Tree Physiology 20, 87–96
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Acclimation of photosynthesis and respiration to simulated climatic warming in northern and southern populations of *Acer saccharum:* laboratory and field evidence

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Received November 18, 1998

Summary Physiological acclimation and genotypic adaptation to prevailing temperatures may influence forest responses to future climatic warming. We examined photosynthetic and respiratory responses of sugar maple (*Acer saccharum* Marsh.) from two portions of the species' range for evidence of both phenomena in a laboratory study with seedlings. A field study was also conducted to assess the impacts of temperature acclimation on saplings subjected to an imposed temperature manipulation (4 ºC above ambient temperature). The two seedling populations exhibited more evidence of physiological acclimation to warming than of ecotypic adaptation, although respiration was less sensitive to short-term warming in the southern population than in the northern population. In both seedling populations, thermal compensation increased photosynthesis by 14% and decreased respiration by 10% in the warm-acclimated groups. Saplings growing in open-top field chambers at ambient temperature and 4 ºC above ambient temperature showed evidence of temperature acclimation, but photosynthesis did not increase in response to the 4 ºC warming. On the contrary, photosynthetic rates measured at the prevailing chamber temperature throughout three growing seasons were similar, or lower (12% lower on average) in saplings maintained at 4 ºC above ambient temperature compared with saplings maintained at ambient temperature. However, the long-term photosynthetic temperature optimum for saplings in the field experiment was higher than it was for seedlings in either the 27 or the 31 °C growth chamber. Respiratory acclimation was also evident in the saplings in the field chambers. Saplings had similar rates of respiration in both temperature treatments, and respiration showed little dependence on prevailing temperature during the growing season. We conclude that photosynthesis and respiration in sugar maple have the potential for physiological acclimation to temperature, but exhibit a low degree of genetic adaptation. Some of the potential for acclimation to a 4 ºC increase above a background of naturally fluctuating temperatures may be offset by differences in water relations, and, in the long term, may be obscured by the inherent variability in rates under field conditions. Nevertheless, physiologically based models should incorporate seasonal acclimation to temperature and permit ecotypic differences to influence model outcomes for those species with high genetic differentiation between regions.

Keywords: acclimation, adaptation, climatic warming, global change, photosynthesis, respiration, sugar maple.

Introduction

One of the predicted consequences of rising atmospheric concentrations of CO_2 and other greenhouse gases is a rise in ground-level air temperatures. Current estimates of the mean global increase in temperature range from 1 to 4.5 ºC by the year 2100, with regional, seasonal, and diurnal heterogeneity (Kattenberg et al. 1996). This projected atmospheric warming has potential consequences for forest ecosystems, as well as for individual tree species. Understanding the nature of temperature adjustments in forest trees (both short-term physiological acclimation and population-level adaptations to climatic regimes) is, therefore, important for predicting forest responses.

Several forest succession models have projected major changes in species composition and biomass accumulation associated with transient forest dieback when climatic changes exceed apparent limits for growth and regeneration of particular species assemblages (Solomon 1986, Pastor and Post 1988, Martin 1992, Shugart et al. 1992). These forest-gap models incorporate temperature response as a parabolic function that predicts maximum growth at temperatures (in growing degree days) found near the north–south midpoint of the current geographic range and zero growth at the northern and southern limits (Solomon 1986, Shugart et al. 1992, reviewed in Schenk 1996, Loehle and LeBlanc 1996). The models assume a single constant temperature optimum for all populations across the range. Because ecotypes or provenances adapted to different environments may vary in some of their growth and survival responses to temperature (Perry 1962, Carter 1996, Kriebel 1957), it is important to determine to what extent such within-species climate adaptation affects the physiological processes that contribute to growth.

Part of the original rationale behind the parabolic temperature response functions of forest-gap models was based on the

shape of the photosynthetic temperature response function (Schenk 1996). An alternative approach is to incorporate physiologically based canopy process models into forest growth models (e.g., Friend et al. 1993). These models usually include temperature effects by varying photosynthetic functions about an optimum temperature, and by relating respiration to temperature exponentially or with an Arrhenius function (Ågren et al. 1991, Ryan 1991). Parameters may be specific to forest types (Wang and Polglase 1995) or to species (Friend et al. 1993), but do not allow for ecotypic differences. Likewise, most process models (with some exceptions, e.g., Amthor 1994*a*) do not incorporate a physiological acclimation potential for photosynthesis or respiration (Körner 1995). Regardless of the modeling approach, it is clear that an understanding of photosynthetic and respiratory responses to rising temperature is essential for modeling forest growth accurately.

The extent to which temperature adjustments in these processes occur in trees is not known. For photosynthesis, the potential for physiological acclimation to environmental temperature is well known (reviewed in Berry and Björkman 1980), but highly variable, ranging from a pronounced shift in temperature optimum, a compensatory increase across all temperatures, or both, to no change, or a negative adjustment. Most of the studies of photosynthetic acclimation in tree species have been done in conifers or eucalypts; very few studies have included temperate deciduous species. Respiratory acclimation to temperature history (a downward adjustment of rates at high growth temperatures) is also documented, but likewise, is not universal (Arnone and Körner 1997 and references therein). Ecotypic and species-level adaptations of both photosynthesis and respiration have been reported (Berry and Björkman 1980, Larigauderie and Körner 1995 and references therein), but again, there is limited information about temperate tree species. Because of the potential importance of temperature adjustments to global change modeling, more information is needed on the type, magnitude and timing of these adjustments in deciduous forest trees.

We examined the potential for temperature acclimation and adaptation of photosynthesis and respiration in sugar maple (*Acer saccharum* Marsh.). Sugar maple is a widely distributed North American temperate deciduous species for which forest succession models predict marked changes in distribution with climatic change (e.g., Solomon 1986, Martin 1992, Post and Pastor 1996). Hypotheses were that photosynthesis and respiration would acclimate to the growth temperature, and that populations from different portions of the range would exhibit ecotypic differences in either immediate temperature response patterns or in acclimation potential. An additional objective was to evaluate the impact of the observed acclimation potential on the long-term responses of saplings growing in the field. We also determined if results obtained under laboratory conditions could predict acclimation in a field study, where temperature increases were superimposed on natural fluctuations in temperature, and where other environmental variables, including vapor pressure deficits and soil water content, were not controlled.

