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Seasonal variation in the temperature response of leaf respiration in *Quercus rubra*: foliage respiration and leaf properties

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Summary

1. Leaf respiratory temperature responses and general leaf properties of *Quercus rubra* were measured throughout the 2003 growing season in a deciduous forest in the north-eastern USA. Measurements were made in the upper and lower portions of the canopy at two sites with different soil water availability. Correlations among respiration and various leaf properties were examined.

2. At a set temperature (10 and 20 °C), area-based leaf respiration rates were higher in both the early and late growing season than in the mid-growing season (0·50 *vs* 0·33 μmol CO_2 m^{-2} s^{-1} at 10 °C, on average). Upper-canopy leaves generally had higher respiration rates than lower-canopy leaves (0·53 *vs* 0·30 μmol CO_2 m^{-2} s^{-1} at 10 °C, on average). At the drier site a more significant seasonal pattern in respiration was observed, while at the more mesic site a stronger canopy-position effect was detected. E_0, a model variable related to the overall energy of activation of respiration, varied only slightly (52 ± 5 kJ mol^{-1} K^{-1}), and was not influenced by season, site or canopy position.

3. Leaf properties (specific leaf area, nitrogen, soluble sugars) also varied with season, site and canopy position. Leaf N and reducing monose were positively correlated with leaf respiration rates. After isolating single factors (season, site, canopy position), reducing monose could partially explain the seasonality in respiration (32–79%), and leaf N (N_{area}) was well correlated with the canopy-position effect.

4. Our results suggest that the temporal and spatial heterogeneities of respiration need to be considered in ecosystem models, but significant simplifications may be made in *Q. rubra* by assuming a constant temperature coefficient (E_0, 52·5 kJ mol^{-1} in this study) or predicting the base respiration rate (R_0) from well understood leaf properties.

Key-words: carbohydrates, dark respiration, deciduous forest, nitrogen, thermal acclimation

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Introduction

Warming will raise global temperatures 1·4–5·8 °C by the end of this century (Hansen *et al*. 1999; IPCC 1999). Furthermore, warming is likely to be more significant at night (Easterling *et al*. 1997; Alward, Detling & Milchunas 1999; IPCC 1999), when respiration is the dominant physiological process in plants. Respiration is a primary biological process regulating the exchange of carbon between the atmosphere and the terrestrial biosphere. It is the small difference between two large fluxes, photosynthesis and respiration (net photosynthesis, 122 GT C $year^{-1}$; autotrophic respiration, 64 GT C $year^{-1}$ plus heterotrophic respiration, 58 GT C $year^{-1}$; Schimel 1995; Hansen *et al*. 1999; Field 2001) that determines the carbon balance of an ecosystem. Globally, plant respiration releases ≈50% of the carbon fixed through net photosynthesis (Amthor 1989; Ryan 1991); of this, 80% of plant respiratory CO_2 is attributable to forest trees (Hall & Scurlock 1993; Houghton 1993). Because plant respiration is highly sensitive to temperature, global warming could dramatically influence the size of the respiratory flux and potentially carbon storage in forest ecosystems. Therefore understanding the temperature response of tree respiration is critical if we are to estimate the potential future forest carbon sink.

Foliar respiration accounts for up to two-thirds of total tree respiration (Hagihara & Hozumi 1991;

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Ryan, Lavigne & Gower 1997) and is the most commonly studied respiratory component of a tree's carbon budget. Typically, leaf respiration rates double for each successive 10 °C increment in temperature (Q_{10}; Ryan 1991), but the value of Q_{10} can be highly variable, ranging between 1·1 and 4·2 (Azcon-bieto & Osmond 1983; Azcon-bieto 1992; Tjoelker, Oleksyn & Reich 2001). Models based on an Arrhenius function are also commonly used to describe the response of respiration to temperature, and have a stronger mechanistic underpinning (Lloyd & Taylor 1994; Turnbull *et al*. 2001). Under natural field conditions, leaves are exposed to many environmental factors that may influence both the rate of respiration and the way it responds to temperature (growth temperature, canopy position, soil moisture; Turnbull *et al*. 2001, 2003). In addition to the short-term respiratory temperature response, longer-term changes in both the respiration rates of leaves and the short-term temperature response may be caused by metabolic adjustments (acclimation).

Although not completely elucidated, close relationships have been found between respiration and a variety of leaf characteristics. For example, a positive leaf nitrogen–respiration relationship, which is attributed to the more general relationship between protein concentration and the associated maintenance requirements, exists across terrestrial ecosystems, functional groups and canopy levels (Ryan 1991, 1995; Reich, Oleksyn & Tjoelker 1996; Ryan *et al*. 1996a; Reich *et al*. 1998a, 1998b; Griffin *et al*. 2001; Griffin, Turnbull & Murthy 2002; Turnbull *et al*. 2003). Similarly, soluble carbohydrate concentrations in leaves may regulate the temperature response by limiting the formation of respiratory substrates (Atkin, Holly & Ball 2000; Griffin *et al*. 2002). A better understanding of these respiration–leaf property relationships may improve our ability to predict physiological adjustments of respiration rates and the respiratory temperature response of plants under future environmental conditions.

In order to scale-up leaf-level results to tree, canopy and ecosystem levels, a better understanding is needed of the patterns and regulation of spatial and temporal variation in the leaf respiratory temperature response. At the individual tree level, previous studies have found that upper-canopy leaves have higher respiration rates than lower-canopy leaves; this phenomenon was attributed to the higher maintenance requirements of the more active photosynthetic apparatus in upper-canopy leaves (Griffin *et al*. 2001, 2002; Tissue *et al*. 2002; Turnbull *et al*. 2003; Whitehead *et al*. 2004). Furthermore, at the ecosystem level, it has been observed that sites with more abundant soil water availability have lower leaf respiration rates (Turnbull *et al*. 2001, 2003). Long-term studies also show significant seasonal and annual variations in respiration in conifer forests and seedlings (Stockfors & Linder 1998; Atkin *et al*. 2000; Vose & Ryan 2002). However, to the best of our knowledge there are no comprehensive studies of the temporal, spatial or canopy-position effects, or their interactions, on tree respiratory temperature responses. Furthermore, it is unclear whether the positive relationships between leaf nitrogen or leaf soluble sugars and the rate of respiration, which were originally described across biomes and functional groups (Reich *et al*. 1998a,b), can explain the spatial and temporal variation of respiratory temperature responses in individual plant species from specific landscapes.

