

## Rapid temperature acclimation of leaf respiration rates in *Quercus alba* and *Quercus rubra*

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**Summary** We conducted controlled (chamber) and natural (field) environment experiments on the acclimation of respiration in *Quercus alba* L. and *Quercus rubra* L. Three-year-old Louisiana, Indiana and Wisconsin populations of *Q. alba* were placed in growth chambers and exposed to alternating 5-week periods of cool (20 °C mean) and warm (26 °C mean) temperatures. We measured respiration rates on fully expanded leaves immediately before and approximately every 2 days after a switch in mean temperature. In a second chamber experiment, 3-year-old potted *Q. alba* seedlings were exposed to alternating warm (26 °C mean) and cool (16 °C mean) temperatures at 4-day intervals. Leaf dark respiration rates were measured on days 2, 3 and 4 after each change in temperature. In a third, field-based study, we measured leaf respiration rates in the same three sources of *Q. alba* and in Arkansas, Indiana and Minnesota sources of *Q. rubra* before and after a natural 16 °C change in mean daily ambient temperature.

We observed rapid, significant and similar acclimation of leaf respiration rates in all populations of *Q. alba* and *Q. rubra*. Cold-origin populations were no more plastic in their acclimation responses than populations from warmer sites. All geographic sources showed lower respiration rates when measured at 24 °C after exposure to higher mean temperatures. Respiration rates decreased 13% with a 6 °C increase in mean temperature in the first chamber study, and almost 40% with a 10 °C increase in temperature in the second chamber study. Acclimation was rapid in all three studies, occurring after 2 days of exposure to changed temperature regimes. Acclimation was reversible when changes in ambient temperature occurred at 4-day intervals.

Respiration response functions,  $\ln(R) = \ln(\beta_0) + \beta_1 T$ , were statistically different among treatments (cool versus warm, first chamber study) and among sources in a pooled comparison. Pair-wise comparisons indicated statistically significant ( $P < 0.05$ ) differences in cool- versus warm-measured temperature/respiration response functions for Indiana and Wisconsin sources of *Q. alba*. Log-transformed base respiration rates were significantly lower during periods of higher mean temperatures. Indiana *Q. alba* showed a significantly higher  $\beta_1$  when plants were grown at 16 °C than when grown at 26 °C.

Acclimation in *Q. alba* was unaccompanied by changes in leaf nitrogen concentration, but was associated with a change in leaf total nonstructural carbohydrate concentration. Total nonstructural carbohydrate concentration was slightly, but statistically, lower (13.6 versus 12%,  $P < 0.05$ ) after a 10 °C increase in temperature.

**Keywords:** adaptation, deciduous, North America, oak, physiology.

### Introduction

Although plant respiration depends on several factors, variation in rate is mainly controlled by temperature (Berry and Raison 1981, Amthor 1989, Ryan 1991, Reich et al. 1996, 1998, Tjoelker et al. 1998). Mass- and area-specific respiration rates typically increase exponentially with temperature, at least when temperatures change over intervals of an hour or less. This temperature response is often modeled by respiration-temperature response functions of the form:

$$R_T = R_{T_{\text{ref}}} Q_{10}^{(T - T_{\text{ref}})/10} \quad (1)$$

or:

$$R_T = \beta_0 e^{\beta_1 T} \quad (2)$$

where  $R_T$  is the observed respiration rate,  $T$  is temperature,  $T_{\text{ref}}$  is a reference temperature and  $R_{T_{\text{ref}}}$ ,  $Q_{10}$ ,  $\beta_0$  and  $\beta_1$  are estimated coefficients. The  $Q_{10}$  may be interpreted as the ratio of respiration measured over a 10-degree span. The equations are equal if we interpret  $\beta_0 = R_{T_{\text{ref}}} Q_{10}^{T_{\text{ref}}/10}$  and  $\beta_1 = \ln(Q_{10})/10$ . The parameter  $\beta_1$  in Equation 2 is similar to  $Q_{10}$  in Equation 1 in that both affect the rate of respiration increase with temperature. Equations 1 and 2 fit individual leaf or plant measurements quite well, but parameter values vary among species, plant condition, current temperature and location (Ryan 1991, Azcon-Bieto 1992, Bolstad et al. 1999, Tjoelker et al. 1999, 2001, Atkin et al. 2000, Turnbull et al. 2001). Estimated  $Q_{10}$  values typically range from 1.2 to 4.0 and can vary with a num-

ber of factors, including species, climate, measurement method, plant N and carbohydrate status, season and measurement temperature (Breeze and Elston 1978, Kajimoto 1990, Ryan 1991, Azcón-Bieto 1992, Stockfors and Linder 1998, Dewar et al. 1999, Tjoelker et al. 2001, Pons and Welschen 2002). The value of  $Q_{10}$  appears to be a nonlinear, decreasing function of measurement temperature, and biases may result if  $Q_{10}$  is assumed to be constant when estimating respiration over a broad range of temperatures (Tjoelker et al. 2001). Observed respiration rates and derived  $Q_{10}$  values may also depend on whether only the leaf, shoot, or whole plant are exposed to short-term temperature changes (Atkin et al. 2000, Griffin et al. 2002). Base respiration ( $R_{Tref}$  or  $\beta_0$ ) may also change as temperature changes, or may vary with other factors (Turnbull et al. 2001). Because  $R_{Tref}$ ,  $\beta_0$  and  $\beta_1$  values have been less widely reported than  $Q_{10}$ , there is little basis for identifying the general relationships between these equation parameters and temperature, species, plant nitrogen status, or other factors.

