Irradiance, temperature and rainfall influence leaf dark respiration in woody plants: evidence from comparisons across 20 sites

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Summary

- Leaf dark respiration (*R*) is one of the most fundamental physiological processes in plants and is a major component of terrestrial CO_2 input to the atmosphere. Still, it is unclear how predictably species vary in *R* along broad climate gradients.
- Data for *R* and other key leaf traits were compiled for 208 woody species from 20 sites around the world. We quantified relationships between *R* and site climate, and climate-related variation in relationships between *R* and other leaf traits.
- Species at higher-irradiance sites had higher mean *R* at a given leaf N concentration, specific leaf area (SLA), photosynthetic capacity (A_{mass}) or leaf lifespan than species at lower-irradiance sites. Species at lower-rainfall sites had higher mean *R* at a given SLA or A_{mass} than species at higher-rainfall sites. On average, estimated field rates of *R* were higher at warmer sites, while no trend with site temperature was seen when *R* was adjusted to a standard measurement temperature.
- Our findings should prove useful for modelling plant nutrient and carbon budgets, and for modelling vegetation shifts with climate change.

Key words: climate gradients, leaf nitrogen, leaf lifespan, photosynthesis, plant metabolism, specific leaf area.

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Introduction

Respiration describes a variety of processes that plants use to generate usable energy (e.g. ATP) and carbon skeletons (needed for biosynthesis). The main substrates for respiration are soluble carbohydrates produced by photosynthesis. Energy is required throughout the plant for growth, nitrate reduction in roots and leaves, symbiotic N_2 fixation, nutrient uptake from the soil, synthesis and phloem-loading of photosynthates, protein and lipid membrane turnover, maintenance of ion gradients between cellular compartments, protecting the photosynthetic apparatus against damage from high light, and repairing damage when this does occur (Amthor, 2000; Cannell & Thornley, 2000; Millar *et al.*, 2003; Raghavendra & Padmasree, 2003). Combined, above- and below-ground respiration from plants represents 30–65% of the total CO_2 released into the atmosphere at the ecosystem level, with leaf respiration contributing between 30 and 60% of this total (Amthor & Baldocchi, 2001; Janssens *et al.*, 2001; Xu *et al.*, 2001).

Although respiration occurs during both day and night (Krömer, 1995), it is most easily measured on leaves in the absence of light so that the respiratory flux of CO_2 (or O_2 uptake) can be distinguished from that caused by photosynthesis. Expressed on a leaf dry-mass basis, this 'dark respiration' (*R*) varies widely between species and shows reasonably consistent relationships with other leaf traits (Reich *et al.*, 1998). In within-site, regional and global interspecific comparisons, *R* has been positively correlated with leaf N concentration (N_{mass}), photosynthetic capacity (A_{mass}) and specific leaf area

(SLA), and negatively correlated with average leaf lifespan (LL) (Ryan, 1995; Reich *et al.*, 1998; Wright *et al.*, 2001; Turnbull *et al.*, 2003). Together, these traits form a spectrum of leaf 'economics' (Wright *et al.*, 2004; Wright *et al.*, 2005a), running from species with potential for quick photosynthetic returns on investments of nutrients and dry mass in short-lived leaves (e.g. many herbs, grasses and deciduous trees) to species with slower potential rates of return, but long-lived leaves (e.g. many evergreen shrubs and trees).

Previously we have quantified broad-scale relationships between site climate and key leaf economic traits, and the degree to which the relationships between leaf traits vary with climate (Wright *et al.*, 2004; Wright *et al.*, 2005b). *R* was not included in these analyses because dealing with climate-related trends in respiration is more complex than for the other leaf traits. Specifically, *R* is strongly temperature-sensitive in the short term (increasing approximately exponentially with temperature), yet can show compensatory adjustment (acclimation) over the longer term (over a few days, weeks or months), with the extent of acclimation varying considerably among species (Larigauderie & Körner, 1995; Atkin & Tjoelker, 2003; Loveys *et al.*, 2003; Atkin *et al.*, 2005). Ideally, these effects should be taken into account when considering relationships between *R* and site temperature, and if we are to model vegetation (and carbon budget) responses to climate change reliably.

In this study we drew together leaf trait data (*R*, leaf lifespan, A_{mass}, N_{mass} and SLA) for species from 20 sites around the world. The sites vary widely in climate and represent a number of predominantly woody biomes (Table 1). There were two aims to the study:

1 To quantify relationships between *R* and site climate. Climate was characterized in terms of temperature, rainfall and solar radiation, all of which strongly influence the primary

Table 1 Details of sample sizes, climate and measurement conditions for the 20 sites at which leaf dark respiration (*R*) was measured