Materials and methods

Plant material

Trees were purchased as 1-year-old bare-root seedlings from commercial nurseries in Tennessee and Michigan. Seeds for both populations were collected in the vicinity of the two nurseries—the Cumberland Plateau area in middle Tennessee (35.5º N, 86º W, TN seedlings), and west central Michigan (44º N, 86º W, MI seedlings). Mean temperature during the growing season is about 4–6 ºC higher at the TN site than at the MI site.

Growth conditions

Growth chamber experiment Seedlings from both geographic sources were planted in 8-dm^3 pots containing Promix BX (Premier Horticulture, Inc, Red Hill, PA). The potted seedlings were placed in a growth chamber maintained at a day/night temperature of 23/10 ºC with a 14-h photoperiod (Trial 1) or in a greenhouse (Trial 2), where temperatures and humidity fluctuated, but a 14-h photoperiod was maintained with supplemental sodium vapor lighting.

After bud break and leaf expansion, seedlings were divided into two groups and moved to two matched growth chambers maintained at a day/night temperature of either 27/14 ºC (cool treatment) or 31/18 ºC (warm treatment). Both chambers provided a 14-h photoperiod, in which light was provided by a combination of high intensity sodium vapor and metal halide lamps providing approximately 500 μmol m^{-2} s^{-1} of photosynthetically active radiation (PAR) at the level of the canopy. Growth chamber humidity was maintained between 65 and 75%. Chamber effects were minimized by switching the cool and warm treatment chambers between Trial 1 and Trial 2. Seedlings were grown at the treatment temperatures for 3 weeks before gas exchange measurements were begun, during which time no additional leaves were produced. Measurements of photosynthesis and respiration in each trial were conducted over a period of approximately 3 months. Seedlings were fertilized monthly (Peters 20,20,20 N,P,K with micronutrients, Grace-Sierra Horticultural Products, Milpitas, CA).

Field experiment Bare-root seedlings from the Tennessee source were planted directly in the ground in open-top chambers (OTCs) at the Global Change Field Research Site on the Oak Ridge National Environmental Research Park as a part of a larger experiment (Norby et al. 1997). Seedlings were planted in spring 1994, and were maintained in naturally varying rainfall and day length. Natural variations in solar radiation were reduced proportionally by covering all sides of the OTCs with 73% shade cloth (maximum PAR = 500 μmol m^{-2} s^{-1}). The ambient OTCs tracked variations in ambient temperatures as measured outside the OTC, and the warm treatment OTCs were maintained at ambient +4 ºC. Treatment temperatures were maintained year round through a combination of evaporative coolers and electrical resistance heaters. In 1994, for example, mean temperatures for the season in the ambient OTCs were 0.4 ± 0.3 ºC above mean ambient temperatures, and mean temperatures in the warm OTCs were 4.0 ± 0.3 ºC above ambient temperatures. Vapor pressures were similar in the two treat-

ment OTCs; leaf-to-air vapor pressure deficits (VPDs) were as much as 1 kPa higher in the warm OTCs compared with the ambient OTCs (Norby et al. 1997). Because an increase in VPD is expected in conjunction with global warming (Kirschbaum 1996), we consider the increase in VPD an inseparable part of the warm treatment. Details of temperature treatments and monitoring systems have been described (Norby et al. 1997). There were three OTCs for each temperature treatment, with ten sugar maples in each OTC (interplanted with red maple). Measurements reported here were taken during the first three seasons of growth, when the trees grew from approximately 0.18 to 2.4 m in height.

Gas exchange measurements

Growth chamber experiment Photosynthesis and respiration were measured with a steady-state open-flow gas exchange system equipped with a minicuvette (Walz, Effeltrich, FRG) and a differential infrared CO_2 analyzer (Binos, Leybold Heraeus, Hanau, FRG). Cuvette temperature was controlled by thermoelectric heating and cooling provided by Peltier elements. Irradiation for the photosynthetic measurements was supplied by a projector lamp with glass heat filters and a neutral gray filter selected to provide approximately 550 µmol m^{-2} s^{-1} of PAR at the leaf, which was determined to be saturating for CO_2 assimilation.

Temperature response curves were constructed for eight plants by raising the temperature in 5 ºC increments from 11 to 36 ºC and allowing leaf gas exchange rate to stabilize at the new temperature. The air stream entering the system was humidified by bubbling it through water. Humidity in the cuvette was controlled by raising the dewpoint temperature of the humidified incoming air in concert with the cuvette temperature, such that dewpoint temperature was 10–12 ºC lower than cuvette temperature, and relative humidity in the cuvette was 50–70%. These relative humidities and resulting cuvette VPDs were comparable to summer midday values in the field experiment (Norby et al. 1997).

In addition to these eight full-response curves, photosynthetic measurements were taken on five to seven plants for each combination of trial, growth temperature, geographic source, and cuvette temperature (16, 26 or 36 ºC). Within each trial, all of the plants were measured at one cuvette temperature before re-equilibrating the photosynthesis system (as described above) to a different temperature and dewpoint.

The response of leaf respiration to cuvette temperature was measured at the end of the dark period with the same gas exchange system. Respiration was measured in one plant at a time, at temperatures of 11, 16, 21, 26, 31, and 36 ºC, from low to high temperature. Five to seven plants were included from each combination of geographic source, growth temperature, and trial.

