Oecologia (1998) 114:471–482 © Springer-Verlag 1998

Peter B. Reich · Michael B. Walters
David S. Ellsworth · James M. Vose · John C. Volin
Charles Gresham · William D. Bowman

Relationships of leaf dark respiration to leaf nitrogen, specific leaf area and leaf life-span: a test across biomes and functional groups

Received: 23 May 1997 / Accepted: 16 December 1997

Abstract Based on prior evidence of coordinated multiple leaf trait scaling, we hypothesized that variation among species in leaf dark respiration rate (R_d) should scale with variation in traits such as leaf nitrogen (N), leaf life-span, specific leaf area (SLA), and net photosynthetic capacity (A_{max}). However, it is not known whether such scaling, if it exists, is similar among disparate biomes and plant functional types. We tested this idea by examining the interspecific relationships between R_d measured at a standard temperature and leaf life-span, N, SLA and A_{max} for 69 species from four functional groups (forbs, broad-leafed trees and shrubs, and needle-leafed conifers) in six biomes traversing the Americas: alpine tundra/subalpine forest, Colorado; cold temperate forest/grassland, Wisconsin; cool temperate forest, North Carolina; desert/shrubland, New Mexico; subtropical forest, South Carolina; and tropical rain forest, Amazonas, Venezuela. Area-based R_d was positively related to area-based leaf N within functional groups and for all species pooled, but not when comparing among species within any site. At all sites, mass-based R_d ($R_{d\text{-mass}}$) decreased sharply with increasing leaf life-span and was positively related to SLA and mass-based A_{max} and leaf N (leaf N_{mass}). These intra-biome relationships were similar in shape and slope among sites, where in each case we compared species belonging to different plant functional groups. Significant $R_{d\text{-mass}}$–N_{mass} relationships were observed in all functional groups (pooled across sites), but the relationships differed, with higher R_d at any given leaf N in functional groups (such as forbs) with higher SLA and shorter leaf life-span. Regardless of biome or functional group, $R_{d\text{-mass}}$ was well predicted by all combinations of leaf life-span, N_{mass} and/or SLA ($r^2 \geq 0.79$, $P < 0.0001$). At any given SLA, $R_{d\text{-mass}}$ rises with increasing N_{mass} and/or decreasing leaf life-span; and at any level of N_{mass}, $R_{d\text{-mass}}$ rises with increasing SLA and/or decreasing leaf life-span. The relationships between R_d and leaf traits observed in this study support the idea of a global set of predictable interrelationships between key leaf morphological, chemical and metabolic traits.

Key words Respiration · Leaf life-span · Specific leaf area · Nitrogen · Functional groups

P.B. Reich (✉)
Department of Forest Resources, University of Minnesota,
St. Paul, MN 55108, USA
Fax 612-625-5212; e-mail: preich@forestry.umn.edu

M.B. Walters
Faculty of Natural Resources and Environmental Studies,
University of Northern British Columbia,
Prince George, BC, Canada V2N 4Z9

D.S. Ellsworth
Department of Applied Science,
Brookhaven National Laboratory,
Upton, NY 11973, USA

J.M. Vose
U.S. Forest Service, Coweeta Hydrological Lab.,
Otto, NC 28763, USA

J.C. Volin
Division of Science, Florida Atlantic University,
Davie, FL 33314, USA

C. Gresham
Baruch Forest Institute, Clemson University,
Georgetown, SC 29442, USA

W.D. Bowman
Mountain Research Station, Institute of Arctic
and Alpine Research, and Department of EPO Biology,
University of Colorado, Boulder, CO 80309, USA

Introduction

Leaf dark respiration is among the most fundamental plant physiological processes and plays a major role in the carbon cycle at scales from the leaf to the globe. Despite its importance, we know far less about local and global patterns of interspecific variation in leaf dark respiration rate (R_d) than for other leaf traits such as nitrogen (N) concentration, net photosynthetic capacity (A_{max}), and life-span. It has long been recognized that R_d and these other leaf traits are related in a general

sense to each other, but a lack of comparable data on R_d among species, ecosystems and biomes limits evaluation of such relations.

R_d has been found to be positively correlated with leaf N in both interspecific (Ryan 1995; Reich et al. 1998b) and broad interpopulation comparisons (Reich et al. 1996), but studies of intraspecific relationships have had mixed results (e.g., Pavlik 1983; Byrd et al. 1992; Poorter et al. 1995). Among species, mass-based A_{max} and leaf N (N_{mass}) levels are usually positively related to each other and negatively related to leaf thickness/density (low specific leaf area, SLA) and longevity (Field and Mooney 1986; Reich et al. 1991, 1992), but we know of no large multi-species data set that examines these relationships involving R_d.

We hypothesize that variation in R_d among species should scale proportionally with variation in A_{max} and associated leaf traits, because high A_{max} requires large complements of enzymes and other metabolites which have substantial maintenance costs and require periodic (and costly) resynthesis. However, it is not known whether such scaling exists, nor, if it does, whether it is similar among disparate biomes and plant functional types. Given the documentation of global convergence in interspecific leaf trait relationships involving A_{max} (Reich et al. 1992, 1997) we hypothesize that a similar convergence exists with respect to interspecific variation in R_d, due to constraints on the combination of leaf traits that occur in any given species (Coley et al. 1985, Field and Mooney 1986, Reich et al. 1992, 1997). For instance, if there was selection for low R_d in low light habitats this would likely result also in low N_{mass} and A_{max}; conversely selection for high N_{mass} and A_{max} in high resource environments would necessarily result in high R_d. Thus, we hypothesize that interspecific relationships of R_d with other leaf traits will be similar among diverse biomes and plant functional groups. To test this and related questions, we quantified R_d, SLA, leaf N and leaf life-span, and their relationships, for 9–15 species within each of six sites representing different broadly-defined biomes traversing the Americas. Our sites represent a range of biomes that vary in growing season length, mean air temperature, elevation, water availability, and soil fertility: alpine tundra and subalpine forest/meadow, Colorado, United States; cold temperate forest and prairie, Wisconsin, United States; humid cool temperate montane forest, North Carolina, United States; arid desert/shrubland, New Mexico, United States; subtropical coastal plain forest, South Carolina, United States; and humid tropical rain forest, Amazonas, Venezuela. At each site we sampled plants from four different functional groups (15–24 of each pooled across sites).

Methods

Sites, species, and leaf traits

Six sites were selected to provide a wide range of ecosystem types (summary data are presented in Table 1). Two sites (Colorado and Wisconsin) were located at the ecotone between biomes and include species common to both biomes.

We studied conifers, hardwood trees and shrubs, and forbs at Niwot Ridge, Colorado, a high elevation site (3200–3500 m) characteristic of alpine tundra and subalpine open forest-meadow of the Rocky Mountains. Soils at the site were largely coarse-textured Inceptisols. In Wisconsin, we studied prairie and understory forbs, woody shrubs, and hardwood and coniferous forest tree species in restored and native cold temperate communities at the University of Wisconsin Arboretum, in Madison. Soils were largely medium-textured silt loams (Alfisols). We studied montane cool temperate forests located at 700–850 m elevation at the Coweeta

Table 1 Description of the six study sites and related ecosystems used in the study. Annual climate data [mean temperature (*Temp*), mean annual precipitation (*Precip*) and potential evapotranspiration (*PET*)] are shown for the meteorological station nearest to the main study area at each site. PET was calculated from open pan evaporation or the equivalent

Site	Location	Ecosystem type	Elevation (m)	Temp (°C)	Precip (mm)	PET (mm)
Niwot Ridge, Colorado, USA	40°03′N, 105°36′W	Alpine tundra and subalpine forest-meadow ecotone	3,200–3,510	−3.7	930	300
Madison, Wisconsin, USA	43°02′N, 89°28′W	Cold temperate forest and prairie	275	8.0	820	700
Coweeta, North Carolina, USA	35°00′N, 83°30′W	Montane temperate forest	700–850	12.5	1829	856
Sevilleta, New Mexico, USA	34°37′N, 106°54 to 106°69′W	Desert grassland, shrubland and pinyon-juniper woodland	1,400–1,890	13.0	222	2428
Hobcaw, South Carolina, USA	33°20′N, 79°13′W	Warm temperate/ subtropical forest and pocosin	3–4	18.3	1295	1656
San Carlos, Amazonas, Venezuela	1°56′N, 67°03′W	Tropical rain forest	120	26.0	3560	1971

Hydrological Laboratory, Otto, North Carolina. Soils at this site were principally clay loam Ultisols. We studied a number of common forbs, broadleafed deciduous and evergreen hardwood and coniferous forest tree species.

Desert shrubland and pinyon-juniper woodland vegetation were studied at Rio Salado in the Sevilleta National Wildlife Refuge, New Mexico, a site representative of Chihuahuan desert grassland and shrubland (1540 m elevation). Several additional species were also studied in the nearby Rio Grande floodplain (1400 m elevation) or in pinyon-juniper woodland in the Los Pinos Mountains (1860 m elevation). Soils are sandy and classified as Aridosols of Haplargids-Torripsamments construction. On the lower coastal plain of South Carolina we studied species from sandy upland pine-dominated forests and forested wetlands on the Hobcaw Forest, which occupies the southern tip of the Waccamaw Peninsula. We studied deciduous and evergreen species from both broad-leafed and needle-leafed species groups. The climate of the area is maritime, warm temperate/humid subtropical. A tropical rain forest site was located in the northern Amazon basin near San Carlos del Rio Negro, Venezuela. Eleven species were studied in primary and secondary rain forest communities (Reich et al. 1991). The San Carlos region is characterized year-round by abundant rainfall and stable, warm temperatures.