Site	References	Biome	No. species (woody/ total)	$T_{ambient}$ (°C)	$T_{measured}$ (°C)	MAT (°C)	Mean annual rainfall (mm)	Mean daily solar radiation (W m^{-2})
Kitajima: Panama	1	Tropical rainforest	6/6	26.0	29	26.3	1657	183
Lee: Cedar Creek, USA	Unpubl.	Temperate forest	1/12	22.0	25	6.3	730	127
Lusk: Concepción, Chile	2, 3, unpubl.	Temperate forest	6/6	16.7	23	12.9	1308	183
Lusk: Los Lleuques, Chile	2, 3, unpubl.	Temperate forest	5/5	12.0	22	6.6	1308	180
Lusk: Puyehue, Chile	2, 3, unpubl.	Temperate rainforest	12/12	13.5	21.8	10.6	3500	167
Mitchell: Coweeta, USA	4, 5, unpubl.	Temperate forest	14/14	19.9	25	11.6	1740	146
Miyazawa: Chiba, Japan	6	Temperate forest	4/4	18.7	27	14.7	1790	136
Mooney: South Africa	7	Temperate forest	5/5	15.2	21	17.0	2500	188
Reich: Colorado, USA	8, 9	Temperate forest	7/10	8.7	25	–1.5	959	142
Reich: North Carolina, USA	8, 9	Temperate forest	9/14	20.5	25	11.6	1740	146
Reich: New Mexico, USA	8, 9	Woodland	8/9	23.3	25	13.5	272	179
Reich: South Carolina, USA	8, 9	Temperate forest	9/10	26.5	25	18.2	1295	152
Reich: Venezuela	8, 9	Tropical rainforest	11/11	26.3	25	26.0	3171	154
Reich: Wisconsin, USA	8, 9	Temperate forest	9/15	21.2	25	8.2	909	134
Tjoelker: Cedar Creek, USA	10, 11, unpubl.	Temperate forest	2/32	20.5	25	6.3	730	127
Veneklaas: Western Australia	12, unpubl.	Woodland	23/25	22.5	25	18.3	690	182
Wright: high rain, high soil P, Australia	13, 14	Temperate forest	18/18	19.5	25	17.5	1148	162
Wright: high rain, low soil P, Australia	13, 14	Woodland	17/17	19.5	25	17.5	1148	162
Wright: low rain, high soil P, Australia	13, 14	Woodland	22/22	18.7	25	17.1	412	177
Wright: low rain, low soil P, Australia	13, 14	Woodland	20/21	18.7	25	17.1	412	177

$T_{ambient}$, mean monthly temperature during the period when measurements were made (typically mid-growing season); $T_{measured}$, mean temperature at which *R* was measured; MAT, mean annual temperature.
Similar sampling protocols were followed for most studies: outer canopy branches were sampled between early and mid-morning and kept in dark, moist and cool conditions (5–10°C) before being warmed to a standard temperature shortly before *R* was measured, *R* being measured in terms of CO_2 efflux using standard infrared gas analysis equipment.
Exceptions
Sampling time: Mitchell (predawn), Kitajima (dawn), Mooney (unknown), Miyazawa (unknown).
Measurement of *R*: Kitajima (*R* measured using oxygen electrode; values converted to CO_2 production by assuming a respiratory quotient of 1.0; Lambers *et al.*, 1998).
Material: Mooney (branches still attached), Kitajima (*R* measured on leaf discs). See Reich *et al.* (1998); Mitchell *et al.* (1999) for justification of measuring *R* on detached branches.
References: 1 (Kitajima *et al.*, 1997); 2, 3 (Lusk, 2001; Lusk *et al.*, 2003); 4, 5 (Bolstad *et al.*, 1999; Mitchell *et al.*, 1999); 6 (Miyazawa *et al.*, 1998); 7 (Mooney *et al.*, 1983); 8, 9 (Reich *et al.*, 1998, 1999); 10, 11 (Craine *et al.*, 1999; Tjoelker *et al.*, 2005); 12 (Veneklaas & Poot, 2003); 13, 14 (Wright *et al.*, 2001; Wright & Westoby, 2002).

productivity of vegetation (Lieth, 1975; Potter & Klooster, 1999; Roderick *et al.*, 2001).

2 To quantify the extent to which relationships between R and the other leaf traits vary according to site climate.

While we are unaware of any previous attempts to quantify relationships between R and either site rainfall or irradiance, there have been a number of comparisons of respiration rates of species originating from sites differing in mean (and growing-season) temperature. These studies can be divided into two types. In the first type, the species have been studied in their natural habitats, with R measured on leaves briefly elevated to a standard temperature before measurement. Mean R at a standard measurement temperature was higher for species from colder sites in three of four such studies (Stocker, 1935; Wager, 1941; Semikhatova *et al.*, 1992); in the fourth, no relationship was evident between R and site temperature (Reich *et al.*, 1998). Both Stocker (1935) and Semikhatova *et al.* (1992) also measured R at approximately ambient field temperatures ($R_{ambient}$), finding no relationship between $R_{ambient}$ and site temperature when comparing rates across sites that differed in climate. Thus the pattern of cold-site species having higher mean R (measured at a standard temperature) appeared simply to reflect greater short-term stimulation of $R_{ambient}$, the difference between ambient and measurement temperatures being greater for these species.

In the second type of study, sets of species originating from thermally contrasting sites have been grown at a standard temperature in growth chambers, and R then measured at this temperature. Results from these studies have suggested that species from colder sites have R generally lower than (Atkin *et al.*, 1997), higher than (Larigauderie & Körner, 1995 for comparisons made at 20 but not 10°C), or similar to species from warmer sites (Atkin & Day, 1990; Collier, 1996). Several similar studies have compared within-species variation, comparing plants originating from thermally contrasting sites but growing them in a common garden and measuring R at a standard temperature. Mean R was higher for plants originating from colder sites in the majority of these studies (Mooney, 1963; Klikoff, 1968; Reich *et al.*, 1996; Oleksyn *et al.*, 1998), but not in all (Chapin & Oechel, 1983). In all these growth-chamber or common-garden experiments, R was given ample time to acclimatize to the standard temperature at which it was measured. Thus it is impossible to infer *post hoc* what trend in R would have been evident for the species (or populations) while growing in their natural habitats, whether R had been measured at ambient field temperatures ($R_{ambient}$) or for leaves briefly elevated to the measurement temperature (as in the first type of study above).

