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Scaling foliar respiration in two contrasting forest canopies

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Summary

1. The responses of night-time dark respiration (R_d) to temperature and leaf characteristics were measured through the canopies of tree species from two distinct forests – an oak-dominated deciduous forest in north-eastern USA, and a conifer-dominated temperate rainforest in New Zealand. These were chosen to examine the extent to which canopy level changes in dark respiration can be applied across forest biomes, and the appropriateness of scaling rules to calculations of whole-canopy carbon efflux.

2. The response of respiration to temperature differed significantly between species and with height in the canopy. This involved changes in both R_d at a reference temperature, and the extent to which R_d increased with temperature (described by the energy of activation, E_o, or the change in R_d over a 10 °C range, Q_{10}). E_o ranged from 25 (lower-canopy leaves) to 53·8 kJ mol^{-1} K^{-1} (upper-canopy leaves) in the deciduous forest, and from 24–37 kJ mol^{-1} K^{-1} in the temperate rainforest site.

3. Relationships between respiratory and leaf characteristics indicated that the instantaneous rate of respiration covaries with soluble sugar concentration and leaf nitrogen, but the temperature response of respiration (E_o or Q_{10}) appears to be driven by leaf N.

4. Scaling leaf respiratory carbon loss to the whole-canopy level indicated that simplifying assumptions regarding the variation in respiration and its temperature response with canopy height tend to underestimate carbon loss if the assumptions are based on lower-canopy leaf physiology, but overestimate carbon loss if the assumptions are based on upper-canopy physiology. Thus, canopy-level differences in leaf respiratory characteristics should be considered in modelling efforts attempting to estimate whole-canopy respiration.

Key-words: Carbohydrates, dark respiration, deciduous forest, podocarp–angiosperm forest, temperature, nitrogen

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Introduction

Although there is debate concerning our ability to predict future temperature change, it is now widely accepted that global temperatures will be 1–6 °C warmer by the year 2100 (Hansen *et al*. 1999; IPCC 2001). This warming will be more pronounced at night when dark respiration (R_d) is the dominant physiological process in vegetation (Easterling *et al*. 1997; Alward *et al*. 1999; IPCC 2001). The degree to which respiration in leaves changes with temperature is highly variable, with Q_{10} values (the increase in respiration rate with a 10 °C increase in temperature) ranging from 1·4–4·0 (Azcón-Bieto 1992). The temperature response of respiration is influenced by measurement temperature (Tjoelker *et al*. 2001); species (Larigauderie & Körner 1995); season (Stockfors & Linder 1998; Atkin *et al*. 2000); growth temperature (e.g. Larigauderie & Körner 1995; Atkin *et al*. 2000); and leaf metabolic state (Berry & Raison 1981). Respiration rate under field conditions will also be a function of temperature and physiological history, as it is subject to acclimation and/or adaptation (Amthor 1989; Atkin *et al*. 2000). Because actual leaf and canopy respiratory carbon release will be influenced by complex interactions between physiological and environmental factors, global warming could have dramatic nonlinear effects

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on system-level carbon, nitrogen and water cycling, and therefore on carbon storage (Dewar *et al*. 1999; Melillo 1999).

The carbon balance of forest ecosystems is defined by the difference between two large fluxes: photosynthetic carbon gain and respiratory carbon loss. On an annual basis, respiration can consume between 30 and 70% of photosynthetic carbon fixation (Amthor 1989; Ryan 1991; Ryan *et al*. 1994; Ryan *et al*. 1996). The processes of photosynthesis and respiration respond independently to environmental variation, and thus have nonlinear effects on forest carbon gain (Ryan 1991; Dewar *et al*. 1999; Gunderson *et al*. 2000). Using data on net CO_2 exchange for a network of sites in Europe, Valentini *et al*. (2000) concluded that the decrease in carbon uptake with increasing latitude was the result of differences in ecosystem respiration rather than differences in gross carbon uptake. Given that, at the global scale, plant respiration results in the release of 60 Gt of carbon annually (Amthor 1997), 80% of which is from forest trees (Houghton 1993), it is essential that respiratory responses of forest trees to environmental variables be better understood. In order to interpret correctly the existing experimental results at the global scale, and to apply this knowledge correctly to predictive models, the uncertainties regarding both short- and long-term responses of respiration to temperature (Grace & Rayment 2000) must be resolved.

While the distribution of respiratory activity (Bolstad *et al*. 1999; Griffin *et al*. 2001; Meir *et al*. 2001) and photosynthetic capacity (Field 1983; Field 1991; Evans 1993; Anten *et al*. 1995; Hollinger 1996) vary through the canopy, the temperature response of these processes at different canopy depths has not been well studied (Bolstad *et al*. 1999). Soluble carbohydrate concentrations may regulate the temperature response, and these carbohydrates in turn vary through the canopy (Atkin *et al*. 2000; Griffin *et al*. 2001). Similarly, leaf nitrogen concentration (N) tends to decrease with canopy depth (Field 1983; Evans 1989; Leuning *et al*. 1991; Ellsworth & Reich 1993; Hollinger 1996), and a general relationship between N and R_d has been reported (Ryan 1991; Ryan 1995; Reich *et al*. 1996, Ryan *et al*. 1996; Reich *et al*. 1998). Hence, the temperature response of respiration might be expected to vary through the canopy of large trees.

In order to scale foliar respiration from leaf to canopy level, we examine the potential for species-level and canopy-level differences in (i) the temperature response of R_d; and (ii) the relationships between R_d and leaf characteristics. R_d of leaves was measured throughout the canopies of three dominant tree species from a temperate deciduous forest in eastern North America and three tree species from a conifer-dominated forest in southern New Zealand. We hypothesized that the response of leaf respiration to temperature would differ with position in the canopy, and would be driven by leaf N and carbohydrate content. Our two research sites comprise two very different forest types. The North American site is a temperate deciduous forest which experiences significant anthropogenic N input (in excess of 4·7 kg N ha^{-1} $year^{-1}$; National Atmospheric Deposition Programme, 2001, personal communication) and summer drought. The New Zealand site is a nutrient-poor conifer-dominated site that experiences high rainfall throughout the year. These distinct sites were chosen to examine the extent to which canopy-level changes in the response of dark respiration to temperature and leaf characteristics can be broadly applied across forest biomes, and to investigate the appropriateness of scaling rules to calculations of whole-canopy respiratory carbon efflux.

Materials and methods

STUDY SITES AND SPECIES

The Black Rock Forest (BRF) is a 1500 ha scientific preserve within the Highlands Province of New York, USA and was established in 1927. The forest is located at a latitude of 41·3° N and a longitude of 74·0° W with elevations ranging from 110–450 m above sea level. Average annual precipitation is 1190 mm. Air temperature is strongly seasonal, with monthly averages ranging from –2·7 °C in January to 23·4 °C in July. The soils are typically shallow, brown forest soils of medium texture, with granite gneiss bedrock or glacial till parent material at depths ranging from 250 mm at elevated sites (Hollis soil) to 1 m at lower sites (Charlton/Paxton soil; Olsson 1981). The forest contains an average of 734 trees ha^{-1} and an average basal area of 21·0 m^2 ha^{-1}. The forest population structure has been described previously (Turnbull *et al*. 2002). A 0·1 ha study plot was established at the bottom of the Cascade Brook watershed at an elevation of 270 m and a slope of <5%. In this plot the canopy height ranges from 20–30 m. Basal area distribution of the three species studied is 41% *Quercus rubra* L., 6% *Quercus prinus* L., 32% *Acer rubrum* L. and 20% other species.

The New Zealand site is located in an extensive, mixed conifer–broadleaved forest at Okarito Forest, Westland (OFW) at latitude 43·2° S and longitude 170·3° E and 50 m elevation above sea level. Because of the prevailing, onshore westerly winds, and the rapid increase in altitude associated with the southern Alps in close proximity east of the forest, annual rainfall is high (≈3400 mm) and evenly distributed throughout the year. Mean annual temperature is 11·3 °C, with a small range between winter and summer of 8·6 °C. The landform at the site is glacial in origin, and the forest is established on terrace outwashes from moraines formed ≈20 000 years ago. The loess is poorly preserved because of erosion and acid dissolution from extreme leaching, resulting from high rainfall (Almond 1996). The soils have a high organic matter content, low permeability and porosity, and are frequently waterlogged. Soils are extremely acid (pH 3·8–4·4 to a depth of 500 mm) with medium total N concentrations

(2·1 mol kg^{-1}) in the upper 150 mm, falling to 0·14 mol kg^{-1} at a depth of 150 mm, and low concentrations of acid-extractable phosphorus and low phosphorus retention (Mew & Lee 1981). Forests of this kind at lowland sites are characterized by a dense, mixed understorey and large, emergent conifers, principally rimu (*Dacrydium cupressinum* Sol. ex Lamb.) (Ogden & Stewart 1995). Our study plot is dominated by 400–600-year-old rimu trees with a mean canopy top height of 20 m. Other conifers and angiosperm species are also present (James & Norton 2002). Miro (*Podocarpus ferruginea* (D. Don) de Laub.) and kamahi (*Weinmannia racemosa* L. f.) are common in the subcanopy, and silver pine (*Manoao colensoi* (Hook.) Molloy), Hall's totara (*Podocarpus hallii* Kirk), Westland quintinia (*Quintinia acutifolia* Kirk) and southern rata (*Metrosideros umbellata* Cav.) are present, but less common. The basal area distribution of the three species studied here is 73% *D. cupressinum*, 12% *W. racemosa*, 10% *Q. acutifolia* and 5% other species.