At each site we selected species expected to provide a gradient of leaf traits (based on prior general knowledge) and that were relatively abundant. Species from four functional groups were studied: forbs, broad-leafed shrubs and trees, and needle-leafed trees (Table 2). All four functional groups were represented in at least five of the six sites. Efforts were made to ensure that both broad-leaf and needle-leaf species with deciduous and evergreen habits were included in the sample population when present at a site. Several leaf traits were measured for numerous individuals of each species. Average leaf life-span was measured primarily using a long-term demographic census of individual leaves, while net photosynthetic capacity under light-saturated conditions was measured in the field under ambient CO_2 concentrations using a standardized protocol (see Reich et al. 1991, 1997).

Since leaf life-span varies substantially among species, and leaf traits within species vary with leaf age as well, contrasts of R_d with A_{max}, leaf N and SLA were made using leaves of a similar "physiological" age rather than a similar chronological age. We used fully expanded young to medium-aged leaves of all species, which corresponds to the period when many leaf traits are relatively stable (Reich et al. 1991, 1996). Gas exchange measurements were made from June to August (1986–1993) in the U.S. and in January in Venezuela (1987–1990). To minimize the potentially confounding influence of shade, to the extent possible we selected "sun" leaves growing in relatively open conditions for all species at all sites. Measurements were made on open-grown plants in all herbaceous dominated communities and usually were made for open-grown trees or shrubs, or saplings or young trees in gaps, or for mature trees in the upper canopy. Although variation in leaf light microenvironment might have impacted on R_d, especially when expressed on an area basis (largely via impacts on SLA), interspecific differences in this study were large enough (e.g., R_d varies 10- and 20-fold on mass and area bases, respectively) that a lack of full control over leaf light microenvironment would not have likely made significant impact on the results. Moreover, since foliage of all species was fully expanded and/or elongated at the time of measurement (but secondary thickening and lignification continue over the leaf life-span), respiration from these leaves can be considered to represent largely maintenance respiration, because growth and construction respiration are minimal (Ryan 1995).

Respiration measurements

Dark respiration (R_d) was measured on detached foliage after > 1 h in darkness, using a portable leaf chamber and infrared gas analyzer operated in the differential mode (ADC model LCA-2, Hoddesdon, Herts., UK). Measurements of R_d were made at 25°C at all sites. Checks of several species were made to determine whether R_d measurements on detached foliage were different than for intact foliage, but no significant differences were found (data not shown). Moreover, K. Mitchell, P. Bolstad and J. Vose (unpublished work) report no difference in respiration rates for intact and detached foliage of four tree species measured across several temperatures. Nonetheless, it is possible that measurements made in this way differ from measurements of intact foliage. However, the magnitude of such potential errors is likely to be small compared to the range of R_d rates (10- to 20-fold) among species and is likely to be systematic (i.e., occur for all species), thus resulting in additional unexplained variability in the results without affecting the general tendencies or patterns.

Data are expressed on both mass and area bases in this study. Expression of net CO_2 exchange rates on both bases is valuable, since each provides different information (Reich et al. 1992; Reich and Walters 1994). Comparing species R_d on a mass basis could be complicated by intraspecific temporal (diel or seasonal) and/or spatial (due to light microenvironment) variation in leaf starch (i.e., changes in starch levels could in theory affect mass-based rates without affecting total R_d per leaf). Although some species show diel variation in mass-based R_d, we have not found this previously in woody plants (e.g., Walters et al. 1993). In surveying the literature for perennial species such as used in this study, we found that starch concentrations of foliage during the active growing season (i.e., significantly after budbreak) vary markedly, and are often higher in evergreen conifers (mean 70 mg/g) than in broad-leaved deciduous species (usually < 30 mg/g)(data not shown). However, such diel and seasonal variation was likely to be randomly incorporated in our data set.

Even assuming that any starch concentration from 0 to 140 mg/g is equally likely in foliage of an evergreen conifer, the standard deviation among random samples would be 41 mg/g (or 4% of total leaf dry mass). Thus, unaccounted-for variation in starch concentration could result in variation in mass-based R_d by 4% on average for evergreen conifers (and by < 2% in species with short-lived leaves). Since the average mass-based R_d for conifers in this study was 5 nmol g^{-1} s^{-1}, unaccounted-for variation in starch means the true mean value is likely somewhere between 4.8 and 5.2 nmol g^{-1} s^{-1}. Given the large interspecific variation in our data set (total range from 3 to 65 nmol g^{-1} s^{-1}; average mass-based R_d for deciduous broad-leaved woody species of 13 nmol g^{-1} s^{-1} and for forbs 27 nmol g^{-1} s^{-1}), it seems likely that intra- and inter-specific variation in starch concentrations would have minimal effect on the interspecific patterns reported in this paper. Alternatively, SLA also changes ontogenetically during the course of leaf development, and varies seasonally and with light environment; and typically, by proportionally more than starch concentrations. Thus, comparing species R_d on an area basis also may be complicated in this or any other study because this measure is also unlikely to be static. The use of a common ontogenetic stage among all species, as done herein, should minimize these concerns for measurements on either basis.

After measuring R_d the projected surface area of the leaf or its silhouette was assessed by a digital image analysis system (Decagon Instruments, Pullman, Wash., USA). All leaves were then dried, weighed and assayed for N concentrations. Total surface area of sampled foliage was also calculated for all species based on their geometry. The results of this study were similar if total rather than projected surface area was used (due to the large interspecific variation). However, the quantitative relations differ slightly, since the ratio of total:projected surface area differs for needle-shaped than planar surfaces. Since projected area was measured, while total surface area was estimated indirectly, area-based data are expressed on a projected area basis.

Data on R_d were compared with data for the following other leaf traits: leaf life-span, SLA, N and A_{max}. These auxiliary data were measured on either the identical leaves (SLA, N) used for R_d measurement, or on leaves from the same branch (leaf life-span and A_{max}). Full details on how each of these were obtained are described in a companion paper (P. Reich, D. Ellsworth, M. Walters, J. Vose, C. Gresham, J. Volin, and W. Bowman, unpublished work). The data set is "species-based". In statistical analyses and the plotted data, individual data points represent the average for a

