

Acclimation of respiratory temperature responses in northern and southern populations of *Pinus banksiana*

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Summary

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Received: 28 May 2008

Accepted: 30 July 2008

- Temperature acclimation of respiration may contribute to climatic adaptation and thus differ among populations from contrasting climates.
- Short-term temperature responses of foliar dark respiration were measured in 33-yr-old trees of jack pine (*Pinus banksiana*) in eight populations of wide-ranging origin (44–55°N) grown in a common garden at 46.7°N. It was tested whether seasonal adjustments in respiration and population differences in this regard resulted from changes in base respiration rate at 5°C (R_5) or Q_{10} (temperature sensitivity) and covaried with nitrogen and soluble sugars.
- In all populations, acclimation was manifest primarily through shifts in R_5 rather than altered Q_{10} . R_5 was higher in cooler periods in late autumn and winter and lower in spring and summer, inversely tracking variation in ambient air temperature. Overall, R_5 covaried with sugars and not with nitrogen. Although acclimation was comparable among all populations, the observed seasonal ranges in R_5 and Q_{10} were greater in populations originating from warmer than from colder sites. Population differences in respiratory traits appeared associated with autumnal cold hardening.
- Common patterns of respiratory temperature acclimation among biogeographically diverse populations provide a basis for predicting respiratory carbon fluxes in a wide-ranging species.

Key words: adaptation, carbohydrates, climate change, jack pine (*Pinus banksiana*), nitrogen, Q_{10} , respiration, temperature acclimation.

New Phytologist (2008) doi: 10.1111/j.1469-8137.2008.02624.x

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Introduction

Respiration is a key determinant of carbon exchange in plants and ecosystems (Ryan, 1991; Valentini *et al.*, 2000). Respiration rates are highly temperature-dependent. In the short term, specific rates of dark respiration in plants increase as an approximate exponential function of ambient temperature. However, there is increasing evidence that thermal acclimation of respiration may occur within 1 or 2 d (Rook, 1969; Teskey & Will, 1999; Atkin *et al.*, 2000; Atkin & Tjoelker, 2003; Bolstad *et al.*, 2003; Atkin *et al.*, 2005a; Lee *et al.*, 2005), raising the possibility of a dynamic temporal response of respiratory metabolism linked to ambient temperature changes.

As a consequence, respiration rates may be constrained across a range of thermal environments compared with expected values based on short-term temperature responses (Tjoelker *et al.*, 1999b; Gifford, 2003; Atkin & Tjoelker, 2003). The metabolic basis of thermal acclimation of the short-term temperature response function of respiration is not fully understood (Atkin & Tjoelker, 2003) but is important in developing and testing physiology-based models that incorporate temperature effects on the carbon cycle (Tjoelker *et al.*, 2001; Gifford, 2003; Wythers *et al.*, 2005; Davidson *et al.*, 2006; King *et al.*, 2006; Atkin *et al.*, 2008).

Thermal acclimation of respiration results in a shift in the shape or elevation of the temperature–response curve.

The instantaneous temperature sensitivity of respiration is often expressed as Q_{10} , the quotient of rates given a 10°C change in temperature. Thermal acclimation may be manifest through changes in Q_{10} (termed type I acclimation) or the base respiration rate at a reference temperature (type II acclimation), which modulates the elevation of the instantaneous temperature–response function (Atkin & Tjoelker, 2003). Adjustments in both Q_{10} and base respiration may occur simultaneously. Changes in base respiration have been hypothesized to involve greater metabolic or anatomic changes and thus to be maximally expressed in plants that develop in contrasting growth temperatures (Loveys *et al.*, 2003; Armstrong *et al.*, 2006). Field-grown *Eucalyptus pauciflora* plants subjected to experimental night-time warming exhibited adjustments in base respiration rate of leaves and not Q_{10} compared with ambient-temperature controls (Bruhn *et al.*, 2007). In general, the relative contribution of type I and type II acclimation to respiratory adjustments in plants is poorly understood.

Across diverse taxa and environments, specific rates of leaf, root, and stem respiration often correlate with tissue nitrogen (N) (Ryan, 1995; Reich *et al.*, 1998, 2008; Tjoelker *et al.*, 2005; Wright *et al.*, 2006). In forest canopies, rates of dark respiration (at a standard temperature) covary with leaf N and carbohydrates (Turnbull *et al.*, 2003; Xu & Griffin, 2006; Tjoelker *et al.*, 2008). Likewise, leaf Q_{10} covaries with leaf N across canopy positions (Turnbull *et al.*, 2003) and sites differing in soil fertility (Turnbull *et al.*, 2005). By contrast, Q_{10} of root respiration in several herbaceous species grown in a range of N supplies was unrelated to root N concentration (Atkinson *et al.*, 2007). Q_{10} is often greater in leaves and roots containing higher concentrations of soluble carbohydrates (Azcón-Bieto *et al.*, 1983; Covey-Crump *et al.*, 2002; but see Atkin *et al.*, 2000; Griffin *et al.*, 2002). Field studies comparing respiration at prevailing ambient temperatures (Lee *et al.*, 2005) and controlled-environment studies comparing respiration in different thermal treatments (Tjoelker *et al.*, 1999b) both show that thermal acclimation of foliar dark respiration is correlated with changes in both leaf N and carbohydrate concentrations. Carbohydrates have received increased attention in studies of temperature acclimation of dark respiration (Dewar *et al.*, 1999; Atkin & Tjoelker, 2003; Xu & Griffin, 2006), particularly with regard to explaining observed constraints on the ratio of respiration to photosynthesis in leaves and plants grown in various environments (Reich *et al.*, 1998; Amthor, 2000; Gifford, 2003; Whitehead *et al.*, 2004; Atkin *et al.*, 2007; Campbell *et al.*, 2007). Thus, changes in both leaf N and soluble carbohydrate contents may be associated with seasonal respiratory adjustments that may be manifest in altered Q_{10} or base respiration rates of the short-term temperature–response functions.