The north-eastern deciduous forests of the USA are regenerating rapidly, and are believed to be important carbon sinks in the northern hemisphere (Myneni *et al*. 2001; Hooker & Compton 2003). Here we measured leaf respiratory temperature responses and leaf properties, and examined the respiration–leaf property relationships of *Quercus rubra* in a north-eastern deciduous forest throughout the 2003 growing season. The forest is located in south-eastern New York State and is actively sequestering carbon in tree biomass (W. Schuster, unpublished data). Measurements were made in both the upper and lower tree canopy at two sites with different water availability. We expected that leaf respiration rates and general leaf properties (specific leaf area, leaf nitrogen, leaf carbohydrates, etc.) would vary with season, site, canopy level or their interactions. For a better mechanistic understanding, we hypothesized that (1) the model parameters of leaf respiratory temperature response (E_0 and R_0, see Materials and methods) would vary with season, site and canopy position; (2) due to the difference in light environment of the two sites, the seasonal effect would be more significant at the drier site, while the canopy effect would be more significant at the more mesic site; (3) the respiration rate would be positively related to leaf nitrogen and soluble sugars (monose and sucrose); and (4) the temporal and spatial patterns in respiration could be explained by different leaf properties (leaf nitrogen, monose and sucrose).

Materials and methods

STUDY SITE AND FIELD PLOTS

Black Rock Forest is a 1500-ha reserve in south-eastern New York State, located at 41°24′ N, 74°01′ W with elevations ranging from 150 to 450 m a.s.l. The air temperature is strongly seasonal, with monthly average temperature ranging from –2·7 °C in January to 23·4 °C in July. The average annual precipitation is 1·2 m (Black Rock Forest climate database). Black Rock Forest is a *Quercus*-dominated secondary growth forest that is a characteristic of the north-eastern USA. Dominant tree species include Red Oak (*Quercus rubra*, 42·3% basal area), Chestnut Oak (*Quercus prinus*, 23·8% basal area) and Red Maple (*Acer rubrum*, 7·6% basal area; Turnbull *et al*. 2001). The soils are typically brown forest soils, acidic and low in nutrients (Lorimer 1981), with granite gneiss bedrock or glacial till parent material at 0·25–1 m depth (Olsson 1981).

The Cascade Brook watershed is a 135-ha plot in the south-eastern portion of Black Rock Forest, with elevation from 210 to 430 m. Two 0·1-ha permanent research sites were established in 1999 at a 270-m lowland and at a 410-m upland site. The two sites differed significantly with respect to water availability, and the distribution of these species along this elevation gradient follows their drought tolerance (Engel *et al*. 2002). In this study, the stable carbon isotope of leaf tissue was measured as an indicator of soil water availability (see 'Leaf analysis'). For detailed descriptions of the two sites see Turnbull *et al*. (2001); Engel *et al*. (2002). Meteorological conditions of the forest are continuously measured and recorded by two standard meteorological stations run by the Black Rock Forest staff.

RESPIRATION MEASUREMENTS

Physiological measurements were made four times during the 2003 growing season: 11–16 June, 30 July–1 August, 17–18 September and 20–23 October. At each site, leaf dark respiration was measured on six fully expanded leaves from three trees from the sunlit upper canopy and the same three trees from the shaded lower canopy. Sampled trees were generally representative in height and crown size.

Dark respiration was measured with infrared gas analysis systems (LI-6400, Li-Cor, Lincoln, NE, USA) equipped with CO_2 and temperature-control modules. Large branches from trees were excised under water in the field in late afternoon and dark acclimated for a minimum of 1·5 h before measurements began. All measurements were made between 5 pm and 2 am in a growth chamber with temperature control (Conviron E15, Winnipeg, Canada). Respiration rates were measured at five to seven temperature set points between 5 and 35 °C (typically 10, 15, 20, 25 and 30 °C). Temperature within the cuvette (enclosing 6 cm^2 leaf area) was controlled to match the ambient air temperature in the growth chamber. During these measurements, air flow through the cabinet ensured the ambient [CO_2] in the cabinet, and thus surrounding the plant material and gas-exchange cuvette, was maintained very close to outside ambient levels. CO_2 partial pressure in the cuvette was maintained at 400 p.p.m. throughout the measurements. At each temperature set point, the leaves were left for 15–20 min to stabilize the respiration rate before recording. The measurements were made on leaves attached to branches at least 1 cm in diameter, and respiration rates were recorded when gas exchange had equilibrated (taken to be when the rate of CO_2 efflux was visually stable and the coefficient of variation for CO_2 partial pressure differential between the sample and reference was <0·3%). Previous studies have shown no differences in leaf respiration rates and respiratory temperature responses measured *in situ* or on detached branches of *Q. rubra* (Mitchell, Bolstad & Vose 1999), and this was verified for *Q. rubra* at our research site (M. H. Turnbull and K.L.G., unpublished data). The respiration rates are reported in area-, mass- and nitrogen-based units. In general, area-based respiration is appropriate for comparison with photosynthetic rates, as the latter is limited by light-harvesting area, while mass- and nitrogen-based units more closely reflect biomass or living tissue maintenance requirements.

The temperature-response curves were analysed using a modified Arrhenius equation described by Lloyd & Taylor (1994), which had been applied to *Q. rubra* by Turnbull *et al*. (2001):

$$R = R_0 e^{\frac{E_0}{R_g}\left(\frac{1}{T_0}-\frac{1}{T_a}\right)} \quad \text{(eqn 1)}$$

where R_0 is the respiration rate at a base temperature T_0 (10 °C, 283 K in our study), T_a is the measurement temperature (K) of R, and R_g is the ideal gas constant (8·314 J mol^{-1} K^{-1}). Originally this type of model was used to describe the temperature response of a simple chemical reaction and E_0 is the energy of activation (kJ mol^{-1}). When applying the model to respiration, we thus simplify and treat the overall chemical processes of respiration as a single reaction. By doing so, E_0 is equivalent to the overall energy of activation, similar but not identical to the energy of activation for a single enzyme reaction. Previous studies have indicated that E_0 appears constant over the physiological temperature range of temperate species (Lyons & Raison 1970). When using this model, the temperature-response curve can be described by the intercept (base respiration rate), which is represented by the parameter R_0, while the curvature (sensitivity of respiratory temperature response) is represented by both R_0 and E_0. The model was fitted using SIGMAPLOT 2001 (SPSS Inc., Chicago, IL, USA). In addition to R_0 (respiration at 10 °C), respiration rate at 20 °C (R_{20}), and the ±7-day night average temperature bracketing the measurement period (R_{ave}), were also calculated.