Although short-term respiration–temperature responses may be well represented by Equations 1 or 2, respiration patterns may be more complex when temperatures vary over longer time intervals. Many plants appear to acclimate to changes in average temperature conditions by adjusting their respiration–temperature response. Respiratory acclimation occurs in many, but not all, taxa (Rook 1969, Chabot and Lewis 1976, Pearcy 1977, Larigauderie and Körner 1995, Saradadevi and Raghavendra 1999, Atkin et al. 2000, Gunderson et al. 2000, Will 2000, Xiong et al. 2000, Pilon and Santamaria 2001, Tjoelker et al. 2001, Griffin et al. 2002). Acclimation is often expressed as an increase in respiration rates in response to lower mean temperatures, when rates are measured at a standard temperature. Acclimation may be modeled by a shift in base respiration rates (change in  $\beta_0$  or  $R_{Tref}$ ), a change in the rate of increase in respiration with temperature (a change in  $Q_{10}$  or in  $\beta_1$ ), or some combination of these responses (Tjoelker et al. 2001).

If acclimation in respiration is widespread and significant, then respiration–temperature relationships under one temperature history may not apply to other histories. Average temperatures in all biomes change over daily, several day and seasonal intervals (Madden 1977, Wedland and Bryson 1981). When response functions are measured over a few hours and applied over longer periods, biases may result (Dewar et al. 1999, Tjoelker et al. 2001, Griffin et al. 2002). Moreover, populations may adapt to regional temperature conditions and differ in leaf respiration rates under common conditions (Criddle et al. 1994, Mitchell et al. 1999, Gunderson et al. 2000), and may differ in acclimation potential.

While acclimation is common, it does not occur in all plant taxa and has not been studied in many widespread species. The occurrence, magnitude and speed of acclimation responses are not well known. This paper describes a set of chamber-based and field studies on respiratory acclimation in seedlings of *Q. alba* and *Q. rubra*. We also report on changes in respiration response function with changes in mean temperature, and whether populations from a continental temperature gradient differ in their acclimation response.

## Methods

Leaf dark respiration rates were measured in two chamber studies and one field study. All studies were conducted on the University of Minnesota, St. Paul campus with 3-year-old plants, hereafter called seedlings. *Quercus alba* seedlings were from sources in northern Louisiana, central Indiana and northern Wisconsin, and *Quercus rubra* seedlings were from central Indiana, northern Minnesota and the uplands of Arkansas. All sources except Minnesota were 2-year-old bare-root stock, lifted in the fall of 1998 and stored at 4 °C until planting. Minnesota seedlings were grown for 2 years in approximately 90 cm<sup>3</sup> plastic plugs, hardened off outdoors in the fall and stored at 5 °C until planting. All seedlings were planted in 12-l pots containing standard potting mix prior to their third growing season, during May and July 1999. Potted plants were placed in a greenhouse for approximately 3 months prior to chamber studies, and ranged between 35 and 50 cm tall. A field site was planted in May 1999 and measurements taken in early summer 2000. Field plants were 20 to 80 cm tall at the time of measurement.

Specific rates of dark net CO<sub>2</sub> efflux on fully expanded leaves (respiration) were measured on intact leaves in the chamber studies and detached leaves in the field studies. Respiration was measured with an LI-6400 gas exchange system (Li-Cor, Lincoln, NE) fitted with a broadleaf cuvette. Respiration rates were observed until readings stabilized, typically after 3 to 10 min. Measurements were made on undamaged, fully expanded leaves near the top of each seedling. Measurements were made on attached (chamber studies) or detached (field study) leaves at the end of a daily dark period. Controlled environment studies were conducted in chambers that were approximately 3 m<sup>3</sup> in volume (Conviro CMP E15, Controlled Environments, Winnipeg, Manitoba, Canada). Plants were placed in a “measurement” chamber for approximately 5 to 10 min before each measurement, and the whole plant exposed to the measurement temperature during this period. This procedure avoided bias due to leaf portion versus whole-plant temperature control during measurement (Atkin et al. 2000, Griffin et al. 2002). Except where noted, both the measurement chamber and the temperature-controlled cuvette of the gas exchange system were set to 24 °C during measurements. Plants were immediately returned to an experimental chamber after measurement.

Experiment 1 focused on the magnitude of respiration changes following a step shift in average temperature. Potted *Q. alba* seedlings from Wisconsin, Louisiana and Indiana geographic sources were randomly selected 80 days after potting and placed in four growth chambers: two for cool and two for warm treatments. The cool treatment was set for 6-h periods each day at 16, 20, 24 and 20 °C; the warm treatment was set for 6-h periods of 22, 26, 30 and 26 °C. Day and night lengths were 15 and 9 h, respectively. Photosynthetic photon flux density was 1100  $\mu\text{mol m}^{-2} \text{s}^{-1}$  at the top of the chamber for 1 h and 600  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for the remainder of the photoperiod. Relative humidity was set at 75% for all chambers. Three seedlings per source were placed in each chamber in late July 1999.

Plants were acclimated in the cool or warm treatment chambers for 5 weeks. At the end of the acclimation period, respiration was measured and the temperature treatment was switched. Respiration at the new temperature was measured every 2 to 3 days for 3 weeks and once more 2 weeks later. The temperature treatment was switched again and respiration was measured every 2 to 3 days for 3 weeks.

Respiration of the same set of five leaves per source per chamber was measured with at least one leaf per seedling in each chamber. In cases where leaves (< 5%) were damaged during measurement, they were replaced with healthy adjacent leaves of similar size and from a similar light environment. At the end of each 5-week acclimation period, and at the end of each measurement period, leaf respiration was measured at 12, 18, 24 and 30 °C in six leaves per source to obtain instantaneous temperature–respiration response functions.