Field experiment Leaf photosynthesis and respiration of saplings in the field were measured with an LI-6200 portable photosynthesis system (Li-Cor, Inc., Lincoln, NE) equipped with a 1-dm^3 (1-liter) leaf cuvette, under conditions of temperature and humidity prevailing in the OTC, rather than under controlled conditions. Because mean air temperatures in the warm treatment averaged 3.6 ºC higher than air temperatures in the ambient temperature treatment, mean leaf temperatures during measurements were correspondingly higher for leaves of trees in the warm OTCs. Illumination during the photosynthetic measurement was provided by a solid-state, 670 nm red-light-emitting diode (LED) lighting system (QB-6200, Quantum Devices, Inc., Barneveld, WI), adjusted to provide 500 µmol m^{-2} s^{-1} at the leaf surface. Gas exchange was measured on fully expanded leaves (third or lower node) in the upper portion of the tree, either on the main stem or, in Year 3, an upper branch. Photosynthetic rates of approximately four saplings per OTC (12 saplings per temperature treatment) were measured on each date. Assessments were made on three to five dates during each growing season of the 3-year period (total of 12 times). Daytime respiration was assessed only in 1996 (Year 3), on five dates, on three saplings per treatment. On each date, respiration was measured at the end of the dark period (nighttime respiration, near dawn), and again in mid-afternoon (daytime respiration). Respiration was measured immediately after a photosynthetic measurement, by covering the cuvette with a dark cloth. On August 9, daytime respiration only was measured in nine trees per treatment.

Data analysis

Gas exchange data from the growth chamber experiment were analyzed by multi-factor analysis of variance (ANOVA). The respiration data and the photosynthesis data from the three-point temperature curves were both analyzed for the main effects of acclimation temperature, geographic source, measurement temperature, and trial (Trial 1 versus Trial 2) and for interactions between these factors. For respiration, the values of Q_{10} (the factor by which the rate increases with a 10 ºC increase in temperature) were determined for individual leaves, by regression of $\log_{10}$ of respiration on leaf temperature. The Q_{10} values were computed from the slopes of these lines, as $Q_{10} = 10^{(10 \times \text{slope})}$. Calculated Q_{10} values were analyzed by a 3-way ANOVA (growth temperature × geographic source × trial). Significance probabilities less than $P = 0.1$ are indicated; higher P-values are reported as non-significant, NS.

To estimate optimum temperature and maximum photosynthesis, photosynthetic–temperature response curves, either for individual leaves or for mean rates at each measurement temperature, were fitted with a quadratic equation of the form (Equation 1, Battaglia et al. 1996):

$$P(T) = P_{\text{opt}} - b(T - T_{\text{opt}})^2,$$

where $P(T)$ represents the (mean) net photosynthetic rate at temperature T in ºC, T_{opt} is the temperature optimum for P, and P_{opt} is the rate at the optimal temperature. The term b describes the relative spread of the parabola (a small value of b indicates a wider parabola than does a large b).

Data from the field experiment were analyzed by ANOVA on each measurement date for the effects of temperature treatment on photosynthesis or respiration. In addition, Equation 1 was used to analyze mean photosynthetic rates from each date as a function of leaf temperature by treatment group, for the entire experiment. Differences in the curves were evaluated

with an *F*-test that is approximate for nonlinear comparisons (Hanson et al. 1988).

Results

Photosynthesis of seedlings in the growth chambers

Measurements of photosynthesis of seedlings in Trials 1 and 2 (as well as preliminary measurements with seedlings grown at day/night temperatures of 23/10 ºC, Figure 1a) revealed a broad temperature response curve, with no distinct temperature optimum for photosynthesis. Despite higher VPDs at higher cuvette temperatures (up to 2 and 3 kPa at 31 and 36 ºC, respectively), there was no marked decrease in photosynthetic rate at high cuvette temperatures. This suggests that photosynthesis in these seedlings was less sensitive to high VPD than in some species (e.g., *Larix decidua,* Tranquillini et al. 1986). Photosynthetic rates were similar at temperatures between approximately 16 and 31 ºC, dropping slightly at 11 and at 36 ºC (Figure 1). Photosynthetic rates were comparable with those reported elsewhere for sugar maple seedlings under a range of conditions (Weber et al. 1985, Ellsworth and Reich 1992, Tschaplinski et al. 1995). A representative temperature response curve from a single MI seedling acclimated to a day/night temperature of 23/10 ºC is shown in Figure 1a. Some individual response functions had less curvature than shown in Figure 1, or a different apparent temperature optimum, and a few had atypical features, such as a maximum rate at 11 ºC or unexpected offsets between temperatures. This variability, as well as the variability in maximum photosynthetic rate, are reflected in Figure 1b, which shows the mean photosynthetic rates from the full-response curves that were generated from seedlings acclimated to the warm and cool treatments (four seedlings per growth temperature). The dashed and dotted lines represent Equation 1 fitted to the photosynthetic rates. Although variability was high, mean photosynthetic rates were higher in the warm-acclimated seedlings than in the cool-acclimated seedlings at all temperatures tested (Figure 1b).

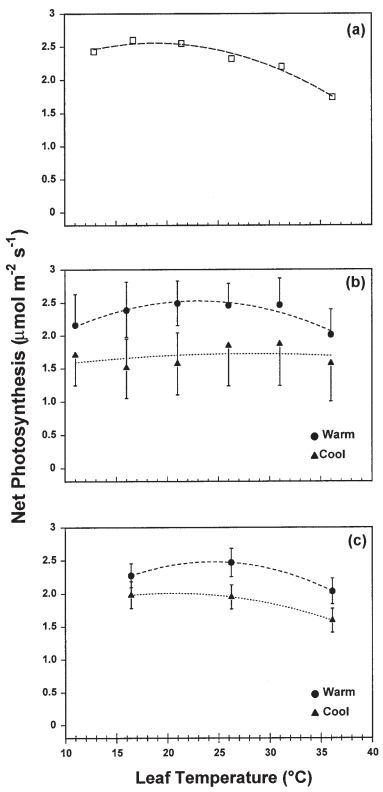

Figure 1. Net photosynthetic responses to measurement temperature in sugar maple seedlings in growth chambers. Dashed and dotted lines represent Equation 1 fit through the means. (a) Responses to measurement temperature of a single seedling growing at a day/night temperature of 23/10 ºC. (b) Instantaneous responses of seedlings grown at either 27/14 ºC (cool treatment, ▲) or 31/18 ºC (warm treatment, ●) Values are means (± SE) of $n = 4$ seedlings. (c) Responses of warm-grown (●) and cool-grown (▲) seedlings to three measurement temperatures. Values are means (± SE) of $n = 24$ seedlings. Data from both geographic sources and trials are combined.

