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LETTER

Scaling of respiration to nitrogen in leaves, stems and roots of higher land plants

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Abstract

Using a database of 2510 measurements from 287 species, we assessed whether general relationships exist between mass-based dark respiration rate and nitrogen concentration for stems and roots, and if they do, whether they are similar to those for leaves. The results demonstrate strong respiration–nitrogen scaling relationships for all observations and for data averaged by species; for roots, stems and leaves examined separately; and for life-forms (woody, herbaceous plants) and phylogenetic groups (angiosperms, gymnosperms) considered separately. No consistent differences in the slopes of these log–log scaling relations were observed among organs or among plant groups, but respiration rates at any common nitrogen concentration were consistently lower on average in leaves than in stems or roots, indicating that organ-specific relationships should be used in models that simulate respiration based on tissue nitrogen concentrations. The results demonstrate both common and divergent aspects of tissue-level respiration–nitrogen scaling for leaves, stems and roots across higher land plants, which are important in their own right and for their utility in modelling carbon fluxes at local to global scales.

Keywords

Leaves, nitrogen, respiration, roots, stems.

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INTRODUCTION

Key metabolic, chemical and structural attributes of leaves of higher plants are often related to each other in similar and predictable ways across the globe, largely independent of growth form, plant functional type or biome (Field & Mooney 1986; Reich *et al.* 1997; Wright *et al.* 2004). These scaling relations are a result of the synergy between physiological, biophysical and evolutionary constraints on leaf phenotypes of all kinds of species in all types of terrestrial ecosystems (Field & Mooney 1986; Reich *et al.* 1997; Wright *et al.* 2004). One such relationship involves two traits known to be functionally related – mass-based dark respiration rate (i.e. respiration per unit dry mass; R, also known as specific respiration rate) and mass-based nitrogen content (N; Ryan 1991; Cannell & Thornley 2000; Amthor & Baldocchi 2001; Gifford 2003; Atkin *et al.* 2005a,b; Bouma 2005; Lambers & Ribas-Carbo 2005). Although considerably fewer measurements have been made of this trait-pair than of, say, photosynthetic capacity and leaf N (Field & Mooney 1986; Reich *et al.* 1997; Wright *et al.* 2004), results to date suggest that there is consistent coupling of leaf R and N among species and communities worldwide (Reich *et al.* 1997; Wright *et al.* 2004). These two traits are key indices of metabolism and chemistry in other plant organs also, such as fine roots (Comas & Eissenstat 2004; Tjoelker *et al.* 2005; Atkinson *et al.* 2007).

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Understanding and characterizing variation in R is of paramount importance for global-change science, as well as fundamental to plant ecology and physiology, because the efflux of CO_2 from plant respiratory processes is a critical and uncertain component of plant, ecosystem and global C budgets (King *et al.* 2006; Houghton 2007). Understanding and quantifying variation in the magnitude of R at a reference temperature as a function of plant chemistry (within and among taxa) and how that base rate varies with temperature (at multiple time steps) remain problematic, despite considerable advances (e.g. Comas & Eissenstat 2004; Bouma 2005; Lee *et al.* 2005; Tjoelker *et al.* 2008). In this study, we focus on the former (respiration–chemistry relations) although we note that the latter has received considerable attention (e.g. Tjoelker *et al.* 2001, 2008; Atkin *et al.* 2005a,b). Without a general model that enables the simulation of R at a reference temperature, models have taken a variety of approaches, including using assumed relationships of R to photosynthesis (Aber *et al.* 1996) or simulating R as a function of N (e.g. Cox *et al.* 2000; Sitch *et al.* 2003). For instance, a number of important regional and global scale models predict R of all tissue types directly from N (e.g. Cox *et al.* 2000; Sitch *et al.* 2003), without knowing whether the same relation applies for leaves, stems and roots, because a lack of any other useful data makes such simplifying assumptions the logical state of affairs. Clearly it is important to know whether or not such generic scaling relations have a sound basis and are broadly applicable.