Three planned statistical analyses were conducted with the results of Experiment 1: a repeated-measures analysis of respiration rates at the end of each treatment period, with treatment, geographic source, cycle, leaf and chamber as main effects, and source by treatment crossed effects; a linear regression of respiration against time since the temperature switch; and a set of tests on respiration response parameters, fit to individual leaves at the end of each temperature treatment. Leaf temperature–respiration models (Equations 1 and 2) showed heteroscedastic residuals when fit by nonlinear regression. A log-transformed model:

$$\ln(R_T) = \beta_0 + \beta_1 T \quad (3)$$

exhibited homoscedastic residuals. Changes in the temperature–respiration response were tested with general linear models (GLM) with  $\ln(R_T)$  as the response variable, temperature as a continuous model variable, source and chamber as categorical variables, and source by temperature and treatment by temperature as crossed effects. *F*-Tests were performed based on a reduced sum of squares approach (Searle 1971), using type III sums of squares. Equation 2 parameters were estimated by nonlinear regression for each source–treatment combination as indicated by GLM results. Differences in Equation 2 and 3 parameters among source–treatment combinations were compared using bivariate Wilk’s lambda-tests (Johnson and Wichern 1982) and Fischer’s “protected” pair-wise *t*-tests (Chew 1977).

Experiment 2 was conducted to determine the speed and repeatability of respiratory acclimation. Nine *Q. alba* seedlings from Louisiana, Indiana and Wisconsin sources were placed in three growth chambers. Chambers were set to alternate between cool and warm temperature regimes on a 4-day cycle. The three chambers were maintained at a relative humidity of 75%, 1-h maximum irradiance ( $1100 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) at midday and half maximum irradiance for an additional 11 h. Cool treatment temperatures were 16 °C during the day and 14 °C at night. Warm treatment day and night temperatures were 26 °C and 24 °C, respectively. Chambers were initially set to the cool treatment. Each temperature treatment was applied for 4 days. Respiration at a leaf temperature of 24 °C was measured once

each day on the second, third and fourth days, beginning approximately 36 h after a shift in chamber temperature. Three leaves from each of the Louisiana, Indiana and Wisconsin sources were measured in each chamber, for a total of nine leaves per source. Leaves were marked and used for repeat measurements. Chamber temperature regimes were switched after the 4th day of measurements. Six changes in treatment regimes were made, yielding three warm treatment and three cool treatment periods. All measured leaves were harvested at the end of the last treatment. A repeated-measures analysis was performed. Treatment, geographic source, chamber, leaf and measurement within leaf were included in the model and *F*-tests performed.

In Experiment 3, leaf dark respiration was measured in field-grown plants to test for acclimation in an outdoor environment. Seedlings planted in spring 1999 were measured in June 2000. Respiration was measured in a set of leaves just before and just after a switch between cool and warm air masses. Seedlings from Minnesota, Indiana and Arkansas *Q. rubra* populations and Wisconsin, Indiana and Louisiana *Q. alba* populations were selected. Two seedlings of each source in each of six replicate blocks were chosen, and one leaf sampled from each seedling at each sampling period. Leaves were sampled before dawn, between 0415 and 0515 h central daylight savings time on June 6 and 7 and again on June 9 and 10, following an increase in ambient air temperatures. Detached leaves were quickly placed in plastic bags and then in a cooler and kept at 10–11 °C. All leaves were transferred to the laboratory immediately after sampling. Leaf bags were placed in a darkened growth chamber and maintained at 24 °C for at least 15 min before measurement. Leaf dark respiration rates were measured at 24.4 °C following protocols described above for the growth chamber experiments. Prior checks revealed no difference in the CO<sub>2</sub> exchange rate of attached leaves compared with detached leaves for up to 6 h following detachment (Mitchell et al. 1999, Lee, unpublished data). A general linear model was fit that included source and period (cool versus warm) as main effects, leaf nested within source/period and source by period interaction effects. Response was partitioned into a series of linear contrasts. Contrasts tested differences among sources within species, and among species and periods (warm and cold). Significant responses were determined by an *F*-test based on the response sum of squares and the mean-square error estimated from the leaf within source/period.

Areas of all freshly harvested leaves were measured with a scanner (ScanMaker Plus E3 with SigmaScan Pro, V4). Measured leaves were dried at 65 to 75 °C for at least 48 h, weighed and specific leaf area (SLA;  $\text{cm}^2 \text{g}^{-1}$ ) calculated. Leaf N and total nonstructural carbohydrates (TNC) were measured on leaves in Experiment 2. Leaves were ground and N determined with a PerkinElmer CHN analyzer (PerkinElmer, Wellesly, MA). Total nonstructural carbohydrate concentrations were determined by a modification of the method described by Haissig and Dickson (1979) and Hansen and Møller (1975). Sugars were extracted from oven-dried (65 °C, 48 h) tissue

powder in methanol–chloroform–water, and tissue residuals were analyzed for starch. Soluble sugars were determined colorimetrically with anthrone reagent at 625 nm within 30 min. Starch in the tissue residual was gelled and converted to glucose with amyloglucosidase. Glucose concentrations were measured with glucose oxidase by mixing the sample with peroxidase–glucose oxidase–*o*-dianisidine dihydrochloride reagent.

## Results

We observed significant, rapid acclimation in leaf respiration rates for both *Q. alba* and *Q. rubra*. Respiration, when measured at 24 °C, was lower after plants had been exposed to higher growth temperatures and higher after plants had been exposed to the lower growth temperatures. Conclusions are similar when respiration was expressed on a leaf area or leaf mass basis, so all results have been expressed on a leaf area basis.

### Experiment 1: Magnitude of response to a step-change in mean temperature

Results from Experiment 1 show a statistically significant shift in respiration related to a change in the temperature regime (Figure 1). Leaf respiration averaged  $0.54 \mu\text{mol m}^{-2} \text{s}^{-1}$  (s.e. =  $0.029 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) when plants were grown under the cool temperature regime, and  $0.48 \mu\text{mol m}^{-2} \text{s}^{-1}$  (s.e. =  $0.020 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) when plants were grown under warm temperatures. Differences among treatments (cool versus warm), geographic source and cycle (first versus second measurement period) were statistically significant ( $P < 0.05$ ,  $P < 0.01$ , GLM treatment effect).