Respiration rates are sometimes higher in populations native to high altitudes and latitudes than in those from lower altitudes and latitudes when grown together and compared in

common gardens (Mooney & Billings, 1961; Reich *et al.*, 1996; Oleksyn *et al.*, 1998), reflecting genetic differentiation, although this is not always the case (Gunderson *et al.*, 2000; Bolstad *et al.*, 2003; Lee *et al.*, 2005). Likewise, the capacity to acclimate to changing temperatures (phenotypic plasticity) may differ genetically among taxa. It has been hypothesized that plants originating in climates with wider temperature fluctuations may exhibit an increased capacity in temperature acclimation of gas exchange traits than those in less extreme, moderate climates (Billings *et al.*, 1971; Cunningham & Read, 2003). However, the evidence is scant and mixed regarding biogeographic differentiation in acclimation capacity of respiratory CO₂ efflux among species or populations (Larigauderie & Körner, 1995; Teskey & Will, 1999; Lee *et al.*, 2005). Thus, the relative importance of temperature acclimation in respiration and population differences in respiratory traits as a driver of respiratory carbon fluxes in plants remains unclear, but knowledge about this would be useful in modeling respiration across temporal and spatial scales in response to climate change.

A study of diverse seed sources of *Pinus banksiana* revealed similar seasonal temperature acclimation of foliar respiration at three geographically diverse sites (Tjoelker *et al.*, 2008). In that study, specific respiration rates at a standard temperature (20°C) inversely tracked variation in ambient air temperature, increasing with cooler temperatures in fall and declining with warming temperatures in spring and summer. The prior study examined relationships between respiration and leaf traits of 20 populations grown in three contrasting common gardens. Herein we examine temperature–response functions of foliar respiration to determine the nature of the observed seasonal adjustments in respiration for a subset of eight diverse populations grown at one of the sites. We focus on the specific respiration rate at the reference temperature of 5°C (R_5) and Q_{10} of instantaneous curves as indicators of changes in base respiration rate and temperature sensitivity, respectively, to provide insight into temperature acclimation that cannot be gained by examining rates at a single temperature. We report specific respiration rates at a standard temperature of 20°C for the populations of the present study elsewhere (Tjoelker *et al.*, 2008). We address the following questions: (i) to what extent do short-term temperature–response functions of foliar dark respiration rates differ seasonally in an evergreen species in terms of changes in R_5 and/or Q_{10} ; (ii) do populations of diverse climatic origins differ in R_5 or Q_{10} and, if so, is acclimation capacity arrayed along climatic clines; and (iii) to what extent are R_5 and Q_{10} correlated with foliar N and total (and in particular, cryoprotectant) carbohydrate concentrations? To address these questions, we used a common-garden plantation of field-grown trees that enabled us to test for genetic differences in response to a range of ambient air temperatures encompassing an annual temperature cycle. We measured rates of needle dark respiration in 33-yr-old trees of eight geographically diverse jack pine (*P. banksiana*) populations

Table 1 Location and climate of origin of geographically diverse seed sources of *Pinus banksiana* selected for study in a common-garden plantation in Minnesota, USA

Provenance ^a	State or Province	Latitude	Longitude	Temperature (°C)			DD
		(°N)	(°W)	January	July	Mean annual	
<i>Northern populations</i>							
Kississing Lake	Manitoba	55.12	101.15	-21.7	18.9	-0.6	982
Nipekamew River	Saskatchewan	54.20	104.92	-20.0	17.8	0.0	1093
Macdowall	Saskatchewan	53.12	106.07	-18.3	18.3	1.1	1260
Lac La Biche	Alberta	55.23	111.92	-17.2	17.2	1.7	1149
<i>Southern populations</i>							
Petawawa Plains	Ontario	45.78	77.38	-13.3	19.4	4.4	1593
Gladstone	Michigan	46.00	86.50	-7.8	19.4	5.6	1538
Fife Lake	Michigan	44.55	85.37	-6.1	20.0	6.7	1816
Mosinee	Wisconsin	44.83	89.67	-8.3	22.2	7.2	1760

^aProvenances are part of a range-wide seed source experiment (see the Materials and Methods section) and are ordered by increasing mean annual temperature. Degree-days (DD) are the cumulative growing-season temperature sums above 5.5°C. Climate data are based on historic climate records obtained before seed collection.

(44–55°N), spanning nearly the entire native climatic range of the species (–0.6 to 7.2°C, mean annual temperature, MAT) and grown together in northern Minnesota, USA.

Materials and Methods

Common-garden site

We used a common-garden plantation of jack pine (*Pinus banksiana* Lamb.) in Cloquet, Minnesota, USA (46.70°N, 92.51°W, elevation 385 m) that was part of a provenance study of seed sources collected from native stands throughout the northern temperate and boreal range of the species and planted at sites in the USA and Canada (Mátyás & Yeatman, 1992). At the site, the mean annual precipitation (1971–2000) is 807 mm and the MAT is 4.6°C, with mean monthly temperatures ranging from –12.7°C in January to 19.6°C in July. A weather station near the plantation (c. 1 km) recorded daily climate data. The soil texture was a loamy sand of typical fertility for the species. The site was planted in May 1966 with 2-yr-old bare-root trees grown from seed in a local nursery. Seedlings were planted at 2.4 m spacing in four-tree row plots of 90 seed sources in five randomized complete blocks. Eight geographically and climatically diverse seed sources were selected for study (Table 1). Earlier studies revealed genetic differentiation among these seed sources, reflecting biogeographic variation within the species (Mátyás & Yeatman, 1992; Savva *et al.*, 2007).

Dark respiration measurements

For each of eight populations, we marked four trees randomly selected for repeated sampling five times throughout the course of a study between October 1997 and the following

August. The sampling dates encompassed mean daily air temperatures ranging from –6.6°C in November to 20.4°C in August. The sample dates and corresponding mean, minimum, and maximum air temperatures (3 d mean, including the day before the 2 d sample period) were: 15–16 October (4.0, –2.6, 10.6°C), 12–13 November (–6.6, –10.2, –3.0°C), 12–13 February (–4.1, –7.8, –0.4°C), 12–13 May (13.4, 5.2, 21.7°C), and 4–5 August (20.4, 13.9, 26.8°C). We sampled the same current-year cohort of fully expanded, mature foliage for the October through May measurements and, in August, the new cohort formed that year. All four trees for each of eight provenances were sampled throughout the course of each 2 d sample period. On each morning between 08:00 and 10:00 h, we used a pole pruner to cut branches from the upper, sunlit portion of the tree crowns, avoiding shade foliage. We moved the cut branches to a laboratory c. 1 km from the plantation site. Two or three twigs bearing current-year needles were cut from each branch, put into bags to slow desiccation, and placed in the dark in a controlled-environment chamber.