The commonly used Q_{10}, a simple parameter to measure respiratory temperature response, can be linked to this model by:

$$Q_{10} = e^{\frac{E_0}{R_g}\left(\frac{1}{T_2}-\frac{1}{T_1}\right)} \quad \text{(eqn 2)}$$

$$T_1 - T_2 = 10\ (°C) \quad \text{(eqn 3)}$$

Clearly Q_{10} is temperature-dependent (Atkin & Tjoelker 2003). In this study, a Q_{10} of 15–25 °C was calculated to facilitate comparison with other studies reporting only Q_{10} values.

LEAF ANALYSIS

All analyses were performed on the same leaf material as was used for respiration measurements. Following the dark respiration measurements, several leaf disks were immediately frozen in liquid nitrogen for carbohydrate analysis. The area of the remaining leaf material

(excluding the midrib and petiole) was determined using a leaf-area meter (Li-3000, Li-Cor), then dried in a 60 °C oven for a minimum of 48 h. The dried leaf material was weighed to calculate specific leaf area (SLA), then ground to fine powder for nitrogen and carbon stable isotope ratio ($\delta^{13}C$) analysis with a Europa 20/20 continuous flow isotope ratio mass spectrometer (CF-IRMS) coupled with an ANCA NT combustion system (PDZ-Europa, Cheshire, UK). Leaf soluble carbohydrates (sucrose and reducing monose, the latter including glucose and fructose) in the harvested leaf discs were determined colorimetrically using the ethanol extraction technique of Hendrix (1993) as described by Griffin, Sims & Seemann (1999), with required modifications. As the Sigma-Aldrich glucose kit #115A, used in the original protocol, is no longer commercially available, glucose kit GATK-20 (Sigma-Aldrich (St Louis, MO, USA) was substituted. The carbohydrate contents were determined by measuring the absorption at 340 nm. All samples were analysed in triplicate and reported as the mean value. Leaf nitrogen results were reported on an area (N_{area}) and mass (N_{mass}) basis. Leaf soluble carbohydrates were reported on an area (monose, M_{area}; sucrose, S_{area}), mass (M_{mass}; S_{mass}) and nitrogen (M_N; S_N) basis.

STATISTICAL ANALYSIS

Because the same trees were sampled on each of the four sampling dates, a repeated-measures ANOVA was used to test for the main effects and interactions of season, site and canopy position on all respiration parameters and leaf properties (STATISTICA, Statsoft Inc., Tulsa, OK, USA). Predetermined comparisons of the respiratory parameters (E_0, R_0) were made among the season, site and canopy position using a simple *t*-test (EXCEL, Microsoft, Seattle, WA, USA). The difference between two groups was considered significant if the probability was <0·05. Multivariant regression was used to analyse the relationships between respiration at 20 °C (R_{20}) and leaf properties, and these correlations were considered significant if the probability of the partial correlation coefficient was <0·05 (STATISTICA). All data were log-transformed to fulfil the assumptions of normality and homoscedasticity.

Results

ENVIRONMENTAL CONDITIONS OF THE RESEARCH SITE IN 2003

The 14-day (±7 days bracketing measurement days) average night temperature across the measurement period peaked in late July (21 °C) then dropped to 5 °C in late October, but there was no difference between the two research sites (Fig. 1b).

The carbon stable isotope ratios ($\delta^{13}C$) of upper-canopy leaves were constantly heavier in the upper site across the entire growing season, indicating higher water-use efficiency and lower water availability. In contrast, $\delta^{13}C$ of the lower-canopy leaves did not show a site effect, as water availability is less likely to affect stomatal openness in the shady, cool lower canopy.

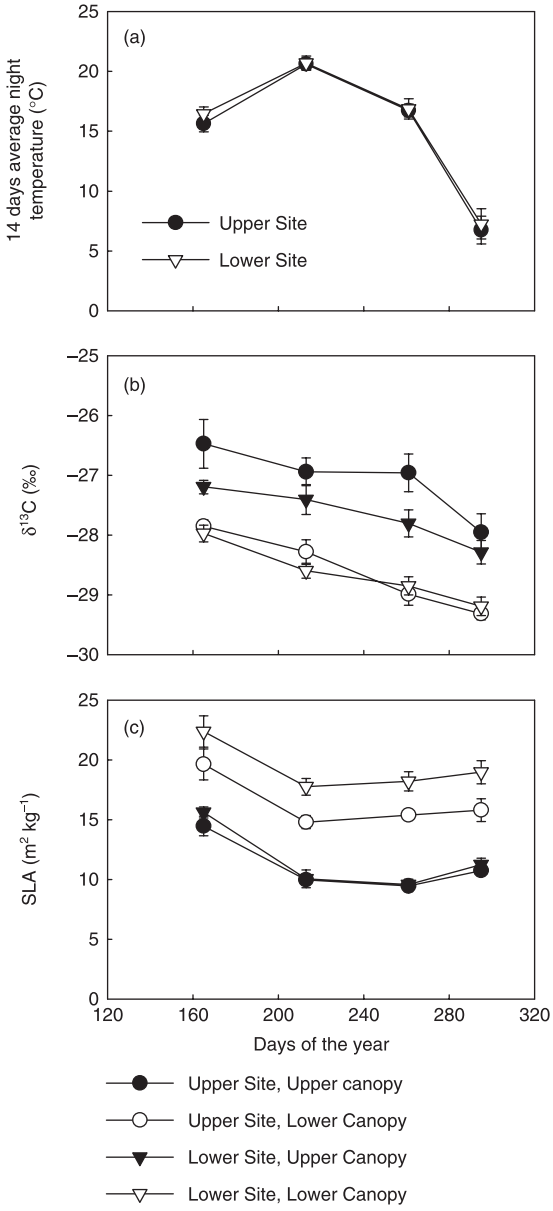

Fig. 1. Seasonal variation of environmental conditions and specific leaf area. (a) 14-day average night temperature during the period of measurement (●, upper site; ▽, lower site); (b) $\delta^{13}C$ of leaf bulk organic material as an indicator of tree water-use efficiency and soil water availability (●, upper site, upper canopy; ○, upper, lower canopy; ▼, lower site, upper canopy; ▽, lower site, lower canopy); (c) specific leaf area. Values shown are means (± SEM) where $n = 14$ (a); $n = 6$ (b,c).