The majority of the studies mentioned above concerned herbs or grasses, mostly or entirely, further complicating any attempt to infer general, climate-related trends in $R_{ambient}$ across the world's vegetation. However, short-term temperature responses of R have been quantified for many species, both woody and herbaceous. Thus for studies where R has been measured on leaves briefly elevated to a standard temperature, but not measured at ambient air temperature, the latter ($R_{ambient}$) can be estimated from the former, either by using species-specific information or by using a general equation describing the short-term temperature response of R (Atkin & Tjoelker, 2003; Atkin *et al.*, 2005). We used both approaches in this study. Data were compiled from source studies where R had been measured on field-grown plants with similar methods. R was measured at a standard temperature within each study (most commonly 25°C, but varying between 20 and 29°C). Two formulations of R were calculated and used in our analyses. First (where necessary) we standardized measured R values to 25°C (R_{25}). Second, we adjusted measured R values to the mean monthly temperature of each site during the time of year when R was measured, this formulation estimating what R would have been had it been measured in the field at ambient temperatures ($R_{ambient}$).

Materials and Methods

Data were compiled from a number of published and unpublished sources (Table 1). A number of criteria had to be met before a source data set was considered suitable. It had to be site-based, so that we could reasonably attach climate data. It had to provide R for at least four co-occurring species at a given site, along with data for at least two of the other leaf traits of interest. It had to provide R measurements made on nonsenescent, fully expanded leaves so that they reflected 'maintenance' respiration (McCree, 1970) more than respiratory costs associated with the conversion of reserve materials into new structure ('growth' respiration). Highly artificial vegetation types such as forestry plantations and crop fields were not included, on the basis that selected genotypes may not represent the long-term adaptation of the taxa to the climate and site. All studies had broadly similar sampling and measurement protocols (e.g. R was measured on foliage from outer canopy branches, generally as CO_2 efflux; details of sampling protocols are given in the footnotes to Table 1). In particular, virtually identical methods were used in studies that one of us (P.B.R.) was directly involved in; together they contributed 80% of the total data set (studies designated as Lee, Reich, Tjoelker, Veneklaas and Wright in Table 1). The total data set consisted of 268 species–site combinations; 23 species occurred at two sites, one species at three sites. For species at 17 of the 20 sites we were able to obtain data for all five of R, A_{mass}, SLA, N_{mass} and LL. Of the 268 species–site combinations, 208 were for woody species (trees or shrubs). Of these species (on which our analyses concentrated), we knew R, SLA and N_{mass} for all 208 species–site combinations, A_{mass} for 193, and LL for 177.

In this study we express leaf R on a dry mass basis. A_{mass} (photosynthetic assimilation capacity) refers to photosynthetic rates measured under near-saturating light conditions, ambient CO_2 concentrations, close-to-ambient air temperatures, and well watered conditions in the growth environment, also expressed on a dry mass basis. A_{mass}, N_{mass} and SLA were measured for fully expanded, nonsenescent leaves. Average LL was estimated either from repeated censuses of leaf populations or by following whole cohorts of leaves from birth to death. The source papers (Table 1) can be consulted for further details about the leaf traits. Trait means were calculated for each species at a site where the mean was not already reported.

Calculation of R_{25} and $R_{ambient}$

The respiration rate at a standard temperature of interest (R_2, at T_2) can be estimated from that measured at another temperature (R_1, at T_1) using the following formula describing the average temperature-response of leaf respiration across 116 terrestrial plant species (Atkin & Tjoelker, 2003; Atkin *et al.*, 2005):

$$R_2 = R_1\{3.09 - 0.0435[(T_2 + T_1)/2]\}^{[(T_2 - T_1)/10]} \qquad \text{Eqn 1}$$

Measured dark respiration rates ($R_{measured}$) were adjusted using this formula, first to 25°C (R_{25}), and second to the long-term mean monthly air temperature during the months when measurements were made ($R_{ambient}$). Another approach for scaling $R_{measured}$ by temperature is to use an appropriate Q_{10} value, this being the ratio of R measured at one temperature to R measured at 10°C lower. The problem is that Q_{10} itself varies with temperature, typically declining with increasing measurement temperature (Tjoelker *et al.*, 2001; Atkin & Tjoelker, 2003). However, as species-specific Q_{10} values were available for the 'Mitchell Coweeta' data set, this second approach (equation 2) was used for these species rather than using equation 1.

$$R_2 = R_1 Q_{10}^{[(T_2 - T_1)/10]} \qquad \text{Eqn 2}$$

For these species (Mitchell Coweeta) the Q_{10} and R values used were those calculated/measured for the upper canopy leaf class of each species, from plants growing at 600–1100 m elevation (Bolstad *et al.*, 1999). The reported R values (measured at 20°C) were scaled first to 25°C (R_{25}) and then to the estimated ambient air temperature ($R_{ambient}$), just as for species at all other sites.

For 170 of the 208 woody species, there was no need to scale R to 25°C as measurements were actually made at that temperature. Adjusting $R_{measured}$ to the long-term average temperature of the measurement period ($T_{ambient}$ in Table 1) allowed us to estimate what R would have been had it been measured in the field at ambient temperature ($R_{ambient}$). That is, we presume that the warming or cooling required to measure R at a standard temperature would have affected ambient rates of R in a manner well described by the equations above. Reversing that process should give reasonable estimates of $R_{ambient}$. While it may seem circular to then compare $R_{ambient}$ to site mean annual temperature (MAT), the same could be said for warming leaves of all species to a standard temperature and then comparing the measured R values with site MAT, given that R would be increased more in species from colder sites. We view both formulations of R (R_{25} and $R_{ambient}$) as relevant for examining how R varies with site climate – the patterns they reveal are complementary. Photosynthetic capacity (A_{mass}) was not adjusted for temperature because it was measured at close-to-ambient air temperatures in all studies, and because it is generally less temperature-sensitive than is R over a comparable temperature range near the temperature optimum for photosynthesis (Hill *et al.*, 1988; Tjoelker *et al.*, 1998; Atkin *et al.*, 2000b).