Because of the relatively flat temperature response curves and the long instrument stabilization times required when changing temperature, the photosynthetic measurements reported hereafter were only taken at 16, 26 and 36 ºC. Mean photosynthetic rates were slightly lower at 36 ºC than at 16 or 26 ºC for all source × growth temperature combinations (Figure 1c). However, the effect of measurement temperature on photosynthetic rates was marginal ($P = 0.09$ for overall cuvette temperature differences).

The most significant factor in the ANOVA of photosynthetic data was the growth temperature. Photosynthetic rates were significantly higher in the warm-acclimated seedlings than in the cool-acclimated seedlings (Figure 1c, $P = 0.02$), and this relationship was maintained in both Trials 1 and 2. Geographic source of the populations was not a significant factor ($P > 0.1$); Trials 1 and 2 differed in the direction of the difference in mean photosynthetic rate ($P = 0.04$ for the source × trial interaction). There was no difference in the way seedlings from the two geographic sources acclimated to growth temperature. Thus, in both MI and TN seedlings, photosynthetic rates were higher in the warm-acclimated seedlings than in the cool-acclimated seedlings, and the source × growth temperature interaction was not significant. Regression of Equation 1 through the data of Figure 1c was also used to quantify the mean photosynthetic temperature response curves from the growth chamber experiment in terms of their temperature optima, T_{opt}, and maximum rates, P_{opt} (Table 1). Apparent temperature optima were similar in the two treatments, 20 °C in the 27/14 °C chamber and 24 °C in the 31/18 °C chamber. The apparent four-degree difference in T_{opt} cannot, however, be evaluated statistically by this method.

Respiration of seedlings in the growth chambers

Foliar respiration rates increased with measurement temperature ($P = 0.01$), and the increase was approximately exponential (Figure 2) (cf. Amthor 1994*b*). Across all measurement temperatures, mean respiration rates were lower for the warm-acclimated seedlings than for the cool-acclimated seedlings (Figure 2a, $P = 0.06$). The degree of respiratory acclima-

Table 1. Photosynthetic temperature response parameters for the growth chamber experiment and in the field. Parameters are defined in the text (Equation 1). In the growth chambers, mean photosynthetic rates at the three measurement temperatures were fitted with Equation 1. For the field experiment, mean photosynthesis and mean leaf temperature for each of 12 sample dates were used for the fits (24 points for the pooled data).

	Growth chamber		Field experiment: OTCs		
	27/14 °C	31/18 °C	Ambient T	Ambient T +4 °C	Pooled
T_{opt} (°C)	20.4	24.1	32.2	36.6	33.6
P_{opt} (μmol m^{-2} s^{-2})	2.00	2.47	6.51	5.58	5.93
b	0.0017	0.0031	0.045	0.015	0.024
R^2	1[1]	1[1]	0.30	0.17	0.16

[1] The fit of Equation 1, a second-order polynomial, to the three means from the growth chamber experiment is estimated without error, and is provided merely to describe the shape of the response.

tion was greater in Trial 1 than in Trial 2, but neither the effect of trial nor the trial × growth temperature interaction was significant. Acclimation was more pronounced for the TN seedlings (Figure 2c) than for the MI seedlings (2b), but geographic source of the seedlings had no effect on respiration rates overall, or at individual measurement temperatures, and the source × growth temperature interaction was not significant.

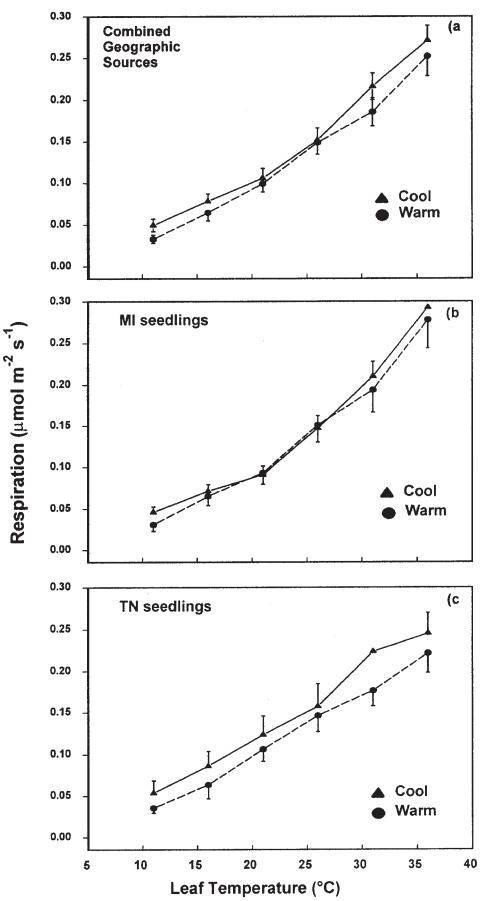

Figure 2. Dependence of leaf dark respiration rate on measurement temperature in sugar maple seedlings grown in chambers set at day/night temperatures of either 27/14 ºC (cool treatment, ▲) or 31/18 ºC (warm treatment, ●). Mean (± SE) responses of seedlings in the two temperature regimes (a) for the two geographic sources combined (n = 24); (b) in the Michigan seedlings (n = 13); and (c) in the Tennessee seedlings (n = 11).