Table 2 List of sites, species, and data

Location	Species	Functional group	Leaf Type	Leaf life span (mo)	SLA ($cm^2 g^{-1}$)	Leaf N ($mg\ g^{-1}$)	$R_{d_{mass}}$ (nmol $g^{-1}s^{-1}$)	$R_{d_{area}}$ (μmol $m^{-2}s^{-1}$)
Colorado	*Acomastylis rosii*	Forb	Broad	2.0	119.0	25.0	20.9	1.8
Colorado	*Bistorta bistortoides*	Forb	Broad	2.0	121.0	39.0	28.4	2.3
Colorado	*Psychrophila leptosepala*	Forb	Broad	2.5	126.0	29.0	15.3	1.2
Colorado	*Salix glauca*	Shrub	Broad	3.0	122.8	26.3	17.7	1.4
Colorado	*S. planifolia*	Shrub	Broad	3.0	123.0	26.7	24.8	2.0
Colorado	*Vaccinium myrtillus*	Shrub	Broad	3.5	171.0	23.4	10.6	0.6
Colorado	*Arctostaphylus uva-ursa*	Shrub	Broad	18.0	78.4	12.3	5.3	0.7
Colorado	*Pinus flexilis*	Tree	Needle	36.0	27.3	11.2	4.0	1.5
Colorado	*Picea engelmanii*	Tree	Needle	90.0	32.7	10.3	3.2	1.0
Colorado	*Abies lasiocarpa*	Tree	Needle	96.0	39.3	10.3	3.5	0.9
N. Carolina	*Podophyllum peltatum*	Forb	Broad	3.0	323.0	41.5	26.8	0.8
N. Carolina	*Veratrum parviflorum*	Forb	Broad	3.6	297.0	–	18.6	0.6
N. Carolina	*Helianthus microcephalus*	Forb	Broad	4.1	251.0	26.2	35.8	1.4
N. Carolina	*Robinia pseudoacacia*	Tree	Broad	4.6	264.0	43.3	32.0	1.2
N. Carolina	*Eupatorium rugesum*	Forb	Broad	4.8	469.0	39.2	44.7	1.0
N. Carolina	*Acer rubrum*	Tree	Broad	5.2	160.0	18.4	12.8	0.8
N. Carolina	*Liriodendron tulipifera*	Tree	Broad	5.3	165.0	22.4	14.0	0.8
N. Carolina	*Quercus coccinea*	Tree	Broad	5.7	118.0	17.3	11.5	1.0
N. Carolina	*Galax aphylla*	Forb	Broad	18.0	125.0	8.9	9.7	0.8
N. Carolina	*Pinus strobus*	Tree	Needle	21.0	92.0	13.5	5.2	0.6
N. Carolina	*P. rigida*	Tree	Needle	33.0	48.9	11.6	5.2	1.1
N. Carolina	*Kalmia latifolia*	Shrub	Broad	36.0	94.5	11.5	8.9	0.9
N. Carolina	*Rhododendron maximum*	Tree	Broad	48.0	48.9	8.6	3.8	0.8
N. Carolina	*Tsuga canadensis*	Tree	Needle	60.0	81.6	9.9	3.1	0.4
New Mexico	*Baccharis angustifolia*	Shrub	Broad	2.5	105.0	19.5	17.3	1.6
New Mexico	*Eleagnus angustifolia*	Tree	Broad	3.0	124.0	39.8	23.4	1.9
New Mexico	*Populus fremontii*	Tree	Broad	3.0	83.8	16.6	14.6	1.7
New Mexico	*Gutierrezia sarothrae*	Forb	Broad	6.0	33.9	16.8	14.3	4.2
New Mexico	*Atriplex canescens*	Shrub	Broad	7.0	39.7	21.0	12.3	3.1
New Mexico	*Prosopis glandulosa*	Shrub	Broad	7.0	51.2	24.9	8.7	1.7
New Mexico	*Quercus turbinella*	Shrub	Broad	8.0	66.0	15.4	9.9	1.5
New Mexico	*Larrea tridentata*	Shrub	Broad	12.0	39.6	19.4	7.8	2.0
New Mexico	*Juniperus monosperma*	Tree	Needle	78.0	12.8	11.7	4.8	3.7
S. Carolina	*Pterocaulon pycnostachyum*	Forb	Broad	5.1	123.6	19.7	15.4	1.2
S. Carolina	*Taxodium distichum*	Tree	Needle	6.5	78.0	11.9	10.3	1.3
S. Carolina	*Vaccinium corymbosum*	Shrub	Broad	7.5	97.9	12.3	12.7	1.3
S. Carolina	*Quercus laevis*	Tree	Broad	7.6	97.6	11.5	6.3	0.6
S. Carolina	*Q. virginia var. geminata*	Tree	Broad	11.0	62.9	15.4	5.7	0.9
S. Carolina	*Vaccinium arboreum*	Shrub	Broad	11.0	80.1	12.1	6.4	0.8
S. Carolina	*Persea borbonia*	Tree	Broad	18.0	90.0	16.4	6.7	0.7
S. Carolina	*Lyonia lucida*	Shrub	Broad	19.5	42.1	9.2	5.8	1.4
S. Carolina	*Pinus serotina*	Tree	Needle	27.0	35.9	8.2	5.0	1.4
S. Carolina	*P. palustris*	Tree	Needle	32.0	39.2	8.2	3.6	0.9
Venezuela	*Manihot esculenta*	Shrub	Broad	1.5	275.1	39.8	33.3	1.2
Venezuela	*Solanum straminifolia*	Shrub	Broad	2.0	287.4	39.2	34.0	1.2
Venezuela	*Cecropia ficifolia*	Tree	Broad	2.7	144.6	24.7	18.0	1.2
Venezuela	*Vismia lauriformis*	Tree	Broad	4.5	114.3	17.9	11.0	1.0
Venezuela	*Vismia japurensis*	Tree	Broad	6.9	105.4	16.4	9.3	0.9
Venezuela	*Bellucia grossularioides*	Tree	Broad	8.4	78.1	16.9	7.9	1.0
Venezuela	*Miconia dispar*	Tree	Broad	12.0	90.3	15.9	5.2	0.6
Venezuela	*Protium* sp.	Tree	Broad	33.0	86.6	8.6	6.0	0.7
Venezuela	*Protium* sp.	Tree	Broad	35.0	82.0	17.7	5.8	0.7
Venezuela	*Ocotea costulata*	Tree	Broad	39.0	76.8	15.0	5.0	0.7
Venezuela	*Licania heteromorpha*	Tree	Broad	40.0	67.3	13.0	5.2	0.8
Wisconsin	*Erythronium americanum*	Forb	Broad	1.9	222.0	42.0	52.0	2.3
Wisconsin	*Silphium terebinthinaceum*	Forb	Broad	3.0	133.0	14.4	17.6	1.3
Wisconsin	*Baptisia leucophaea*	Forb	Broad	3.5	106.3	35.9	36.3	3.4
Wisconsin	*Echinacea purpurea*	Forb	Broad	4.0	128.5	15.0	17.2	1.3
Wisconsin	*Silphium integrifolium*	Forb	Broad	4.0	116.3	16.6	19.1	1.6
Wisconsin	*Sanguinaria canadensis*	Forb	Broad	4.0	321.0	53.6	65.0	2.0
Wisconsin	*Populus deltoides*	Tree	Broad	5.0	110.0	23.6	14.0	1.3
Wisconsin	*P. tremuloides*	Tree	Broad	5.0	121.0	22.1	22.3	1.8
Wisconsin	*Acer rubrum*	Tree	Broad	5.5	166.0	21.0	12.4	0.7
Wisconsin	*A. saccharum*	Tree	Broad	5.5	125.0	18.5	7.0	0.6
Wisconsin	*Quercus ellipsoidalis*	Tree	Broad	6.0	95.0	21.0	13.1	1.4
Wisconsin	*Pinus strobus*	Tree	Needle	21.0	74.0	17.0	4.7	0.6

Table 2 (Continued)

Location	Species	Functional group	Leaf Type	Leaf life span (mo)	SLA (cm^2g^{-1})	Leaf N ($mg\ g^{-1}$)	$R_{d_{mass}}$ (nmol $g^{-1}s^{-1}$)	$R_{d_{area}}$ (μmol $m^{-2}s^{-1}$)
Wisconsin	*P. banksiana*	Tree	Needle	27.0	41.0	12.4	6.0	1.5
Wisconsin	*P. sylvestris*	Tree	Needle	27.0	34.0	13.9	6.2	1.8
Wisconsin	*Picea glauca*	Tree	Needle	60.0	35.0	12.4	4.0	1.1

single species at a single site. A simple linear regression model was not appropriate to describe the relations between R_d and other leaf traits for pooled data, for data at each site, or for data within each functional group (pooled across sites), because (1) the R_d data were not normally distributed (Shapiro-Wilk W-test, $P < 0.01$), (2) some relationships were not linear, and (3) there was patterned heteroscedasticity in the residuals (usually a funnel shape) of all simple linear regressions. Therefore, we used logarithmic (base-10) transformations to normalize the data distribution, linearize the regression functions and stabilize the error term variances where appropriate. The transformed data were normally distributed. Log transformations are often suitable for biological data, especially for interspecific data, because of the common adherence of such data to power laws (Peters 1983). Such an approach has been used previously for examination of leaf trait relations (e.g., Coley 1988; Reich et al. 1991, 1992, 1997). When leaf traits are used in regression as the independent variable, there is no random sampling variation associated with them because the species were selected by the investigators (based on approximate knowledge of the species leaf traits) to provide a roughly continuous range of leaf traits, and hence type I regression is appropriate (Steel and Torrie 1980).

Data were analyzed using multiple regression (JMP Statistical Software, SAS Institute). We statistically compared relationships between sites using linear contrasts (separate and same slopes analyses) of the transformed variables. We used this technique to test the hypothesis that different equations describe these relationships in different ecosystems.

Results

Respiration in relationship to other leaf traits within and among biomes

Mass-based dark respiration rates ($R_{d\text{-mass}}$, base temperature 25°C) ranged from 3 to 65 nmol g^{-1} s^{-1} among all species (Table 2, Fig. 1). $R_{d\text{-mass}}$ was closely related to and declined precipitously with increasing leaf life-span, and increased linearly with increasing N_{mass} and SLA. Area-based R_d varied from 0.4 to 4.0 μmol m^{-2} s^{-1} among species and declined with leaf life-span and SLA, but highly variably, and increased with area-based leaf N (Fig. 1).

The relationship between $R_{d\text{-mass}}$ and leaf life-span was strong at each of the six sites and for all data pooled ($r^2 > 0.7$, Fig. 2). Separate slopes analyses were made to test whether the slopes of the lines varied among sites (Table 3), and if they did not, same slopes analyses were used to test for differences in the intercept (i.e., the relative position or elevation of the lines). Based on these analyses, sites did not differ significantly in the slope or intercept of the $R_{d\text{-mass}}$:leaf life-span relationship. A similar approach to analyzing site differences is used for all subsequent relationships. Individual site and pooled data are both shown because it is difficult to see individual site relationships in pooled data (even if separate symbols are used), or the general relationship from separate individual plots. In Figs. 2 and 3 sites are paired by mean annual temperature and figures are arrayed left to right from cold to warm. $R_{d\text{-area}}$ was very weakly, but significantly correlated with leaf life-span (log-transformed) using the pooled data set ($P < 0.01$, $r^2 = 0.10$). However, this relationship was significant ($P < 0.05$) for only one of the six sites.