RESPIRATION MEASUREMENTS

Physiological measurements presented here were undertaken during summer (June 2000 at BRF; January 2001 at OFW). Measurements of leaf dark respiration were made on fully expanded leaves from three levels (upper, mid- and lower) within the canopies of each experimental tree. Canopy access was gained at BRF using a 20 m boom 'cherry-picker' and at OFW using a 22 m permanent tower. For *Q. rubra* and *Q. prinus* at BRF and *D. cupressinum* at OFW, the upper-canopy level consisted of fully sunlit leaves from the top of the forest canopy. For *A. rubrum* at BRF and *Q. acutifolia* and *W. racemosa* at OFW, upper-level leaves were partially sunlit in the mid-stratum of the forest. At least six leaves (from at least two separate branches on three individual trees) were measured for each species per canopy level. Leaf carbohydrate, total N and specific leaf area (SLA) analyses were performed on the same leaves used for gas-exchange measurements.

Dark respiration measurements were made using gas analysis systems (Li-Cor model 6400, Lincoln, NE, USA) equipped with CO_2 control modules. Response curves were generated following measurements of steady-state responses of leaf dark respiration (R_d) to four different cuvette temperatures (≈12, 18, 24 and 28 °C) which were set using thermoelectric coolers. These experimental temperatures represented a range of approximately ±7 °C around the ambient minimum temperature during the study period. Responses were modelled according to actual leaf temperatures achieved at these temperature set points (≈13, 18, 22 and 25 °C, respectively). External CO_2 (C_a) was maintained at ambient atmospheric partial pressure (36 Pa). Measurements were made at each temperature set point when respiratory gas exchange had equilibrated (taken to be when the coefficient of variation for the CO_2 partial pressure differential between the sample and reference analysers was <1%). This condition was typically achieved ≈10 min after the stable temperature set point had been reached. Measurements were made at night (after 2200 h) in the dark using individual leaves on large branches excised under water from trees in the field. Previous studies have shown no differences in respiration between *in situ* leaves and leaves from detached branches in a range of deciduous species, including *Q. rubra* and *A. rubrum* (Mitchell *et al.* 1999). We also confirmed that this applies for the New Zealand forest species (unpublished results). Photosynthetic capacity (A_{max}) was determined under saturating photon flux density (1500–2000 μmol m^{-2} s^{-1}) and ambient C_a (36 Pa) and 25 °C during the previous daytime period for *in situ* leaves, adjacent in the canopy to those subsequently used for respiration determinations. All gas-exchange measurements are presented on the basis of half leaf surface area.

Analysis of temperature response curves was performed using a modification of an Arrhenius function described by Lloyd & Taylor (1994), where respiration rate at a given temperature is given by:

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

where R_0 is the respiration rate at the base temperature T_0 (here 10 °C), T_a is leaf temperature (K), R_g is the gas constant (8·314 J mol^{-1} K^{-1}), and E_o is a parameter related to the energy of activation which describes the magnitude of the temperature response. Nonlinear curve fitting was performed using the Marquardt–Levenberg algorithm (SIGMAPLOT ver. 2·0, 1994, Jandel Corp.). In order to facilitate comparisons with other investigations, the parameter Q_{10} was also calculated (the ratio of R_d at 25 °C divided by R_d at 15 °C). Q_{10} should be used with caution as the value changes according to the temperature range used (Amthor 1989; Ryan *et al.* 1994).

MODELLED STAND FOLIAR CARBON LOSS

The calculated temperature response (equation 1) was used to predict leaf respiration from actual air temperatures during a 2-week period centred on when gas exchange measurements were made. The instantaneous rates were then scaled to the stand level (R_{can}) by multiplying by the leaf area index for each forest (5·8 m^2 m^{-2} for BRF and 5·4 m^2 m^{-2} for OFW) and by total area (1 ha). Two separate model calculations were made in order to illustrate the impact of simplifying assumptions regarding the variation in respiration and its temperature response with canopy height. In the first, the distributed foliar characteristics model, the vertical distribution of the respiration rate and temperature response of respiration were considered explicitly, along with the vertical distribution of leaf area and contribution to leaf area made by the three major component species for each forest (based on stem basal area). For BRF, vertical leaf area distribution

was considered to be the same as that determined previously for an oak-dominated deciduous forest (Hutchison *et al*. 1986). At OFW, vertical leaf area distribution was inferred from photographs of tree crowns (Whitehead *et al*. 2002). Within each 1 m segment of the canopy, the appropriate fraction of total leaf area was allocated to those species and leaf types present according to the contribution each species made to stem basal area. In the second model calculation, the constant foliar characteristics model (with the additional designation of lower, mid- or upper canopy), all leaves for a given species were assumed to have the respiration rate and temperature response measured for that species in only the lower, mid- or upper canopy, respectively. All calculations were made on a 20 min time scale and then summed for the duration of the night-time period (2100–0700 h). Canopy assimilation rate (A_{can}) during the day was also calculated for the two forests using a process-based model (Whitehead *et al*. 2002).

LEAF ANALYSES

All analyses were determined on leaf material harvested directly following respiratory measurements. Specific leaf area was calculated following determination of individual leaf area and dry weight. Soluble sugar content of leaves was determined colorimetrically using an ethanol extraction technique described by Griffin *et al*. (1999). Total N content of leaves was determined on dried and ground material using an NCS autoanalyser (Carlo Erba NCS 2500, Milan, Italy).

STATISTICAL ANALYSIS

Two-way ANOVA was used to test for the main effects and interactions of species and canopy level on respiration parameters (S-PLUS ver. 3·3, MathSoft Inc., Seattle, USA). A nested model (individual leaves nested within trees) was used to account for leaf *vs* tree variation in parameters (Underwood 1981). Differences were considered significant if probabilities (P) were <0·05. Treatment means were compared by least significant difference to determine whether means of the dependent variable were significantly different at $P = 0·05$ (Sokal & Rohlf 1981).

Results

In both forests the response of respiration to temperature differed between species and with position in the canopy. At BRF, *A. rubrum* displayed a less pronounced increase in respiration with increasing temperature than did either *Q. rubra* or *Q. prinus* (Fig. 1). The effects of species and stratum on the temperature response of respiration were also exemplified in the parameters E_o and Q_{10} (Table 1). For both these parameters *A. rubrum* had lower values than the other two species, and leaves in the upper-canopy stratum had higher values than those in the mid- and lower strata. E_o ranged from 25·2 in lower-canopy leaves of *A. rubrum* to 53·9 kJ mol^{-1} K^{-1} in upper-canopy leaves in *Q. prinus* (Table 1). Leaf respiration differed significantly between canopy strata, with R_{10} ($P < 0·01$) and R_{25} ($P < 0·001$) significantly smaller in lower-canopy than in upper-canopy leaves (Table 1). There were significant differences in respiration between species at both high (R_{25}, $P < 0·001$) and low temperature (R_{10}, $P = 0·02$). At OFW, *D. cupressinum* displayed the most pronounced increase in respiration with increasing temperature, particularly in upper- and mid-canopy leaves (Fig. 1). E_o and Q_{10} both differed significantly among species (Table 1). Although there was a trend for both parameters to be greater in the upper canopy than the lower, this was much less pronounced than for BRF. E_o ranged from 23·9 in lower-canopy leaves of *Q. acutifolia* to 38·3 kJ mol^{-1} K^{-1} in mid- and upper canopy leaves in *W. racemosa* (Table 1). Leaf respiration differed significantly among strata, with both R_{10} ($P < 0·001$) and R_{25} ($P < 0·001$) significantly smaller in lower-canopy than upper-canopy leaves (Table 1).

Leaf characteristics differed among species, and displayed significant responses to canopy position (Table 2). At BRF, SLA responded to canopy position ($P < 0·0001$) and was significantly larger in *A. rubrum* (15·2 in upper canopy compared to 17·6 m^2 kg^{-1} in lower canopy) than in both *Q. rubra* (10·3–17·4 m^2 kg^{-1}) and *Q. prinus* (9·0–14·9 m^2 kg^{-1}). The SLA responded similarly to canopy position at OFW. Nitrogen concentration on both a mass and area basis differed significantly among species at both sites, and was greatest in *Q. rubra* at BRF and *D. cupressinum* at OFW. N_{area} decreased significantly with depth in the canopy in both forests ($P < 0·001$ at BRF; $P < 0·0001$ at OFW). In contrast, N_{mass} was much more constant through the canopy strata. At BRF and OFW, leaf soluble sugar content was greatest in the two *Quercus* species (BRF) and *D. cupressinum* (OFW), and decreased in lower-canopy leaves. At OFW, the range of values between canopy strata in SLA, N_{area} and soluble sugars was greatest in *D. cupressinum* and much less pronounced in *W. racemosa* and *Q. acutifolia*, as the latter were shaded subcanopy trees.