Unfortunately, our ability to widely predict R is constrained by limitations both empirical and theoretical (Cannell & Thornley 2000; Amthor & Baldocchi 2001; Gifford 2003; Comas & Eissenstat 2004; Atkin *et al.* 2005a,b; Bouma 2005; Lambers & Ribas-Carbo 2005). Although the *total* respiration of entire plants scales isometrically with the *total* amount of N per plant, across a wide range of plant sizes (Reich *et al.* 2006), whole-plant N data are extremely scarce, so the utility of this relationship in C modelling is limited, and in any case it may also provide limited insight into tissue-level scaling relations. This is because the relationship between whole-plant respiration and N is an aggregate function of (i) changes with plant size in the proportional distribution of biomass and N to organs (leaves, stems and roots) that differ chemically, structurally and metabolically, and (ii) potential changes with plant size in N concentration and R for each organ type. Hence, the mass-based (i.e. specific) R–N relationships of leaves, stems or roots are not necessarily also isometric.

It is widely recognized (Amthor 1994, 2000; Cannell & Thornley 2000; Amthor & Baldocchi 2001; Atkin & Tjoelker 2003; Gifford 2003; Comas & Eissenstat 2004; Atkin *et al.* 2005a,b; Bouma 2005; Lambers & Ribas-Carbo 2005) that R (regardless of organ type) is strongly influenced by the concentration of key enzymes and co-factors (comprising much of total N in plant tissues) that drive metabolic processes, and also by the concentration of the substrates for metabolic processes, i.e. carbohydrates (Atkin & Tjoelker 2003; Atkin *et al.* 2005a,b). Indeed, Ryan (1991) suggested that there should be a general R–N relationship for every plant organ, and all organ types examined collectively, because of the central and common role N plays in metabolic processes in plant tissues.

This role takes several forms. In leaves, stems and roots, most of the N in plant cells is associated with protein. Moreover, much of respiration involves maintenance, repair and replacement of proteins as well as the maintenance of photosynthetic activity that includes provision of ATP for sucrose synthesis and energy for phloem loading (Amthor 1994, 2000; Cannell & Thornley 2000; Amthor & Baldocchi 2001; Atkin & Tjoelker 2003; Gifford 2003; Comas & Eissenstat 2004; Atkin *et al.* 2005a,b; Bouma 2005; Lambers & Ribas-Carbo 2005). The idea of a general R–N relation (for all organs) has some support from the relatively few – usually site-specific or organ-specific – data available (Maier *et al.* 1998; Pregitzer *et al.* 1998; Reich *et al.* 1998; Burton *et al.* 2002; Vose & Ryan 2002; Tjoelker *et al.* 2005; Atkinson *et al.* 2007). However, it is not clear whether general R–N relationships exist for roots or stems, nor how similar these relationships (if indeed general) are to those found for leaves, as to this point there has not been a comprehensive comparison of R–N scaling among plant organs.

To enable such an analysis, we compiled a new data set that enabled us to test, for the first time, whether general R–N relationships exist for leaves, roots and stems, and to test for differences among organ-types in these relationships. We use these data to address two main questions: firstly, considered across a variety of taxa and plant groups sampled from many different habitats, whether general R–N relationships can be discerned for roots and stems, as has been found for leaves; and, secondly, whether or not a similar relationship between R and N exists across these three organ-types that obviously differ in structure and function. The three plant groups were herbaceous angiosperms (herbs), woody angiosperms and woody gymnosperms, and were selected *a priori* because, among the studied taxa, they represent the simplest divisions based on important aspects such as phylogeny and life-form that also resulted in sufficient sample sizes.

Our specific hypotheses were: (i) that the proportional scaling of R to N represents a fundamental biological relationship that is likely similar in diverse plants and organs, and hence slopes of R–N relationships would be similar for leaves, stems and roots, yet at the same time; (ii) the intercepts of the three organ-specific relationships were likely to differ – as respiratory costs related to N partitioning or tissue architecture or associated with processes such as protein turnover, phloem loading, nutrient uptake and N

assimilation could differ systematically among organs (Cannell & Thornley 2000; Amthor & Baldocchi 2001; Gifford 2003; Comas & Eissenstat 2004; Atkin *et al.* 2005a,b; Bouma 2005; Lambers & Ribas-Carbo 2005). Given the fundamental role that enzymes play in metabolic processes, the hypothesis of a similar scaling of the proportional response of R to variation in N in different organs seems parsimonious, is consistent with whole-plant results (Reich *et al.* 2006), and is consistent with the greater generality of scaling slopes than of intercepts (and elevations of lines), as has been demonstrated in previous work with leaves (Wright *et al.* 2004). The common perception of leaves as sites of intense metabolic activity leads to a simple hypothesis of greater R per unit N in leaves than roots or stems (i.e. a different intercept), perhaps due to a greater fraction of N being allocated to metabolic activities in the former than the latter. In contrast, Cannell & Thornley (2000) suggested that energy (i.e. ATP, NADPH) from the light reactions of photosynthesis might offset respiratory costs associated with adenylate production, reducing the consumption of carbon substrates and CO_2 evolution below that which might be expected for a given N content. If this were true, rates of R per a common N would likely be lower in leaves than in roots or stems. In addition to addressing questions of fundamental ecophysiological importance, improved quantification of these relationships should aid efforts to model regional and global C-cycles (Cox *et al.* 2000; King *et al.* 2006; O. Atkin, personal communication), given that the availability of data for organ N concentrations, although patchy, is considerable and growing at a global scale.