Mean Q_{10} values calculated from 11 to 36 ºC ranged from 2.13 to 2.49; however, Q_{10} values were not significantly affected by either acclimation temperature or geographic source of the seedlings. For many individual leaves, there appeared to be a break at 21 ºC in the increase in the $\log_{10}$ of respiration with increasing measurement temperature. That is, the increase was linear only in the range from 21 to 36 ºC, with higher or lower slopes below 21 ºC (cf. Figure 3). There were two consequences of this nonlinearity. First, respiration rates were lower for warm-acclimated seedlings than for cool-acclimated seedlings (Figure 3a, circles) at low measurement temperatures, regardless of seedling source. Second, at high measurement temperatures, respiration rates were lower in TN seedlings than in MI seedlings (Figure 3a, open symbols), regardless of growth temperature. Respiration rates measured at 26 ºC were similar for all seedlings (Figure 3a). Because of the break at 21 ºC, we also calculated Q_{10} values separately for the 21 to 36 ºC range. Mean Q_{10} values calculated for this temperature range varied from 1.74 to 2.15 (Table 2), and were significantly higher in MI seedlings than in TN seedlings (P = 0.0285), implying a greater impact of increases in measurement temperature above 21 ºC in the MI seedlings (Figure

Table 2. Effects of geographic source and growth temperature on Q_{10} values for leaf dark respiration measured at temperatures from 21 to 36 ºC. Means are of 12 (MI) or 11 (TN) Q_{10} values (SD in parentheses). Significance values: P = 0.0285 for geographic source; growth temperature, trial, and all interactions were ns.

	Growth temperature regime (day/night, ºC)	
Geographic source	27/14	31/18
Michigan	2.16 (0.47)	2.12 (0.44)
Tennessee	1.85 (0.56)	1.74 (0.53)

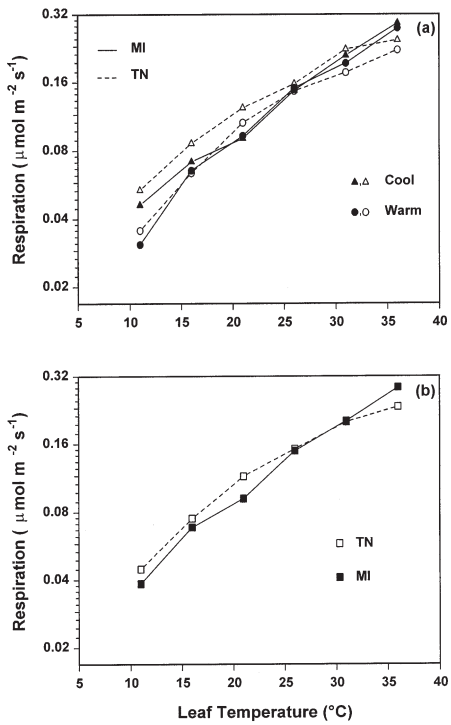

Figure 3. Leaf respiration rate (log scale) plotted against leaf temperature: (a) for each geographic source and growth temperature combination (n = 11–13); and (b) by geographic source (n = 22–26), with data for the two growth temperatures combined.

3b). Growth temperature did not influence Q_{10} even in the 21 to 36 ºC temperature range.

Photosynthesis in the field

Net photosynthetic rates measured in saplings in the ambient OTCs over three growing seasons were higher, on average, than those measured in seedlings in the growth chambers, although the range of values measured in the two studies overlapped. Mean photosynthetic rates of saplings in the ambient temperature OTCs varied from 3.2 to 8.8 μmol m^{-2} s^{-1} during the 3-year period. These variations reflect responses to natural variations including soil water content, humidity, and temperature as well as differences associated with developmental stage, leaf age, and canopy position (cf. Ellsworth and Reich 1992, 1993).

On each sampling date, net photosynthetic rates of saplings in the warm OTCs (measured at the prevailing temperatures, which averaged 3.6 ºC higher than in the ambient OTCs) were similar to, or slightly lower than, those of saplings in the ambient temperature OTCs (Figure 4). The mean difference between temperature treatments was 0.73 μmol m^{-2} s^{-1} over the three-season period, and the differences were significant on only three dates (Figure 4). There was no evidence of a decrease in the difference between treatments over the course of a growing season that could be interpreted as gradual acclimation to the elevated growth temperature. In general, the first measurement(s) of each season showed the least detrimental effect of the warm treatment (Figure 4). Regression of Equation 1 through the mean photosynthetic rates from each sampling as a function of leaf temperature (Figure 5, Table 1) showed that temperature explained only 16 to 30% of the variation in photosynthesis, based on a parabolic model. Also, the apparent temperature optima (T_{opt}) were higher for saplings in the OTCs than for seedlings in the laboratory (Table 1). Regression of Equation 1 through each treatment group also suggested a higher optimal temperature for photosynthesis for saplings in the warm OTCs than for saplings in the ambient-temperature OTCs (Table 1), but parameter estimates from the two curves were not significantly different. Figure 5 shows data from both treatment groups represented by the same temperature relationship (Table 1), along with additional data from 1996 (n = 3). The variability in photosynthesis associated with other influences during the growing season was still apparent. For example, the points lying substantially beneath the curve at the lowest temperatures were all taken in either April

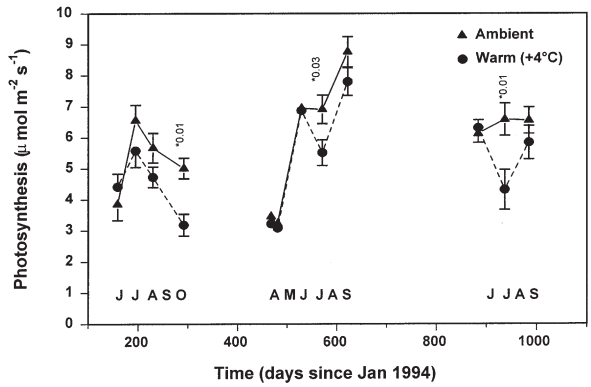

Figure 4. Net photosynthesis of fully expanded leaves of sugar maples grown in open-top chambers for three years. Symbols: ▲ = saplings grown at ambient temperature; ● = saplings grown at ambient + 4 ºC. Values are means (n = 8–12), the vertical bars = 1SE. The P-values are indicated when less than 0.10.