RESPIRATORY TEMPERATURE RESPONSE COEFFICIENT (E_0)

E_0 was unaffected by season, site, canopy position ($F = 0–2·5$, $P > 0·07$, ANOVA), and the influence of season × canopy position and season × site × canopy position interactions was only marginally significant

Table 1. Model parameters of respiratory temperature response in all season/site/canopy position combinations

Model parameter	Sampling period	Upper site		Lower site	
		Upper canopy	Lower canopy	Upper canopy	Lower canopy
E_0 (kJ mol^{-1})	06/11–06/16	51·0 (3·0)^{abc}	54·8 (1·9)^{ab}	57·6 (1·1)^{a}	51·2 (1·3)^{bc}
	07/30–08/01	52·5 (1·9)^{bc}	52·1 (1·3)^{bc}	49·5 (2·4)^{bc}	56·7 (3·1)^{ab}
	09/17–09/18	55·4 (1·5)^{ab}	55·1 (2·7)^{abc}	47·0 (2·4)^{c}	55·6 (1·9)^{ab}
	10/20–10/23	52·0 (1·2)^{bc}	49·7 (2·7)^{bc}	51·5 (2·8)^{abc}	48·2 (3·2)^{bc}
R_0 (area, 10 °C) (μmol m^{-2} s^{-1})	06/11–06/16	0·64 (0·06)^{a}	0·43 (0·06)^{bcd}	0·51 (0·03)^{ab}	0·28 (0·03)^{e}
	07/30–08/01	0·39 (0·01)^{d}	0·20 (0·02)^{f}	0·45 (0·05)^{bcd}	0·21 (0·03)^{ef}
	09/17–09/18	0·39 (0·04)^{d}	0·21 (0·02)^{ef}	0·60 (0·05)^{a}	0·17 (0·01)^{f}
	10/20–10/23	0·59 (0·04)^{a}	0·47 (0·06)^{abcd}	0·64 (0·06)^{a}	0·40 (0·03)^{cd}
R_0 (mass, 10 °C) (μmol kg^{-1} s^{-1})	06/11–06/16	8·5 (0·42)^{a}	8·0 (0·57)^{ab}	7·9 (0·42)^{ab}	6·1 (0·44)^{cd}
	07/30–08/01	3·9 (0·19)^{ef}	2·9 (0·18)^{h}	4·4 (0·29)^{e}	3·6 (0·43)^{efgh}
	09/17–09/18	3·6 (0·25)^{efg}	3·2 (0·29)^{fgh}	5·6 (0·32)^{d}	3·0 (0·20)^{gh}
	10/20–10/23	6·3 (0·39)^{cd}	7·4 (0·54)^{abc}	7·1 (0·47)^{bc}	7·6 (0·53)^{abc}

E_0 is a parameter equivalent to the energy of activation for respiration as an overall reaction, and is similar, but not identical, to the energy of activation for a single enzyme reaction.
R_0 (on an area basis and a mass basis) is the base respiration rate at 10 °C.
Values shown are means (± SEM) where $n = 6$. Means were compared in pairs among all 16 season/site/canopy position combinations by *t*-test. If two values are followed by the same letter, they are not significantly different at $P = 0·05$.

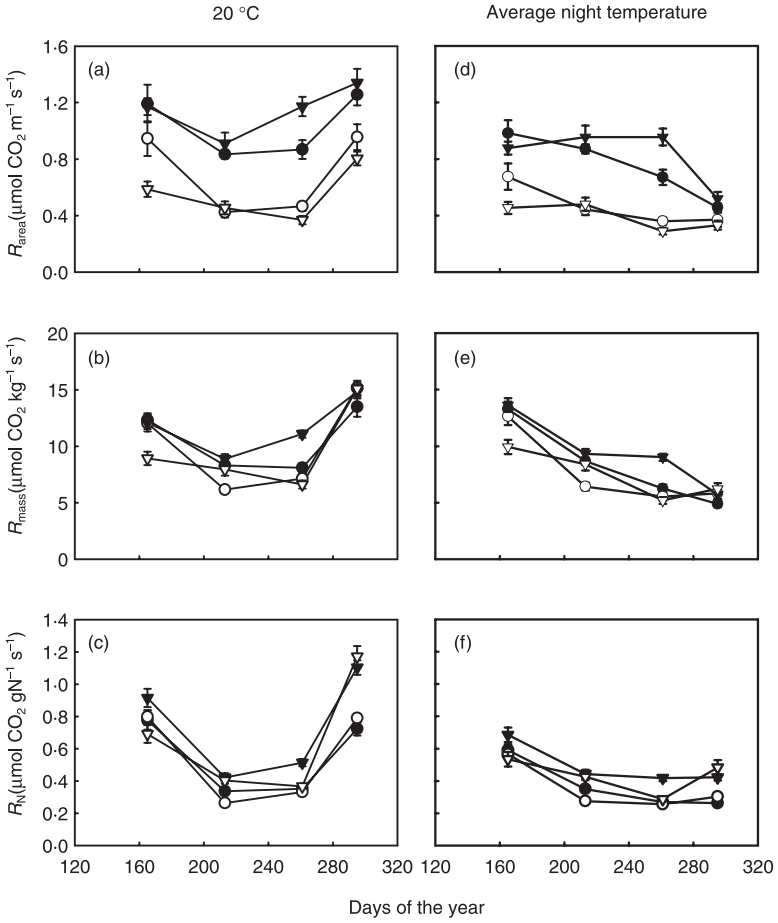

Fig. 2. Seasonal variation of dark respiration rates estimated from fitted temperature-response curves (Fig. 2) for *Quercus rubra* leaves in four site–canopy position combinations. Parameters R_{area} (upper panel); R_{mass} (middle panel); R_N (lower panel) are area-, biomass- and nitrogen-based dark respiration rates calculated from the fitted responses. Respiration rates at 20 °C (a–c) or at the 14-day average night temperature bracketing the measurement period (d–f) are plotted. Values shown are means (± SEM), $n = 6$. Symbols as in Fig. 1(b,c).

($F = 2·8$, $P = 0·05$, ANOVA). Only the upper-canopy leaves from the lower site showed a distinctively high (mid-June) or low (mid-September) E_0 (Table 1, *t*-test). Averaged across all season–site–canopy-position combinations, E_0 was 52·5 kJ mol^{-1}, with a small deviation of ±10% (5 kJ mol^{-1}). Q_{10} (15–25 °C) of all season–site–canopy-position combinations ranged from 1·93 to 2·24, with an average of 2·09.

LEAF RESPIRATION RATES

In all site–canopy-position combinations, R_{area} (at 10 and 20 °C) displayed a strong and consistent seasonal pattern (Table 1; Fig. 2a). R_{area} in late October and mid-June was significantly higher than in late July and mid-September. Upper-canopy leaves displayed higher R_{area} at both sites. Site alone did not have a significant effect on R_{area}, but site × canopy position and season × site interaction were all significant ($F = 4·1–6·5$, $P < 0·02$, ANOVA). In general, leaves from the upper site showed more seasonal variation, while leaves from the lower site showed more canopy-position variation (Fig. 2a). The seasonal trends in R_{mass} and R_N are similar to, but stronger than, the trends in R_{area} (Table 1; Fig. 2a–c). Canopy-position effects were much smaller in both R_{mass} and R_N, although still highly significant (Table 1; Fig. 2).