Climate data and data analysis

Long-term climate data were taken from (1) the sites themselves, where measurements had been made; (2) the nearest weather stations, with temperature data scaled where necessary by an altitudinal lapse rate of 0.6°C per 100 m (Körner, 1999); (3) a global $0.5 \times 0.5°$ data set of MAT, rainfall and solar radiation (New *et al.*, 1999). Climate variables were summed (total annual rainfall) or averaged (mean daily temperature and irradiance) across all months of the year, and across the growing season (months where the mean air temperature was = 5°C; see Additional analyses).

The majority of herbaceous species (herbs and grasses) in the data set were sampled from sites representing only a limited climatic range (three-quarters coming from sites experiencing between 6.3 and 8.2°C MAT and 690 and 730 mm annual rainfall). By contrast, each of the various woody plant functional types (shrubs, deciduous trees, broad-leaf evergreen trees, needle-leaf evergreen trees) were sampled from a broad range of sites, spanning at least 19°C in MAT and 1000 mm in annual rainfall. Consequently, we concentrated on woody species in our analyses, although some trends involving the herbaceous species are also reported. Site rainfall was strongly right-skewed across the data set and was $\log_{10}$-transformed for all analyses. MAT and irradiance were left untransformed as their distribution was approximately normal. MAT and irradiance were positively correlated across sites (correlation $r = 0.48$, $P = 0.031$); MAT and rainfall, and rainfall and irradiance, were unrelated (both $P > 0.4$).

There was considerable variation among species for each leaf trait. R_{25} varied 16-fold across the data set, $R_{ambient}$ 47-fold, SLA 22-fold, N_{mass} eightfold, A_{mass} 41-fold, and LL 70-fold. All leaf traits were strongly right-skewed and were $\log_{10}$-transformed before analysis. Standard bivariate regression was used for quantifying relationships between R and climate variables, and between R and the other leaf traits. Multiple regression was used for quantifying the effect of climate on R–trait relationships. In these analyses a significant coefficient for the climate variable indicates that the 'elevation' (intercept) of the trait relationship varies with climate.

Additional analyses

We ran a number of additional analyses to test whether our results were sensitive to the method by which $R_{ambient}$ and R_{25} were calculated. Our overriding conclusion was that they were not. In the first set of analyses, R_{25} and $R_{ambient}$ were calculated using several different Q_{10} values and equation 2. For leaves experiencing moderate temperatures, such as between 15 and 25°C, Q_{10} ranges between 1.4 and 4.2, but the majority of values fall between 2.0 and 2.6 (Larigauderie & Körner, 1995; Tjoelker *et al.*, 2001). Using a range of Q_{10} values between 1.4 and 4.2, we found the same patterning of *R* by climate (or lack thereof), and the same effects of climate on *R*–trait relationships as with R_{25} and $R_{ambient}$ calculated using equation 1, with only one exception. With Q_{10} values between 3.9 and 4.2, the MAT effect on the R_{25}–A_{mass} regression became weakly negative ($P = 0.042$) rather than nonsignificant (see Results). In the second set of analyses, $R_{ambient}$ was recalculated by adjusting $R_{measured}$ to the mean temperature during the entire growth season, rather than to the mean temperature for just the months when measurements were made. Equation 1 was used for these calculations, and growth season was defined as months where the mean air temperature was = 5°C. This recalculation of $R_{ambient}$ to growing-season temperature did not change our findings in any qualitative sense. Finally, instead of using MAT in regression analyses, we substituted the average temperature during the growth season, as well as the version of $R_{ambient}$ adjusted to this temperature. Again, there was close agreement between these results and those we report in Results, but in this case with a stronger $R_{ambient}$–site temperature correlation ($r = 0.58$ compared with $r = 0.39$, both $P < 0.001$). In conclusion, the patterns we observed between *R* and climate among woody species were robust to a whole range of different assumptions made in the calculations of R_{25} and $R_{ambient}$.

Results

Relationships between *R* and site climate

Across the 208 woody species, R_{25} was unrelated to site MAT, annual rainfall or average site irradiance (all $P > 0.130$; Fig. 1a–c). $R_{ambient}$ was also unrelated to rainfall ($P = 0.078$) and irradiance ($P = 0.787$), but was positively correlated with MAT ($r^2 = 0.15$, $P < 0.001$; Fig. 1d–f). Despite the positive relationship between $R_{ambient}$ and MAT, we note that there was *c.* 10-fold variation among species in *R* at any given MAT (or rainfall, or irradiance).

Among the 60 herbs and grasses in the original data set, R_{25} was negatively related to MAT ($r^2 = 0.09$, $P = 0.020$) and irradiance ($r^2 = 0.11$, $P = 0.008$), and positively correlated with rainfall ($r^2 = 0.15$, $P = 0.002$). $R_{ambient}$ was also negatively related to irradiance ($r^2 = 0.11$, $P = 0.009$) and positively correlated with rainfall ($r^2 = 0.09$, $P = 0.022$), but showed no relationship with MAT ($P = 0.820$). As these species were sampled from only a very limited climatic range (see Materials and Methods), these results do not necessarily reflect trends over broader climatic gradients.

Modulation of trait relationships by climate

The following analyses concern woody species only. As expected (Reich *et al.*, 1998), R_{25} and $R_{ambient}$ were positively correlated with SLA, N_{mass} and A_{mass}, and negatively correlated with LL (all $P < 0.001$; regression details in Table 2). The relationships involving A_{mass} and LL were generally stronger than those involving SLA or N_{mass}. R_{25} was more tightly related to SLA and N_{mass} than was $R_{ambient}$; both formulations of *R* were correlated with A_{mass} and LL, with similar strength (Table 2).