Acclimation was rapid (Figure 1); respiration appeared to shift to new rates within 3 to 5 days of the change in mean temperature. Large differences due to the switch in temperature were always observed in the first post-switch measurement. Consistent differences in mean respiration were observed for all sources and temperature transitions. Respiration during cool treatments remained above the mean observed during preceding warm treatments, and respiration during warm treatments was always below rates observed during preceding cool treatments. There were no trends in respiration after the initial post-switch measurements ( $P > 0.1$ , regression slope within treatment of respiration versus time). Therefore, acclimation appeared to have been completed by our first measurement, between 38 and 70 h after a change in temperature regimes.

Respiration–temperature response functions changed significantly as a result of treatment (cool versus warm mean temperatures) and geographic source (Table 1). The response appears to be, more often, a result of changes in the base respiration rate ( $\ln(\beta_0)$ ) than of the rate of increase with temperature ( $\beta_1$ ). Treatment, source and measurement temperature effects were statistically significant in the general linear model ( $P < 0.05$ ,  $F$ -test), whereas the temperature by treatment effects were not significant ( $P > 0.1$ ). This indicates a statistically sig-

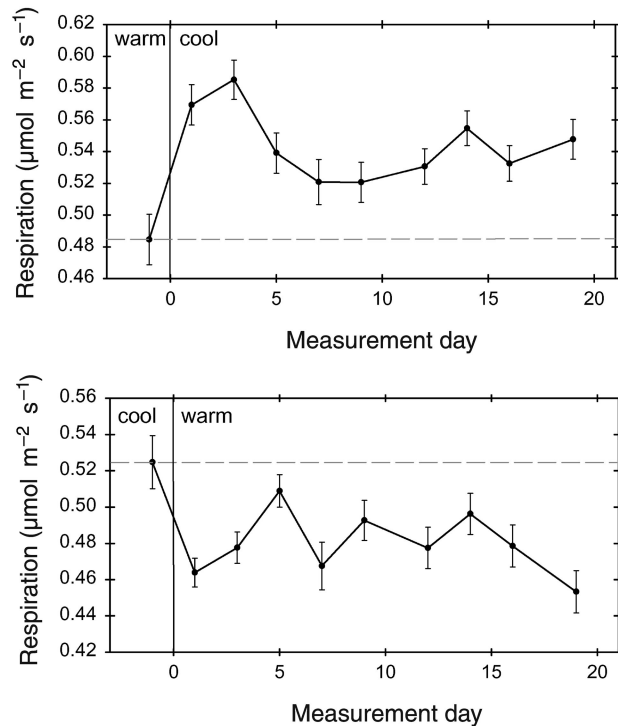


Figure 1. Mean leaf dark respiration rates ( $\pm 2$  SE) at 24 °C versus days since a switch in ambient temperature regimes. The switch in temperature was imposed immediately after measurements on day zero. Data are for *Q. alba* sources and are averaged across trees and chambers in Experiment 1 ( $n = 20$  at each measurement time).

nificant difference in the intercepts (source-based mean respiration), but no difference in the slope of the temperature factor,  $\beta_1$  by definition, when pooled data are analyzed in a GLM.

Regression-based estimates of respiration/temperature response functions (Table 1) are consistent with the GLM results. Model fits indicate a larger and more consistent acclimation response in  $\ln(\beta_0)$  than in  $\beta_1$ . Estimated  $\ln(\beta_0)$  values were statistically different among temperature treatments for the Indiana and Wisconsin sources ( $P < 0.05$ , protected  $t$ -test), but not for the Louisiana source ( $P > 0.1$ , protected  $t$ -test). Differences in  $\beta_1$  as a result of temperature treatments were not statistically significant for any sources ( $P > 0.1$ , protected  $t$ -test). When compared within treatments, the Indiana source in the warm treatment had a significantly lower  $\ln(\beta_0)$  and higher  $\beta_1$  than the other two sources ( $P < 0.05$ , protected  $t$ -test). No other among-source differences were statistically different.

### Experiment 2: Response to frequent shifts in mean daily temperature

The results from Experiment 2 demonstrate that respiratory acclimation is both rapid and reversible (Figure 2). Respiration rates measured at 24 °C decreased when plants were switched from cool (14/16 °C) to warm (24/26 °C) growth temperatures, and increased when plants were switched from warm to cool regimes. Both responses were repeated through



Table 1. Estimated respiration/temperature response coefficients derived from fits of Equation 3,  $\ln(R_T) = \beta_0 + \beta_1 T$ . All sources are *Q. alba*. Respiration was measured at 12, 18, 24 and 30 °C. Abbreviations:  $R_T$  = observed respiration;  $T$  = temperature;  $T_{\text{ref}} = 24$ , a reference temperature; and  $\ln(\beta_0)$  and  $\beta_1$  are estimated coefficients. Coefficients for Equation 1 are calculated by  $Q_{10} = e^{10\beta_1}$ ,  $R_{T_{\text{ref}}} = \beta_0/Q_{10}^{-T_{\text{ref}}/10}$ .