Leaf R_d at the average minimum night-time temperature for each site (June average minimum at BRF was 17·2 ± 0·53 °C; January minimum at OFW was 11·4 ± 0·50 °C) was calculated from the respiration response characteristics (Fig. 1; Table 1) to reflect respiration under ambient conditions. Respiration rates expressed on a leaf area basis (R_{area}) differed between species at both sites, and were significantly greater in upper-canopy leaves than in mid- and lower-canopy leaves (Table 3). At BRF, R_{area} ranged from 0·98 μmol m^{-2} s^{-1} in upper-canopy leaves of *Q. prinus* to 0·49 μmol m^{-2} s^{-1} in lower-canopy leaves of *A. rubrum*. At OFW R_{area} values were smaller, reflecting lower air temperature, and ranged from 0·80 in upper-canopy leaves of *D. cupressinum* to 0·22 μmol m^{-2} s^{-1} in lower-canopy

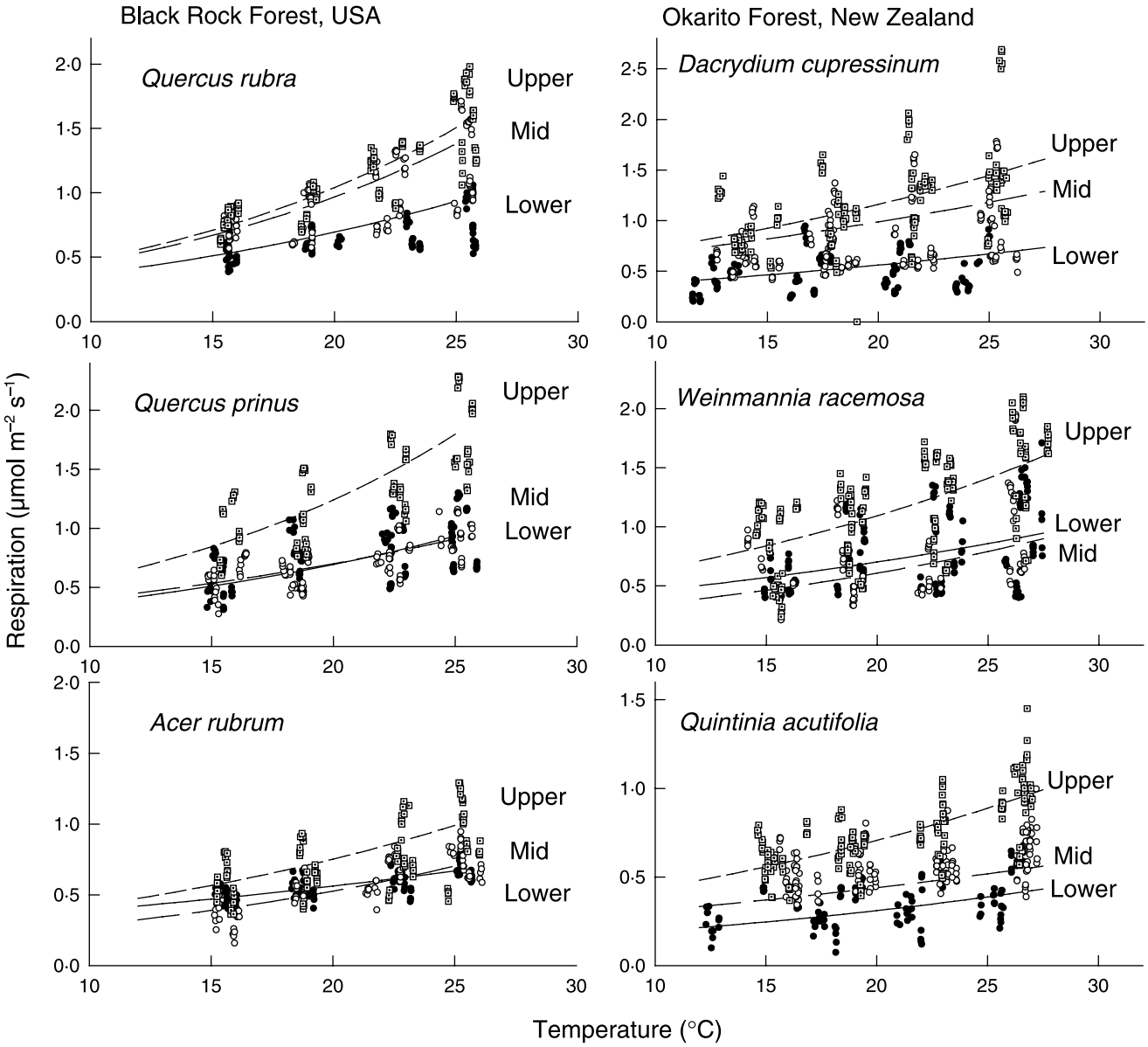

Fig. 1. Response of respiration rate, R_d, to temperature for leaves at different canopy levels of *Quercus rubra, Quercus prinus* and *Acer rubrum* at Black Rock Forest, NY, USA and *Dacrydium cupressinum, Weinmannia racemosa* and *Quintinia acutifolia* at Okarito Forest, Westland, NZ. Data are shown for upper-canopy (□), mid-canopy (○) and lower-canopy (●) leaves. The curves describe modelled responses derived using the mean parameters from 6 to 7 replicate response curves at each canopy level (individual curves fitted using a modification of the Arrhenius equation described by Lloyd & Taylor 1994). For statistical comparison of respiration parameters, see Table 1.

leaves of *Q. acutifolia*. When expressed on a mass basis, patterns of variation in respiration rate (R_{mass}) were less clear, displaying a significant species effect ($P = 0{\cdot}031$) at BRF and a significant canopy position effect at OFW ($P < 0{\cdot}001$). At OFW, R_{mass} was generally smaller in lower-canopy leaves. The response of respiration on a nitrogen basis (R_N) also differed between the two forest sites, with no canopy position effect in the deciduous BRF, but a significant canopy position effect at evergreen OFW. At OFW, R_N tended to decrease in lower-canopy leaves.

At BRF, the magnitude of the temperature response of leaf respiration (E_o) was positively correlated with N_{area} (Fig. 2a; $r^2 = 0{\cdot}29$–$0{\cdot}31$, Table 4). The slope of these responses did not differ between species. In contrast, E_o was not related to leaf soluble sugar content (Fig. 2b). R_{25} was strongly correlated with N_{area} (Fig. 2c; r^2 ranged from 0·28 in *Q. rubra* to 0·77 in *Q. prinus* and 0·83 in *A. rubrum*, Table 4), but weakly correlated with soluble sugar content in *Q. prinus* only (Fig. 2d). Relationships between respiration parameters and leaf characteristics were less clear at OFW. In contrast to findings for deciduous forest species at BRF, at OFW E_o was not significantly related to N_{area} (Fig. 2e), although a weak relationship was observed for *D. cupressinum*. E_o was not related to leaf soluble sugar content (Fig. 2f). R_{25} at OFW was correlated with N_{area} in *D. cupressinum* and *Q. acutifolia* (Fig. 2g; Table 4). R_{25} was not significantly related to leaf soluble sugar content at OFW (Fig. 2h).

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Table 1. Modelled dark respiration parameters calculated from fitted temperature response curves (Fig. 1) as a function of canopy height in three tree species from a deciduous forest (Black Rock Forest, NY, USA) and three species from a conifer-dominated temperate rainforest (Okarito Forest, Westland, NZ)