Across the 208 woody species, both R_{25} and $R_{ambient}$ increased with increasing site irradiance at a given N_{mass}, SLA,

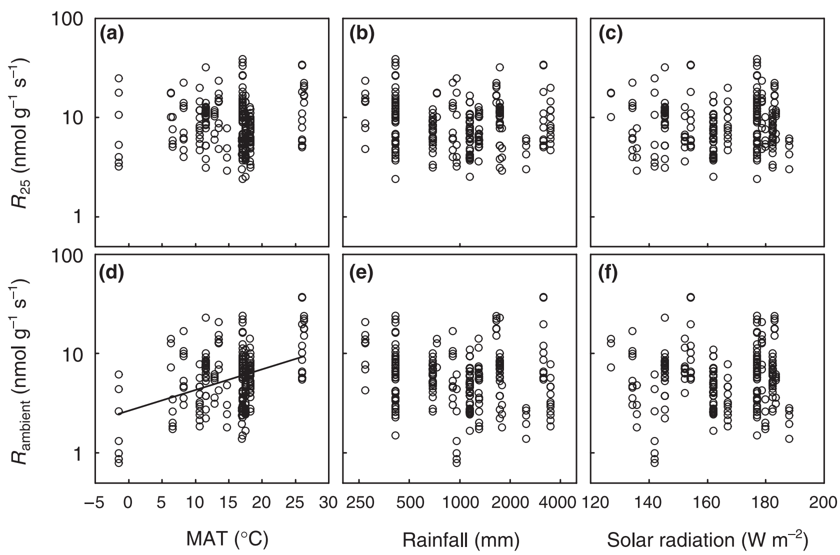

Fig. 1 Relationships between dark respiration (R_{25} and $R_{ambient}$) and site climate for 208 tree and shrub species from 20 sites. The only statistically significant relationship was between $R_{ambient}$ and mean annual temperature (d), for which the fitted regression line had the following parameters: $\log_{10} R_{ambient} = 0.021$ MAT + 0.43; $r^2 = 0.15$. Sensitivity analyses (see Materials and Methods) showed that these findings were still seen when a wide range of different Q_{10} values were used to calculate $R_{ambient}$.

Table 2 Regression equations predicting leaf dark respiration (R) as a function of other leaf traits across the 208 woody species

Equation	r^2
$\log R_{25} = 0.595 \log \text{SLA} - 0.169$	0.36
$\log R_{ambient} = 0.622 \log \text{SLA} - 0.396$	0.26
$\log R_{25} = 0.889 \log N_{mass} + 0.788$	0.45
$\log R_{ambient} = 1.003 \log N_{mass} + 0.593$	0.39
$\log R_{25} = 0.624 \log A_{mass} - 0.211$	0.49
$\log R_{ambient} = 0.754 \log A_{mass} - 0.623$	0.48
$\log R_{25} = -0.511 \log \text{LL} + 1.542$	0.55
$\log R_{ambient} = -0.623 \log \text{LL} + 1.503$	0.55

Units: R_{25} and $R_{ambient}$, nmol g^{-1} s^{-1}; specific leaf area (SLA), cm^2 g^{-1}; leaf N concentration (N_{mass}), %; photosynthetic capacity (A_{mass}), nmol g^{-1} s^{-1}; leaf lifespan (LL), months.
Sample size: for relationships involving N_{mass} or SLA, $n = 208$ species; for A_{mass}, $n = 193$; for LL, $n = 177$.

A_{mass} or LL (regression coefficient for irradiance significantly positive in all cases, all $P = 0.005$; Table 3). The $R_{ambient}$–SLA relationship is depicted in Fig. 2(a) (in which species have been coded into irradiance classes for illustrative purposes only).

There was no effect of site rainfall on regressions of either R_{25} or $R_{ambient}$ on either N_{mass} or LL. However, site rainfall had a significantly negative effect on regressions of either formulation of R with both SLA and with A_{mass} (all $P < 0.001$). That is, at a given SLA or A_{mass}, dark respiration was higher at lower-rainfall sites (regression details in Table 3). This is depicted in Fig. 2(b), where species have been coded into rainfall classes.

MAT had no effect on regressions of R_{25} on any of N_{mass}, SLA, A_{mass} or LL. However, $R_{ambient}$ increased with increasing MAT at a given N_{mass}, SLA, A_{mass} or LL (main MAT effects all $P < 0.001$; Table 3). This is illustrated in Fig. 2(c), where species have been coded into MAT classes. The trends concerning site rainfall and irradiance can be contrasted with those concerning MAT: whereas the MAT effects on $R_{ambient}$ were observed whether or not variation in the other leaf traits was simultaneously controlled, there were no apparent rainfall or irradiance effects on leaf R except in the multiple regressions.

Independence of climate effects on trait relationships

More complex regression models were used to assess the extent to which the various climate effects were independent of each other. In regressions predicting either R_{25} or $R_{ambient}$ from SLA, the effect of irradiance was still significantly positive, and that of rainfall still significantly negative, when both climate variables were included in analyses (irradiance and rainfall terms all $P < 0.002$). The influence of rainfall on R–A_{mass} relationships was still evident when irradiance was added to the models (rainfall terms $P < 0.003$), although in these analyses irradiance itself was only marginally significant at best (predicting R_{25}, $P = 0.054$; predicting $R_{ambient}$, $P = 0.134$). Finally, the positive MAT term in each of the $R_{ambient}$ regressions was still found when rainfall and/or irradiance were added to any of the models (MAT terms all $P < 0.001$). In summary, the irradiance and rainfall effects on R–SLA relationships were substantially independent, whereas their

Table 3 Regression equations expressing leaf dark respiration (R) as a function of other leaf traits and site climate across the 208 woody species