Six-point temperature–response functions (5–30°C in 5°C intervals, low to high) were determined, with the exception of the first sampling period in which we did not measure at 5°C and confirmed that the order of temperature measurement did not affect the results. Temperatures were obtained by changing the air temperature of the growth chamber. At measurement, we placed the intact twigs inside sealed cuvettes to minimize leaks around the gaskets. Between each step change in temperature, we waited c. 20 min for the temperature to stabilize before measuring the samples in random order. On average, steady-state measures were recorded after 6 min. Rates of net CO₂ efflux were measured using infrared gas analyzers and cuvettes (LCA-3 and PLC-C, Analytical Development Co. Ltd, Hoddesdon, UK), operating in an open

configuration. We removed water vapor from the analyzer air stream using desiccants in order to standardize measurement conditions and eliminate concerns about the accuracy of measuring and correcting for water vapor dilution effects. The reference CO₂ concentration averaged 380 μmol mol⁻¹ and was stabilized by sampling air through a void volume. On each sampling date, we completed the measures of respiration within a 6 h period using two identical calibrated gas exchange systems operating concurrently. Rates of respiration on detached branches or leaves in a range of tree species have been shown to be stable for several hours or longer (Mitchell *et al.*, 1999; Ow *et al.*, 2008) and this was confirmed in our study by testing for time trends, repeating measures, and inspecting curve fits for individual samples. Rates of respiration were expressed on a needle dry mass basis (R , nmol g⁻¹ s⁻¹).

We determined the fresh mass and oven-dry mass (65°C) of the needles to determine water content as ((fresh mass – dry mass)/dry mass). The dry mass of the woody twig constituted an average of 16% of the total sample dry mass. In a separate analysis, paired measures of respiration rates of intact twigs (needles and twig) vs detached needles revealed that the respiratory CO₂ efflux from the woody twig, presumably including any wound respiration from the cut end of the twig, constituted, on average, only 5.4% (± 2.3% SEM, $n = 32$) of the total CO₂ efflux of the intact twig with needles.

Needle nitrogen and carbohydrates

We determined N and carbohydrate concentrations on the same needle samples used in the dark respiration measurements of all four trees of eight populations and five dates. The needle N and carbohydrate data are reported elsewhere as part of a larger multi-site study (Tjoelker *et al.*, 2008). Herein we examine needle N and carbohydrate data in relation to respiratory temperature–response parameters not shown elsewhere. In brief, oven-dried (65°C) and powdered needle tissue was used to determine N concentration by coupled CN and mass spectroscopy (University of California – Davis, Stable Isotope facility, Davis, CA, USA). Total nonstructural carbohydrates were determined using a methanol, chloroform, and water extraction and spectrophotometric procedures described in Tjoelker *et al.* (2008).

In addition to the carbohydrate analyses of all sample dates, we quantified the concentrations of soluble sugars related to cold-temperature acclimation. Two contrasting sample dates in late autumn (November) and the following spring (May) of the same needle age-class cohort were selected. Soluble sugars were extracted from the dried needle samples as described earlier and the concentrations of raffinose (a trisaccharide composed of galactose, glucose, and fructose), sucrose (a disaccharide, glucose + fructose), and the monosaccharides glucose and fructose were quantitatively determined using a HPLC system (Waters Associates, Milford, MA, USA) fitted with a Sugar Pack I column and a refractive index detector

(Waters 410) as described in Pukacka & Pukacki (1997). The flow rate was 0.5 ml min⁻¹ and the temperature was 90°C. Peaks were identified and concentrations of carbohydrates were determined according to carbohydrate standard chromatograms.

Data analysis

The response of specific respiration rate (R , nmol g⁻¹ s⁻¹) to temperature (5–30°C) was modeled using the following function:

$$R = R_5 Q_{10}^{\frac{(T-5)}{10}} \quad \text{Eqn 1}$$

where R_5 is the estimated specific respiration rate at the reference temperature of 5°C and T is the measurement temperature. The Q_{10} describes the proportional increase in rate with a 10°C increase in temperature and represents the value for the entire measurement temperature range (5–30°C). We fitted individual curves to each sample using nonlinear regression. Of the 160 temperature–response curves analyzed, one curve was removed for lack of fit.

We used a repeated-measures analysis of variance to examine the effects of population (7 d.f.), sampling date (4 d.f.) and population × sampling date (28 d.f.) on the fitted parameters R_5 and Q_{10} . The F statistic for the between-population effect used the nested effect of tree within population (24 d.f.) as the expected mean square for the denominator. In addition, we tested preplanned contrasts of northern vs southern populations (see Table 1). The F statistic for sampling date and the population × sampling date effects used the residual error term. Sampling date effects were also examined separately within each population using analysis of variance. Hypothesized relationships between climate variables of seed-source origin and response variables of population means were examined using correlation and type I regression analyses. In all data analyses, we used statistical analysis software (JMP 7.02 for Macintosh, SAS Institute, Cary, NC, USA).

The degree of temperature acclimation for each population was calculated as an acclimation ratio (A):

$$A = 1 - \left(\frac{\text{LTR}_{10} - 1}{Q_{10} - 1} \right) \quad \text{Eqn 2}$$

where LTR_{10} is the long-term Q_{10} of needle R across the five sampling periods for rates estimated at the 3 d mean ambient temperatures, and Q_{10} is the short-term temperature sensitivity for each sampling period (Atkin *et al.*, 2005b). LTR_{10} was determined by fitting a temperature–response function (described earlier) to *in situ* respiration rates across the five sample dates for each sampled tree of each population. The index takes into account long-term adjustments in