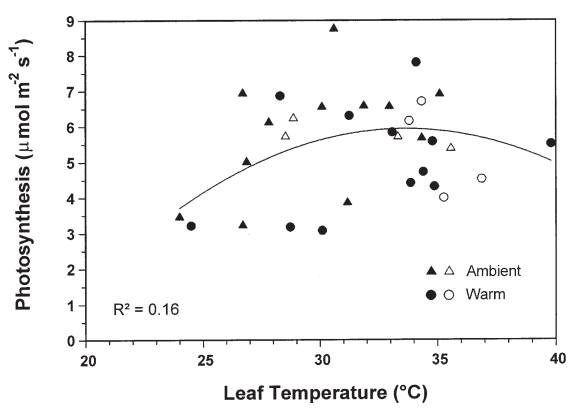

Figure 5. Net photosynthetic rates from Figure 4 plotted against mean prevailing leaf temperature during the measurements for saplings in the ambient treatment (▲, △) and warm (ambient + 4 ºC) treatment (●, ○). Dotted lines represent the fit of Equation 1 through the pooled data from both treatments. Open symbols represent the means of the additional 1996 sampling (n = 3).

or October. Nevertheless, a regression of either the differences or ratios in mean rates on ambient temperatures (Figure 6) showed that the detrimental effects of elevated temperatures were slightly greater at leaf temperatures above the inflection point, or T_{opt} (27.4 ºC). Nevertheless, leaf temperature explained only a small portion of the variability in temperature effects.

Respiration in the field

Both daytime and nighttime respiration rates were similar in saplings in the two sets of open-top chambers (Figure 7). Respiration rates were, on average, only 3 to 5% higher in the warm OTCs than in the ambient OTCs over the season, and only one *P*-value was below 0.1 (Figures 7a and 7b). Plots of mean respiration rates as a function of mean temperature (Figures 7c and 7d) suggest that prevailing temperature was not a strong determinant of respiration rates during the summer.

Discussion

Photosynthesis

Despite differences in growing season temperatures at the source sites of the two populations of sugar maple, seedlings in the growth chamber experiment showed more evidence of acclimation to growth temperature than of inherited population-level adaptation to climate, particularly with respect to photosynthesis. Analysis of variance failed to detect differences in mean photosynthetic rates associated with seed source that would have suggested increased P_{opt} as an adaptation to non-optimal climates in the source region. Neither were significant ecotypic differences in temperature optima detected between the seedling populations, but maintaining optimum rates of photosynthesis over a broad range of temperatures would lessen the importance of ecotypic adaptations to specific climate patterns. These results contrast with the ecotypic differences reported by Kriebel (1957) for summer leaf injury and drought survival in sugar maple, characteristics that correlated well with temperature at the site of seed origin. Our results are similar to those of Ledig and Korbobo (1983) who found no differences in photosynthetic temperature optima among populations of sugar maple from an altitudinal gradient, and no population × temperature interactions; however, photosynthetic rates were highest in the population from the highest elevation. Ferrar et al. (1989) found differences in temperature optima between populations from contrasting thermal environments in *Eucalyptus pauciflora* Sieber *ex* A. Spreng., but not in *E. camaldulensis* Dehnh., in which the two populations had very similar responses to temperature. The authors attributed this similarity to the wide distribution of *E. camaldulensis*, and to the presumably large amount of inherent variability. Sugar maple is also a widely distributed species, with high genetic variation within and among stands in a region, and low genetic variation between regions (Gunter et al. 1999). Low regional differentiation is consistent with the small physiological differences observed in our study between seedlings from different regions.

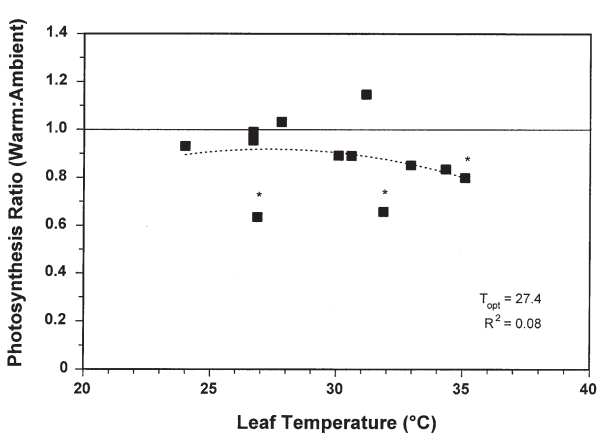

Figure 6. Photosynthetic rate of saplings grown at ambient +4 °C relative to that of saplings grown at ambient temperature. Values are based on measurements in the field on 12 dates (see Figure 4). The dotted line and inflection point (estimated as T_{opt}) were derived from Equation 1. Asterisks indicate dates on which differences between growth temperature treatments were significant (see Figure 4).

The broad temperature range for optimal photosynthetic performance in sugar maple made it difficult to detect shifts in optima with growing temperature. Curve fitting (Figure 1c, Table 1) with Equation 1 provided a graphic illustration of the higher P_{opt} of seedlings in the warm treatment compared with seedling in the cool treatment (Figures 1b and 1c). Curve fitting with Equation 1 also indicated a possible increase in T_{opt}, and a slightly more narrow parabola (larger *b*, Table 1) of seedlings in the warm treatment compared with seedlings in the cool treatment. Unfortunately, quadratic fits through the means from data based on three cuvette temperatures (Figure 1c, Table 1) do not provide estimates of error for these parameters. However, the observed response is consistent with a pattern of acclimation that is referred to by Prosser (1986) as thermal compensation—a translational (in this case, upward) shift in the rate function with acclimation temperature. Photosynthesis consistently declined at measurement temperatures above 31 ºC in both groups of seedlings, but the translational increase in photosynthesis across the temperature range (Figure 1) partially compensated for this decrease such that rates would be similar at 31 ºC in the cool-acclimated seedlings and 35 ºC in the warm-acclimated seedlings.