	Canopy			Canopy			Canopy			
	Upper	Mid	Lower	Upper	Mid	Lower	Upper	Mid	Lower	ANOVA statistics
Black Rock Forest (USA)	*Quercus rubra*			*Quercus prinus*			*Acer rubrum*			
R_{10} (μmol CO_2 m^{-2} s^{-1})	0·49 (0·02)^{bc}	0·46 (0·03)^{b}	0·42 (0·04)^{b}	0·58 (0·08)^{c}	0·41 (0·05)^{b}	0·37 (0·03)^{ab}	0·42 (0·04)^{b}	0·31 (0·03)^{a}	0·39 (0·03)^{ab}	Sp 0·02 Pos 0·01 Sp × P NS
R_{25} (μmol CO_2 m^{-2} s^{-1})	1·53 (0·11)^{d}	1·42 (0·16)^{d}	1·13 (0·18)^{c}	1·77 (0·13)^{e}	0·90 (0·06)^{bc}	0·95 (0·11)^{bc}	1·00 (0·09)^{c}	0·74 (0·05)^{ab}	0·66 (0·03)^{a}	Sp <0·001 Pos <0·001 Sp × P NS
E_o (kJ mol^{-1} K^{-1})	53·7 (3·3)^{c}	51·6 (3·9)^{c}	44·2 (4·7)^{bc}	53·9 (5·2)^{c}	38·0 (3·3)^{b}	43·3 (6·3)^{bc}	39·9 (3·6)^{b}	42·0 (2·0)^{bc}	25·2 (3·1)^{a}	Sp 0·01 Pos 0·01 Sp × P NS
Q_{10}	2·13 (0·09)^{c}	2·07 (0·11)^{c}	1·87 (0·11)^{bc}	2·16 (0·15)^{c}	1·71 (0·08)^{b}	1·86 (0·15)^{bc}	1·76 (0·09)^{b}	1·80 (0·05)^{b}	1·43 (0·06)^{a}	Sp 0·04 Pos 0·03 Sp × P NS
Okarito Forest (NZ)	*Dacrydium cupressinum*			*Weinmannia racemosa*			*Quintinia acutifolia*			
R_{10} (μmol CO_2 m^{-2} s^{-1})	0·73 (0·06)^{c}	0·67 (0·03)^{c}	0·38 (0·04)^{ab}	0·65 (0·08)^{c}	0·35 (0·08)^{ab}	0·46 (0·06)^{b}	0·44 (0·03)^{b}	0·31 (0·02)^{ab}	0·20 (0·03)^{a}	Sp 0·05 Pos <0·001 Sp × P NS
R_{25} (μmol CO_2 m^{-2} s^{-1})	1·46 (0·15)^{c}	1·19 (0·07)^{bc}	0·71 (0·12)^{ab}	1·39 (0·13)^{c}	0·81 (0·22)^{b}	0·88 (0·12)^{b}	0·89 (0·05)^{b}	0·52 (0·04)^{ab}	0·37 (0·05)^{a}	Sp NS Pos <0·001 Sp × P NS
E_o (kJ mol^{-1} K^{-1})	31·8 (2·9)^{ab}	26·0 (2·6)^{a}	26·4 (4·6)^{a}	37·1 (4·2)^{b}	38·3 (6·3)^{b}	29·1 (5·1)^{ab}	33·3 (2·7)^{b}	23·9 (3·1)^{a}	32·4 (4·2)^{b}	Sp 0·05 Pos NS Sp × P NS
Q_{10}	1·57 (0·06)^{ab}	1·45 (0·05)^{a}	1·45 (0·09)^{a}	1·71 (0·11)^{b}	1·74 (0·16)^{b}	1·53 (0·10)^{ab}	1·60 (0·06)^{ab}	1·41 (0·06)^{a}	1·59 (0·10)^{ab}	Sp 0·05 Pos NS Sp × P NS

R_{10} is respiration rate at the base temperature (10 °C) used to fit equation 1 to actual responses. R_{25} denotes respiration rates calculated from the fitted responses at 25 °C. E_o is a modelled parameter related to the energy of activation. Q_{10} denotes the relative change in respiration rate with a 10 °C increase in temperature (15–25 °C). Values shown are means (± SEM) where $n = 6–7$. Significance of treatment effect for species (Sp), canopy position (Pos) and the interaction between species and canopy position (Sp × P) are indicated as the P value or as nonsignificant (NS). Different letters within rows indicate statistically different values at $P < 0·05$ based on the least significant difference test of treatment means.

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Table 2. Leaf characteristics at different canopy levels of three tree species from a deciduous forest (Black Rock Forest, NY, USA) and three species from a conifer-dominated temperate rainforest (Okarito Forest, Westland, NZ)

	Canopy			Canopy			Canopy			
	Upper	Mid	Lower	Upper	Mid	Lower	Upper	Mid	Lower	ANOVA statistics
Black Rock Forest (USA)	*Quercus rubra*			*Quercus prinus*			*Acer rubrum*			
SLA ($m^2\ kg^{-1}$)	10·3 (0·31)^{a}	13·5 (0·85)^{b}	17·4 (2·15)^{cd}	9·0 (0·25)^{a}	14·7 (1·0)^{b}	14·9 (0·61)^{b}	15·2 (1·14)^{bc}	17·0 (0·58)^{cd}	17·6 (0·45)^{d}	Sp <0·0001 Pos <0·0001 Sp × P 0·035
N_{mass} (mmol N g^{-1})	1·59 (0·03)^{bc}	1·73 (0·05)^{c}	1·75 (0·02)^{c}	1·33 (0·03)^{a}	1·29 (0·04)^{a}	1·38 (0·05)^{ab}	1·56 (0·04)^{bc}	1·55 (0·03)^{bc}	1·44 (0·04)^{ab}	Sp <0·01 Pos NS Sp × P 0·05
N_{area} (mmol N m^{-2})	155 (3·5)^{d}	129 (4·3)^{cd}	107 (12·5)^{bc}	147 (5·5)^{d}	89 (4·6)^{ab}	93 (3·8)^{ab}	105 (8·2)^{b}	92 (3·3)^{ab}	72 (3·2)^{a}	Sp <0·001 Pos <0·001 Sp × P NS
Sugars (g m^{-2})	2·80 (0·27)^{cd}	2·07 (0·36)^{bc}	1·81 (0·18)^{ab}	3·64 (0·45)^{d}	3·04 (0·31)^{cd}	2·99 (0·13)^{cd}	1·15 (0·15)^{a}	1·67 (0·39)^{ab}	1·25 (0·15)^{a}	Sp <0·01 Pos NS Sp × P NS
Okarito Forest (NZ)	*Dacrydium cupressinum*			*Weinmannia racemosa*			*Quintinia acutifolia*			
SLA ($m^2\ kg^{-1}$)	4·86 (0·32)^{a}	6·43 (0·35)^{ab}	7·55 (0·27)^{b}	7·90 (0·61)^{b}	7·90 (0·99)^{b}	7·91 (0·41)^{b}	10·8 (0·20)^{cd}	12·1 (0·38)^{d}	13·2 (0·53)^{e}	Sp 0·013 Pos 0·022 Sp × P NS
N_{mass} (mmol N g^{-1})	0·93 (0·03)^{e}	0·84 (0·02)^{d}	0·84 (0·05)^{d}	0·69 (0·04)^{b}	0·68 (0·02)^{ab}	0·66 (0·02)^{a}	0·79 (0·03)^{c}	0·72 (0·03)^{bc}	0·70 (0·02)^{b}	Sp <0·0001 Pos 0·01 Sp × P NS
N_{area} (mmol N m^{-2})	186 (7·9)^{f}	133 (6·1)^{e}	114 (7·8)^{de}	91 (5·4)^{cd}	90 (6·1)^{cd}	85 (4·2)^{bc}	73 (2·4)^{abc}	60 (2·9)^{ab}	54 (2·2)^{a}	Sp <0·0001 Pos <0·001 Sp × P <0·01
Sugars (g m^{-2})	9·76 (1·25)^{c}	5·67 (0·64)^{ab}	5·72 (0·84)^{ab}	6·76 (0·85)^{b}	7·33 (0·83)^{bc}	6·26 (0·52)^{b}	6·26 (1·30)^{b}	5·39 (0·75)^{ab}	3·12 (0·50)^{a}	Sp NS Pos <0·01 Sp × P 0·03

Values shown are means (± SEM) where $n = 6–7$. Significance of treatment effect for species (Sp), canopy position (Pos) and the interaction between species and canopy position (Sp × P) are indicated as the P value or as nonsignificant (NS). Different letters within rows indicate statistically different values at $P < 0·05$ based on the least significant difference test of treatment means.

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Table 3. Night respiration for leaves at different canopy levels of three tree species from a deciduous forest (Black Rock Forest, NY, USA) and three species from a conifer-dominated temperate rainforest (Okarito Forest, Westland, NZ)

	Canopy			Canopy			Canopy			
	Upper	Mid	Lower	Upper	Mid	Lower	Upper	Mid	Lower	ANOVA Statistics
Black Rock Forest (USA)	*Quercus rubra*			*Quercus prinus*			*Acer rubrum*			
R_{area} (μmol CO_2 m^{-2} s^{-1})	0·83 (0·04)^{d}	0·78 (0·06)^{cd}	0·67 (0·08)^{bc}	0·98 (0·10)^{e}	0·59 (0·05)^{ab}	0·58 (0·05)^{ab}	0·63 (0·06)^{bc}	0·46 (0·03)^{a}	0·49 (0·02)^{a}	Sp <0·001 Pos 0·026 Sp × P NS
R_{mass} (μmol CO_2 kg^{-1} s^{-1})	8·57 (0·41)^{ab}	10·5 (0·98)^{b}	12·7 (3·05)^{c}	8·87 (0·90)^{ab}	8·47 (0·38)^{ab}	8·55 (0·68)^{ab}	8·91 (0·63)^{ab}	7·93 (0·54)^{a}	8·84 (0·45)^{ab}	Sp 0·031 Pos NS Sp × P NS
R_N (μmol CO_2 mol N^{-1} s^{-1})	5·39 (0·41)^{ab}	6·08 (0·52)^{bc}	5·45 (0·34)^{ab}	6·74 (0·78)^{c}	6·65 (0·41)^{c}	6·23 (0·48)^{bc}	5·65 (0·24)^{ab}	5·00 (0·24)^{a}	6·16 (0·33)^{bc}	Sp NS Pos NS Sp × P NS
Okarito Forest (NZ)	*Dacrydium cupressinum*			*Weinmannia racemosa*			*Quintinia acutifolia*			
R_{area} (μmol CO_2 m^{-2} s^{-1})	0·80 (0·07)^{c}	0·73 (0·04)^{c}	0·41 (0·05)^{ab}	0·72 (0·08)^{c}	0·39 (0·09)^{ab}	0·50 (0·06)^{b}	0·48 (0·03)^{b}	0·37 (0·02)^{ab}	0·22 (0·03)^{a}	Sp 0·05 Pos <0·0001 Sp × P NS
R_{mass} (μmol CO_2 kg^{-1} s^{-1})	3·93 (0·44)^{abc}	4·69 (0·34)^{cd}	3·07 (0·34)^{a}	5·73 (0·80)^{d}	2·91 (0·66)^{a}	4·11 (0·59)^{abc}	5·32 (0·42)^{c}	3·93 (0·22)^{abc}	3·08 (0·50)^{a}	Sp NS Pos <0·001 Sp × P NS
R_N (μmol CO_2 mol N^{-1} s^{-1})	4·31 (0·36)^{ab}	5·61 (0·35)^{bc}	3·77 (0·40)^{a}	7·96 (0·90)^{d}	4·22 (0·90)^{ab}	6·33 (0·98)^{cd}	6·93 (0·76)^{cd}	5·52 (0·31)^{bc}	4·50 (0·80)^{ab}	Sp <0·001 Pos <0·01 Sp × P NS