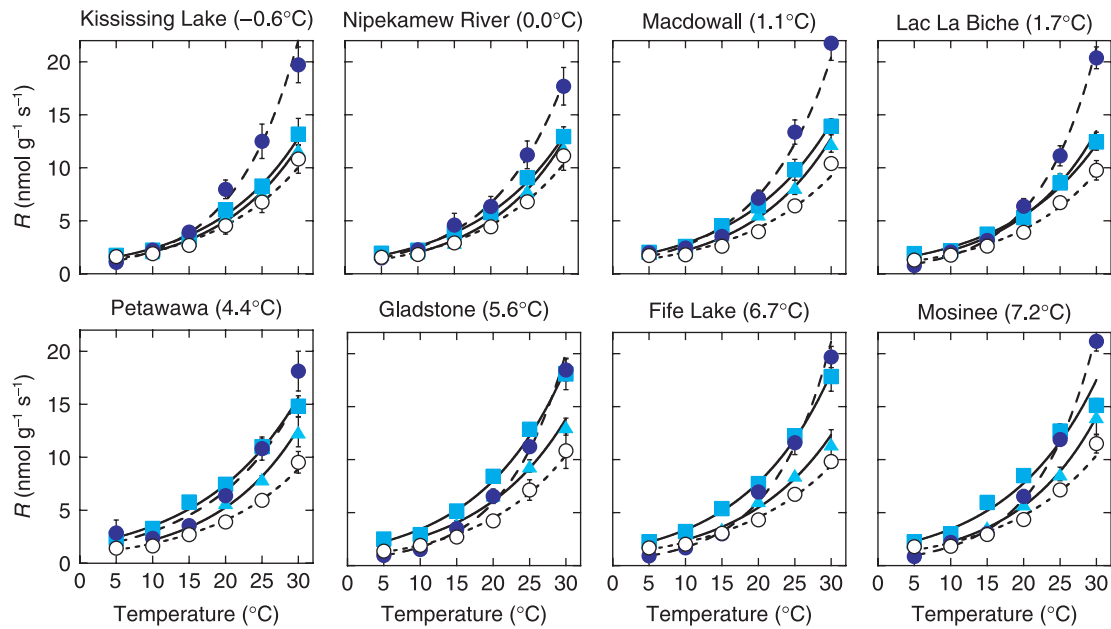


Fig. 1 Seasonal variation in temperature response of dark respiration in eight geographically diverse populations of *Pinus banksiana* grown in a common garden in Minnesota, USA. Corresponding mean annual temperatures at seed origin are shown. Mean values (± 1 SEM) of specific respiration rates (R , $\text{nmol g}^{-1} \text{s}^{-1}$) of current-year foliage ($n = 4$) are shown for trees measured in October (triangles), November (squares), February (closed circles), and May (open circles). Exponential fits are shown (see the Materials and Methods section). For clarity, August data are not shown.

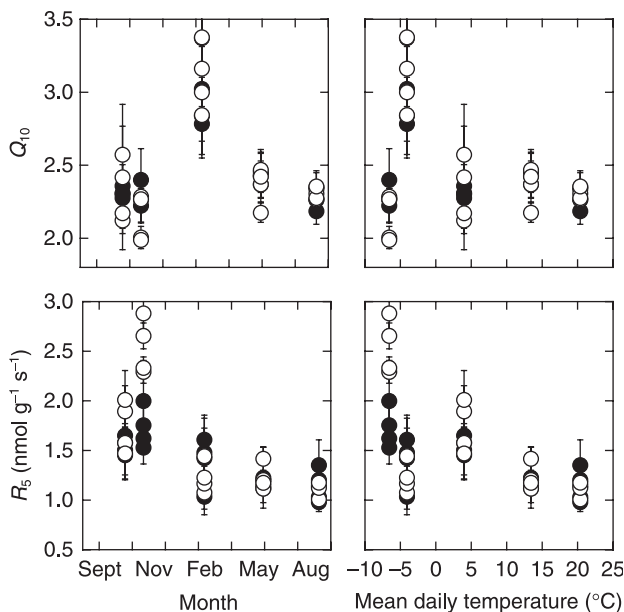


Fig. 2 Seasonal changes in the respiratory temperature–response parameters of needles of *Pinus banksiana* populations. Mean (± 1 SEM) values of Q_{10} (5–30°C) and base respiration rates at 5°C (R_5 , $\text{nmol g}^{-1} \text{s}^{-1}$) are shown in relation to 3 d mean daily temperature for each of five sampling dates for populations of northern (closed circles) and southern (open circles) geographic origin (see Table 1).

respiration rates as well as short-term temperature responses, each expressed in equivalent form as a Q_{10} (Atkin *et al.*, 2005b). An A value of 0 indicates no acclimation (i.e. LTR_{10} and Q_{10} are equal) and a value of 1 indicates complete acclimation or homeostasis.

Results

Seasonal adjustments in temperature–response parameters of respiration

Inspection of the fitted temperature–response functions revealed adjustments in the elevation (R_5) and slope (Q_{10} , 5–30°C) of the curves in each population throughout the year-long study (Fig. 1, Table 2). In general, seasonal adjustments were manifest primarily through changes in R_5 of the temperature–response functions among the five sample dates. Overall, mean R_5 of the populations was higher during cold than during warm periods (date effect, $P < 0.0001$). Q_{10} also varied among sample dates (date effect, $P < 0.0001$) and was markedly higher in February than on the remaining dates (Fig. 2). R_5 was negatively correlated with the mean daily temperature of the 3 d sample periods ($r = -0.61$, $P < 0.0001$, $n = 40$, Fig. 2), which is consistent with patterns of respiration measured at a standard temperature (20°C) in these and other populations at three sites (Tjoelker *et al.*, 2008). Correlation coefficients between R_5 and mean daily temperatures calculated for 7, 14, and 30 d intervals before

Table 2 Seasonal variation in temperature–response parameters and acclimation of needle dark respiration ($\text{nmol g}^{-1} \text{s}^{-1}$) of geographically diverse populations of *Pinus banksiana* grown in a common garden in Minnesota, USA