Thermal acclimation has been documented for photosynthesis of some evergreen tree species under field conditions, based on seasonal trends in temperature response. Seasonal acclimation entailed a shift in temperature optima (*Eucalyptus pauciflora*, Slatyer and Morrow 1977, *E. camaldulensis*, Ferrar et al. 1989), a translational increase in warmer months (*P. strobus* L., Jurik et al. 1988), or both (*Pinus taeda* L., Strain 1976). Growth chamber temperature manipulations of seedlings have also indicated that the patterns of thermal acclimation involve various combinations of shifted T_{opt} with temperature, higher P_{opt} in warmer conditions, and little effect of growth temperature (Strain et al. 1976, Read 1990, Tranquillini et al. 1986, Slatyer 1977, Domingo and Gordon 1974). Several *Eucalyptus* species exhibited the reverse response, a decrease in P_{opt} at high growth temperatures (Ferrar et al. 1989). Of equal note, broad photosynthetic temperature

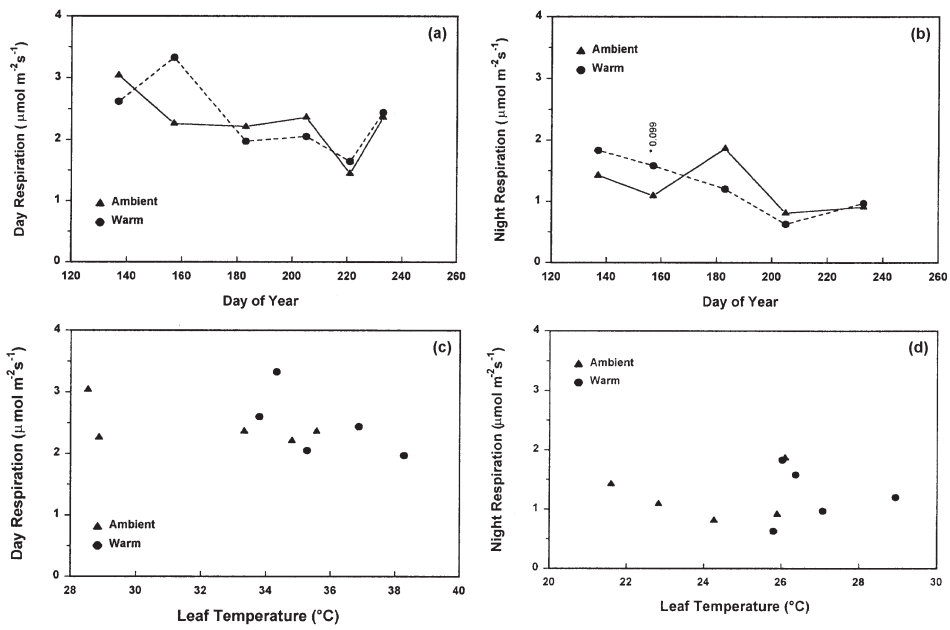

Figure 7. Leaf dark respiration rates measured during the day (a and c) and at the end of the night (b and d) in saplings in the field experiment. Measurements were made throughout the summer of 1996. Data are plotted against time (a and b) and against prevailing temperature (c and d). Symbols: ▲ = means for saplings in the ambient treatment; ● = means for saplings in the warm (ambient +4 ºC) treatment. Values represent means of three saplings, except on Day 221 (a only), when $n = 9$ because of the additional sampling of daytime respiration in August. The only P-value less than 0.10 is indicated.

optimum ranges have been associated with growth at cool temperatures (Ferrar et al. 1989), warm temperatures (Tranquillini et al. 1986), and with high diurnal temperature variation at the site of origin (Read 1990). Because these contrasting acclimation patterns exist and do not seem well correlated with climatic patterns, we suggest that a clear ecological explanation of species differences has not been demonstrated.

Deciduous species are exposed to less extreme temperature fluctuations than evergreen species, so it is notable that they also have a capacity for acclimation. The extent to which the acclimation potential affects photosynthetic rates in the field within this smaller range of temperatures, and in the context of a 4 ºC warming, is difficult to assess. In our field study, photosynthesis was not measured at multiple temperatures on a given date, so a shift in temperature optimum with treatment or seasonally could not be determined, and a major shift with a 4 ºC warming was not predicted from the growth chamber experiment. On the other hand, mean daily temperatures in the field in midsummer were higher than the temperatures in the growth chamber experiment (Norby et al. 1997), and adjustment to these warmer conditions may account for the higher apparent T_{opt} in the field (Table 1). However, if photosynthetic response to the 4 ºC temperature manipulation in the field had mimicked the laboratory responses (Figure 1), rates at the prevailing temperatures of the warm OTCs would have been 15 to 30% higher over most of the temperature range (up to about 30 °C), and similar at very high temperatures. However, mean photosynthetic rates of saplings in the warm OTCs were similar or lower than the mean rates of saplings in the ambient OTCs, not higher, as in the laboratory study. It is possible that higher VPDs in the warm OTCs than in the ambient OTCs accounted for the lower photosynthetic rates, either directly or indirectly through feedbacks to soil water availability. Although photosynthesis of seedlings in the growth chambers appeared relatively insensitive to VPD, VPD can affect photosynthesis in sugar maple seedlings under some conditions (Ellsworth and Reich 1992, Weber et al. 1985). Soil water content was usually slightly lower in the warm OTCs than in the ambient OTCs (e.g., 21 versus 25%, and 17 versus 21%, v/v; Edwards and Norby 1999). Although these differences were relatively small, they could have reduced photosynthesis in the warm OTCs on some dates, because low soil water content or decreased leaf water potential can reduce photosynthesis in sugar maple (Ellsworth and Reich 1992, Tschaplinski et al. 1995). Increased respiration rates in saplings in the warm OTCs could not account for the decreased net photosynthetic rates, because respiration rates were similar in saplings in the two treatments (Figure 7). Although the ratio of photosynthesis in the warm OTCs to that in the ambient OTCs (Figure 6) was usually less than one, the mean decrease was only 12%, and the long-term response could be modeled as a single curve through both treatments. The most detrimental effects of the ambient +4 ºC treatment were usually associated with high ambient temperatures, e.g., those in July. An exception occurred in late October 1994, when photosynthetic rates declined faster in leaves in the warm OTCs than in leaves in the ambient OTCs although some leaves had already been lost from saplings in both treatments.