Respiration rates are calculated from modelled responses (Table 1) at the average minimum night-time temperature for each site during a 2-week period (17·2 °C for Black Rock Forest and 11·4 °C for Okarito Forest). Values shown are means (± SEM) where n = 6–7. Significance of treatment effect for species (Sp), canopy position (Pos) and the interaction between species and canopy position (Sp × P) are indicated as the P value or as nonsignificant (NS). Different letters within rows indicate statistically different values at $P < 0·05$ based on the least significant difference test of treatment means.

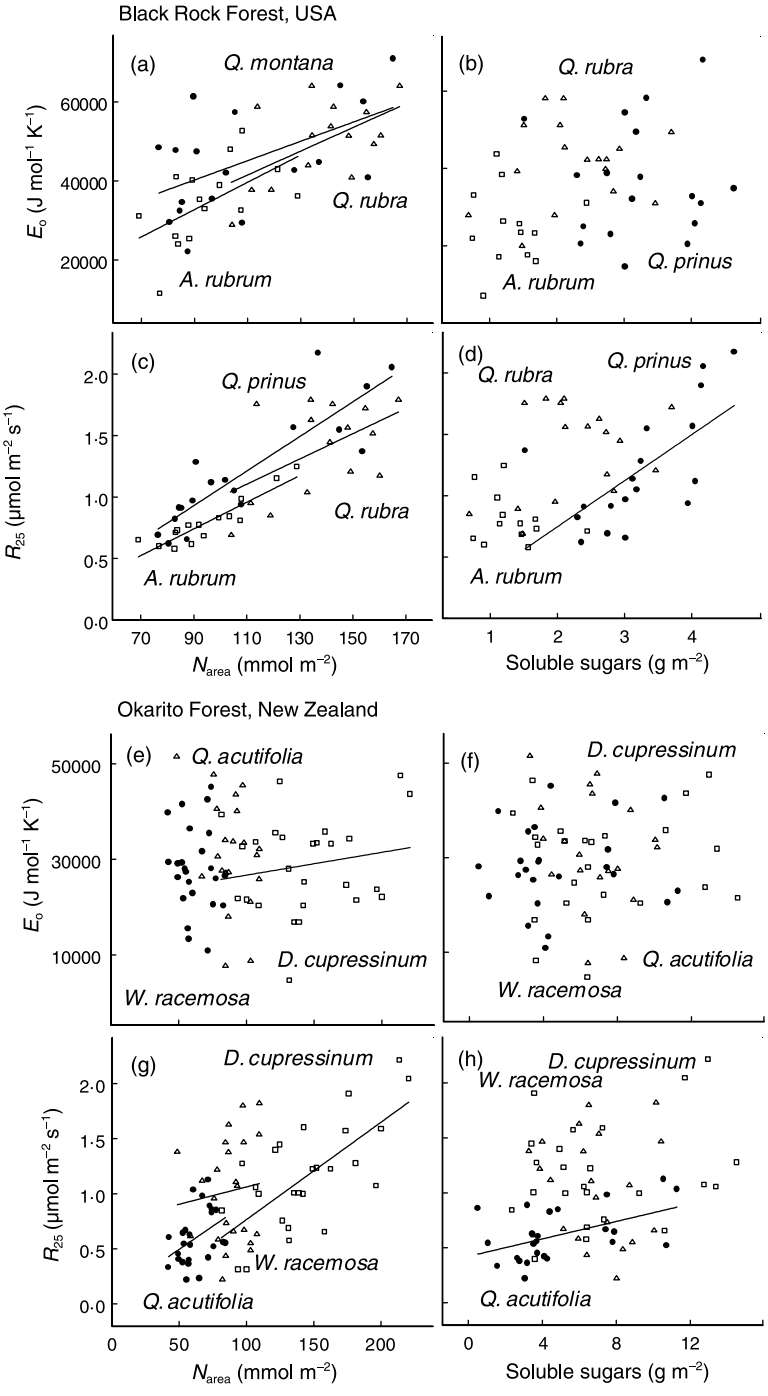

Fig. 2. Relationships between respiratory (E_o and R_{25}) and leaf characteristics (N_{area} and soluble sugar content) for leaves of *Quercus rubra* (△), *Quercus prinus* (●) and *Acer rubrum* (□) from Black Rock Forest, NY, USA and *Weinmannia racemosa* (△), *Quintinia acutifolia* (●) and *Dacrydium cupressinum* (□) trees from Okarito Forest, Westland, NZ. For statistical comparison of leaf characteristics and respiration parameters, see Tables 2 and 3, respectively.

Leaf-level responses to ambient temperature conditions were scaled to reflect night-time respiratory carbon loss at the whole-canopy level (Fig. 3). The results are expressed as the difference between the constant physiology and distributed physiology models. At both sites there were clear differences in canopy respiration rates, depending on the model calculation. At BRF, assuming all leaves had the characteristics of those in the mid-canopy provided a respiratory loss estimate closest to that obtained using the distributed model. The lower-canopy constant physiology model consistently underestimated the distributed physiology model by as much as 39 mmol m^{-2} per night, while the upper-canopy constant physiology model consistently overestimated the distributed physiology model by as much as 32 mmol m^{-2} per night. Both upper- and lower-canopy constant physiology models displayed the strongest temperature sensitivity, with the greatest deviations from the distributed physiology model occurring at warmer temperatures. At OFW, respiratory loss was less variable due to more constant field temperature. Here, assuming all leaves had the characteristics of those in the upper canopy provided the respiratory loss estimate closest to that obtained using the distributed model. The mid- and lower-canopy constant physiology models consistently underestimated the distributed physiology model by as much as 29 and 87 mmol CO_2 m^{-2} per night, respectively.

When the above responses to actual temperature variations are totalled for the 2-week period bracketing our measurement nights, it is possible to calculate total foliar carbon efflux and the extent to which simplifying assumptions affect calculated respiratory carbon loss under field conditions. Total canopy foliar carbon efflux (R_{can}) over the 2-week period was 2·26 mol m^{-2} at BRF and 2·23 mol m^{-2} at OFW. This corresponded to total canopy foliar assimilation (A_{can}) during the same period of 10·3 mol m^{-2} at BRF (daily A_{can}/R_{can} of $4{\cdot}51 \pm 0{\cdot}34$) and 5·73 mol m^{-2} at OFW (daily A_{can}/R_{can} of $2{\cdot}59 \pm 0{\cdot}09$). At BRF, if all leaves in the canopy were assumed to have constant physiological characteristics, then total leaf carbon loss over the 2-week period varied from 1·93 (assuming the properties of the lower-canopy leaves) to 2·58 mol m^{-2} (assuming the properties of the upper-canopy leaves) (Table 5). These estimates were 14·7% less and 14·2% greater than that of the distributed physiology model. If the canopy was assumed to consist entirely of mid-canopy leaves, the estimate of total leaf carbon loss was not greatly different (–5·6%) from the distributed physiology model calculation. At the OFW site, stand foliar respiration rate was estimated at 2·23 mol m^{-2}, similar to that at BRF, with the mid- and lower-canopy constant models underestimating the respiratory loss calculated by the distributed model by 14·5 and 46·9%, respectively. When expressed on a mass basis, canopy respiratory carbon efflux at BRF (32·0 mol kg^{-1}) was twice that at OFW (16·4 mol kg^{-1}; Table 5). On a mass basis, the constant physiology estimates of carbon efflux at BRF were much closer to the distributed physiology estimate throughout the canopy (+3·7 to –5·7% for the lower and upper canopy estimates, respectively). However, at OFW, mass-based estimates did little to bring the constant physiology model calculations together or reduce their deviation from the distributed model calculation.