Provenance ^a		October	November	February	May	August	SEM	F	Date ($P > F$)
<i>Northern populations</i>									
Kississing Lake	R_5	1.45	1.53	1.61	1.23	1.20	0.23	0.64	0.64
	Q_{10}	2.36	2.40	2.78	2.46	2.19	0.15	2.23	0.11
	A	0.23	0.23	0.42	0.28	0.13	0.07	2.14	0.13
Nipekamew River	R_5	1.50	1.75	1.48	1.20	0.98	0.19	2.44	0.092
	Q_{10}	2.30	2.26	2.84	2.43	2.34	0.16	2.11	0.13
	A	0.33	0.30	0.50	0.38	0.35	0.06	1.76	0.19
Maddowall	R_5	1.58	2.00	1.42	1.12	1.35	0.22	2.22	0.12
	Q_{10}	2.31	2.22	3.02	2.43	2.26	0.12	8.01	0.0012*
	A	0.31	0.18	0.51	0.36	0.30	0.08	2.05	0.16
Lac La Biche	R_5	1.65	1.62	1.03	1.15	1.03	0.13	5.88	0.0047*
	Q_{10}	2.28	2.27	3.37	2.37	2.35	0.12	16.38	< 0.0001*
	A	0.18	0.20	0.57	0.25	0.23	0.10	2.41	0.096
<i>Southern populations</i>									
Petawawa Plains	R_5	1.58	2.65	1.44	1.12	1.01	0.21	9.61	0.0005*
	Q_{10}	2.42	2.00	2.84	2.37	2.31	0.22	1.96	0.15
	A	0.39	0.22	0.54	0.43	0.40	0.08	2.16	0.12
Gladstone	R_5	2.01	2.33	1.23	1.17	1.18	0.17	10.85	0.0002*
	Q_{10}	2.17	2.27	3.00	2.42	2.35	0.11	8.79	0.0007*
	A	0.17	0.25	0.52	0.33	0.28	0.08	2.92	0.057
Fife Lake	R_5	1.89	2.29	1.17	1.42	1.12	0.16	9.33	0.0005*
	Q_{10}	2.12	2.28	3.16	2.17	2.28	0.13	11.06	0.0002*
	A	0.19	0.34	0.61	0.28	0.33	0.08	4.36	0.016*
Mosinee	R_5	1.47	2.88	1.08	1.20	1.14	0.17	20.40	< 0.0001*
	Q_{10}	2.57	1.99	3.38	2.47	2.27	0.21	6.07	0.0048*
	A	0.36	0.06	0.58	0.35	0.26	0.09	4.74	0.012*

^aSee Table 1 for provenance information. Parameters and least-squares means (± 1 SEM) for sampling date effects are derived from the short-term response of net CO_2 exchange to measurement temperature using nonlinear regression. R_5 is the specific respiration rate ($\text{nmol g}^{-1} \text{s}^{-1}$) at 5°C and Q_{10} is the temperature coefficient ($5\text{--}30^\circ\text{C}$). A is the acclimation ratio, an index of the degree of temperature acclimation (see the Materials and Methods section).

*, $P \leq 0.05$.

sampling were progressively weaker and statistically nonsignificant with increasing interval length compared with the 3 d mean (not shown). In comparison, the correlation between mean Q_{10} and mean daily temperature of the 3 d sample period was also significant ($r = -0.32$, $P = 0.04$, $n = 40$), although it was leveraged by high values in February that differed markedly from November observations at a comparable mean daily temperature (Fig. 2).

R_5 exhibited a significant interaction effect of sample date and population ($P = 0.003$). Mean R_5 was nearly 50% higher in the southern than in the northern population group on the November sampling date (2.54 vs 1.73 $\text{nmol g}^{-1} \text{s}^{-1}$); however, populations did not differ among the four remaining dates (Fig. 2). Q_{10} did not differ among populations ($P = 0.65$) or between the northern and southern population groups (group effect, $P = 0.65$, Fig. 2). Overall, mean acclimation ratios (A) differed among sample dates ($P < 0.0001$, Table 2); however, neither A nor the mean long-term temperature sensitivity (LTR_{10}), which averaged 1.92, differed among populations or between population groups.

Biogeographic variation in temperature–response parameters and acclimation capacity

We examined correlations of the means and ranges in R_5 and Q_{10} with geographic and climatic variables of seed-source origin for the eight sampled populations. The examined correlations differed in magnitude and sign when compared among the individual sampling dates examined separately (not shown), suggesting that temporal plasticity in acclimation of respiration differed among populations. As evidence of this, among populations, the range in mean R_5 values across pooled sampling dates increased with increasing MAT (Fig. 3) and growing degree-days (not shown) at seed origin. Similarly, the range in Q_{10} values across the five sampling dates was positively correlated with MAT (Fig. 3) and growing degree-days at seed origin. However, the ranges in R_5 and Q_{10} were unrelated to the annual range in mean monthly temperatures (July minus January) at seed origin. The combined effects of changes in both R_5 and Q_{10} were reflected in an increasing seasonal range in acclimation ratios (A) with increasing MAT

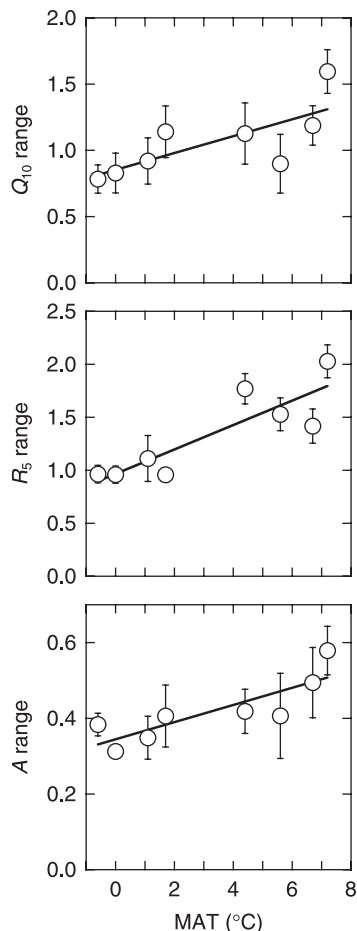


Fig. 3 Seasonal range in temperature–response parameters and temperature acclimation of respiration of eight geographically diverse populations of *Pinus banksiana* in relation to mean annual temperature (MAT) at seed origin. The mean range (\pm SEM, $n = 4$ trees per population) in values of Q_{10} (5–30°C), base respiration rate at 5°C (R_5 , $\text{nmol g}^{-1} \text{s}^{-1}$), and acclimation ratio (A) among five measurement dates are shown. Correlations: Q_{10} ($r = 0.74$, $P = 0.03$), R_5 ($r = 0.86$, $P = 0.006$), and A ($r = 0.84$, $P = 0.01$).

of seed origin (Fig. 3). Thus, populations originating in southern, warmer climates exhibited a greater range in seasonal acclimation in temperature–response parameters than those originating in northern populations from colder climates.