MATERIALS AND METHODS

The data set used in this study consisted of 2510 paired observations of tissue (root, stem or leaf) N concentration and respiration rate (as net CO_2 efflux) derived both from peer-reviewed publications and from unpublished data contributed by the authors (Table S1). In total, the measurements concerned 287 species from 47 sites (468 species-site combinations in aggregate for leaves, stems and roots) spread across most major terrestrial biomes. The 2510 observations include 267 from the previously most comprehensive analysis, restricted only to leaves (Wright *et al.* 2004). The new, greatly expanded data set also includes data for roots of various sizes as well as data for stems ranging from fine woody branches to large tree boles. However, the number of species, species-site combinations and total observations for which stem measurements are available (16, 20 and 380, respectively) is much lower than for roots (83, 108, 744) or leaves (267, 340, 1386).

To reconcile measurement temperature differences among studies, we adjusted respiration rates to a common measurement temperature (20 °C) using a well-validated (Tjoelker *et al.* 2001) published temperature model (Tjoelker *et al.* 2001; Atkin *et al.* 2005a,b). Although this equation describes the general relationship between the Q_{10} of respiration and short-term measurement temperature, real variation in temperature–response relationships still exist, but are unknown for the vast majority of data in our paper. However, as respiration is universally highly responsive to short-term temperature variation, it seemed prudent to use the general model to adjust measurement temperatures to a common temperature. Given that 86% of the observations in the paper were made between 20 and 25 °C (91% between 18 and 26 °C), adjustments across a large temperature range were made for a relatively small fraction of the entire data set in any case. Moreover, in general, fits were similar but slightly better (for each organ type or combinations of group and organ type) and slopes were similar but slightly lower using the adjusted than original respiration values. Most important to this paper, the main conclusions would be similar if we reported data under measurement rather than standardized temperature measurement conditions.

The majority of data (87% of observations) were obtained by measuring CO_2 evolution with the remainder obtained by measuring O_2 consumption. We used a respiratory quotient of 1.0 to convert these to CO_2 evolution; using a quotient of 0.9 or 1.1 did little to alter the overall relationships. Lab-grown plants tended to have higher respiration and higher nitrogen values on average for each organ type than field-grown plants, but with considerable overlap, and all data for each organ type fit a common relationship. Additionally, although bole respiration data in large trees are potentially problematic because respired CO_2 from other sources may be transported in xylem sap (Teskey & McGuire 2007), we include them in our analyses because measured stem CO_2 fluxes represent from 82% to 97% of total stem respiration (Saveyn *et al.* 2008), and note that our results are similar with or without them. To evaluate the consistency of R–N scaling, we used reduced major axis regression (Wright *et al.* 2004; Reich *et al.* 2006) to compare the scaling exponents of the power function (hereafter described as the slope of the log–log relationship) within and among the three major organs, among major plant groupings and among organs within each plant group.

RESULTS

Among all measured plant organs and 287 species, N varied *c.* 275-fold and R *c.* 4000-fold. For all organs and three plant groups pooled (n = 2510 measurements), R increased with tissue N ($P < 0.001$, $R^2 = 0.68$, Figs 1 and 2; Table 1), with the scaling exponent = 1.27 (95% CI 1.23–1.30). Hence, two-thirds of all variation in respiration was associated with variation in tissue N concentration across the diverse data.