Treatment	Source	$\ln(\beta_0)$	$\beta_1$	$R_{T_{\text{ref}}}$	$Q_{10}$
Cool	Indiana	-2.71 ab	0.0855 a	0.517	2.35
	Louisiana	-2.71 ab	0.0872 a	0.542	2.39
	Wisconsin	-2.59 a	0.0868 a	0.605	2.38
Warm	Indiana	-3.16 c	0.0964 b	0.430	2.62
	Louisiana	-2.65 a	0.0823 a	0.511	2.28
	Wisconsin	-2.76 bc	0.0875 a	0.478	2.40

several cycles for all populations (Figure 2). Differences in respiration in response to temperature regimes were statistically significant (GLM,  $P < 0.01$ ), whereas differences among time periods and chambers were not (GLM,  $P > 0.10$ ). Variations within temperature treatments were small relative to variation among treatments; mean respiration rates on days 2, 3, and 4 of a treatment were not significantly different ( $P > 0.1$ , repeated measures factor, and  $t$ -test on regression of respiration versus time within treatment).

Mean leaf N concentration and standard deviations in Experiment 2 were  $18.3 \pm 0.86$  (warm treatment) and  $17.7 \pm 1.07$  mg g<sup>-1</sup> (cool treatment). The difference between treatments was not significant ( $P > 0.1$ ,  $t$ -test). In the same experiment, TNC differed between temperature treatments (Figure 3), averaging 12.0% under the higher temperatures and 13.6% under the lower temperatures. Differences were weakly significant ( $P < 0.1$ , arcsine transformed  $t$ -test).

### Experiment 3: Field response

Measurements on field-grown plants were generally consistent with those made on plants in the chamber studies. Mean daily temperatures were near 14.5 °C from Julian day 153 to 157 (Figure 4). Mean daily temperatures increased to between 25 and 30 °C from Julian day 159 to 163. Leaf respiration rates at 24.4 °C averaged  $2.2 \mu\text{mol m}^{-2} \text{s}^{-1}$  on days 156 and 157, during the cool period, and decreased to  $1.6 \mu\text{mol m}^{-2} \text{s}^{-1}$  on Julian day 161, after a 2-day exposure to a warm air mass. The decreases were highly significant ( $t$ -test,  $P < 0.01$ ) when pooled across all sources and both species.

Differences in respiration rates among populations (Figure 5) were not significant ( $P > 0.1$ ,  $F$ -test in GLM) in the field study, and contradict the chamber-based results in Experiment 1. In this field study, we found no evidence for regional or local adaptation to temperature regimes (e.g., Reich et al. 1996), although we measured relatively few sources and leaves.

There was a larger, statistically significant ( $P < 0.05$ ,  $F$ -test, GLM contrast), acclimation response in *Q. rubra* than in *Q. alba* (mean of all sources Figure 5). Leaf respiration measured at 24.4 °C declined in *Q. alba* by  $0.37 \mu\text{mol m}^{-2} \text{s}^{-1}$  with

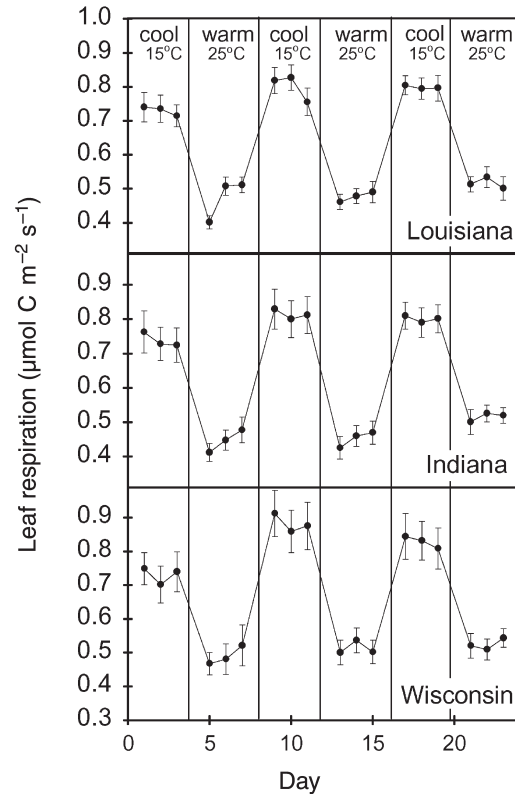


Figure 2. Mean leaf dark respiration rates ( $\pm 2$  SE) at 24 °C for three sources of *Q. alba* in response to rapid changes in temperatures.

a 12.1 °C increase in 5-day mean temperature, versus a decrease of  $0.73 \mu\text{mol m}^{-2} \text{s}^{-1}$  in *Q. rubra*. Respiration rates per unit area were higher under the cool growth temperature regimes for all *Q. rubra* sources when compared with all *Q. alba*

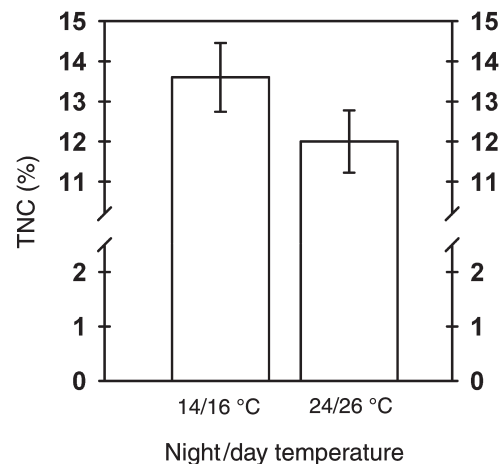


Figure 3. Leaf total nonstructural carbohydrates (TNC) in *Q. alba* in Experiment 2 in the warm and cool temperature regimes ( $\pm 2$  SE). Leaf TNC was significantly higher in the cool treatment than in the warm treatment ( $P < 0.05$ , arcsine transformed  $t$ -test).