At all sites and for pooled data ($r^2 = 0.72$), there were highly significant $R_{d\text{-mass}}$ – leaf N_{mass} relations (Fig. 2). The $R_{d\text{-mass}}$ – N_{mass} slopes were not different among sites,

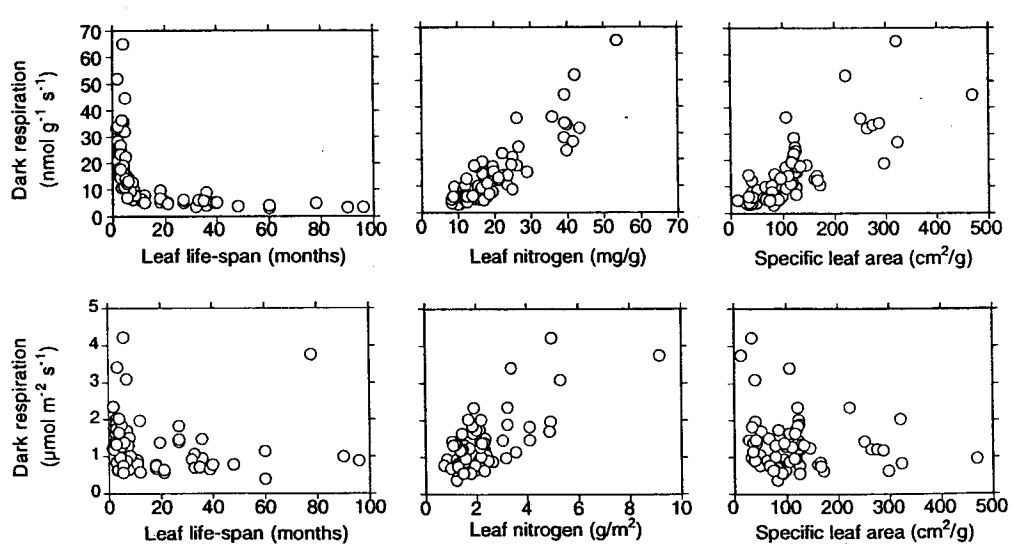

Fig. 1 Mass- and area-based dark respiration rates for 69 species from six biomes pooled, in relation to leaf life-span, mass- and area-based leaf N, and specific leaf area (SLA, cm^2/g)

Table 3 Summary of multiple regression relationships to test for significant relationships and site differences. Effects were considered not significant (NS) when $P > 0.05$

Dependent variable	Independent variable			Whole model		Site (intercept)		Slope (interaction)	
	Variable	P	F ratio	P value	r^2	P	F ratio	P	F
$R_{d_{mass}}$	Leaf life span	<0.0001	202.6	<0.0001	0.79	NS		NS	
$R_{d_{mass}}$	SLA	<0.0001	175.7	<0.0001	0.76	<0.0001	9.0	NS	
$R_{d_{mass}}$	Leaf N_{mass}	<0.0001	172.7	<0.0001	0.76	NS		NS	
$R_{d_{area}}$	Leaf life span	0.02	6.5	<0.0001	0.50	<0.0001	9.8	NS	
$R_{d_{area}}$	Leaf N_{area}	0.01	7.2	<0.0001	0.49	0.02	3.1	NS	
$R_{d_{area}}$	SLA	NS		<0.0001	0.45	<0.0001	9.0	NS	
A_{mass}	$R_{d_{mass}}$	<0.0001	223.4	<0.0001	0.82	<0.0001	5.1	NS	
A_{area}	$R_{d_{area}}$	<0.0001	16.6	<0.0001	0.64	<0.0001	9.4	0.0008	5.0

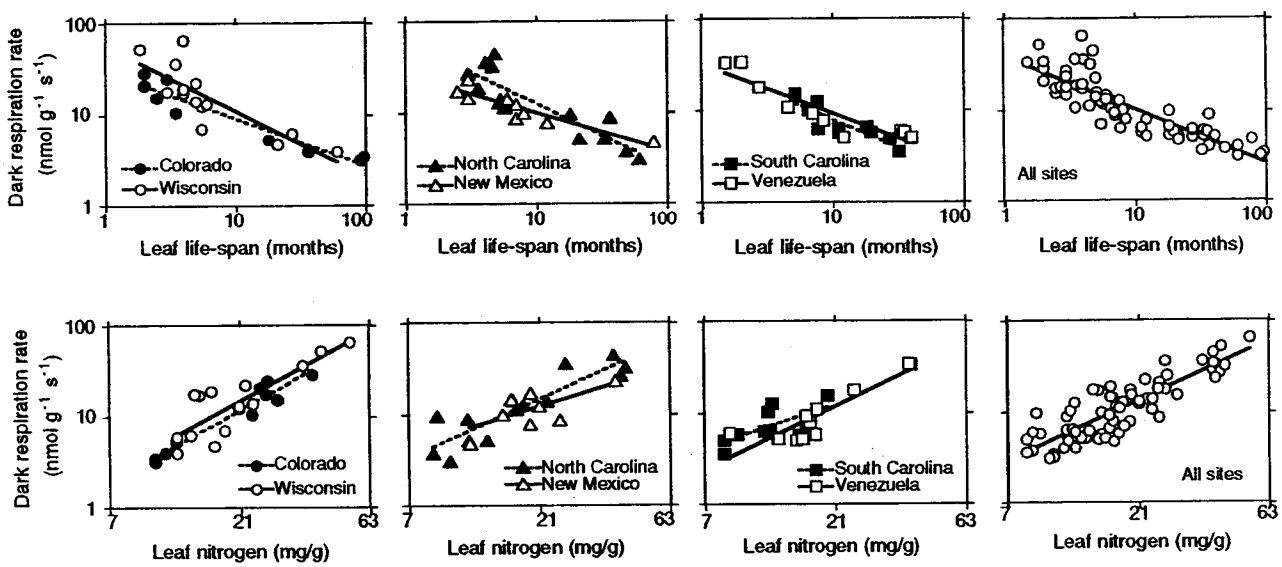

Fig. 2 Mass-based dark respiration rate (nmol g^{-1} s^{-1}) in relation to leaf life-span (months) and mass-based leaf nitrogen (mg/g) for species in each of six diverse ecosystems. Sites and ecosystems are arranged from *left* to *right panels* by ranking (low to high) of mean annual temperature (alpine tundra/subalpine forest, Colorado; cold temperate forest and prairie, Wisconsin; mesic temperate forest, North Carolina; desert and scrub, New Mexico; warm temperate forest, South Carolina, tropical rain forest, Venezuela). All regressions for Figs. 2 and 3 were significant at $P < 0.001$ (based on simple linear regressions of base-10 logarithmically transformed data). Correlation coefficients (r^2) for leaf $R_{d\text{-mass}}$ vs. leaf life-span: CO (0.92), WI (0.70), NC (0.78), NM (0.75), SC (0.72) and VEN (0.85). The pooled regression relationship: $\log(R_{d\text{-mass}}) = 1.60–0.59 \times \log(\text{leaf life-span})$, $r^2 = 0.74$. Correlation coefficients (r^2) for leaf $R_{d\text{-mass}}$ vs.leaf nitrogen (mg/g): CO (0.94), WI (0.71), NC (0.80), NM (0.58), SC (0.42, $P = 0.05$) and VEN (0.80). Regression relationships for pooled data; $\log(R_{d\text{-mass}}) = -0.69 + 1.37 \times \log(N_{mass})$, $r^2 = 0.74$

nor did the intercepts differ (i.e., sites did not differ in this relationship). $R_{d\text{-area}}$ was significantly correlated with N_{area} using the pooled data set ($r^2 = 0.36$), but this relationship was not significant ($P < 0.05$) at any of the six sites (data not shown). As explained below in the Discussion, these apparent discrepencies between mass- and area-based relationships result from differential variation in SLA and N among species (see Reich and Walters 1994 for detailed explanation).

$R_{d\text{-mass}}$ was significantly related to SLA at every site (average $r^2 = 0.75$) and for all data pooled (Fig. 3). For the pooled data, SLA accounted for the vast majority of variation in $R_{d\text{-mass}}$, and the intercepts were also significantly different, but not the slopes (Table 3). In essence the proportional scaling of $R_{d\text{-mass}}$ to SLA was similar at all sites, but for common SLA, $R_{d\text{-mass}}$ was higher in desert shrubland (New Mexico) than in other sites.

A_{mass} and $R_{d\text{-mass}}$ were closely related among species at every site (Fig. 3, mean $r^2 = 0.78$ for linear relations). These relations were slightly better fit with a second-order polynomial model for four of six individual sites, and were clearly not linear for all data pooled ($r^2 = 0.78$ for polynomial fit). For any given $R_{d\text{-mass}}$, species in tropical rain forest (warmest site) tended to have the highest A_{mass} with alpine/subalpine species from Colorado (coldest site) having the lowest A_{mass}. A_{area} and $R_{d\text{-area}}$ were significantly related in four of six sites ($P < 0.05$), but weakly correlated ($r^2 = 0.30$) using pooled data.