	Equation	r^2	β_1	β_2
1	$\log R_{25} = 0.742 \log \text{SLA} + 0.005\ \text{RAD} - 1.295$	0.45	0.744	0.345
2	$\log R_{ambient} = 0.772 \log \text{SLA} + 0.005\ \text{RAD} - 1.547$	0.33	0.638	0.291
3	$\log R_{25} = 0.941 \log N_{mass} + 0.003\ \text{RAD} + 0.330$	0.49	0.713	0.182
4	$\log R_{ambient} = 1.058 \log N_{mass} + 0.003\ \text{RAD} + 0.100$	0.42	0.662	0.161
5	$\log R_{25} = 0.644 \log A_{mass} + 0.003\ \text{RAD} - 0.670$	0.51	0.718	0.162
6	$\log R_{ambient} = 0.775 \log A_{mass} + 0.003\ \text{RAD} - 1.131$	0.50	0.713	0.147
7	$\log R_{25} = -0.525 \log \text{LL} + 0.003\ \text{RAD} + 1.029$	0.59	−0.763	0.188
8	$\log R_{ambient} = -0.641 \log \text{LL} + 0.004\ \text{RAD} + 0.858$	0.59	−0.766	0.195
9	$\log R_{25} = 0.727 \log \text{SLA} -0.294 \log \text{RAIN} + 0.473$	0.47	0.729	−0.365
10	$\log R_{ambient} = 0.777 \log \text{SLA} -0.346 \log \text{RAIN} + 0.360$	0.37	0.643	−0.355
11	$\log R_{25} = 0.647 \log A_{mass} -0.169 \log \text{RAIN} + 0.255$	0.53	0.721	−0.206
12	$\log R_{ambient} = 0.783 \log A_{mass} -0.223 \log \text{RAIN} - 0.010$	0.53	0.720	−0.224
13	$\log R_{ambient} = 0.655 \log \text{SLA} + 0.023\ \text{MAT} - 0.805$	0.44	0.542	0.424
14	$\log R_{ambient} = 1.005 \log N_{mass} + 0.021\ \text{MAT} + 0.271$	0.55	0.628	0.391
15	$\log R_{ambient} = 0.695 \log A_{mass} + 0.017\ \text{MAT} - 0.782$	0.58	0.640	0.313
16	$\log R_{ambient} = -0.572 \log \text{LL} + 0.020\ \text{MAT} + 1.172$	0.69	−0.684	0.376

All climate variables were significant ($P = 0.005$). Relative contributions of leaf and climate variables to each regression can be ascertained from their standardized partial regression coefficients (β_1 and β_2, respectively).
Units: specific leaf area (SLA), cm^2 g^{-1}; leaf N concentration (N_{mass}), %; photosynthetic capacity (A_{mass}), nmol g^{-1} s^{-1}; leaf lifespan (LL), months; solar radiation (RAD), W m^{-2}; rainfall (RAIN), mm; mean annual temperature (MAT), °C.
Sample size: for relationships involving N_{mass} or SLA, $n = 208$ species; for A_{mass}, $n = 193$; for LL, $n = 177$.

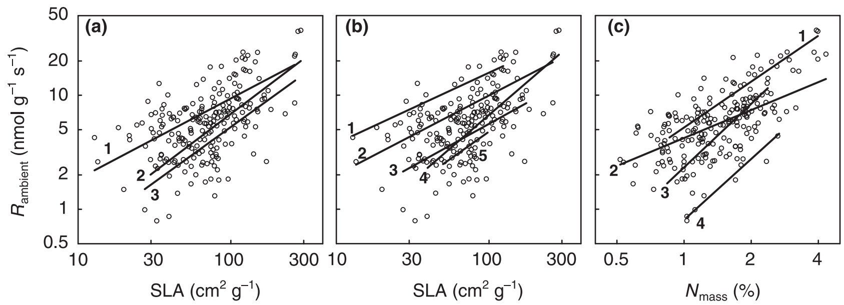

Fig. 2 Patterning of $R_{ambient}$–trait relationships by climate (208 woody species). (a) $R_{ambient}$ vs specific leaf area (SLA), with regression lines shown for species coded into irradiance classes. Classes: 1 (127–150); 2 (150–170); 3 (170–190 W m^{-2}). Classes were defined on an arithmetic scale as irradiance was approximately normally distributed. (b) $R_{ambient}$ vs SLA, with regression lines shown for species coded into annual rainfall classes. Classes: 1 (200–400); 2 (400–800); 3 (800–1600); 4 (1600–3200); 5 (> 3200 mm). Classes were defined on a log scale because rainfall was strongly right-skewed (approximately log-normally distributed). (c) $R_{ambient}$ vs leaf N concentration (N_{mass}), with regression lines shown for species coded into mean annual temperature (MAT) classes. Classes: 1 (20–30); 2 (10–20); 3 (0–10); 4 (–10 to 0°C). Classes were defined on an arithmetic scale as MAT was approximately normally distributed.

effects on R–A_{mass} relationships were at least partially conflated. By contrast, the MAT effects on $R_{ambient}$ relationships were independent of the effects of the other climate variables.

Discussion

Consequences for leaf dry mass and nutrient economics

The climate-related trends in R found in our analyses were of sufficient magnitude to have potentially important consequences for the dry mass and nutrient economics of leaves, and thus for whole-plant carbon balance. Below we give six examples comparing two hypothetical woody species occurring in different climate zones, based on regression equations in Table 3:

1 Comparing two species, each with leaf N_{mass} of 1.4% (mean log N_{mass} for woody species in the data set), both R_{25} and $R_{ambient}$ would be 30% higher for a species occurring at a site with 180 W m^{-2} mean irradiance than for one at 140 W m^{-2} (Table 3, equations 3 and 4). Heath forest in Malaysia (146 W m^{-2} irradiance) and rainforest on Barro Colorado Island, Panama (180 W m^{-2}) are vegetation types with similar MAT and annual rainfall that approximately fit this climate contrast (climate data from Wright *et al.*, 2004).

