at the Macon site. Thermal acclimation of respiration, and perhaps acclimation of other physiological processes that we did not measure, was insufficient to compensate for a 1.4°C increase in mean growing season temperature in the provenance of loblolly pine used in this study.

Rook (1969) reported a similar degree of thermal acclimation of R_d with increasing temperatures in *Pinus radiata* seedlings grown at 33/28°C or 15/10°C day/night temperatures, as did Bolstad et al. (2003) when investigating acclimation of respiration in *Quercus alba* and *Quercus rubra* saplings in both a controlled environment and a field experiment. In a growth chamber study, shoot dark respiration was 40% lower in loblolly pine seedlings grown and measured at 35°C compared to seedlings grown at 25°C and measured at 35°C (Teskey and Will 1999). In the present study, even under the variable temperature

conditions at the field sites, the observed amount of respiratory acclimation was similar to that achieved in the loblolly pine growth chamber study. Unlike respiration, there was no evidence of photosynthetic acclimation across sites. Acclimation of respiration but not photosynthesis has been reported in other tree species (Ow et al. 2008; Warren 2008).

In summary, growing season temperatures had a very large effect on biomass accumulation in loblolly pine seedlings, more so than PPFD or VPD, which did not vary as much as temperature, across this transect. Thermal acclimation of leaf dark respiration was evident but its role in mitigating the effect of thermal stress on growth was not clear. Super- and sub-optimal temperatures had essentially the same net effect on growth. Even in the presence of thermal acclimation of respiration, the large and linear response of biomass growth to temperature, as demonstrated by the 18% difference in growth across a 1.4°C change in mean growing season temperature, suggests that future changes in temperature may have substantial effects on growth of this species. However, we expect that the effect of increasing temperature can be negative or positive, depending on whether the plants are located in supra- or sub-optimum portions of their range.

References

Atkin OK, Tjoelker MG (2003) Thermal acclimation and the dynamic response of plant respiration to temperature. Trends Plant Sci 8:343–351. doi:10.1016/S1360-1385(03)00136-5

Battaglia M, Beadle S, Loughhead S (1996) Photosynthetic temperature responses of *Eucalyptus globulus* and *Eucalyptus nitens*. Tree Physiol 16:81–89

Bolstad PV, Reich P, Lee T (2003) Rapid temperature acclimation of leaf respiration rates in *Quercus alba* and *Quercus rubra*. Tree Physiol 23:969–976

Bongarten BC, Teskey RO (1987) Dry-weight partitioning and its relationship to productivity in loblolly pine seedlings from seven sources. For Sci 33:255–267

Cantin D, Tremblay MF, Lechowicz MJ, Potvin C (1997) Effects of CO₂ enrichment, elevated temperature, and nitrogen availability on the growth and gas exchange of different families of jack pine seedlings. Can J For Res 27:510–520. doi:10.1139/cjfr-27-4-510

Grace J, Berninger F, Nagy L (2002) Impacts of climate change on the tree line. Ann Bot (Lond) 90:537–544. doi:10.1093/aob/mcf222

Gunderson CA, Norby RJ, Wullschleger SD (2000) Acclimation of photosynthesis and respiration to simulated climatic warming in northern and southern populations of *Acer saccharum*: laboratory and field evidence. Tree Physiol 20:87–96

Hawkins BJ, Kiiskila SBR, Henry G (1999) Biomass and nutrient allocation in Douglas fir and amabilis fir seedlings: influence of growth rate and temperature. Tree Physiol 19:59–63. doi:10.1887/0750305711

Hellmers H (1962) Temperature effect on optimum tree growth. In: Kozlowski TT (ed) Tree growth. The Ronald Press Company, New York, pp 275–287

Juntilla O, Nilsen J (1993) Growth and development of northern forest trees as affected by temperature and light. In: Alden J, Mastrantonio JL, Odum S (eds) Forest development in cold climates. Plenum, New York, pp 43–57

Lee TD, Reich PB, Bolstad PV (2005) Acclimation of leaf respiration to temperature is rapid and related to specific leaf area, soluble sugars and leaf nitrogen across three temperate deciduous tree species. Funct Ecol 19:640–647. doi:10.1111/j.1365-2435.2005.01023.x

Mäkelä A, Hari P, Berninger F, Hänninen H, Nikinmaa E (2004) Acclimation of photosynthetic capacity in Scots pine to the annual cycle of temperature. Tree Physiol 24:369–376

McKeand SE, Crook RP, Allen HL (1997) Genotypic stability effects on predicted family responses to silvicultural treatments in loblolly pine. South J Appl For 21:84–89

Meehl GA, Stocker TF, Collins WD, Friedlingstein P, Gaye AT, Gregory JM, Kitoh A, Knitti R, Murphy JM, Noda A, Raper SCB, Watterson IG, Weaver AJ, Zhao Z-C (2007) Global climate projections. In: Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt M, Tingor M, Miller HL (eds) Climate change 2007: the physical science basis. Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge, pp 749–845