Differences in R_d-N among functional groups

Mean values for R_d and other leaf traits differed among functional groups, although there is substantial variation within each group (Table 4). On average, the forbs had highest $R_{d\text{-mass}}$, SLA, and N_{mass}, and shortest leaf

Table 4 Mean leaf traits (± 1 SD) for functional groups, pooled across sites

Functional group	Number of species	$R_{d_{mass}}$ (nmol g^{-1} s^{-1})	$R_{d_{area}}$ (μmol $m^{-2}s^{-1}$)	R_d/N (μmol $gN^{-1}s^{-1}$)	Specific leaf area (cm^2/g)	leaf N_{mass} (mg/g)	leaf N_{area} (g/m^2)	Leaf life span
Forbs	16	27.3 (15.6)	1.72 (0.98)	1.00 (0.25)	188 (29)	28.2 (13.1)	1.9 (1.2)	4.5 (3.8)
Broad-leafed shrubs	15	14.4 (9.4)	1.43 (0.63)	0.67 (0.21)	112 (20)	20.9 (9.5)	2.4 (1.4)	9.4 (9.2)
Broad-leafed trees	24	11.4 (7.0)	0.99 (0.39)	0.57 (0.18)	112 (9)	19.2 (8.0)	1.8 (0.5)	13.3 (14.0)
Needle-leafed trees	14	4.9 (1.8)	1.27 (0.82)	0.43 (0.15)	48 (6)	11.6 (2.3)	3.1 (2.0)	43.9 (27.0)

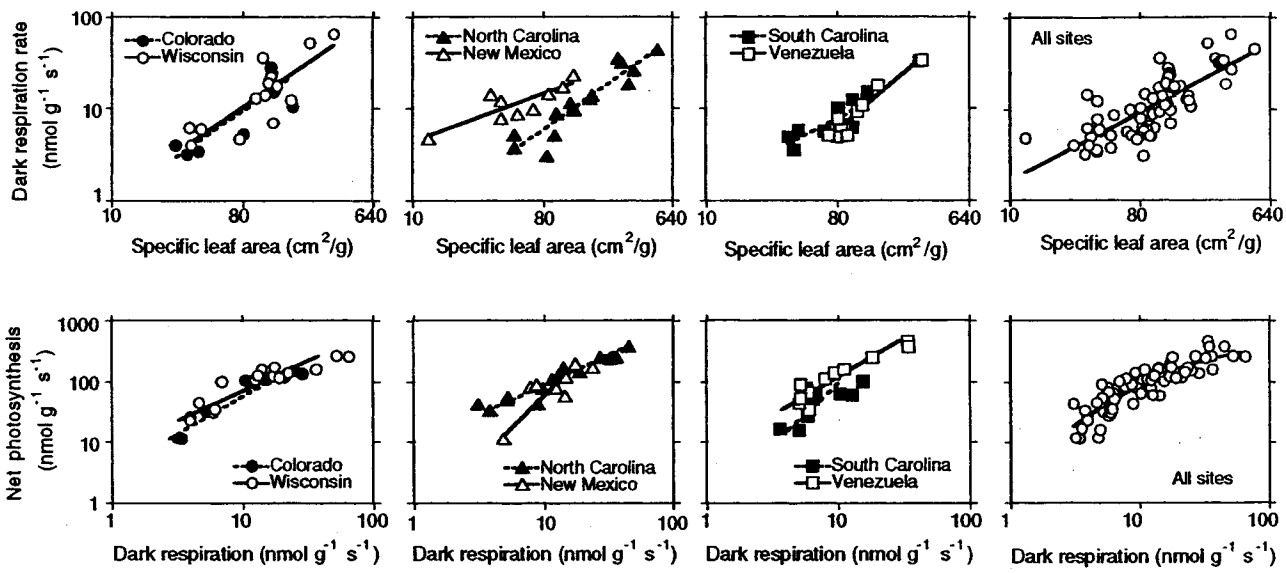

Fig 3 Mass-based dark respiration rate ($R_{d\text{-}mass}$, nmol g^{-1} s^{-1}) in relation to specific leaf area (cm^2/g), and mass-based net photosynthetic rates (nmol g^{-1} s^{-1}) in relation to $R_{d\text{-}mass}$, for species in six diverse ecosystems. All other details as in Fig. 2. Correlation coefficients (r^2) for leaf $R_{d\text{-}mass}$ vs. SLA: CO (0.73), WI (0.68), NC (0.86), NM (0.72), SC (0.59, P = 0.009) and VEN (0.94). Regression relationships for pooled data: $\log(R_{d\text{-}mass}) = -0.64 + 0.85 \times \log(\text{SLA})$, r^2 = 0.60. Correlation coefficients (r^2) for linear regressions of leaf A_{mass} vs. $R_{d\text{-}mass}$: CO (0.92), WI (0.80), NC (0.91), NM (0.69), SC (0.51, P = 0.02) and VEN (0.88). These relations were more accurately fit with polynomial regression for all sites except NC and VEN; and these correlation coefficients increased by between 0.06 to 0.10 over the linear ones

life-span, with needle-leafed conifers at the other extreme, and broad-leafed shrubs and trees intermediate. Although $R_{d\text{-}mass}$ in conifers was only 18–43% as great as in the other functional groups, $R_{d\text{-}area}$ was in a comparable range. The R_d-leaf N relationships were generally highly significant in all functional groups (Fig. 4, Table 5). However, they differed in several important ways among groups. In general, at any given level of leaf N (mass or area), R_d tended to be lowest in needle-leafed conifers, intermediate in the two broad-leafed groups (which were similar) and highest in the forbs.

Mass-based R_d – N relationships were significant at each site and for every functional group. In contrast, area-based R_d – N relations were significant for all functional groups, but not among species at any site.

R_d in relation to multiple leaf trait combinations

We explored additional ways of examining leaf trait, site and functional group effects on R_d. Using multiple regression, neither site nor any interaction involving site was significant ($P > 0.1$) in models with R_d as the dependent variable and including site and two or three of the following (leaf life-span, N and SLA) as independent factors. This indicates that site differences in R_d relations (noted in analyses which included sites and single leaf traits) disappeared when two or more leaf traits were included as independent factors in the analysis. $R_{d\text{-}area}$ was significantly related to the combination of N_{area} and leaf life-span (r^2 = 0.62) or N_{area} and SLA (r^2 = 0.49) (Table 6). Multiple regressions showed, regardless of biome, that $R_{d\text{-}mass}$ was highly correlated with the dual combinations of N_{mass} and SLA, leaf life-span and SLA, and N_{mass} and leaf life-span (all $P < 0.001$, $r^2 \geq 0.79$, Fig. 5, Table 6). At any level of SLA, $R_{d\text{-}mass}$ rises with increasing N_{mass} and/or decreasing leaf life-span; and at any level of N_{mass}, $R_{d\text{-}mass}$ rises with increasing SLA and/or decreasing leaf life-span. Using multiple regression (Table 6), $R_{d\text{-}mass}$ was significantly related to leaf life-span, leaf N_{mass} and SLA (and no interactions) (all factors $P < 0.001$, r^2 = 0.85) and the observed:predicted relationship was close to the 1:1 line (Fig. 6). Thus, leaf structure, longevity and chemistry collectively are highly associated with leaf $R_{d\text{-}mass}$.

Table 5 Regression statistics describing the relationship between R_d and leaf nitrogen content. For mass-based regressions the dependent variable is $\log_{10} R_{d\text{-mass}}$ (nmol g^{-1} s^{-1}) and the independent variable is $\log_{10} N_{mass}$ (mg/g). For area-based regressions, the dependent variable is $R_{d\text{-area}}$ (μmol m^{-2} s^{-1}) and the independent variable is N_{area} (g/m^2). Species arranged by functional groups for data pooled from six biomes: forbs; broad-leafed shrubs; broad-leafed deciduous trees; and needle-leafed evergreen trees

Group	n	Mass-based regressions				Area-based regressions			
		Y-intercept	slope	$P<F$	r^2	Y-intercept	slope	$P<F$	r^2
Forbs	15	0.10	0.91	0.0001	0.74	0.03	0.77	0.0001	0.74
Broad-leafed shrubs	15	−0.32	1.10	0.0001	0.69	−0.08	0.80	0.0001	0.57
Broad-leafed trees	24	−0.62	1.28	0.0001	0.72	−0.19	0.68	0.011	0.26
Needle-leafed evergreen trees	13	0.06	0.55	0.088	0.24	−0.44	1.05	0.0001	0.85
All species	68	−0.69	1.37	0.0001	0.74	−0.11	0.63	0.0001	0.38