2 Comparing two species, each with A_{mass} of 63.5 nmol g s^{-1} (mean log A_{mass} for woody species), a species occurring at 180 W m^{-2} irradiance would have 26% higher R_{25} or 30% higher $R_{ambient}$ than one at 140 W m^{-2} (Table 3, equations 5 and 6).

3 Comparing two species, each with SLA of 69 cm^2 g^{-1} (mean log SLA for woody species), one growing at 500 mm annual rainfall would average 50% higher R_{25} and 62% higher $R_{ambient}$ than one growing at a site experiencing 2000 mm annual rainfall (Table 3, equations 9 and 10).

4 Comparing two species each with A_{mass} of 63.5 nmol g s^{-1}, one growing at 500 mm annual rainfall would average 26% higher R_{25} and 36% higher $R_{ambient}$ than one growing at a site experiencing 2000 mm annual rainfall (Table 3, equations 11 and 12).

5 Comparing two woody species, each with SLA of 69 cm^2 g^{-1} (mean log SLA for woody species), one growing at 20°C MAT would average 69% higher $R_{ambient}$ than one growing at a site with 10°C MAT (Table 3, equation 13).

6 Comparing two species, each with N_{mass} of 1.4%, one growing at 20°C MAT would average 62% higher $R_{ambient}$ than one growing at a site with 10°C MAT (Table 3, equation 14). Note that the bivariate trend between $R_{ambient}$ and MAT (Fig. 1d) indicated a trend of almost exactly the same magnitude (61%; regression details in figure legend).

Site temperature: conflict with previous results

On average, we found that woody species from warmer sites had higher estimated field rates of R ($R_{ambient}$) than species from colder sites, while no difference was seen when R was compared at a standard temperature (R_{25}). What could account for the discrepancy between our findings and those from several previous reports (see Introduction)? One possibility is differences in sample size. Stocker (1935) studied three tropical, 31 temperate-zone and three arctic species; Wager (1941) compared 15 arctic species with 10 temperate species; Semikhatova *et al.* (1992) compared temperate, subarctic and arctic species in a study concerning 23 species in total. Further, Stocker's (1935) comparison of R measured at approximately ambient temperatures involved just two shrub species from Greenland (R measured at 10°C) and three tree species from Java (R measured at 30°C). The larger sample size used for the present study (208 woody species from 20 sites) should, on the face of it, represent a considerably more representative sample for detecting broad climate-related trends. A second possible reason for the discrepancies is that there are actually different trends in R with site temperature for woody species than for grasses and herbs. While we cannot suggest any plausible reason why this should be so, it is notable that the majority of species studied by Semikhatova *et al.* (1992) and Wager (1941) were herbaceous, and results congruent with theirs were found among the climatically limited sample of grasses and herbs in our data set. Additional data would be required to evaluate this possibility. A third possibility is that our estimates of $R_{ambient}$ only poorly reflected actual rates of R for plants growing in the field. Against this possibility, our sensitivity analyses (see Methods) suggested that the results were quite robust: the same pattern of results was evident when we used a wide range of Q_{10} values in the calculation of $R_{ambient}$, or when we used the average temperature during the entire growth season in the calculations, rather than the mean temperature for the measurement period only.

Possible mechanisms underlying trends concerning site temperature

Our results for woody species indicated that, on average, field rates of dark respiration ($R_{ambient}$) were 1.6-fold higher for species growing at sites with 20°C MAT than in species at sites with 10°C MAT. This is intermediate between what would be seen within the 'average' species over that temperature range (ratio of 2.4; equation 1), and what would be observed if there was no overall trend in $R_{ambient}$ with site temperature among species. This finding suggests that, compared with well known short-term temperature responses of R across species (Tjoelker *et al.*, 2001; Atkin & Tjoelker, 2003), R measured in the field at ambient site temperatures may reflect partial adjustments in rates via the combined effects of acclimation, adaptation and species-sorting along geographical temperature gradients. In animals, resting metabolic rate (RMR) is roughly analogous to dark (maintenance) respiration in plants (Reich, 2001). Indeed, within a number of animal lineages, mass-normalized RMR tends to be faster in species inhabiting warmer regions (Gillooly *et al.*, 2001; Clarke & Fraser, 2004). Just as reported here for $R_{ambient}$ in woody plants, in teleost fish, short-term, within-species responses in RMR to a given change in temperature tend to be greater than the mean difference in RMR among species for the same difference in habitat temperature (Clarke & Johnston, 1999). Specifically, in that study the average Q_{10} within species was 2.4, whereas the mean difference in RMR for a 10°C difference in habitat temperature was 1.8. Within individual species, increases in R (or RMR) with temperature are generally ascribed to inevitable temperature-associated changes in membrane fluidity and in the kinetics of biochemical reactions, as well as a general ramping-up of metabolism at higher temperature, for example because of greater ATP demands for biosynthesis, transport, protein turnover and phloem-loading of photosynthates (Lambers *et al.*, 1998; Atkin *et al.*, 2000a; Gillooly *et al.*, 2001; Atkin *et al.*, 2005). It seems likely that the between-species pattern in R reflects similar underlying physiological changes with increasing temperature, only reduced somewhat by acclimation, adaptation and species-sorting. Further studies would be required to quantify the genotypic and phenotypic (acclimatory) contributions to these trends.

Considering the between-species trend, a key question is whether faster R actually represents a higher cost to life associated with life at generally higher temperatures? That is, is the overall respiratory cost higher for a given rate of growth (or carbon fixation, or nutrient uptake)? Here we dealt with leaf-level data, so we cannot easily extrapolate the results to whole-plant costs. However, we note that the magnitude of the shift in $R_{ambient}$ with site temperature was still similar when covariation in other leaf traits (e.g. A_{mass} or N_{mass}) was accounted for, consistent with the idea that higher temperatures inevitably lead to higher respiratory costs.