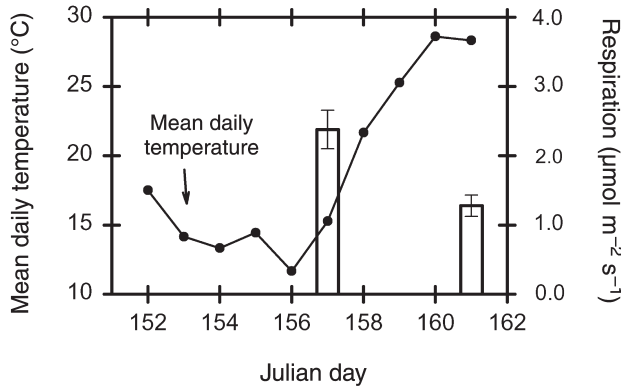


Figure 4. Mean leaf dark respiration rates ( $\pm 2$  s.e.) when measured at 24.4 °C and mean daily temperatures for field-grown plants. Means are averaged across three geographic sources of *Q. alba* and three geographic sources of *Q. rubra*. Mean respiration rates decreased significantly ( $P < 0.05$ ) and rapidly in response to an increase in ambient temperature. Means did not vary significantly ( $P < 0.05$ ) among sources that represented continental climatic gradients.

sources, and *Q. rubra* respiration rates were comparable to *Q. alba* rates under warm growing conditions (Figure 5).

## Discussion

Our results demonstrated significant, rapid and reversible respiratory acclimation in both *Q. alba* and *Q. rubra*. Acclimation resulted in changes in leaf respiration rate of up to 100%, depending on the experiment, source and species. Our results are noteworthy because of the magnitude and speed of the respiratory acclimation response and because similar responses were observed in different populations of two common and widespread deciduous species.

Our results add to a growing list of studies that report respi-

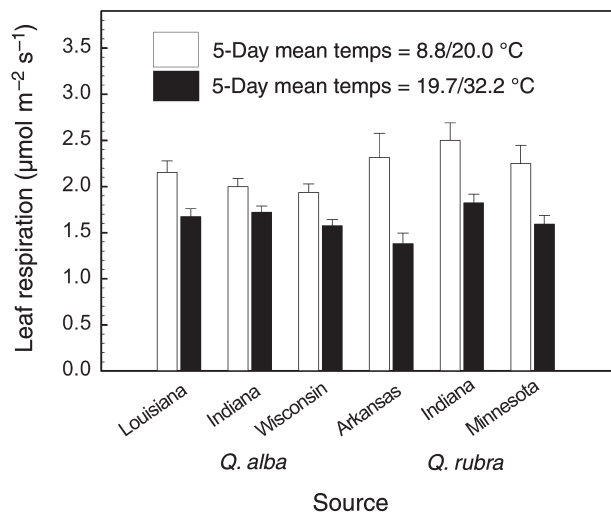


Figure 5. Mean leaf dark respiration rates ( $\pm 2$  s.e.) at 24.4 °C of three source populations of field-grown *Q. alba* and *Q. rubra* seedlings following 5 days of cool compared to warmer mean daily temperatures.

ratory acclimation in tree species (Rook 1969, Sorensen and Ferrell 1973, Chabot and Lewis 1976, Pearcy 1977, Paembonen et al. 1991, Larigauderie and Körner 1995, Saradadevi and Raghavendra 1999, Teskey and Will 1999, Tjoelker et al. 1999, Atkin et al. 2000, Gunderson et al. 2000, Will 2000, Xiong et al. 2000, Pilon and Santamaria 2001, Tjoelker et al. 2001, Griffin et al. 2002). Nearly all species have shown an increase in respiration in response to decreases in mean temperatures, with acclimation ranging from full to partial. This contrasts with a broader range of acclimation responses observed for annual and perennial herbaceous plants (Larigauderie and Körner 1995). Acclimation may be more common in long-lived woody species that are exposed to a broad range of temperatures (Criddle et al. 1994).

Acclimation may improve carbon balance, broadening the range of climatic conditions over which carbon gain can occur. Photosynthesis has been reported to acclimate to temperature, although comparisons are available for relatively few woody plant species (Chabot and Lewis 1976, Slayter 1977, Tranquillini et al. 1986, Battaglia et al. 1996, Teskey and Will 1999). Temperature response studies on a number of species show that photosynthesis rates remain relatively constant over a broad range of temperatures (Chabot and Lewis 1976, Aubuchon et al. 1978, Jurik 1986, Jurik et al. 1988, Gunderson et al. 2000). Photosynthetic rates in *Q. alba* and *Q. rubra* generally remain near maximum between 18 and 30 °C. If respiration rates acclimate over the same temperature range, as the present study indicates, photosynthesis relative to respiration will be greater at higher temperatures, which would result in a more positive carbon balance than would otherwise have been predicted.

Our results suggest that there is no adaptive variation in acclimation response along the climatic gradient represented by our three populations of *Q. alba* and *Q. rubra*. Populations were selected along a large latitudinal gradient, with concomitant gradients in mean growing season and annual temperatures. Previous studies have reported ecotypic differences in respiration and photosynthesis as a result of temperature adaptation (Billings et al. 1971, Ledig and Korbor 1983, McNulty et al. 1988, Criddle et al. 1994). In those studies, respiration rates from cold-origin populations were higher than warm-origin populations when compared under similar conditions. In contrast, we saw no significant trends associated with climate or latitude of the source populations. Respiration rates in *Q. alba* from Louisiana were similar to those from Wisconsin, and there were no differences between *Q. rubra* Arkansas and Minnesota respiration rates. Long-term mean temperatures during the growing season differed by more than 9 °C among source locations, yet plants from these sources exhibited similar respiration rates when grown together. Our results are consistent with previous work conducted primarily on herbaceous plants (Larigauderie and Körner 1995), in which no adaptive variation was found in a large number of taxa with both alpine and lowland distributions.