Biogeographic variation in needle cryoprotectant sugars

In November, northern populations had higher mean concentrations of both raffinose (group contrast, $P = 0.068$) and sucrose ($P < 0.0001$) and lower concentrations of glucose ($P = 0.004$) than did the southern populations (Table 3). Moreover, the concentrations of both raffinose and sucrose were each negatively correlated with MAT at seed-source origin, while glucose exhibited a positive correlation (Fig. 4). In addition, in November the populations and groups

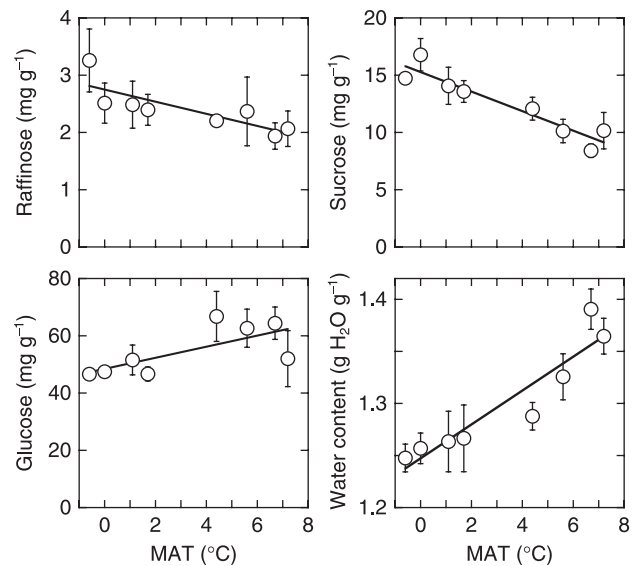


Fig. 4 Needle concentrations of soluble sugars and water content in relation to mean annual temperature (MAT) at seed origin for eight populations of *Pinus banksiana*. Mean values (\pm SEM, $n = 4$) are shown for needles sampled in November. Correlations: raffinose ($r = -0.82$, $P = 0.013$), sucrose ($r = -0.94$, $P = 0.0005$), glucose ($r = 0.71$, $P = 0.05$), and water content ($r = 0.93$, $P = 0.0007$).

($P < 0.0001$) differed in needle water content, exhibiting a positive correlation with MAT at seed-source origin (Fig. 4). Thus, in late autumn, northern populations originating in colder climates had comparatively lower water contents and higher concentrations of two cryoprotectant sugars, raffinose and sucrose than did southern populations originating in warmer climates. Raffinose was not detected in needles in May and sucrose concentrations were generally 10–20% of values observed in November (Table 3). Fructose did not differ between population groups in November, but was higher in northern than in southern populations in May ($P = 0.020$).

Relationships between R_5 , Q_{10} , nitrogen, and soluble sugars

To examine the relationships between seasonal changes in the temperature–response parameters (R_5 and Q_{10}), nitrogen, and carbohydrates, we pooled all data of all four trees of eight populations across the five sample dates, using individual values of each sample. Overall, R_5 was positively correlated with total soluble sugar concentration ($r = 0.52$, $P < 0.0001$, $n = 159$) and not with N concentration. Using mean values of the eight populations sampled across the five dates increased the strength of the correlation between R_5 and soluble sugars (Fig. 5). By contrast, Q_{10} (5–30°C) was not correlated with either soluble sugar or N concentrations. Thus, seasonal and population variation in R_5 was largely associated with concomitant changes in soluble carbohydrate concentrations.

Table 3 Soluble sugar concentrations and water content in geographically diverse populations of *Pinus banksiana* grown in a common garden in Minnesota, USA

Provenance ^a	Month	Raffinose (mg g ⁻¹)	Sucrose (mg g ⁻¹)	Glucose (mg g ⁻¹)	Fructose (mg g ⁻¹)	Water content (g H ₂ O g ⁻¹ dry mass)
<i>Northern populations</i>						
Kississing Lake	November	3.3 ± 0.5	14.7 ± 0.4	46.6 ± 1.8	25.8 ± 2.4	1.25 ± 0.01
	May	– ^b	3.1 ± 0.5	36.2 ± 3.6	18.1 ± 3.0	0.90 ± 0.07
Nipekamew River	November	2.5 ± 0.4	16.8 ± 1.4	47.5 ± 1.9	26.4 ± 0.9	1.26 ± 0.01
	May	–	2.5 ± 0.2	19.6 ± 1.6	14.6 ± 0.7	0.90 ± 0.05
Macdowall	November	2.5 ± 0.4	14.1 ± 1.6	51.6 ± 5.2	30.1 ± 1.8	1.26 ± 0.03
	May	–	1.8 ± 0.1	26.6 ± 3.3	11.8 ± 1.2	0.97 ± 0.06
Lac La Biche	November	2.4 ± 0.3	13.6 ± 0.9	46.7 ± 2.4	27.1 ± 1.9	1.27 ± 0.03
	May	–	2.1 ± 0.2	35.7 ± 4.7	20.2 ± 2.5	0.94 ± 0.02
<i>Southern populations</i>						
Petawawa Plains	November	2.2 ± 0.1	12.1 ± 1.0	66.8 ± 8.7	35.5 ± 5.8	1.29 ± 0.01
	May	–	2.3 ± 0.2	32.0 ± 2.0	11.6 ± 2.0	0.94 ± 0.03
Gladstone	November	2.4 ± 0.6	10.1 ± 1.0	62.6 ± 6.7	33.1 ± 4.7	1.33 ± 0.02
	May	–	1.7 ± 0.2	23.8 ± 2.0	10.5 ± 1.1	1.00 ± 0.03
Fife Lake	November	1.9 ± 0.2	8.4 ± 0.6	64.4 ± 5.6	23.1 ± 2.0	1.39 ± 0.02
	May	–	1.8 ± 0.1	29.8 ± 2.0	15.1 ± 2.1	0.95 ± 0.04
Mosinee	November	2.1 ± 0.3	10.2 ± 1.6	52.0 ± 9.8	21.1 ± 4.6	1.36 ± 0.02
	May	–	1.7 ± 0.2	26.3 ± 2.9	14.1 ± 1.5	0.92 ± 0.03
<i>Population effect</i>						
November	<i>F</i>	1.08	5.92	1.99	2.00	6.42
	<i>P</i> > <i>F</i>	0.40	0.0004*	0.099	0.097	0.0003*
May	<i>F</i>	–	3.65	3.87	3.08	0.65
	<i>P</i> > <i>F</i>	–	0.0080*	0.0059*	0.018*	0.71
<i>Group contrast</i>						
November	<i>F</i>	3.64	31.90	9.94	0.13	31.00
	<i>P</i> > <i>F</i>	0.068	< 0.0001*	0.0043*	0.72	< 0.0001*
May	<i>F</i>	–	8.19	0.56	6.20	0.64
	<i>P</i> > <i>F</i>	–	0.0086*	0.46	0.020*	0.43

^aSee Table 1 for provenance information.