Table 4. Summary of regression statistics for significant relationships ($P < 0{\cdot}05$) between respiratory (E_o and R_{25}) and leaf characteristics (N_{area} and soluble sugar content) for leaves of *Quercus rubra*, *Quercus prinus* and *Acer rubrum* from Black Rock Forest, NY, USA (BRF) and *Weinmannia racemosa*, *Quintinia acutifolia* and *Dacrydium cupressinum* trees from Okarito Forest, Westland, NZ (OFW)

Dependent variable	Independent variable	Species	Site	Regression relationship	r^2
E_o (kJ mol^{-1} K^{-1})	N_{area}	*Q. rubra*	BRF	$8300 + (302 \times N_{area})$	0·31
		Q. prinus	BRF	$18210 + (245 \times N_{area})$	0·29
		A. rubrum	BRF	$1710 + (345 \times N_{area})$	0·31
R_{25} (μmol CO$_2$ m$^{-2} \times$ s^{-1})	N_{area}	*Q. rubra*	BRF	$-0{\cdot}025 + (0{\cdot}010 \times N_{area})$	0·27
		Q. prinus	BRF	$-0{\cdot}337 + (0{\cdot}014 \times N_{area})$	0·77
		A. rubrum	BRF	$-0{\cdot}236 + (0{\cdot}011 \times N_{area})$	0·83
		W. racemosa	OFW	NS	NS
		Q. acutifolia	OFW	$0{\cdot}080 + (0{\cdot}008 \times N_{area})$	0·17
		D. cupressinum	OFW	$-0{\cdot}120 + (0{\cdot}009 \times N_{area})$	0·47
R_{25} (μmol CO$_2$ m^{-2} s^{-1})	Soluble sugars	*Q. rubra*	BRF	NS	NS
		Q. prinus	BRF	$-0{\cdot}003 + (0{\cdot}375 \times \text{SolSug})$	0·42
		A. rubrum	BRF	NS	NS
		W. racemosa	OFW	NS	NS
		Q. acutifolia	OFW	$0{\cdot}420 + (0{\cdot}040 \times \text{SolSug})$	0·25
		D. cupressinum	OFW	NS	NS

Discussion

RESPONSE OF RESPIRATION TO TEMPERATURE

Our results show that the response of respiration to temperature may differ significantly in leaves of different canopy strata, and that these differences can alter calculated estimates of stand respiratory carbon efflux. The significant differences observed in leaf-level respiration rates between different canopy positions and in scaled canopy-level fluxes may have important mechanistic implications for whole-tree and ecosystem responses to variations in night-time temperature. Given that leaf respiratory response to temperature is a function of temperature and physiological history (Amthor 1989; Atkin *et al*. 2000) and varies with site (Turnbull *et al*. 2001), these findings indicate a need for further investigations into within-stand variation in the temperature responses of respiration in trees. Such investigations are essential to inform models that extrapolate from leaf-level to ecosystem- and landscape-level responses.

While the two oak species studied at BRF (*Q. rubra* and *Q. prinus*) showed similar responses to temperature, respiration in *A. rubrum* was considerably less sensitive (lower E_o and Q_{10}). These values for E_o are consistent with those previously obtained at this site (Turnbull *et al*. 2001), but differ from the temperature responses of similar species in other studies (Bolstad *et al*. 1999; Amthor 2000) which found that Q_{10} rarely differed among species. Here we found significant differences between species, with values of Q_{10} ranging from 1·4–2·2. These values are at the low end of published values for Q_{10} (Azcón-Bieto 1992) and are likely to be due to seasonal differences. Our measurements were made when the active metabolic state of leaves and higher temperatures may reduce the temperature response of respiration (Stockfors & Linder 1998; Atkin *et al*. 2000). Temperature responses at OFW were generally more muted than at BRF, with E_o values in the range 24–38 kJ mol^{-1} K^{-1} (Q_{10} values in the range 1·4–1·7). There are few, if any, previous studies of equivalent species with which to assess these values. A review of *Pinus* spp. found Q_{10} values in the range 1·9–2·3 (Ryan *et al*. 1994). This places *D. cupressinum* (range of Q_{10} 1·45–1·57) below other coniferous species.

An important finding of our investigation was the trend in all species, in both forests, toward a less accentuated response of respiration to temperature (lower E_o and Q_{10}) with depth in the canopy. Although the canopy position effect on E_o and Q_{10} was statistically significant only at BRF, a clear trend was also displayed at OFW. This finding is of interest given its implications for modelling forest carbon budgets and appropriate sampling protocols. Few studies have investigated variation in the temperature response of R_d, but many more have investigated the effects of growth temperature (e.g. Larigauderie & Körner 1995; Atkin *et al*. 2000); geographical location (e.g. Gunderson *et al*. 2000); elevation (Mitchell *et al*. 1999); CO_2 concentration (e.g. Amthor 2000; Tissue *et al*. 2002); and canopy position (e.g. Bolstad *et al*. 1999; Griffin *et al*. 2001) on respiration rate at a given temperature. We found that canopy-level differences in temperature response functions of respiration resulted from changes in both R_{10} and E_o. This is consistent with the findings of Griffin *et al*. (2002), but differs from those of Bolstad *et al*. (1999), who found that differences among species and canopy position were almost solely dependent on changes in respiration at the reference temperature (R_{Tref}) and not Q_{10}.

RESPIRATION AT AMBIENT TEMPERATURE

At BRF, canopy position differences in respiration rates were observed on a leaf area basis, but not when rates

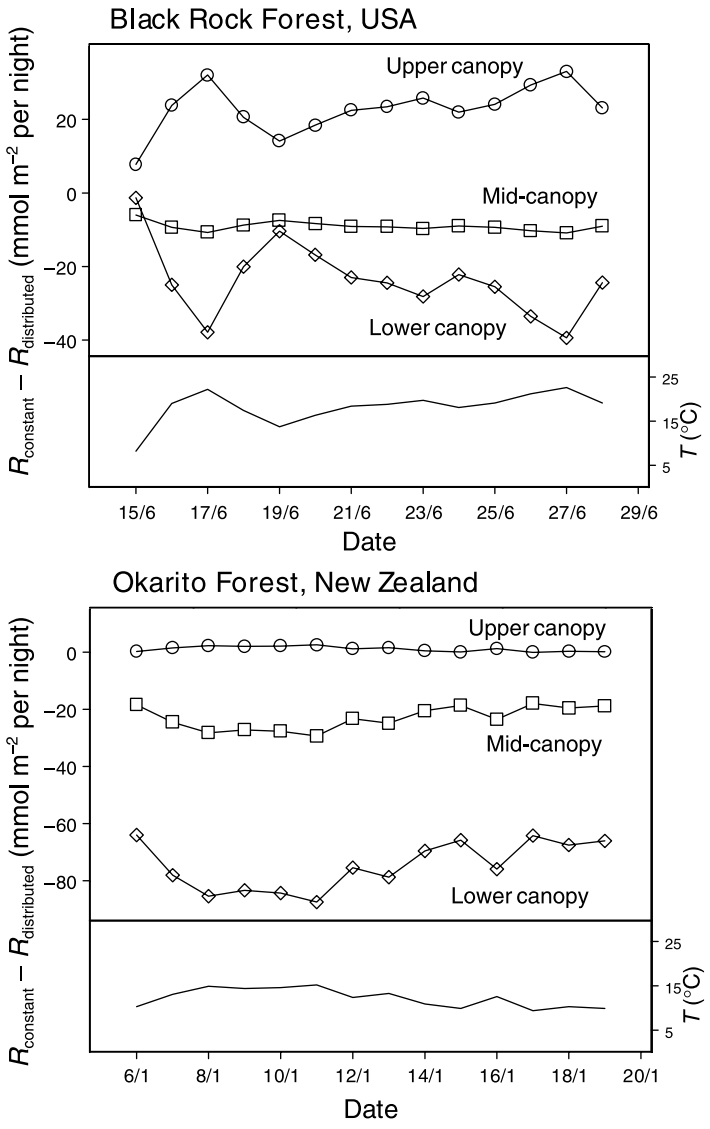

Fig. 3. Differences between two model calculations of canopy respiratory carbon release for a deciduous forest (Black Rock Forest, NY, USA) and a conifer-dominated temperate rainforest (Okarito Forest, Westland, NZ). Respiration rates are calculated from modelled responses (Table 1) using actual field temperatures (T) over the night period (2100–0700). The constant foliar characteristics models assume all leaves in the mixed canopies have the physiological properties of either lower-, mid- or upper-canopy leaves, respectively. In the distributed foliar characteristics model, leaves were assigned the appropriate response characteristics according to position in the canopy. For detailed modelling assumptions, see Methods. Note the different y-axis scales for each forest.