Possible mechanisms underlying trends concerning site irradiance

Below we list several mechanisms that could lead to species growing at higher-irradiance sites tending to have higher R (at a given leaf N, SLA, A_{mass} or LL). However, two caveats should be noted. First, as many studies that we cite were within-species comparisons, the mechanisms should not be extrapolated uncritically to differences among species (just as for temperature-related effects, discussed above). Second, while the processes we describe mostly take place in the light, it is likely that there is a carry-over effect with increased respiratory demands in the light, resulting in enhanced respiratory capacity, and thus higher rates in the dark also.

Protein turnover Damage to the D1 protein of photosystem II is particularly common under high light, leading to increased rates of degradation and resynthesis of the damaged proteins (Shyam *et al.*, 1993; Anderson *et al.*, 1997). These processes consume energy: approx. 2–20% of leaf proteins are turned over daily, representing from 20 to 60% of total respiration in mature leaves (Penning de Vries, 1975; de Visser *et al.*, 1992; Bouma *et al.*, 1994; Zerihun *et al.*, 1998).

Reactive oxygen species (ROS) High light (particularly under cold temperatures) leads to the accumulation of excess redox equivalents (e.g. NADPH) in chloroplasts which, in turn, can lead to formation of ROS that damage chloroplast pigments and membrane lipids. Plants can use various means to lower an excess of redox equivalents in the chloroplasts (Atkin *et al.*, 2000c), including exporting excess NADPH to the mitochondria via the oxaloacetate–malate shuttle where it can be oxidized via the nonphosphorylating, alternative oxidase (AOX) respiratory pathway (Purvis, 1997; Maxwell *et al.*, 1999). Repairing damage caused by ROS also incurs respiratory costs, as does quenching of ROS, for example via mitochondrial ascorbate synthesis as part of the ascorbate–glutathione cycle (Smirnoff, 2000; Millar *et al.*, 2003).

Xanthophyll cycle Ascorbate synthesis also plays a role in regulating production of photoprotective xanthophyll pigments (Demmig-Adams & Adams, 1996). Hence a greater need for xanthophylls for species at high-irradiance sites contribute to higher *R*.

Where photosynthetic capacity is enhanced because of high irradiance, there would be a higher demand for cytosolic ATP (needed to support sucrose synthesis) and higher rates of phloem loading of photosynthates (Krömer, 1995; Hoefnagel *et al.*, 1998; Atkin *et al.*, 2000c). However, it is unclear whether this would lead to higher rates of *R* at a given A_{mass}, as we found here, as opposed to higher *R* considered on its own, which was not observed.

Possible mechanisms underlying trends concerning site rainfall

There are several ways that coping with frequently dry conditions could potentially lead to higher *R* (at a given SLA or A_{mass}).

Photoinhibition Low rainfall probably results in reduced stomatal conductance and thus reduced availability of CO_2 for photochemistry, increasing the likelihood of photoinhibition. Although the xanthophyll cycle generally can deal with this quite effectively (Demmig-Adams & Adams, 1996), increased *R* could still result, for example by the oxaloacetate–malate shuttle or via the role respiration plays in ascorbate synthesis (both described above).

Maintenance of solute gradients Many plants in low-rainfall habitats maintain high concentrations of osmotically active compounds in the vacuoles of leaf cells (Lambers *et al.*, 1998). The energy costs of maintaining these gradients could also contribute to higher *R*.

Additional considerations

Additional factors need to be considered in order to assess how accurately the measured rates of *R* truly reflect leaf respiration. For example, leaf respiration during daylight may be suppressed, maintained or (less commonly) stimulated relative to that occurring at night (Krömer, 1995; Atkin *et al.*, 2000c), yet our study was based only on measurements of dark respiration. Further, mitochondrial CO_2 production and O_2 consumption may be affected differently by light and temperature, and species may differ in this regard (Brooks & Farquhar, 1985; Atkin *et al.*, 2000b), yet *R* was measured for most species in terms of CO_2 efflux only. On the other hand, there could be carry-over effects that counteract these concerns. For example, if increased AOX activity (detected via O_2 consumption) went hand-in-hand with increases in the capacity of other respiratory enzymes, this could also lead to higher respiratory CO_2 production.

Conclusions

Our results indicated that dark respiration rates of field-grown plants vary systematically with site climate: after covariation in other leaf traits had been accounted for, woody species occurring at hotter, drier or higher-light sites had higher mean *R*. For site rainfall and irradiance, these trends were apparent for both $R_{ambient}$ and R_{25}. To our knowledge, no study has previously assessed links between *R* and site irradiance. Moreover, while previous studies have linked variations in *R* with site rainfall at the regional level (Wright *et al.*, 2001), none has assessed patterns across global spatial scales and/or over such a large sample of species and vegetation types. Our analysis reveals significant temperature-related trends for $R_{ambient}$ but not for R_{25}. Considered together with the sensitivity analyses, these results suggest that species typical of warmer sites would have higher *R* if the measurements were made at ambient field temperature, at a standard time of year (e.g. mid-growing season). Ideally, site temperature-related trends in *R* would be assessed with field measurements standardized in ways such as these, but insufficient data exist as yet.

The data used in this study were measured during relatively well watered times of year during the growth season, and the frequency of favourable growth periods also varies with site climate. Thus the patterns cannot be extrapolated directly to differences in leaf or whole-plant *R* considered over the course of a year, or over the lifetime of a plant. Nevertheless, with care, our findings should prove useful for modelling plant nutrient and carbon budgets, and for modelling vegetation shifts with climate change.

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