Similarly strong relations were seen for leaves ($P < 0.001$, $R^2 = 0.66$, $n = 1386$), stems ($P < 0.001$, $R^2 = 0.80$, $n = 380$) and fine roots ($P < 0.001$, $R^2 = 0.62$, $n = 744$) examined among all plant taxa (scaling exponents ranged from 1.34 to 1.64; Fig. 1). Examining each plant group separately (pooled across organs), there were strong R–N relations for gymnosperms ($P < 0.001$, $R^2 = 0.66$, $n = 1216$), woody angiosperms ($P < 0.001$, $R^2 = 0.62$, $n = 1069$) and herbs ($P < 0.001$, $R^2 = 0.57$, $n = 225$; scaling exponents ranged from 1.16 to 1.31, Table 1, Fig. 2). The consistently greater than isometric (>1) scaling of R to N in all organs and all plant groups indicates R per unit N is as a rule higher in tissues with higher metabolic rates. This is likely due to generally faster turnover rate of proteins, maintenance of solute gradients, and ion transport in more metabolically active tissues (Bouma 2005) as well as a disproportionate increase in N in metabolically active pools relative to structural N with increasing tissue N

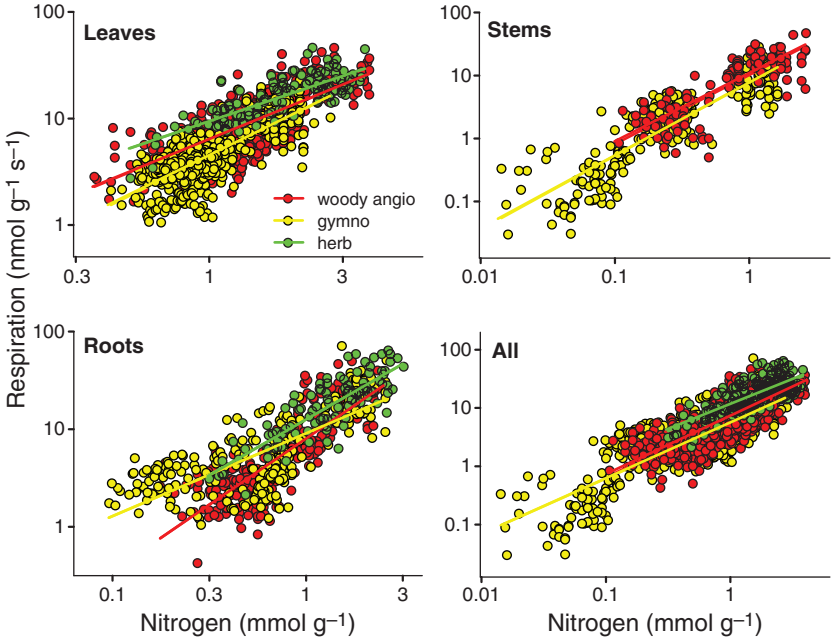

Figure 1 Mass-based dark respiration (nmol g^{-1} s^{-1}) in relation to tissue nitrogen concentration (mmol g^{-1}). Both are expressed on a logarithmic ($base_{10}$) basis. Data are shown for different organ types (and for all organ types pooled), with plant groups labelled with different colours. To improve visibility of each panel, scales are not identical among panels; however, the axis ratios are the same, hence slopes may be compared among panels. Plant groups include herbaceous angiosperms (herb), woody angiosperms (woody angio) and woody gymnosperms (gymno). Statistics shown in Table 1.