^bNot detected. Mean values (± 1 SEM) are shown (*n* = 4 trees per provenance).

*, *P* ≤ 0.05.

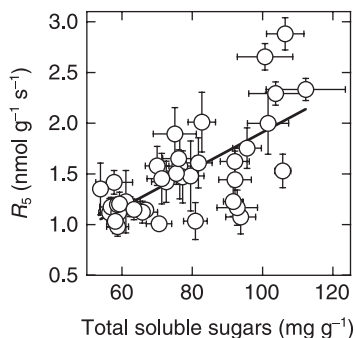


Fig. 5 Relationship between base respiration rate at 5°C (R_5) and total soluble sugars in needles of *Pinus banksiana*. Mean values (± 1 SEM, *n* = 4 trees) are shown for each of eight populations and five sampling dates ($r = 0.70$, $P < 0.0001$, $n = 40$).

Discussion

Is seasonal acclimation in foliar respiration rate in an evergreen related to changes in R_5 or Q_{10} ?

From five sets of complete temperature–response curves for four individuals of each of eight populations, we observed a temporal pattern in base respiration rate at 5°C (R_5) in fully developed needles of all eight populations consistent conceptually with an acclimation response associated with changes in prevailing ambient air temperatures, and consistent empirically with temperature acclimation seen in 20 *P. banksiana* populations at three different sites and measured only at a single temperature (20°C, Tjoelker *et al.*, 2008). Seasonal temperature acclimation was largely the result of a downward adjustment in R_5 with warming and an upward adjustment with cooling. These adjustments of R_5 – the elevation (i.e. intercept) of the short-term temperature–response functions – are consistent with a type II temperature acclimation response (Atkin & Tjoelker, 2003). Given that Q_{10} and R_5 are derived from curve-fitting procedures on the same individual samples, the parameter values are not strictly independent. Yet, these parameters differed from each other in their pattern of variation among sample periods. The pattern of variation in R_5 and stronger association of R_5 than

Q_{10} with ambient air temperature changes provide evidence that a change in base respiration rate was the predominate factor underpinning respiratory temperature acclimation. A study of *P. banksiana* seedlings in controlled environments shows comparable acclimation responses of dark respiration to a range of growth temperatures (Tjoelker *et al.*, 1999a,b). Thus, our findings in this evergreen species indicate that similar adjustments in base respiration rates can occur across thermally contrasting seasons as well as in plants grown at contrasting temperatures. This finding was somewhat surprising given that growth temperature effects on leaf development are hypothesized to have larger effects on respiratory gas exchange physiology than shorter-term temperature effects on reversible physiological plasticity (Atkin & Tjoelker, 2003; Loveys *et al.*, 2003; Armstrong *et al.*, 2006; but see Bolstad *et al.*, 2003; Lee *et al.*, 2005; Bruhn *et al.*, 2007).

Q_{10} values (5–30°C) were markedly higher in the midwinter (February) sampling date, suggesting that adjustments in the temperature sensitivity of the temperature–response function (type I acclimation) also contribute to seasonal acclimation. Higher Q_{10} values in winter have been observed in other evergreen species (Stockfors & Linder, 1998; Atkin *et al.*, 2000). In addition, respiration is known to increase rapidly upon thawing and warming of cold-hardened tissues. Although we observed relatively low R_5 values on the February sampling date, respiration rates at higher temperatures (> 20°C) were among the highest observed in the study.

Inferring temperature acclimation from field-based measurements of foliar respiration rates is problematic because temporal changes may also reflect the effects of confounding factors such as leaf age and plant phenology (see later discussion). In this study, a comparison of needle age-class cohorts in October showed that rates measured at a standard temperature (20°C) were, on average, 16% (\pm 4% SEM) lower in needles formed the previous year than in the current year ($n = 48$). This likely represents the upper end of the magnitude of an annual seasonal effect of increasing needle age on maintenance respiration rates of fully formed needles, since trees held their needles for 2 yr in this study. Thus, the increase in rates during a cooling autumn period is counter to a presumed decline in rate with increasing age. Moreover, temperature acclimation of comparable magnitude has been observed in comparisons that largely avoided leaf age, phenology, or seasonal confounding in *P. banksiana* (Tjoelker *et al.*, 1999a,b) and other species (Stockfors & Linder, 1998; Teskey & Will, 1999; Atkin *et al.*, 2000; Bolstad *et al.*, 2003; Lee *et al.*, 2005), suggesting that the responses of *P. banksiana* observed in this study likely represent, in large part, thermal acclimation.

Do populations of diverse climatic origin differ in respiratory temperature responses?

We found evidence that seasonal adjustments in respiration rates were comparatively more important in constraining

respiration rates than inherent biogeographic variation in temperature–response parameters in *P. banksiana*. Overall, the acclimation ratios indicate a partial temperature acclimation response of low to intermediate magnitude (Atkin *et al.*, 2005b). Likewise, a companion study of 20 diverse seed sources of the species, including the eight populations herein, with increased replication ($n = 6$ trees per population) across three common gardens, revealed population differences in respiration rate (at 20°C) on some dates and some sites, but no consistent genetic differentiation in respiration associated with geographic or climatic clines (Tjoelker *et al.*, 2008). The four northern and four southern populations examined here appeared to differ in magnitude of cold-temperature acclimation, suggesting that plasticity in thermal acclimation may exhibit genetic variation along climatic clines. However, significant differences in R_5 and Q_{10} among the populations were observed in only one of five measurement periods when trees were subjected to cooling and subfreezing fall temperatures (R_5 in November) or midwinter (Q_{10} in February) in the common garden. This suggests that cold-temperature acclimation may differ among these seed sources more so than acclimation to high temperatures. However, further study is needed to confirm this interpretation.