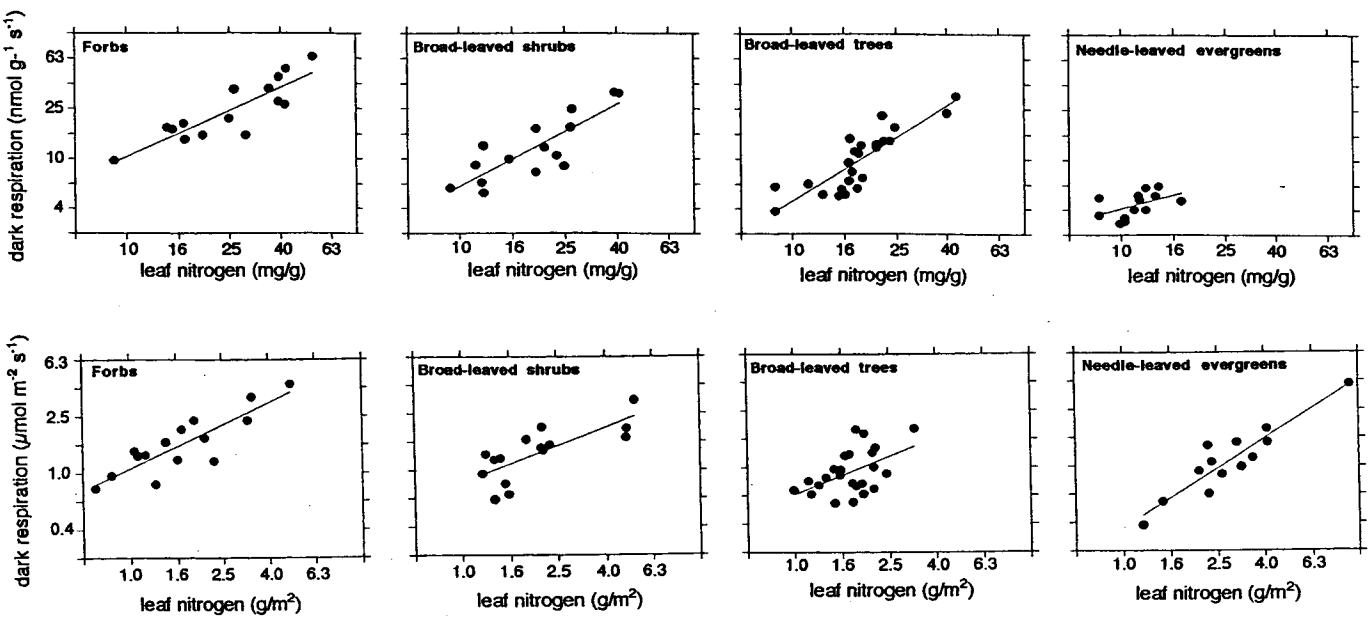

Fig. 4 Mass- and area-based dark respiration rates in relation to mass- and area-based leaf N for species pooled across sites, grouped into functional groups (based on simple linear regressions of base-10 logarithmically transformed data). All regressions were significant at $P < 0.001$, except for mass-based R_d-N in the conifers ($P = 0.08$). Regression relationships are given in Table 5

Unlike site, functional group was a significant factor in multiple regression analyses for R_d even when leaf life-span, leaf N_{mass} and SLA were included in the model, and it slightly increased the explained variance (all factors $P < 0.05$, whole model $r^2 = 0.89$). This resulted from significantly higher $R_{d\text{-mass}}$ for forbs than for woody plants (shrubs, broad-leafed trees and conifers were similar) standardized to a common SLA, N_{mass} and leaf life-span. Thus, predicting $R_{d\text{-mass}}$ based solely on leaf traits for this data set would slightly underpredict measured values for forbs. However, given the relatively small sample size in each functional group, only one or two samples can markedly alter these relationships. A data set with greater numbers of species in each functional group would be needed to clarify whether or not functional groups did generally differ in R_d-leaf trait relationships even after standardizing for SLA, N_{mass} and leaf life-span.

Site differences in leaf traits and their relationship to climate

For all species and sites pooled, $R_{d\text{-mass}}$ measured at 25°C was approximately 13% of A_{mass} (measured at ambient conditions usually between 20 and 30°C), which would correspond to 9.5% of A_{mass} at 20°C, and 6% of A_{mass} at 15°C assuming a common Q_{10} of 2 for respiration and minimal variation in A_{mass} over that temperature range. Measures of $R_{d\text{-mass}}$ (made at 25°C) were not directly related to variation among sites in mean annual temperature (data not shown), nor was annual or growing season temperature significant in multiple regression analyses. However, the ratio A_{mass}: $R_{d\text{-mass}}$ increased with mean annual temperature ($P = 0.05$, $r^2 = 0.66$). Respiration measured at 25°C represented the largest fraction (16%) of A_{mass} in the coldest site (Colorado) and the lowest proportion (8%) in the warmest site (Amazonas). Given the relatively low number (six) of sites in the current study, clarification of the generality of this pattern will await a comparison based on a larger number of sites. Additionally, this pattern should not be interpreted as suggesting that the in situ relationship between A_{mass} and R_d varies across

Table 6 Summary of significant multiple regression relationships. All dependent and independent variables are on a $\log_{10}$ basis. Site was not a significant factor in any multiple regression analysis. All factors included were significant at $P < 0.001$. Units and abbreviations: mass-based dark respiration ($R_{d_{mass}}$), nmol g^{-1} s^{-1}; mass-based leaf N (N_{mass}), mg/g; specific leaf area (SLA), cm^2/g; leaf life-span (months); area-based dark respiration ($R_{d_{area}}$), μmol m^{-2} s^{-1}; area-based leaf N (N_{area}), g/m^2

Dependent variable	Regression relationship	r^2
$\log (R_{d_{mass}})$	$= 0.08 + 0.66 \times \log (N_{mass}) + 0.20 \times \log (SLA) - 0.28 \times \log$ (leaf life span)	0.85
	$= 0.78 + 0.34 \times \log (SLA) - 0.44 \times \log$ (leaf life span)	0.79
	$= -0.94 + 0.37 \times \log (SLA) + 1.00 \times \log (N_{mass})$	0.79
	$= 0.39 + 0.77 \times \log (N_{mass}) - 0.34 \times \log$ (leaf life span)	0.84
$\log (R_{d_{area}})$	$= 0.07 + 0.77 \times \log (N_{area}) - 0.23 \times \log$ (leaf life span)	0.64
	$= -0.95 + 1.00 \times \log (N_{area}) + 0.37 \times \log (SLA)$	0.50

sites, with R_d a greater fraction of net photosynthesis at colder sites. It is likely that such large inter-site differences would not occur for plants if both A_{mass} and R_d were measured in their native thermal environments, since much lower average growing season air temperatures at high elevations in Colorado (maximum mean monthly temperature of 8°C) than in Amazonas would proportionally reduce in situ respiration rates more than photosynthesis.

Discussion

Variation in R_d-leaf trait relationships among biomes and functional groups

These data generally support the main hypothesis, that interspecific multiple leaf trait relationships involving R_d will be similar among both diverse biomes and plant functional groups. However, this similitude holds true more for cross-site than cross-functional group comparisons when individual pairs of traits are compared, rather than multiple trait combinations. Consistent regressions for data from six biomes suggests that the interspecific relationships between R_d and individually, leaf life-span, N_{mass}, SLA, and A_{mass}, are universal across diverse sites, ecosystems and biomes, with patterns as depicted in Figs. 1–5. Taken together with data from companion papers (Reich et al. 1997, 1998a), these data demonstrate that regardless of terrestrial ecosystem type, species with short leaf life-spans generally have "thin" (high SLA) leaves with high N_{mass}, high A_{mass}, and high $R_{d\text{-}mass}$, with the reverse true for species with tough, long-lived leaves. Species tend to have a set of linked leaf traits, with SLA, leaf life-span, leaf N_{mass}, A_{mass} and $R_{d\text{-}mass}$ of each species generally falling together somewhere along a continuum of these coordinated leaf traits (Reich et al. 1997).

For species within four broad functional groups, R_d was highly significantly related to leaf N on both mass and area bases. The proportional variation in R_d with respect to N was roughly similar among functional groups, but at any given level of leaf N, R_d was highest in forbs (with high SLA and short leaf life-spans) and lowest in needle-leafed conifers (with low SLA and long leaf life-spans). This is likely due to the combined interrelationships of SLA, leaf life-span, N and R_d (see below). Moreover, it suggests that modeling R_d based on leaf N alone is likely to be more accurate within functional groups than for all species pooled, while a better approach would utilize a combination of leaf traits rather than N alone.

These data on functional group differences indicate that in a common environment forbs likely have higher respiratory costs for any given level of leaf N than woody broad-leafed species, with needle-leafed conifers having the lowest. Forbs also have greater maximum photosynthetic gains at a given level of leaf N than than woody broad-leafed species with needle-leafed conifers again having the lowest (Reich et al. 1998a). These functional group differences are largely due to their differences in leaf morphology (SLA) which additively (along with leaf N) influence both R_d (this paper) and photosynthetic capacity (Reich et al. 1998a). Such functional group differences in potential carbon gains and losses per unit standing pool of N could play an important role in the carbon balance of individual plants and differentially influence relative success of different species in varying resource habitats where R_d carbon costs vary as a proportion of photosynthetic carbon inputs.

Although several previous studies have addressed relationships between A_{max} and other leaf traits, there are far fewer reports comparing R_d with leaf traits (but see Ryan 1995; Reich et al. 1996). Those studies comparing interspecific or interpopulation variation in R_d-N suggest there is often a linear increase in $R_{d\text{-}mass}$ with increasing N_{mass}, comparable to that seen in our broad survey. Similarity in the mass-based R_d-N relationship among species in six biomes supports the idea that this is a broad universal relationship *among species*. However, this broad relationship is stable across only the entire array of plant species, since in fact there are different R_d-N relationships among functional groups, associated with their differences in SLA and leaf-lifespan.