There are several reasons why the capacity for photosynthetic acclimation to temperature seen under laboratory conditions was not apparent in the field. Prosser (1986) distinguished acclimation under controlled conditions from what he called acclimatization to natural environments. In natural environments, organisms must respond not only to unpredictably irregular temperature cycles, but also to many other variables (e.g., photoperiod, thermal range, and season) that can influence the extent to which the capacity for metabolic compensation is expressed. In addition, a synthesis of assimilation data across three summers is confounded by other influences on assimilation (e.g., changes in leaf N, variable soil

water content, VPD, etc.), as well as potential feedbacks of the treatments on those variables. Also, any seasonal temperature acclimation is incorporated into the combined response functions, potentially obscuring the acclimation.

Respiration

In contrast to photosynthesis, respiration in the two sugar maple populations studied in the growth chambers showed some degree of adaptation at the population level, and some acclimation to prevailing growth temperatures. The temperature coefficient for respiration, Q_{10}, was significantly lower in TN seedlings than in MI seedlings (Table 2). A lower Q_{10} for populations in the warmer portions of the range would be of adaptive value in reducing respiratory carbon losses in midsummer, and in reducing losses during episodic high temperature events. Similarly, a lower Q_{10} would moderate the impact of environmental warming on these populations. Adjustments in respiration to an incremental temperature increase were also demonstrated, particularly in the TN seedlings. Respiration in seedlings from both sources responded to prevailing temperature with a translational acclimation to lower rates in seedlings grown in the warm chambers. This type of respiratory acclimation has been demonstrated for several species, including several trees, but the degree of acclimation has varied (see references in Amthor 1994*b,* Larigauderie and Körner 1995, Arnone and Körner 1997, Tranquillini et al. 1986). A complete acclimation would result in identical respiration rates when measured at the growth temperatures. Although this was not the case for seedlings in the growth chamber study (Figure 2a), respiration rates of the saplings in the ambient and warm OTCs were similar on most dates. Respiration rates were not strongly linked to prevailing temperature, indicating that respiration may also acclimate to seasonal temperature changes (Figure 7), although other environmental factors or phenological changes may influence leaf biochemistry and thus respiration, independently of temperature effects.

Larigauderie and Körner (1995) introduced the term long-term acclimation ratio (LTR_{10}) to assess the effects of temperature on respiration rates. They defined LTR_{10} as the ratio of respiration rates in plants grown and measured at a given temperature (e.g., 20 ºC) to respiration rates in plants grown and measured at a temperature 10 ºC lower (e.g., 10 ºC). Based on LTR_{10} values, Larigauderie and Körner (1995) concluded that one third of 19 alpine and lowland plant species had a high degree of acclimation, whereas the others did not and were likely to experience increased carbon losses in response to warming climate. The degree of acclimation was not linked to plant origin, and the adaptive value of the different species' responses remains to be elucidated (Arnone and Körner 1997). Nevertheless, the occurrence of varying degrees of acclimation in this study and many others suggests that modeling the response of plant respiration to climate change should not assume a constant Q_{10} relationship, but should include an appropriate acclimation potential component.

Conclusions

The sugar maple populations in this study illustrate the potential of the species to adjust to past and future climatic warming. Both genetic adaptation (in Q_{10} of respiration) and phenotypic plasticity (physiological acclimation of respiration and photosynthesis) were exhibited, but acclimation was the predominant component of the adjustment. In the field study, saplings demonstrated respiratory acclimation comparable with that predicted from the growth chamber results, but the pattern of photosynthetic response to elevated temperature differed between the laboratory and field studies. The difference in photosynthetic responses may be attributed to the influence of other factors (environmental and developmental) on photosynthesis over the course of three field seasons, obscuring a long-term relationship with temperature conditioning. Additionally, it is possible that differences in water relations of saplings in the two field treatments offset the temperature acclimation.

Because experimental systems for regulating the temperature of large trees have not been perfected, and we do not have the technology to warm whole stands or ecosystems, models will continue to be used to predict long-term responses to climate change at those scales. Based on current information about foliar responses, physiologically based models should be able to incorporate temperature acclimation, although establishing the genetic and environmental determinants of different patterns remains a challenge. The degree of ecotypic difference in temperature responses varies among species and for species that exhibit high genetic differentiation, it may be necessary to model forest succession differently for different ecotypes.

Acknowledgments

We thank Lisa G. Wiggins for her technical contributions to the growth chamber gas exchange measurements, made during her participation in the U.S. Department of Energy Science and Engineering Research Semester Program. Assistance with data collection in the field experiment was provided by Emily Childs, Sheri Wampler, Michael Battaglia, Yomari Marrero, Maria Verbrugge, Sarah Schweitzer and Kristina Kipping. We thank P.J. Hanson and J.S. Amthor for their helpful comments on a previous version of the manuscript. The field experiment was conducted at the Global Change Field Research Site on the Oak Ridge National Environmental Research Park. Research sponsored by the Program for Ecosystem Research and the Global Change Research Program of the Environmental Sciences Division, U.S. Department of Energy, under contract DE-AC05-96OR22464 with Lockheed Martin Energy Research Corp. This project contributes to the Global Change and Terrestrial Ecosystems core project of the International Geosphere-Biosphere Programme. Publication No. 4924, Environmental Sciences Division, Oak Ridge National Laboratory.

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