Respiration rates estimated at the average field night temperatures corresponding to the measurement periods (±7 days) shed light on the actual *in situ* respiration rates. In general, respiration rates gradually declined through the growing season, reflecting the combined effects of respiratory acclimation and temperature change (Fig. 1). Furthermore, the seasonal variation of R_{ave} was smaller than respiration rates at a set temperature (e.g. 20 °C, Fig. 2).

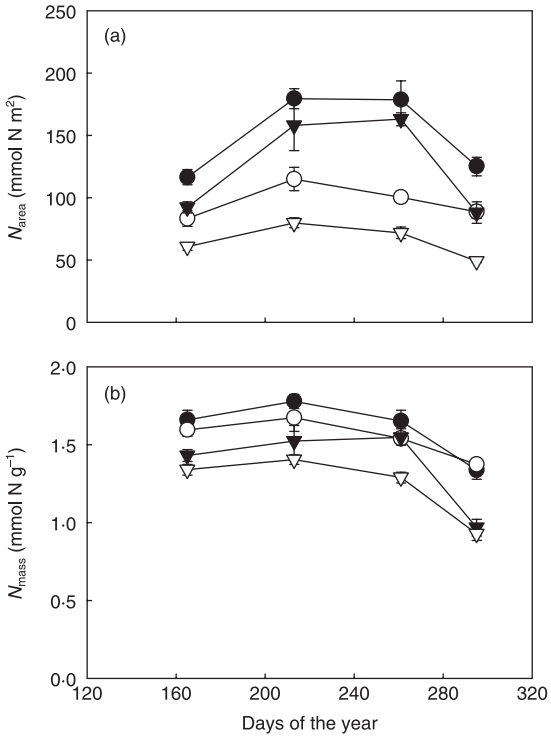

Fig. 3. Seasonal variation in leaf nitrogen in the four site–canopy-position combinations with leaf nitrogen expressed on an (a) area basis; (b) mass basis. Values shown are means (± SEM), $n = 6$. Symbols as in Fig. 1(b,c).

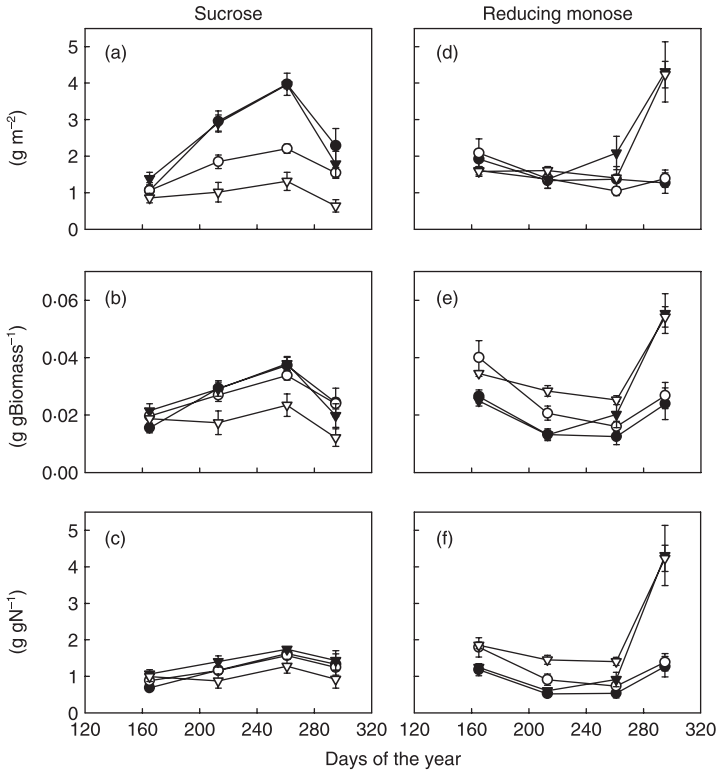

Fig. 4. Seasonal variation in leaf sucrose and reducing monose (including glucose and fructose) in the four site–canopy-position combinations. Concentrations are presented for area (upper panel); mass (middle panel); nitrogen (lower panel). Values shown are means (± SEM) where $n = 6$. Symbols as in Fig. 1(b,c).

LEAF NITROGEN

N_{area} was significantly affected by season, site and canopy position ($F = 47$–139, $P < 0{\cdot}0001$, ANOVA). The seasonal pattern in N_{area} was uniform across all site and canopy-position combinations, but the inverse of the pattern in respiration rates (Fig. 3). The site and canopy effects were also clear. Upper-site leaves and upper-canopy leaves had higher N_{area} (37 and 72% higher than lower-site and lower-canopy leaves, respectively).

Different seasonal patterns were observed in N_{mass}. From June to September N_{mass} varied only slightly, but then declined significantly in late October. Significant site and canopy-position effects on N_{mass} were observed, but the magnitude of these differences was smaller than that in N_{area}.

LEAF SUGARS

Although non-structural carbohydrate pools may turn over quickly, observed leaf sucrose and monose of *Q. rubra* still displayed a clear seasonal pattern. Leaves of *Q. rubra* contained similar amounts of sucrose and reducing monose (e.g. range $0{\cdot}5$–4 g m^{-2} on an area basis throughout the growing season), but the seasonal patterns were clearly different. The observed leaf sucrose concentration (S_{area}, S_{mass}, S_N) increased through the growing season until late October, when the concentration dropped; reducing monose showed the inverse pattern (Fig. 4). In combination, the low sucrose and high reducing monose levels in leaves during mid-June are consistent with the active leaf growth during this period, while the decline of sucrose and increase in reducing monose in late October can be attributed to translocation prior to leaf loss. The canopy and site effects were more complex. S_{area} and S_{mass} increased much faster in upper-canopy leaves through the growing season, especially at the lower site. The site and canopy effects on S_{mass} and S_N were all absent ($F = 0{\cdot}06$–$2{\cdot}88$, $P > 0{\cdot}10$, ANOVA; Fig. 4b,c). Site and canopy position had little effect on M_{area} ($F = 0{\cdot}36$–$3{\cdot}69$, $P > 0{\cdot}07$, ANOVA) but significantly affected M_{mass} and M_N ($F = 9{\cdot}2$–$24{\cdot}8$, $P < 0{\cdot}006$, ANOVA; Fig. 4e,f).