Table 5. Modelled canopy foliar respiratory carbon release (R_{can}) for a deciduous forest (Black Rock Forest, NY, USA) and a conifer-dominated temperate rainforest (Okarito Forest, Westland, NZ)

	Foliar characteristics			
		Constant; canopy:		
	Distributed	Lower	Mid	Upper
Area-based				
Black Rock Forest (USA)				
R_{can} (mol m^{-2})	2·26	1·93	2·13	2·58
% Difference		−14·7	−5·6	+14·2
Okarito Forest (NZ)				
R_{can} (mol m^{-2})	2·23	1·19	1·91	2·25
% Difference		−46·9	−14·5	+0·70
Mass-based				
Black Rock Forest (USA)				
R_{can} (mol kg^{-1})	32·0	33·2	31·1	30·2
% Difference		+3·7	−2·9	−5·7
Okarito Forest (NZ)				
R_{can} (mol kg^{-1})	16·4	9·41	13·1	12·6
% Difference		−42·7	−20·4	−23·0

Respiration rates are calculated from modelled responses (Table 1) using actual field temperatures (Fig. 3) and are presented as the total carbon released per m^2 ground area or per kg of leaf mass over a 2-week period during the growing season. For detailed modelling assumptions see caption for Fig. 3 and Methods. Percentage difference refers to difference between constant and distributed foliar characteristics model calculations.

were scaled by either SLA or leaf N concentration. The consistency in R_{mass} and R_N between canopy levels indicates a strong coupling between factors influencing respiration and those affecting leaf characteristics. We conclude from these results that differences in dark respiration are most probably based on the effects that canopy position has on demand for energy associated with leaf maintenance (Lambers *et al.* 1998). Higher respiration rates in upper-canopy leaves of *Q. rubra* and *Q. prinus* corresponded with greater foliar concentrations of soluble sugars and lower SLA (Table 2). This is consistent with previous findings (Azcón-Bieto & Osmond 1983; Tissue *et al.* 2002), although relationships between respiration and leaf carbohydrate content are often not clear (Atkin *et al.* 2000). In contrast, at OFW, canopy position differences in respiration rates were observed on a leaf area, leaf mass and leaf N basis. In all three species, R_{area}, R_{mass} and R_N decreased with depth in the canopy. This inconsistency in R_{mass} and R_N with depth in the canopy is because SLA and N_{area} displayed modest changes with canopy depth, but R_{area} decreased strongly in mid- and lower-canopy leaves.

RELATIONSHIPS BETWEEN RESPIRATION AND LEAF CHARACTERISTICS

Canopy depth differences in R_{area}, N_{area} and soluble sugars allow us to investigate the likely physiological mechanisms underpinning respiration rate and its temperature response. We found that R_{25} was positively associated with N_{area} at both sites. This is consistent with previous studies (Reich *et al.* 1998; Bolstad *et al.* 1999; Mitchell *et al.* 1999), and is considered to reflect the close relationship between leaf N concentration and maintenance respiration (Amthor 1989; Ryan 1991). R_{25} was also positively correlated with leaf soluble sugar content in both forests. In contrast, the response of respiration to temperature (E_o, Q_{10}) was associated with N_{area} only. This relationship was strong at BRF, but much less clear at OFW. At OFW, the

dominant canopy tree, *D. cupressinum*, displayed only a weak relationship between E_o and N_{area}. The other two species at OFW were shaded subcanopy trees with little range in leaf N content. The temperature response of respiration is related to metabolic activities such as growth, the maintenance of ion gradients, protein turnover and cellular repair, phloem loading and, in some cases, excess carbohydrate consumption, all of which are likely to vary with canopy depth (Penning de Vries 1975; De Visser *et al*. 1992). Because all measurements here were made on fully expanded leaves, it seems unlikely that growth processes were affected significantly, and therefore the observed results are probably related to maintenance processes. We conclude from these relationships that, while the instantaneous rate of respiration is related to substrate availability (or metabolic activity that covaries with substrate availability) and leaf N, the temperature response of respiration (as indicated by E_o) appears to be driven almost solely by leaf N and maintenance processes.

SCALING OF RESPIRATION FROM LEAF TO CANOPY

Assessing the impact of the observed variation in leaf-level respiratory physiology requires the results to be scaled to the stand level. On a leaf area basis, R_{can} was similar for the two forest stands (2·2 mol m^{-2} over a 2-week period during the growing season). This reflects the fact that the OFW trees displayed higher R_{10} but lower E_o values, and experienced cooler minimum temperatures in summer than BRF species. When expressed on a mass basis, the greater SLA of leaves at BRF compared with OFW resulted in an R_{can} for BRF which was twice that at OFW (Table 4). These values for the foliar component of stand respiration at BRF and OFW are comparable with those published previously for deciduous (Vose & Bolstad 1999) and coniferous (Ryan *et al*. 1994; Law *et al*. 2001) forests.

Our results demonstrate that forest structure and the location of individual leaf measurements can have a significant effect on the model outcome. When scaling our results to the stand level at BRF, we find that simplifying assumptions regarding the variation in respiration rate and the temperature response of respiration with canopy height underestimate actual carbon loss if based on lower- or mid-canopy physiology. We overestimate the actual carbon loss if calculations are based on upper-canopy physiology. Furthermore, when the effects of the observed variation in respiration rate and its temperature response with canopy depth are taken into consideration, differences between the distributed and constant physiology model calculations are greatest at higher temperatures. In general, the difference between model calculations was minimized at BRF when the constant physiology model was based on the mid-canopy leaves. Although this proved to be the case in a mixed deciduous forest with three dominant species and a closed canopy, our conclusions are quite different for OFW, a temperate mixed rainforest dominated by a single conifer (*D. cupressinum*) and with much less defined canopy layering. At OFW, the constant physiology calculation based on upper-canopy leaves was not greatly different from the distributed model, as *D. cupressinum* represents almost 75% of total leaf area, and the open canopy structure means that differences between upper- and mid-canopy leaves are small.

SLA changes with canopy depth (Ellsworth & Reich 1993; Hollinger 1996), and N is related to respiration rate (Reich *et al*. 1996; Ryan *et al*. 1996; Reich *et al*. 1998; Tissue *et al*. 2002), so it should be possible to scale foliar respiration from leaf to canopy level using mass- or N-based measures. When we scaled from leaf to canopy respiration at BRF using R_{mass} rather than R_{area}, the simplified constant-characteristics model calculations for the three canopy levels were similar to the calculation where the actual distribution of leaf characteristics was taken into account (a maximum deviation of −5·7% for the upper-canopy constant-characteristics calculation). However, this simplified scaling based on R_{mass} did little to improve the constant physiology calculations at OFW, as in this forest stand R_{mass} decreased with depth in the canopy. Therefore, while it may be possible to use simplifying assumptions regarding respiratory carbon loss in more complex models containing ecosystem physiology, some caution must be used when selecting representative leaves to generate empirical relationships between respiration and temperature. This has important implications for accurate modelling of respiratory carbon fluxes from forests, particularly for models that assume single temperature responses among species and with depth in canopies. Given the importance of respiration in influencing net carbon sequestration in forest communities, such calculations will be an important underpinning of our understanding of the ecology of forests in response to environmental change.

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References

Almond, P.C. (1996) Loess, soil stratigraphy and Aokautere ash on late Pleistocene surfaces in south Westland, New Zealand: interpretation and correlation with the glacial stratigraphy. *Quaternary International* **34–36**, 163–176.

Alward, R.D., Detling, J.K. & Milchunas. D.G. (1999) Grassland vegetation changes and nocturnal global warming. *Science* **283**, 229–231.

Amthor, J.S. (1989) *Respiration and Crop Productivity*. Springer-Verlag, New York.

Amthor, J.S. (1997) Plant respiratory response to elevated CO_2 partial pressure. *Advances in Carbon Dioxide Effects Research* (eds L.H. Allen Jr, M.B. Kirkham, D.M. Olszyk & C.E. Whitman), pp. 35–77. American Society of Agronomy, Madison, WI.

Amthor, J.S. (2000) Direct effect of elevated CO_2 on nocturnal *in situ* leaf respiration in nine temperate deciduous tree species is small. *Tree Physiology* **20**, 139–144.

Anten, N.P.R., Schieving, F. & Werger, M.J.A. (1995) Patterns of light and nitrogen distribution in relation to whole canopy carbon gain in C_3 and C_4 mono- and dicotyledonous species. *Oecologia* **101**, 504–513.

Atkin, O.A., Holly, C. & Ball, M.C. (2000) Acclimation of snow gum (*Eucalyptus pauciflora*) leaf respiration to seasonal and diurnal variations in temperature: the importance of changes in the capacity and temperature sensitivity of respiration. *Plant, Cell and Environment* **23**, 15–26.

Azcón-Bieto, J. (1992) Relationships between photosynthesis and respiration in the dark in plants. *Trends in Photosynthesis Research* (eds J. Barber, M.G. Guerrero & H. Medrano), pp. 241–253. Intercept Ltd, Andover, Hampshire, UK.

Azcón-Bieto, J. & Osmond, C.B. (1983) Relationship between photosynthesis and respiration. The effect of carbohydrate status on the rate of CO_2 production by respiration in darkened and illuminated wheat leaves. *Plant Physiology* **71**, 574–581.

Berry, J.A. & Raison, J.K. (1981) Responses of macrophytes to temperature. *Physiological Plant Ecology I. Responses to the Physical Environment* (eds O.L. Lange, P.S. Nobel, C.B. Osmond & H. Zeigler), pp. 277–238. Springer-Verlag, Berlin.

Bolstad, P.V., Mitchell, K. & Vose, J.M. (1999) Foliar temperature–respiration response functions for broad-leaved tree species in the southern Appalachians. *Tree Physiology* **19**, 871–878.

De Visser, R., Spitters, C.J.T. & Bouma, T.J. (1992) Energy costs of protein turnover: theoretical calculation and experimental estimation form regression of respiration on protein concentration of full-grown leaves. *Molecular Biochemical and Physiological Aspects of Plant Respiration* (eds H. Lambers & L.H.W. Van der Plas), pp. 493–508. Academic Press, The Hague, the Netherlands.