It is important to point out why $R_{d\text{-}mass}$-N_{mass} relationships do not differ among biomes (Fig. 2, Table 3), despite the fact that the overall relationship for pooled data includes a series of slightly, but significantly different relationships for functional types that differ in SLA and leaf life-span. Comparison of species at each site includes contrasting species that broadly differ in leaf traits and range from low N_{mass}, low SLA and long

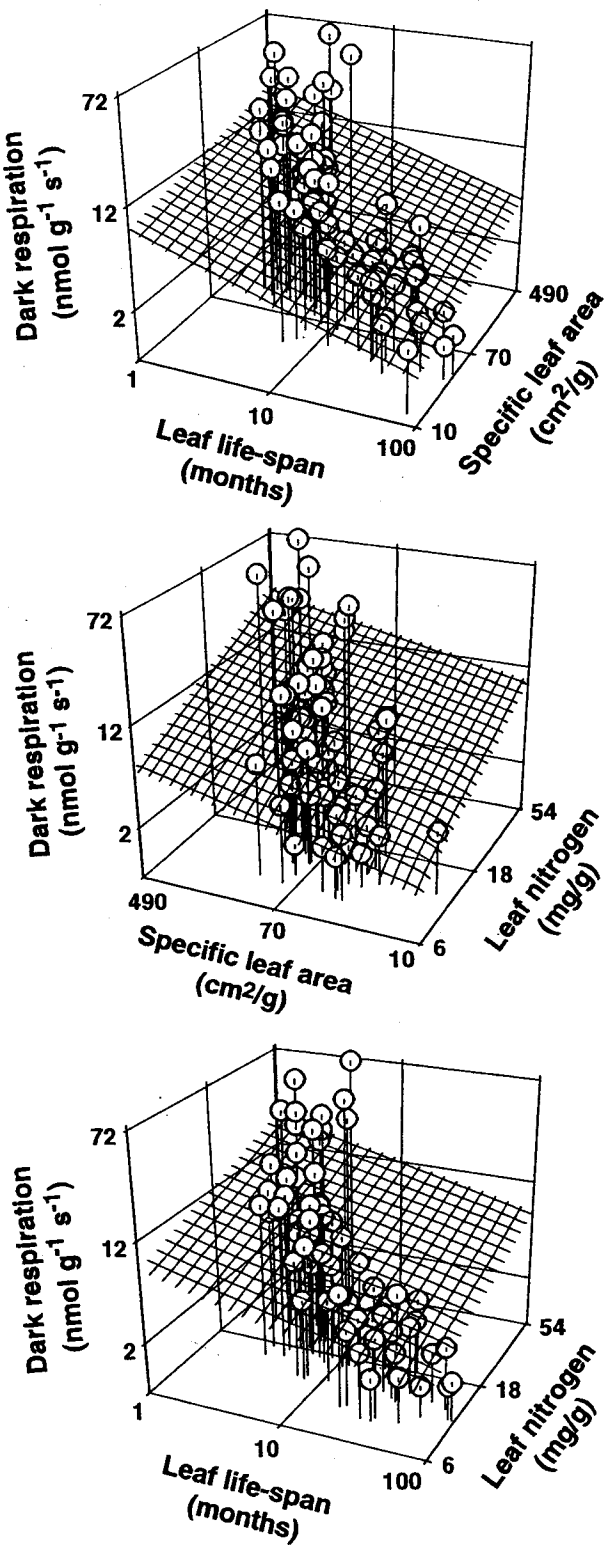

Fig. 5 Leaf dark respiration in relation to the combination of SLA and leaf N, SLA and leaf life-span, and leaf N and leaf life-span, for 69 species from six biomes. Regression statistics are given in Table 6

leaf life-span to high N_{mass}, high SLA and short leaf life-span; thus the comparison simultaneously spans gradients of all three leaf traits. Hence, given that species with a comparable range of linked traits are found on all sites, the site-specific R_d–N relationships (across a range

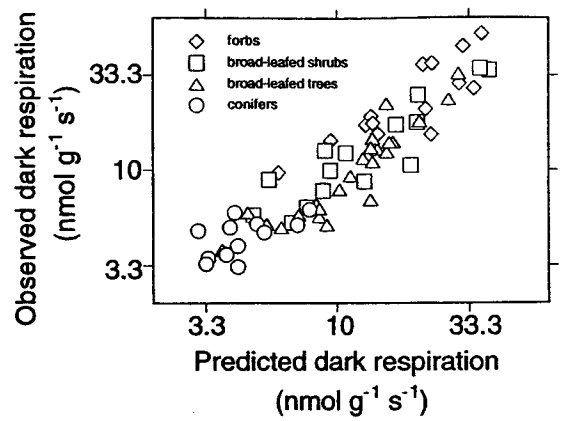

Fig. 6 Observed vs. predicted leaf dark respiration rate for species from four functional groups and six biomes, using multiple regression of respiration on the combination of leaf life-span, specific leaf area, and mass-based leaf N (regression given in Table 6)

of species) follow roughly the same overall pattern, because they all contrast the same multiple trait gradient. In contrast, within-group R_d–N relationships differ among functional groups because each group differs in leaf traits.

Area- and mass-based expression and interpretation

The $R_{d\text{-mass}}$ -N_{mass} relationship was significant, not only among species at each site, but among species within functional groups pooled across sites. In contrast, variation in $R_{d\text{-area}}$ among species was unrelated to N_{area} in any site in this study, but was strongly correlated with N_{area} within functional groups across sites. These data suggest that there is not a fundamental $R_{d\text{-area}}$ -to-N_{area} relationship *among all species*. This mirrors the finding of no generalized A_{area} – N_{area} relationship among species (Reich et al. 1991, 1992, 1998a). Species with vastly different SLA and N_{mass} can have similar N_{area}, giving rise to considerable scatter in the $R_{d\text{-area}}$ – N_{area} relationship among the range of species found at a site. However, within a group where SLA and N_{mass} do not vary as widely, the $R_{d\text{-area}}$-to-N_{area} relationship is significant, because leaves with higher N_{area} also tend to have equal or higher N_{mass}.

The slopes of the overall (all species) R_d-N relationships were lower when both variables were expressed on an area than a mass basis (Table 5). This is consistent with comparisons of area- and mass-based A_{max}-N relations (Reich and Walters 1994). Since the slope of these contrasting relationships has the same units (change in R_d per unit change in leaf N, μmol CO_2 g^{-1}N s^{-1}) one might intuitively ask whether the slopes should be the same regardless of whether leaf traits are expressed on a mass vs. area basis? Prior examination of mass and area-based net CO_2 exchange relationships for each of 23 species (Reich and Walters 1994) provided a simple explanation that reconciled these differences. Within species, variation in SLA and N_{mass} was related;

i.e., as SLA decreased N_{mass} also decreased, but proportionally more slowly, so that N_{area} increased. Thus, "thicker" leaves (low SLA) tended on average to have lower N_{mass} (and due to a stable A_{mass} -N_{mass} relation, lower A_{mass}) but higher N_{area} than thinner leaves. Given a negative intercept of the linear A_{mass}-N_{mass} relationship in every species, A_{mass} per unit N_{mass} declines with increasing N_{mass}. This tendency towards decreasing A per N with increasing N_{area} decreased the rate at which A_{area} increased with N_{area}, resulting in a lower slope on an area basis. The same explanation holds for this interspecific study of R_d. As SLA varies among species, those with lower SLA tend to have lower N_{mass}, but N_{mass} varies proportionally less than SLA (data not shown), and thus species with lower SLA tend to have higher N_{area} ($r^2 = 0.51$, $P < 0.0001$). Given the negative intercept and general consistency of the overall $R_{d\text{-}mass}$-N_{mass} relationship, these patterns of covariance in SLA and N_{mass} lead to a lesser slope of R_d-N on an area basis (since leaves with high N_{area} tend not to have high N_{mass}). In summarizing about area vs. mass based comparisons, the similarity of units of slope may provide a false sense that these two R_d-N relationships are measuring the same thing, when in reality they are measuring relationships of R_d and N along different gradients of multiple leaf traits.

Why is there a close association among R_d and other leaf traits?

Our multi-biome and multi-functional group results demonstrate fundamental repeatable patterns of variation among R_d and other measures of leaf structure, longevity, and chemistry. Combinations of leaf traits act together – increasingly long-lived leaves generally have lower SLA, N_{mass}, and A_{mass}, which collectively drive $R_{d\text{-}mass}$ down. What factors contribute to this close association of variation in R_d and several related leaf characteristics among species?