Ecosystem carbon balance and respiration models should incorporate an acclimation response. Many models include a form of Equation 1 or 2, but use fixed parameters that do not

represent acclimation (e.g., Running and Coughlan 1988, Bonan 1991, Aber et al. 1996, but see McGuire et al. 1992). Our results indicate that acclimation may be more accurately modeled through temperature-dependent changes in  $\beta_0$  or  $R_{Tref}$ , both because of the rapid acclimation responses shown here and because of the sensitivity of the temperature response function to instantaneous temperature conditions (Tjoelker et al. 2001). Accurate prediction of respiration may require models that incorporate some time-weighted function of recent temperature. Substrate-based models may also be used, as they show promise in predicting changes in respiration and photosynthesis with temperature (Dewar et al. 1999). However, time to full acclimation has been reported on the order of 10 days or longer. These periods are substantially longer than those observed in the present study and some others (Atkin et al. 2000, Griffin et al. 2002).

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#### References

- Aber, J.D., P.B. Reich and M.L. Goulden. 1996. Extrapolating leaf  $\text{CO}_2$  exchange to the canopy: a generalized model of forest photosynthesis compared with measurements by eddy correlation. *Oecologia* 106:257–265.
- Amthor, J.S. 1989. Respiration and crop productivity. Springer-Verlag, Berlin, 215 p.
- Atkin, O.K., C. Holly and M.C. Ball. 2000. Acclimation of snow gum (*Eucalyptus pauciflora*) leaf respiration to seasonal and diurnal variations in temperature: the importance of changes in the capacity and temperature sensitivity of respiration. *Plant Cell Environ.* 23:15–26.
- Atkin, O.K., E.J. Edwards and B.R. Loveys. 2000. Response of root respiration to changes in temperature and in its relevance to global warming. *New Phytol.* 147:141–154.
- Aubuchon, R.R., D.R. Thompson and T.M. Hinckley. 1978. Environmental influences on photosynthesis within the crown of white oak. *Oecologia* 35:295–306.
- Azcón-Bieto, J. 1992. Relationships between photosynthesis and respiration. The effect of carbohydrate status on the rate of  $\text{CO}_2$  production by respiration in darkened and illuminated wheat leaves. *Plant Physiol.* 71:574–581.
- Battaglia, M.C. Beadle and S. Loughhead. 1996. Photosynthetic temperature response of *Eucalyptus globulus* and *Eucalyptus nitens*. *Tree Physiol.* 16:81–89.
- Berry, J.A. and J.K. Raison. 1981. Responses of macrophytes to temperature. In *Physiological Plant Ecology I. Responses to the Physical Environment*. Eds. O.L. Lange, P.S. Nobel, C.B. Osmond and H. Zeigler. Springer-Verlag, Berlin, pp 277–338.
- Billings, W.D., P.J. Dodfrey, B.F. Chabot and D.P. Bourque. 1971. Metabolic acclimation to temperature in Arctic and alpine ecotypes of *Oxyria digyna*. *Arctic Alp. Res.* 3:277–289.
- Bolstad, P.V., K. Mitchell and J.M. Vose. 1999. Foliar temperature–respiration response functions for broad-leaved tree species in the southern Appalachians. *Tree Physiol.* 19:871–878.
- Bonan, G.B. 1991. Seasonal and annual carbon fluxes in a boreal forest landscape. *J. Geophys. Res.* 96:17,329–17,338.
- Chabot, B.F. and A.R. Lewis. 1976. Thermal acclimation of photosynthesis in northern red oak. *Photosynthetica* 10:176–183.
- Chew, V. 1977. Comparisons among treatment means in an analysis of variance. Agricultural Research Service, USDA, Washington, DC, 64 p.
- Criddle, R.S., M.S. Hopkins, E.D. McArthur and L.D. Hansen. 1994. Plant distribution and the temperature coefficient of metabolism. *Plant Cell Environ.* 17:233–243.
- Dewar, R.C., B.E. Medlyn and R.E. McMurtrie. 1999. Acclimation of respiration photosynthesis ratio to temperature: insights from a model. *Global Change Biol.* 5:615–622.
- Griffin, K.L., M. Turnbull, R. Murthy et al. 2002. Leaf respiration is differentially affected by leaf vs. stand-level night-time warming. *Global Change Biol.* 8:479–485.
- Gunderson, C.A., R.J. Norby and S.D. Wullschlegler. 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.
- Haissig B.E. and R.E. Dickson. 1979. Starch measurement in plant tissue using enzymatic hydrolysis. *Physiol. Plant.* 47:151–157.
- Hansen J. and I. Møller. 1975. Percolation of starch and soluble carbohydrates from plant tissue for quantitative determination and anthrone. *Analyt. Biochem.* 68:87–94.
- Johnson, R.W. and D.W. Wichern. 1982. Applied multivariate statistical analysis. Prentice-Hall, Englewood Cliffs, NJ, 594 p.
- Jurik, T.W. 1986. Seasonal patterns of leaf photosynthesis capacity in successional northern hardwood tree species. *Am. J. Bot.* 73: 131–138.
- Jurik, T.W., J.A. Weber and D.M. Gates. 1988. Effects of temperature and light on photosynthesis of dominant species of a northern hardwood forest. *Bot. Gaz.* 149:203–208.
- Kajimoto, T. 1990. Photosynthesis and respiration of *Pinus pumila* needles in relation to needle age and season. *Ecol. Res.* 5:333–340.
- Larigauderie, A. and C. Körner. 1995. Acclimation of leaf dark respiration to temperature in alpine and lowland plant species. *Ann. Bot.* 76:245–252.
- Ledig, F.T. and D.R. Korboro. 1983. Adaptation of sugar maple populations along altitudinal gradients: photosynthesis, respiration, and specific leaf weight. *Am. J. Bot.* 70:256–265.
- Madden, R.A. 1977. Estimates of the autocorrelations and spectra of seasonal mean temperatures over North America. *Mon. Weather Rev.* 105:9–18.
- McGuire, A.D., J.M. Melillo, L.A. Joyce, D.W. Kicklighter, A.L. Grace, B. Moore, III and C.J. Voorsmarty. 1992. Interactions between carbon and nitrogen dynamics in estimating net primary productivity for potential vegetation in North America. *Global Biogeochem. Cycles* 6:101–124.
- McNulty, A.K., W.R. Cummins and A. Pellizzari. 1988. A field survey of respiration rates in leaves of arctic plants. *Arctic* 41:1–5.
- Mitchell, K.A., P.V. Bolstad and J.M. Vose. 1999. Interspecific and environmentally induced variation in foliar dark respiration among eighteen southeastern deciduous tree species. *Tree Physiol.* 19: 861–870.
- Paembonan, S.A., A. Hagihara and K. Hozum. 1991. Long-term measurement of  $\text{CO}_2$  releases from the aboveground parts of a hinoki forest tree to air temperature. *Tree Physiol.* 8:399–405.
- Pearcy, R.W. 1977. Acclimation of photosynthetic and respiratory carbon dioxide exchange to growth temperature in *Atriplex lentiformis* (Torr.) Wats. *Plant Physiol.* 59:795–799.
- Pilon, J. and L. Santamaria. 2001. Seasonal acclimation in the photosynthetic respiratory temperature responses of three submerged freshwater macrophyte species. *New Phytol.* 151: 659–670.