Dewar, R.C., Medlyn, B.E. & McMurtrie, R.E. (1999) Acclimation of the respiration photosynthesis ratio to temperature: insights from a model. *Global Change Biology* **5**, 615–622.

Easterling, D.R., Horton, B., Jones, P.D. *et al.* (1997) Maximum and minimum temperature trends for the globe. *Science* **277**, 364–367.

Ellsworth, D.S. & Reich, P.B. (1993) Canopy structure and vertical patterns of photosynthesis and related leaf traits in a deciduous forest. *Oecologia* **96**, 169–178.

Evans, J.R. (1989) Photosynthesis and nitrogen relationships in leaves of C_3 plants. *Oecologia* **78**, 9–19.

Evans, J.R. (1993) Photosynthetic acclimation and nitrogen partitioning within a lucern canopy. II. Stability through time and comparison with a theoretical optimum. *Australian Journal of Plant Physiology* **20**, 69–82.

Field, C.B. (1983) Allocating leaf nitrogen for the maximization of carbon gain: leaf age as a control on the allocation program. *Oecologia* **56**, 341–347.

Field, C.B. (1991) Ecological scaling of carbon gain to stress and resource availability. *Response of Plants to Multiple Stresses* (eds H.A. Mooney, W.E. Winner & E.J. Pell), pp. 35–65. Academic Press, New York.

Grace, J. & Rayment, M. (2000) Respiration in the balance. *Nature* **404**, 819–820.

Griffin, K.G., Sims, D.A. & Seemann, J.R. (1999) Altered night-time CO_2 concentration affects the growth, physiology and biochemistry of soybean. *Plant, Cell and Environment* **22**, 91–99.

Griffin, K.L., Tissue, D.T., Turnbull, M.H., Schuster, W.S.F. & Whitehead, D. (2001) Leaf dark respiration as a function of canopy position in *Nothofagus fusca* trees grown at ambient and elevated CO_2 partial pressures for six years. *Functional Ecology* **15**, 497–505.

Griffin, K.L., Turnbull, M.H. & Murthy, R. (2002) Canopy position affects the temperature response of leaf respiration in *Populus deltoides*. *New Phytologist* **154**, 609–619.

Gunderson, C.A., Norby, R.J. & Wullschleger, S.D. (2000) Acclimation of photosynthesis and respiration to simulated climatic warming in northern and southern populations of *Acer saccharum*: laboratory and field evidence. *Tree Physiology* **20**, 87–96.

Hansen, J., Ruedy, R., Glascoe, J. & Sato, M. (1999) GISS analysis of surface temperature change. *Journal of Geophysical Research* **104**, 30997–31022.

Hollinger, D.Y. (1996) Optimality and nitrogen allocation in a tree canopy. *Tree Physiology* **16**, 627–634.

Houghton, R.A. (1993) The role of the world's forests in global warming. *World Forest for the Future: Their Use and Conservation* (eds K. Ramakrishna & G.M. Woodwell), pp. 21–58. Yale University Press, New Haven, CT.

Hutchison, B.A., Matt, D.R., McMillen, R.T., Gross, L.J., Tajchman, S.J. & Norman, J.M. (1986) The architecture of a deciduous forest canopy in eastern Tennessee. *Journal of Ecology* **74**, 635–676.

IPCC (2001) *Third Assessment Report of Working Group I*. Intergovernmental Panel on Climate Change. United Nations Environmental Programme, Geneva, Switzerland.

James, I.L. & Norton, D.A. (2002) Helicopter based natural forest management for New Zealand's rimu (*Dacrydium cuprinessum*, Podocarpeae) forests. *Forest Ecology & Management* **155**, 337–346.

Lambers, H., Chapin, F.S. III & Pons, T.L. (1998) *Plant Physiological Ecology*. Springer-Verlag, New York.

Larigauderie, A. & Körner, C. (1995) Acclimation of leaf dark respiration to temperature in alpine and lowland plant species. *Annals of Botany* **76**, 245–252.

Law, B.E., Kelliher, F.M., Baldocchi, D.D. *et al.* (2001) Spatial and temporal variation in respiration in young ponderosa pine forest during a summer drought. *Agricultural and Forest Meteorology* **110**, 27–43.

Leuning, R., Cromer, R.N. & Rance, S. (1991) Spatial distributions of foliar nitrogen and phosphorus in crowns of *Eucalyptus grandis*. *Oecologia* **88**, 504–510.

Lloyd, J. & Taylor, J.A. (1994) On the temperature dependence of soil respiration. *Functional Ecology* **8**, 315–323.

Meir, P., Grace, J. & Miranda, A.C. (2001) Leaf respiration in two tropical rainforests: constraints on physiology by phosphorus, nitrogen and temperature. *Functional Ecology* **15**, 378–387.

Melillo, J.M. (1999) Warm, warm on the range. *Science* **283**, 183–184.

Mew, G. & Lee, R. (1981) Investigation of the properties and genesis of West Coast wetland soils, South Island, New Zealand. 1. Type localities, profile morphology, and soil chemistry. *New Zealand Journal of Science* **24**, 1–24.

Mitchell, K.A., Bolstad, P.V. & Vose, J.M. (1999) Interspecific and environmentally induced variation in foliar dark respiration among eighteen southeastern deciduous tree species. *Tree Physiology* **19**, 861–870.

Ogden, J. & Stewart, G.H. (1995) Community dynamics of the New Zealand conifers. *Ecology of the Southern Conifers* (eds N.J. Enright & R.S. Hill), pp. 81–119. Smithsonian Institution Press, Melbourne.

Olsson, K.S. (1981*) Soil Survey of Orange County, New York*. USDA Soil Conservation Service, US Government Printing Office, Washington, DC.

Penning de Vries, F.W.T. (1975) The cost of maintenance processes in plant cells. *Annals of Botany* **39**, 77–92.

Reich, P.B., Oleksyn, J. & Tjoelker, M.G. (1996) Needle respiration and nitrogen concentration in Scots Pine populations from a broad latitudinal gradient: a common garden test with field-grown trees. *Functional Ecology* **10**, 768–776.

Reich, P.B., Walters, M.B., Ellsworth, D.S. *et al.* (1998) Relationships of leaf dark respiration to leaf nitrogen, specific leaf area, and leaf life-span: a test across biomes and functional groups. *Oecologia* **114**, 471–482.

Ryan, M.G. (1991) Effects of climate change on plant respiration. *Ecological Applications* **1**, 157–167.

Ryan, M.G. (1995) Foliar maintenance respiration of subalpine and boreal trees and shrubs in relation to nitrogen content. *Plant, Cell and Environment* **18**, 765–772.

Ryan, M.G., Linder, S., Vose, J.M. & Hubbard, R.M. (1994) Dark respiration in pines. *Ecological Bulletins* **43**, 50–63.

Ryan, M.G., Hibberd, R.M., Pongracic, S., Raison, R.J. & McMurtrie, R.M. (1996) Foliage, fine-root, woody tissues and stand respiration in *Pinus radiata* in relation to nitrogen status. *Tree Physiology* **16**, 333–343.

Sokal, R.R. & Rohlf, F.J. (1981) *Biometry*. Freeman, New York.

Stockfors, J. & Linder, S. (1998) The effect of nutrition on the seasonal course of needle respiration in Norway spruce stands. *Trees* **12**, 130–138.

Tissue, D.T., Lewis, J.D., Wullschleger, S.D., Amthor, J.S., Griffin K.L. & Anderson, O.R. (2002) Leaf respiration in sweetgum (*Liquidambar styraciflua* L.) at different canopy positions grown in ambient and elevated CO_2 in the field. *Tree Physiology* in press.

Tjoelker, M.G., Oleksyn, J. & Reich, P.B. (2001) Modelling respiration of vegetation: evidence for a general temperature-dependent Q_{10}. *Global Change Biology* **7**, 223–230.

Turnbull, M.H., Whitehead, D., Tissue, D.T., Schuster, W.F.S., Brown, K.J. & Griffin, K.L. (2001) The response of leaf respiration to temperature and leaf characteristics in three deciduous tree species differs at sites of contrasting soil moisture. *Tree Physiology* **21**, 571–578.

Turnbull, M.H., Whitehead, D., Tissue, D.T. *et al.* (2002) Photosynthetic characteristics in canopies of *Quercus rubra*, *Quercus prinus* and *Acer rubrum* differ in response to soil water availability. *Oecologia* **130**, 515–524.

Underwood, A.J. (1981) Techniques of analysis of variance in experimental marine biology and ecology. *Oceanography and Marine Biology Annual Reviews* **19**, 513–605.

Valentini, R., Mateucci, G., Dolman, A.J. *et al.* (2000) Respiration as the main determinant of carbon balance in European forests. *Nature* **404**, 861–864.

Vose, J.M. & Bolstad, P.V. (1999) Challenges to modelling NPP in diverse eastern deciduous forests: species-level comparisons of foliar respiration responses to temperature and nitrogen. *Ecological Modelling* **122**, 165–174.

Whitehead, D., Walcroft, A.S., Griffin, K.L. *et al.* (2003) Scaling carbon uptake from leaves to canopies: insights from two forests with contrasting properties. *Forests at the Land–Atmosphere Interface* (eds M. Mencuccini & J. Grace). CAB International, Wallingford, Oxon, UK, in press.

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