LEAF ONTOGENY

There was a significant effect of canopy position on leaf thickness ($F = 172$, $P < 0{\cdot}0001$, ANOVA; Fig. 1d) and, as expected, lower-canopy leaves had a much higher SLA. Although the leaves were visually mature in mid-June, higher SLA indicated that leaves were still actively growing, which is also reflected in the change in leaf nitrogen and soluble sugars from mid-June to late July. During the remainder of the growing season, SLA increased only slightly from late July to October. Additionally, in the lower canopy, leaves from the upper site were significantly thicker.

CORRELATIONS BETWEEN RESPIRATION RATE AND LEAF PROPERTIES

A multivariant regression was first applied to all data throughout the season, site and canopy positions to examine the general relationship between leaf respiration (at 20 °C, area-, mass- and nitrogen-based: $R_{20(area)}$, $R_{20(mass)}$, $R_{20(N)}$) and leaf properties (N_{area}, N_{mass}, M_{area}, M_{mass}, M_N, S_{area}, S_{mass}, S_N). Then regressions were performed on particular subsets of the data to isolate the three individual factors. For example, to isolate the seasonal effect, regressions were run on leaf data sets of four site–canopy position combinations (UU, UL, LU, LL; Table 2). The multiple correlation coefficients of regressions and partial correlation coefficients of each leaf property are presented in Table 2.

Multivariant regression on all data illustrated that $R_{20(area)}$ was significantly correlated with N_{area} and M_{area}, but $R_{20(mass)}$ was correlated only with M_{mass}. Sucrose, the main storage and transport sugar, was not significantly correlated with leaf respiration, regardless of the unit of expression. However, only a small part of the overall variation in leaf respiration was explained by the leaf properties examined (25–36%). Once factors were isolated, regression correlations among respiration and leaf properties were specific to season, site or canopy position. Seasonal variations in respiration rates were partially related to variations in reducing monose, especially for $R_{20(N)}$. On the other hand, canopy-position effects on respiration were well explained by N_{area} (Table 2), but N_{mass} could not explain the canopy effects. Finally, site variation in R_{20} could not be well explained by nitrogen or soluble sugars. In most cases, sucrose (S_{area}, S_{mass}, S_N) was not significantly correlated with respiration.

Discussion

MODEL PARAMETERS OF RESPIRATORY RESPONSE TO TEMPERATURE

In the Arrhenius model, the response of respiration to leaf temperature is partially represented by the parameter E_0, which linearly determines ln R. Variations in E_0 are related to the cumulative change in the energy of activation for respiration as an overall reaction, and shed light on possible biochemical/physiological adjustments in respiration (such as temperature acclimation). In our study, the average E_0 is very similar to previously reported values for *Q. rubra* (Turnbull *et al*. 2003) measured early in the growing season (June). Furthermore, E_0 was not influenced by season, site or canopy position, and the influence of season × canopy position and season × site × canopy position interactions was only marginally significant. The deviation from the mean value was small (10%; Table 1). This constant E_0 suggests that the energy of activation of dark respiration as an overall reaction is stable, and is influenced only slightly by environmental conditions in *Q. rubra*, indicating uniform substrate source and reaction pathways. On the other hand, R_0 not only determines the base respiration rate (intercept of modelled temperature response), but also affects the respiratory temperature response. The variation in the respiratory temperature response observed in this experiment appears to be mainly related to a significant variation in R_{10} (Tables 1 and 2). The constant E_0 and variable R_0 are consistent with some previous observations (Bolstad, Mitchell & Vose 1999; but cf. Griffin *et al*. 2001); further studies are needed to examine whether the pattern is generalizable in diverse plant species and growth conditions. If expressed as Q_{10} (15 *vs* 25 °C), the average respiratory temperature response is 2·09, also comparable with recent studies on Red Oak and other related species (Bolstad *et al*. 1999; Amthor 2000; Turnbull *et al*. 2001, 2003).

RESPIRATORY ACCLIMATION TO SEASONAL TEMPERATURE CHANGE

The leaf respiratory response to temperature is known to be a function of both temperature and physiological history (Amthor 1989; Atkin *et al*. 2000). Seasonal variation and thermal acclimation of respiration have been reported mostly in conifers or in tree seedlings (Stockfors & Linder 1998; Atkin *et al*. 2000; Oleksyn *et al*. 2000; Vose & Ryan 2002). Here we observed similar patterns in ≈100-year-old *Q. rubra* trees, characterized by reduced leaf respiration rates (at a set temperature, e.g. 10 or 20 °C) and lower sensitivity to temperature in the warm mid-growing season, compared with significantly higher respiration rates and a more sensitive temperature response in the cooler early and late growing season (Figs 1 and 3). The obvious thermal acclimation partly offset the effect of seasonal temperature variation on *in situ* leaf respiration rates. In general, the respiration rates at the ±7-day average night temperature gradually decrease over the 5-month period (Fig. 3), indicating declining leaf-level carbon loss and physiological activities throughout the growing season.

Temperature acclimation of respiration has been suggested to be of two types (Atkin & Tjoelker 2003). Type I acclimation is characterized predominantly by a change in Q_{10} (which can be calculated from E_0 in the model used in this study, equations 2 and 3), with little or no change in the respiration rate at a base temperature (R_0), and is probably affected by substrate availability, adenylate restriction, or both. By contrast, Type II acclimation is associated with a change in both R_0 and the respiration rate at moderately higher temperatures (e.g. 20 °C), and has been attributed to temperature-mediated changes in respiratory capacity. In our study, a constant E_0 and variable R_0 across the growing season suggests typical type II seasonal temperature acclimation in *Q. rubra*. Therefore we speculate that mechanisms directly influencing respiratory capacity, such as enzyme activity and concentration, or overall

Table 2. Summary of multivariant correlation analysis between R at 20 °C (R_{20}) and leaf properties (leaf nitrogen, reducing monose and sucrose) in *Quercus rubra*