Morison JIL, Lawlor DW (1999) Interactions between increasing CO₂ concentration and temperature on plant growth. Plant Cell Environ 22:659–682. doi:10.1046/j.1365-3040.1999.00443.x

Norby RJ, Long TM, Hartz-Rubin JS, O'Neill EG (2000) Nitrogen resorption in senescing tree leaves in a warmer, CO₂-enriched atmosphere. Plant Soil 224:15–29. doi:10.1023/A:1004629231766

Olszyk DM, Johnson MG, Tingey DT, Rygiewicz PT, Wise C, Van Ess E, Benson A, Storm MJ, King R (2003) Whole-seedling biomass allocation, leaf area, and tissue chemistry for Douglas-fir exposed to elevated CO₂ and temperature for 4 years. Can J For Res 33:269–278. doi:10.1139/x02-186

Overdieck D, Ziche D, Böttcher-Jungclaus K (2007) Temperature responses of growth and wood anatomy in European beech saplings grown in different carbon dioxide concentrations. Tree Physiol 27:261–268. doi:10.1007/3-540-32733-9

Ow LF, Griffin KL, Whitehead D, Walcroft AS, Turnbull MT (2008) Thermal acclimation of leaf respiration but not photosynthesis in *Populus deltoides × nigra*. New Phytol 178:123–134. doi:10.1111/j.1469-8137.2007.02357.x

Paembonan SA, Hagihara A, Hozumi K (1991) Long-term measurement of CO₂ release from the aboveground parts of a Hinoki Forest tree in relation to air temperature. Tree Physiol 8:399–405

Peltola H, Kilpelainen A, Kellomaki S (2002) Diameter growth of Scots pine (*Pinus sylvestris*) trees grown at elevated temperature and carbon dioxide concentration under boreal conditions. Tree Physiol 22:963–972

Raich JW, Russell AE, Kitayama K, Parton WJ, Vitousek PM (2006) Temperature influences carbon accumulation in moist tropical forests. Ecology 87:76–87. doi:10.1890/05-0023

Rasmussen L, Beier C, Bergstedt A (2002) Experimental manipulations of old pine forest ecosystems to predict the potential tree growth effects of increased CO₂ and temperature in a future world. For Ecol Manag 158:179–188. doi:10.1016/S0378-1127(00)00677-0

Reich PB, Oleksyn J (2008) Climate warming will reduce growth and survival of Scots pine except in the far north. Ecol Lett 11:588–597. doi:10.1111/j.1461-0248.2008.01172.x

Rook DA (1969) The influence of growing season temperatures on photosynthesis and respiration of *Pinus radiata* seedlings. NZ J Bot 7:43–55

Rustad LE, Campbell JL, Marion GM, Norby RJ, Mitchell MJ, Hartley AE, Cornelissen JHC, Gurevitch J (2001) A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. Oecologia 126:543–562. doi:10.1007/s004420000544

Sallas L, Luomala EM, Utriainen J, Kainulainen P, Holopainen JK (2003) Contrasting effects of elevated carbon dioxide concentration and temperature on Rubisco activity, chlorophyll fluorescence, needle ultrastructure and secondary metabolites in conifer seedlings. Tree Physiol 23:97–108

Sonesson J, Eriksson G (2000) Genotypic stability and genetic parameters for growth and biomass traits in a water × temperature factorial experiment with *Pinus sylvestris* L. seedlings. For Sci 46:487–495

Teskey RO (1997) Combined effects of elevated CO_2 and air temperature on carbon assimilation of *Pinus taeda* trees. Plant Cell Environ 20:373–380. doi:10.1046/j.1365-3040.1997.d01-75.x

Teskey RO, Will RE (1999) Acclimation of loblolly pine (*Pinus taeda*) seedlings to high temperatures. Tree Physiol 19:519–525. doi:10.1887/0750305711

Tjoelker MG, Oleksyn J, Reich PB, Żytkowiak R (2008) Coupling of respiration, nitrogen, and sugars underlies convergent temperature acclimation in *Pinus banksiana* across wide-ranging sites and populations. Glob Change Biol 14:1–16. doi:10.1111/j.1365-2486.2008.01548.x

Warren CR (2008) Does growth temperature affect the temperature responses of photosynthesis and internal conductance to CO_2? A test with *Eucalyptus regnans*. Tree Physiol 28:11–19

Way DA, Sage RF (2008) Elevated growth temperatures reduce the carbon gain of black spruce [*Picea mariana* (Mill.) B.S.P.]. Glob Change Biol 14:624–636. doi:10.1111/j.1365-2486.2007.01513.x

Weston DJ, Bauerle WL (2007) Inhibition and acclimation of C_3 photosynthesis to moderate heat: a perspective from thermally contrasting genotypes of *Acer rubrum* (red maple). Tree Physiol 27:1083–1092. doi:10.1007/3-540-32733-9