- Pons, T.L. and R.A.M. Welschen. 2002. Overestimation of respiration rates in commercially available clamp-on leaf chambers. Complications with measurement of net photosynthesis. *Plant Cell Environ.* 25:1367–1372.
- Reich, P.B., J. Oleksyn and M.G. Tjoelker. 1996. Needle respiration and nitrogen concentration in Scots pine populations from a broad latitudinal range: a common garden test with field-grown trees. *Funct. Ecol.* 10:768–776.
- Reich, P.B., M.B. Walters, D.S. Ellsworth, J.M. Vose, J.C. Volin, M. Gresham and W.D. Bowman. 1998. Relationships of leaf dark respiration to leaf N, specific leaf area and leaf-span: a test across biomes and functional groups. *Oecologia* 114:471–482.
- Rook, D.A. 1969. The influence of growing temperature on photosynthesis and respiration of *Pinus radiata* seedlings. *N.Z. J. Bot.* 7:43–55.
- Running, S. and J. Coughlin. 1988. A general model of forest ecosystem processes for regional applications. I. Hydrologic balance, canopy gas exchange, and primary production processes. *Ecol. Model.* 42:125–154.
- Ryan, M.G. 1991. Effects of climate change on plant respiration. *Ecol. Appl.* 1:157–167.
- Saradadevi, K. and A.S. Raghavendra. 1999. Dark respiration protects photosynthesis against photoinhibition in mesophyll protoplasts of pea (*Pisum sativum*). *Plant Physiol.* 99:1232–1237.
- Searle, S.R. 1971. *Linear models*. Wiley, New York, 532 p.
- Slyter, R.O. 1977. Altitudinal variation in the photosynthetic characteristics of snow gum, *Eucalyptus pauciflora* Sieb. ex Spreng. III. Temperature response of material grown in contrasting thermal environments. *Aust. J. Plant Physiol.* 4:301–312.
- Sorensen, F.C. and W.K. Ferrell. 1973. Photosynthesis and growth of Douglas-fir seedlings when grown in different environments. *Can. J. Bot.* 51:1689–1698.
- Stockfors, J. and S. Linder. 1998. The effect of nutrition on the seasonal course of needle respiration in Norway spruce stands. *Trees* 12:130–138.
- Teskey, R.O. and R.E. Will. 1999. Acclimation of loblolly pine (*Pinus taeda*) seedlings to high temperatures. *Tree Physiol.* 19: 519–525.
- Tjoelker, M.G., J. Oleksyn and P.B. Reich. 1998. Acclimation of respiration to temperature and CO<sub>2</sub> in seedlings of boreal tree species in relation to plant size and relative growth rate. *Global Change Biol.* 5:679–691.
- Tjoelker, M.G., P.B. Reich and J. Oleksyn. 1999. Changes in leaf nitrogen and carbohydrates underlie temperature and CO<sub>2</sub> acclimation of dark respiration in five boreal tree species. *Plant Cell Environ.* 22:767–778.
- Tjoelker, M.G., J. Oleksyn and P.B. Reich. 2001. Modeling respiration of vegetation: evidence for a general temperature-dependent  $Q_{10}$ . *Global Change Biol.* 7:223–230.
- Tranquillini, W., W.M. Havranek and P. Ecker. 1986. Effects of atmospheric humidity and acclimation temperature on the temperature responses of photosynthesis in young *Larix decidua* Mill. *Tree Physiol.* 1:37–45.
- Turnbull, M.H., D. Whitehead, D.T. Tissue, W.S.F. Schuster, K.J. Brown and K.L. Griffin. 2001. Responses of leaf respiration to temperature and leaf characteristics in three deciduous tree species vary with site water availability. *Tree Physiol.* 21:571–578.
- Wendland, W. and R. Bryson. 1981. Northern hemisphere airstream regions. *Mon. Weather Rev.* 109:255–270.
- Will, R. 2000. Effect of different daytime and nighttime temperature regimes on the foliar respiration of *Pinus taeda*: predicting the effect of variable temperature on acclimation. *J. Exp. Bot.* 351: 1733–1739.
- Xiong, F.S., E.C. Mueller and T.A. Day. 2000. Photosynthetic and respiratory acclimation and growth response of Antarctic vascular plants to contrasting temperature regimes. *Am. J. Bot.* 87: 700–710.