Cold hardiness is a critical adaptive trait in ensuring survival of temperate and boreal trees. Seasonal plasticity in acclimation among populations may, in part, reflect differences in the phenology of autumn cold hardening and concomitant changes in nonstructural carbohydrate and N concentrations, as observed in populations of *Pinus sylvestris* (Reich *et al.*, 1996; Oleksyn *et al.*, 2000, 2003). As evidence, needles of northern populations had comparatively lower R_5 , reduced water content, and increased raffinose and sucrose accumulation in November. These metabolic changes, reflecting cellular dehydration and an increase in cryoprotectant sugars, are associated with differences in the timing or magnitude of cold hardening among populations and species (Ögren *et al.*, 1997; Ögren, 1999; Klotke *et al.*, 2004).

That southern populations exhibited evidence of a greater plasticity in seasonal adjustments in R_5 and Q_{10} than northern seed sources appears contrary to the prediction that taxa originating in colder climates with wider temperature fluctuations exhibit increased capacity in temperature acclimation of CO_2 exchange rates, potentially leading to a greater degree of homeostasis when subjected to wide ambient temperature fluctuations (Billings *et al.*, 1971; Cunningham & Read, 2003). Billings *et al.* (1971) demonstrated a greater temperature acclimation of dark respiration in alpine than in arctic ecotypes of *Oxyria digyna* and attributed increased plasticity in acclimation capacity to greater climate variation at seed-source origin of the alpine than of the arctic populations. By comparison, Larigauderie & Körner (1995) found no consistent differences in acclimation among alpine and lowland taxa. Likewise, climatically diverse seed sources of *Pinus taeda* (Teskey & Will, 1999), *Acer rubrum*, and *Quercus alba*,

Q. rubra (Lee *et al.*, 2005) did not differ in plasticity of temperature acclimation of foliar dark respiration. In our study, mean values of the temperature–response parameters generally did not differ among populations on individual dates, and thus populations exhibited comparable mean amounts of thermal acclimation of respiration throughout much of the year. Nonetheless, the observed ranges in parameter values suggest that temperature–response functions of dark respiration were more stable (less plastic), and corresponding range in acclimation ratios lower across seasons in northern than in southern populations of *P. banksiana*.

Do R_5 and Q_{10} covary with foliar N and carbohydrate concentrations?

The positive correlation between R_5 and soluble sugar concentration in needles across populations and sample dates suggests that substrate availability and/or demand may be related to base respiration rates, especially during colder autumn and winter months when soluble carbohydrate concentrations, and particularly glucose, increased markedly (see also Tjoelker *et al.*, 2008). Although glucose and fructose are the primary monosaccharides catabolized by glycolysis, generating pyruvate, the initial substrate for the tricarboxylic acid cycle (i.e. mitochondrial dark respiration), it is unlikely that respiration is governed simply by substrate supply, but also by adenylate demand (Atkin & Tjoelker, 2003). Cold temperatures often result in increased concentrations of soluble carbohydrates in plants, in part reflecting decreased sink demands (Farrar & Williams, 1991). Concomitant increases in soluble carbohydrates and specific respiration rates in response to cold temperatures are often observed in controlled environments (Tjoelker *et al.*, 1999b; Atkin *et al.*, 2000; Covey-Crump *et al.*, 2002) and in field studies (Lee *et al.*, 2005; but see McCutchan & Monson, 2001). Although correlative evidence with respect to temperature effects *per se*, this observation is consistent with the prediction that temporal changes in the degree of substrate and/or adenylate limitations to respiration affect respiratory CO_2 efflux. Our findings indicate that seasonal respiratory adjustments were primarily mediated through changes in base respiration rate and concomitant changes in sugars and less so via changes in foliar N.

Overall, seasonal adjustments in R_5 and Q_{10} were unrelated to changes in foliar N concentrations, in agreement with findings for roots by Atkinson *et al.* (2007). However, adjustments in foliar N concentrations have been observed in plants grown or exposed to different temperatures (Tjoelker *et al.*, 1999b; Weih & Karlsson, 2001; Lee *et al.*, 2005) with the largest changes occurring in tissues that develop in contrasting thermal environments (Loveys *et al.*, 2003). We did not observe consistent intraspecific differences in needle N in this species, although specific rates of respiration at 20°C and needle N were positively correlated when comparing popula-

tions across three common gardens in a range of climates (Tjoelker *et al.*, 2008). Hence, variation in bulk leaf N may correlate with changes in specific respiration rates, as a result of the association of N with metabolic capacity as observed in many studies, especially broad comparisons of taxa and diverse sites. However, the respiration–nitrogen relationship may be masked, in part, when variation in substrate concentration, as in this study, is large. Thus, respiration rates may be predicted using both N and carbohydrates, as evident in the larger study of specific rates of respiration at 20°C (Tjoelker *et al.*, 2008).

Taken together our findings suggest that seasonal acclimation of foliar respiration in an evergreen was related to adjustments in the short-term temperature–response functions. Changes in base respiration rate, R_5 , appeared more important than changes in Q_{10} . Base respiration rate across seasons and populations was correlated with nonstructural soluble carbohydrates, perhaps reflecting shifts in substrate and/or adenylate limitations to respiratory processes. These findings support the concept of a substrate-based model of respiratory acclimation (Dewar *et al.*, 1999; Whitehead *et al.*, 2004), providing a linkage to photosynthetic carbon fixation and temporal changes in pools of soluble sugars, and perhaps constraining respiration–photosynthesis relationships. Moreover, our finding of common patterns of thermal acclimation of dark respiration among diverse populations of a wide-ranging tree species may simplify and improve process-based models that simulate respiratory carbon flux across large spatial scales.

Acknowledgements

This work was supported by the National Science Foundation (IBN-EEP 9630241), the Wilderness Research Foundation, the F. B. Hubachek Endowment at the University of Minnesota, and Texas AgriLife Research. We thank Ron Severs for assistance at the University of Minnesota, Cloquet Forestry Research Center. We thank Cindy Buschena and Ann Karpinski for technical assistance and Anna Szadel for assistance with the carbohydrate analyses with support of the Polish Academy of Sciences, Institute of Dendrology.

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