		$R_{20(area)}$ (μmol CO_2 m^{-2} s^{-1})				$R_{20(mass)}$ (μmol CO_2 kg^{-1} s^{-1})				$R_{20(N)}$ (μmol CO_2 g^{-1} N s^{-1})		
			Partial correlation coefficient				Partial correlation coefficient				Partial correlation coefficient	
Effects isolated	Data group	R^2	N_{area} (mmol N m^{-2})	M_{area} (g m^{-2})	S_{area} (g m^{-2})	R^2	N_{mass} (mmol N g^{-1})	M_{mass} (g g^{-1})	S_{mass} (g g^{-1})	R^2	M_N (g g^{-1} N)	S_N (g g^{-1} N)
(n = 96)	All	**0·36*****	**0·39*****	**0·46*****	–0·007 ns	**0·22*****	–0·03 ns	**0·32****	–0·12 ns	**0·42*****	**0·61*****	–0·04 ns
Season	UU	**0·40***	–0·19 ns	**0·54****	–0·07 ns	**0·66*****	–0·35 ns	**0·51***	–0·56**	**0·48****	**0·57****	–0·25 ns
(n = 24)	UL	0·29 ns	–0·18 ns	**0·46***	0·04 ns	**0·44****	–0·28 ns	0·39 ns	–0·20 ns	**0·41*****	**0·57****	0·04 ns
	LU	0·23 ns	0·26 ns	0·39 ns	–0·27 ns	**0·34***	0·10 ns	0·31 ns	–0·36 ns	**0·57*****	**0·72*****	–0·24 ns
	LL	**0·64*****	–0·19 ns	**0·73*****	0·14 ns	**0·66*****	0·26 ns	**0·72*****	0·11 ns	**0·80*****	**0·89*****	0·11 ns
Canopy	13 Jun US	**0·73***	0·62 ns	0·30 ns	**0·66***	0·19 ns	–0·04 ns	0·06 ns	0·41 ns	0·41 ns	0·30 ns	0·53 ns
position	13 Jun LS	**0·91*****	**0·93*****	–0·08 ns	–0·72*	0·54 ns	0·25 ns	–0·67*	–0·61 ns	0·41 ns	–0·57 ns	–0·63*
(n = 12)	31 Jul US	**0·91*****	**0·86****	–0·57 ns	0·02 ns	0·73*	0·49 ns	–0·79**	0·11 ns	**0·50***	–0·70*	0·03 ns
	31 Jul LS	**0·92*****	**0·85****	–0·12 ns	0·23 ns	0·32 ns	0·48 ns	–0·13 ns	0·15 ns	0·12 ns	0·05 ns	0·30 ns
	21 Sep US	**0·91*****	**0·68***	0·29 ns	0·44 ns	0·43 ns	0·53 ns	0·20 ns	0·39 ns	0·13 ns	0·04 ns	0·27 ns
	21 Sep LS	**0·99*****	**0·97*****	–0·63 ns	0·06 ns	**0·87****	**0·81****	–0·70*	–0·04 ns	0·56*	–0·61*	0·42 ns
	17 Oct US	**0·92***	**0·93*****	0·36 ns	–0·04 ns	0·73*	0·60 ns	0·43 ns	–0·56 ns	0·54 ns	0·39 ns	–0·50 ns
	17 Oct LS	**0·92*****	**0·90*****	0·59 ns	–0·26 ns	0·21 ns	0·34 ns	0·13 ns	–0·12 ns	0·47 ns	**0·64***	–0·31 ns
Site	13 Jun UC	0·47 ns	–0·26 ns	**0·64***	0·23	0·32 ns	–0·48 ns	0·22 ns	–0·18 ns	0·44 ns	0·61 ns	0·27 ns
(n = 12)	13 Jun LC	**0·85*****	**0·85****	0·05 ns	–0·29*	0·35 ns	0·59 ns	–0·02 ns	–0·10 ns	0·02 ns	–0·04 ns	–0·12 ns
	31 Jul UC	0·37 ns	0·48 ns	0·04 ns	–0·17 ns	0·22 ns	–0·30 ns	0·16 ns	–0·44 ns	0·13 ns	–0·17 ns	0·35 ns
	31 Jul LC	0·21 ns	0·39 ns	0·10 ns	–0·07 ns	0·06 ns	–0·03 ns	0·02 ns	–0·19 ns	0·33 ns	0·49 ns	–0·11 ns
	21 Sep UC	0·23 ns	0·23 ns	0·27 ns	0·20 ns	0·22 ns	–0·29 ns	0·41 ns	0·29 ns	0·17 ns	0·26 ns	0·37 ns
	21 Sep LC	**0·77****	**0·67***	0·50 ns	0·42 ns	0·47 ns	0·44 ns	0·48 ns	0·41 ns	0·32 ns	0·57 ns	0·42 ns
	17 Oct UC	**0·67***	**0·79****	**0·69***	–0·25 ns	**0·61***	0·59 ns	**0·67***	–0·38 ns	**0·82*****	**0·90*****	–0·08 ns
	17 Oct LC	**0·72***	**0·79***	**0·70***	–0·08 ns	0·21 ns	0·28 ns	0·43 ns	0·13 ns	**0·77****	**0·85****	–0·13 ns

Original data were log-transformed. Multiple correlation coefficients (R^2), partial correlation coefficients (r) of each leaf property and statistical significance levels are shown (*, $P < 0·05$, **, $P < 0·01$, ***, $P < 0·001$).

UU, Upper site, upper canopy; UL, upper site, lower canopy; LU, lower site, upper canopy; LL, lower site, lower canopy; US, upper site; LS, lower site; UC, upper canopy; LC, lower canopy.

Bold type highlights significant R^2, which can be attributed to some positive partial correlations, and all significant positive partial correlation coefficients.

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demand for respiratory products, are likely to be primarily responsible for the seasonal variation of respiratory response to temperature in *Q. rubra*. For example, active growth in mid-June and material translocation in late autumn would require more energy and carbon skeletons, which are mainly products of respiratory processes.

RESPIRATION–LEAF PROPERTY RELATIONSHIPS

Correlations among leaf respiration, nitrogen and soluble sugars have been reported in many studies (Ryan 1991, 1995; Reich *et al*. 1996; Ryan *et al*. 1996a; Noguchi & Terashima 1997; Reich *et al*. 1998a, 1998b; Atkin *et al*. 2000; Griffin *et al*. 2001, 2002; Tissue *et al*. 2002; Vose & Ryan 2002; Turnbull *et al*. 2003). Although it has been suggested that respiration is determined by multiple factors (Tissue *et al*. 2002), most previous work investigated the relationships between respiration and individual leaf properties (but cf. Tjoelker, Reich & Oleksyn 1999). As different leaf properties can affect respiration interactively, a simple correlation analysis may be biased. The multivariant regression analysis used in our study can decrease the risk of such biased estimations, as the effects of multiple factors are accounted for. In general, our findings are consistent with the previously reported positive correlation between respiration, nitrogen and soluble sugars. Furthermore, by isolating the effects of the various environmental factors, we found that the seasonal and canopy-position effects are associated with different leaf properties. In this case, N_{area} was well correlated with the canopy-position effect on $R_{20(area)}$; while reducing monose, especially M_N, a direct substrate of respiration, was well correlated with R_{20} over the course of the growing season (Table 2).