As a working hypothesis, our explanation for these patterns involves boundaries set by functional relationships, biophysical constraints, ecological adaptation and evolutionary selection (Chapin 1980; Field and Mooney 1986; Reich et al. 1992, 1997, 1998a). From a strictly physiological perspective $R_{d\text{-}mass}$ likely scales with A_{mass} and N_{mass} since leaves with high A_{mass} have large complements of N-rich enzymes and other metabolites which have substantial maintenance respiration costs and require periodic (and costly) resynthesis. Thus, there are reasonable grounds for the linkages between $R_{d\text{-}mass}$, A_{mass} and N_{mass} but why is $R_{d\text{-}mass}$ also so well related to leaf life-span and SLA? The combination of high mass-based N, R_d and A_{max} entails specific trade-offs, since such leaves are fragile (high SLA and low toughness), short-lived, desirable to herbivores because of high N, and less well physically defended against biotic (herbivory) and abiotic (physical weathering and stress) agents (Coley et al. 1985; Coley 1988; Reich et al. 1991, 1992). Lower SLA and longer leaf life-span have been associated with (1) greater allocation of biomass to structural rather than metabolic components of the leaf; (2) potentially different intra-leaf allocation of N; (3) greater within-leaf shading; and (4) potential diffusion limitations to net CO_2 uptake (see discussion in Reich et al. 1992, 1998a). The first of these could directly result in lower $R_{d\text{-}mass}$ as well as in A_{mass}, but the link to $R_{d\text{-}mass}$ of the others is not so clear. However, if these factors collectively reduce A_{mass} as appears likely (e.g., Reich et al. 1997), interspecific variation in $R_{d\text{-}mass}$ probably follows closely along. Although it is possible that species could have intrinsically high $R_{d\text{-}mass}$ and low A_{mass}, there is no apparent advantage to this combination and it is unlikely that neither adaptation nor acclimation would act to proportionally balance out carbon costs and gains.

Relationships of R_d and related leaf traits to plant ecological distributions

For plants adapted to grow fast, it makes sense that they have high maintenance and growth $R_{d\text{-}mass}$ since this would fuel growth and maintain metabolic activities related to high carbon gain potential (Lambers and Poorter 1992). Selection may be strong for high A_{mass}, and $R_{d\text{-}mass}$ may follow suit due to the A_{max}-R_d linkage. In contrast, species with inherently low maximum growth rates and mass-based N, A_{max} and R_d tend to regenerate in low light, low nutrient, or otherwise stressed environments (Chapin 1980; Reich et al. 1992, 1997; Walters et al. 1993). These slow-growing species often occupy sites where conditions tend to limit the achieved capture of CO_2 and therefore likely act to select against high N status, high metabolic capacity and associated respiratory costs, and for slow leaf turnover rates (Walters et al. 1993; Walters and Reich 1996; Reich et al. 1998b). Survival and/or the duration of nutrient and carbon use (Aerts 1990) may be the targets of selection, rather than a high maximum growth potential, in such microhabitats. For plant species adapted to deep shade, low $R_{d\text{-}mass}$ may help maintain positive carbon balances under conditions where high rates of carbon assimilation can not be realized (and associated high R_d costs would be disadvantageous from a carbon balance perspective), and thus be an advantage (Walters and Reich 1996). In such a case $R_{d\text{-}mass}$ might be a higher target of selection than A_{mass}, and A_{mass} might follow $R_{d\text{-}mass}$ due to their close linkage. It is possible that plants adapted to low resource environments other than deep shade also have low R_d as part of a strategy that enhances positive carbon balance and/or survival under adverse conditions even if low N_{mass} and low N and C turnover rates are the primary objects of selection (Chapin 1980; Aerts 1990; Reich et al. 1992).

Implications and conclusions

The results of this study suggest that there are common R_d-leaf trait relationships among species within widely

disparate biomes and also within functional groups if variation in SLA is simultaneously accounted for. These findings have several implications. First, these relationships allow quantitative comparisons of R_d for species of differing plant types and in widely differing ecosystems. We can now speculate with some degree of confidence that any given species will likely have comparable R_d as species with comparable leaf structure, longevity and/or N, from either the same or other functional group, ecosystem or biome. We can with more confidence predict the ordering of species R_d rankings and their absolute values based on combinations of leaf traits and/or functional groupings. Second, the uncovering of the generality of R_d and related leaf-trait relationships should allow the incorporation of such relationships into ecosystem to global scale models of carbon balance (Running and Hunt 1993; Ryan et al. 1994; Aber et al. 1996). Since leaf traits such as leaf N and SLA that are related to R_d and A_{max} are relatively easy to measure in the field and may be potentially estimated accurately from remotely sensed data (e.g., Wessman et al. 1988), collectively they provide a useful foundation for the development of scaling-based ecosystem or regional models (Running and Hunt 1993; Aber et al. 1996). Thus, evidence of functionally based R_d and related leaf-trait scaling relationships among species across functional groups and biomes should help us understand better both the diversity of species R_d and related ecophysiological characteristics, and the ways in which these aggregate to influence ecosystem level carbon cycling.

Acknowledgements This research was partially supported by National Science Foundation Grants BSR 8819718, BSR 8857129, and IBN9296005, and by the NSF Long-Term Ecological Research Program. We thank Chris Uhl, Brian Kloeppel, Dan Bahauddin and many others who contributed to this work in a wide variety of ways, and Mike Ryan for helpful criticism.

References

Aber JD, Reich PB, Goulden ML (1996) Extrapolating leaf CO_2 exchange to the canopy: a generalized model of forest photosynthesis validated by eddy correlation. Oecologia 106:267–275

Aerts R (1990) Nutrient use efficiency in evergreen and deciduous species from heathlands. Oecologia 84:391–397

Byrd GT, Sage RF, Brown RH (1992) A comparison of dark respiration between C_3 and C_4 plants. Plant Physiol 100:191–198

Chapin FS III (1980) The mineral nutrition of wild plants. Annu Rev Ecol Syst 11:233–260

Coley PD (1988) Effects of plant growth rate and leaf lifetime on the amount and type of anti-herbivore defense. Oecologia 74:531–536

Coley PD, Bryant JP, Chapin, FS III (1985) Resource availability and plant anti-herbivore defense. Science 230:895–899

Field C, Mooney HA (1986) The photosynthesis-nitrogen relationship in wild plants. In: Givnish T (ed) On the economy of plant form and function. Cambridge University Press, Cambridge, pp 25–55

Lambers H, Poorter H (1992) Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. Adv Ecol Res 23:187–261

Pavlik BM (1983) Nutrient and productivity relations of the dune grasses *Ammophila arenaria* and *Elymus mollis*. I. Blade photosynthesis and nitrogen use efficiency in the laboratory and field. Oecologia 57:227–232

Peters RH (1983) The ecological implications of body size. Cambridge University Press, Cambridge

Poorter H, Vijver C van de, Boot RG, Lambers H (1995) Growth and carbon economy of a fast-growing and a slow-growing grass species as dependent on nitrate supply. Plant Soil 171:217–227

Reich PB, Walters MB (1994) Photosynthesis-nitrogen relations in Amazonian tree species. II. Variation in nitrogen vis-à-vis specific leaf area influences mass- and area-based expressions. Oecologia 97:73–81

Reich PB, Uhl C, Walters MB, Ellsworth DS (1991) Leaf lifespan as a determinant of leaf structure and function among 23 tree species in Amazonian forest communities. Oecologia 86:16–24

Reich PB, Walters MB, Ellsworth DS (1992) Leaf lifespan in relation to leaf, plant and stand characteristics among diverse ecosystems. Ecol Monogr 62:365–392

Reich PB, Oleksyn J, Tjoelker MG (1996) Needle respiration and nitrogen concentration in Scots pine populations from a broad latitudinal range: a common garden test with field grown trees. Funct Ecology 10:768–776

Reich PB, Walters MB, Ellsworth DS (1997) From tropics to tundra: global convergence in plant functioning. Proc Nat Acad Sci 94:13730–13734

Reich PB, Ellsworth DS, Walters MB (1998a) Leaf structure (SLA) modulates photosynthesis relations: evidence from within and across species, functional groups, and biomes. Funct Ecol (in press)

Reich PB, Walters MB, Tjoelker MG, Vanderklein D, Buschena C (1998b) Photosynthesis and respiration rates depend on leaf and root morphology and nitrogen concentration in nine boreal tree species differing in relative growth rate. Funct Ecol (in press)

Running SW, Hunt ER (1993) Generalization of a forest ecosystem process model for other biome, BIOME-BGC, and an application for global-scale models. In: Ehleringer JR, Field CB (eds) Scaling physiological processes: leaf to globe. Academic Press, San Diego, pp 141–158

Ryan MG (1995) Foliar maintenance respiration of subalpine and boreal trees and shrubs in relation to nitrogen content. Plant, Cell Environ 18:765–772

Ryan MG, Linder S, Vose JM, Hubbard RM (1994) Dark respiration of pines. Ecol Bull 43:50–63

Steel RGD, Torrie JH (1980) Principles and procedures of statistics. A biometrical approach 2nd ed. McGraw-Hill, New York

Walters MB, Reich PB (1996) Are shade tolerance, survival, and growth linked? Low light and nitrogen effects on hardwood seedlings. Ecology 77:841–853

Walters MB, Kruger EL, Reich PB (1993) Growth, biomass distribution and CO_2 exchange of northern hardwood seedlings in high and low light: relationships with successional status and shade tolerance. Oecologia 94:7–16

Wessman CA, Aber JD, Peterson D, Melillo J (1988) Remote sensing of canopy chemistry and nitrogen cycling in temperate forest ecosystems. Nature 335:154–156