In our study, changes in N_{area} were well correlated with the respiratory variations caused by the canopy-position effect, but not with the seasonal variations in respiration (Table 2). Similarly, it has been shown that temporal variations in photosynthetic capacity are not always explained by leaf nitrogen (Wilson, Baldocchi & Hanson 2000; Dungan, Whitehead & Duncan 2003), and previous studies attribute the lack of correlation to a seasonally dependent fractional allocation of leaf nitrogen to Rubisco (Wilson *et al*. 2000). This mechanism, however, is not likely to apply to respiration, as the concentration of respiratory enzymes is generally in excess for the observed respiration rates, and the proportion of respiratory enzymes in total protein is too low to be affected significantly by nitrogen availability (Amthor 1991).

It has been proposed that the relationship between respiration rate and nitrogen is derived from the more general relationship between nitrogen and protein concentration, which is linked to maintenance respiration (Ryan 1991; Vose & Ryan 2002). In the light of this model we speculate that, in our study, N_{area} did not explain the seasonal variation in $R_{20(area)}$ due to the involvement of non-maintenance respiration components. Seasonally, many other physiological processes (such as growth, translocation, nitrogen metabolism, herbivore defence) can override the nitrogen–maintenance respiration relationship, as they also depend on products of respiration (such as energy and secondary metabolites). Interestingly, we found that N_{area} is correlated well with the variation in R_{area} with canopy position, but N_{mass} could not explain the canopy-position effect on R_{mass} (Table 2). This pattern matches the observation of Tissue *et al*. (2002) in *Liquidambar styraciflua*, and indicates that the $R_{20(area)}$–N_{area} relationship may be derived mainly from the variation in leaf thickness or cellular density in the different canopy heights. This pattern is also consistent with the general nitrogen–maintenance respiration model, as thicker leaves would contain more nitrogen per unit area and have a higher demand for maintenance respiration on an area basis (R_{area}).

It has been suggested that, at moderately high temperatures, respiration rates can be limited by the availability of substrates (Atkin & Tjoelker 2003), thus we examined variation in leaf non-structural carbohydrates as a factor possibly regulating respiration and thermal acclimation. Although non-structural carbohydrate pools may turn over quickly and vary from day to day (Griffin *et al*. 2002), previous studies had found a positive correlation between leaf soluble sugar (or total non-structural carbohydrates) and the rate of respiration (Noguchi & Terashima 1997; Atkin *et al*. 2000; Griffin *et al*. 2001; Turnbull *et al*. 2003). In our study, overall, reducing monose was significantly correlated with respiration but sucrose was not, indicating that the pool of reducing monose influences respiration rates more directly (Table 2). Furthermore, reducing monose explained the seasonal variation of respiration better than it explained the site or canopy-position effects (Table 2), so it appears to be more closely related to seasonal thermal acclimation or phenology than to general physiological function. This observation is consistent with the model of Dewar, Medlyn & McMurtrie (1999), who found that adjustments in leaf sugars are responsible for the thermal acclimation and constant respiration to photosynthesis ratio ($R : P$). However, very few previous studies have examined the relationship between respiration and particular pools of soluble sugars (Azcon-bieto & Osmond 1983). We suggest that further studies in diverse species are warranted to establish the generality of this relationship.

SITE AND CANOPY-POSITION EFFECTS ON RESPIRATION RATE

Overall respiration rates in our study are comparable with (but slightly lower than) those previously reported at this site (Turnbull *et al*. 2001, 2003), and the canopy-position effect was consistent with that

observed by Turnbull *et al*. (2001, 2003). Turnbull *et al*. (2001) also attributed site effects to differences in water availability or demand for energy associated with leaf maintenance. By extending the measurements to the entire growing season, we found that the site and canopy depth could influence leaf respiration in a more complex way. In general, leaf respiration was affected more strongly by canopy position at the lower, more mesic site, but more significant seasonal variations were found at the upper, drier site (Fig. 3). The effects can be attributed primarily to the light environment at these two sites, which indirectly affects respiration rates by influencing the spatial distribution of the photosynthetic apparatus and the demand for maintenance metabolism. At the lower site, where the tree canopy is much deeper (≈30 m), the lower-canopy leaves are in a relatively constant low-light environment. Thus less photosynthetic apparatus would be invested in the lower-canopy leaves, leading to a lower maintenance demand on respiratory products. At the upper site, the lower canopy experiences a more dramatic seasonal variation in light, as more light can penetrate the shallow canopy (≈10 m) in early summer and late autumn. During this period, upper-site trees tend to allocate more photosynthetic machinery to the lower-canopy leaves, and this would result in a higher demand for growth/maintenance respiration. Finally, the canopy depth and tree height at these two sites are determined by the long-term difference of soil water availability, which is derived from local topography (Engel *et al*. 2002; Shaman *et al*. 2002). Following this logic, our results shed light on how the local topographic heterogeneity can shape tree respiratory fluxes. Other observations, such as the consistently higher leaf N_{area} and N_{mass} at the upper site (Fig. 4) and thinner lower-canopy leaves at the lower site (Fig. 1d), further support this deduction.

INDICATIONS FOR ECOSYSTEM MODELLING

Ecosystem modellers are aware of the temperature response of respiration, and draw from gas-exchange measurements to parameterize their models (Foley 1994; Dewar *et al*. 1999; Melillo 1999). However, studies on the temporal and spatial heterogeneity of the temperature response of respiration in forests are limited. Typically in these models, one fixed respiration rate is used and then adjusted by a fixed Q_{10} (usually assumed to be 2; for review see Ryan *et al*. 1996b). Our results show significant effects of season, site, canopy position and their interactions on the response of respiration to temperature. The phenomenon indicates that more detailed gas-exchange measurements are required to parameterize the complicated temporal and spatial variation of leaf respiration in order to estimate plant respiratory CO_2 efflux correctly.

In the Arrhenius equation used, two parameters, R_0 and E_0, affect the thermal sensitivity of respiration. In this study, E_0 was nearly constant, and most of the temporal and spatial variation in the leaf respiratory temperature response was determined by changes in R_0. If such patterns are proven to be widespread, this could simplify the treatment of respiration in ecosystem models by assuming a constant E_0 (52·5 kJ mol^{-1} K^{-1} for *Q. rubra* in our study). In contrast, detailed measurements of R_0 should be made to parameterize the models. Based on the respiration–leaf property correlations, it may also be possible to predict R_0 from some leaf properties (such as nitrogen or reducing monose). Such simplifications may apply to north-eastern deciduous forest dominated by *Q. rubra* and other *Quercus* species with similar physiological characteristics (Mitchell *et al*. 1999; Turnbull *et al*. 2001, 2003).

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