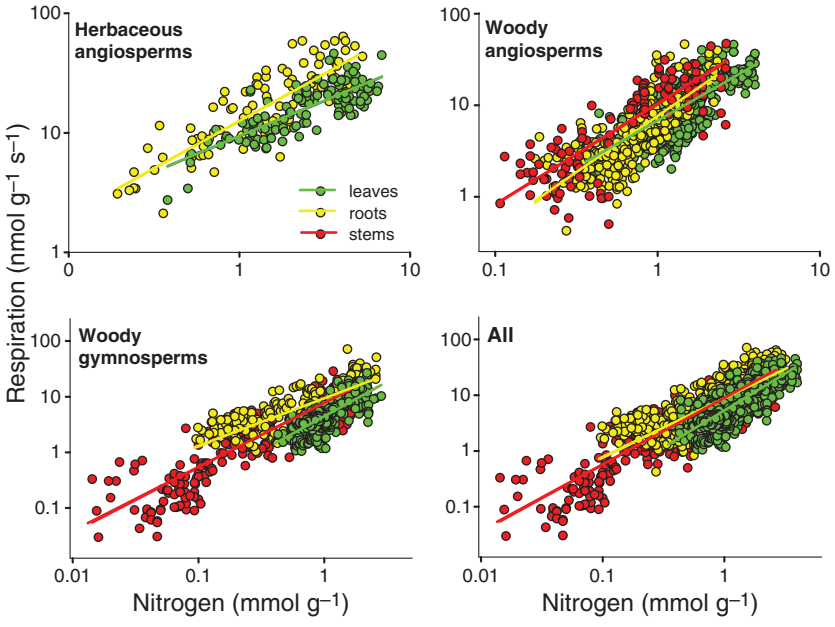

Figure 2 Mass-based dark respiration (nmol g^{-1} s^{-1}) in relation to tissue nitrogen concentration (mmol g^{-1}). Both are expressed on a logarithmic ($base_{10}$) basis. Data are shown for different plant groups and for all plant groups pooled, with organ types labelled with different colours. Note, to improve visibility of each panel, scales are not identical among panels; however, the axis ratios are the same, hence slopes may be compared among panels. Statistics shown in Table 1.

Table 1 Scaling of dark respiration rate (nmol g^{-1} s^{-1}) and tissue N concentration (mmol g^{-1}) by all combinations of organ types and plant groups. Plant groups include woody gymnosperms (Gymno), woody angiosperms (Woody Angio), and herbaceous angiosperms (Herb)

Organ type	Plant group	*n*	Intercept	Exponent	Lower CI	Upper CI	R^2
All	All	2510	0.833	1.268	1.234	1.303	0.683
Leaves	All	1386	0.691	1.639 a	1.578	1.703	0.657
Stems	All	380	1.024 a	1.344 b	1.278	1.413	0.801
Roots	All	744	0.980 a	1.352 b	1.277	1.430	0.620
All	Gymno	1216	0.786 a	1.178 a	1.131	1.227	0.655
All	Woody Angio	1069	0.839	1.311 b	1.252	1.374	0.623
All	Herb	225	0.985 b	1.156 a	1.031	1.297	0.571
Leaves	Gymno	680	0.645	1.660 a	1.553	1.774	0.561
Stems	Gymno	252	0.993	1.323 b	1.239	1.412	0.783
Roots	Gymno	284	1.012	1.120 c	1.012	1.239	0.573
Leaves	Woody Angio	584	0.753 a	1.411 a	1.307	1.522	0.534
Stems	Woody Angio	128	1.053 b	1.315 a	1.170	1.478	0.696
Roots	Woody Angio	357	0.915	1.597 b	1.489	1.714	0.687
Leaves	Herb	122	0.911	1.078 a	0.935	1.242	0.622
Roots	Herb	103	1.079	1.343 b	1.184	1.524	0.712

All relations were significant ($P < 0.001$).
Significant differences ($P < 0.05$) in slopes among relations (for data subsets selected as appropriate contrasts, these are set apart by empty rows) shown by lack of shared letters; for contrasts with shared slopes, differences in intercepts shown in the same way. All equations were fit using the log–log version of the equation: $Y = Y_0 M^b$. Reduced major axis intercepts and slopes (exponents) are shown, as well as the lower and upper 95% confidence interval (CI) of the exponent, and R^2. n = number of observations.

concentration (Field & Mooney 1986; Reich *et al.* 1997). This may reflect advantageous N allocation under conditions conducive to rapid metabolic processing (Field & Mooney 1986; Reich *et al.* 1997).

There were no consistent differences in organ-specific R–N slopes. The R–N slope for leaves was significantly greater than for roots for all data pooled and within the gymnosperm data set, but was significantly shallower than for roots within the angiosperm herbaceous and angiosperm woody data sets (Table 1). Likewise, the slopes for stems could be lower or higher than for either leaves or roots depending on the data set. In contrast, leaves had lower R at a given N than roots or stems in all data sets (Figs 1 and 2).

The data set with all observations (n = 2510) includes leaf, stem or root data from species with only one or a few observations, as well as data from species with many observations, both among but especially within sites. To evaluate whether the relationships noted in Table 1 were influenced by being statistically leveraged towards species measured frequently at individual study sites, we also evaluated the relations using values averaged for each species-site combination (n = 468). The R–N scaling relations examined in Table 1 were similar on this latter basis (data not shown); hence an observation-centric and a species-centric approach both lead to similar conclusions.

The complete data set also includes observations from many species for which there are data for only one or two of the three tissue types. To assess whether the relations using all available data were consistent with relations where data for each organ were obtained from common species, we also assessed relationships based on species averages for the 67 species with both leaf and root data and for the 11 species with stem, leaf and root data (Fig. 3). The results were generally similar to those using the 468 species-site averages (data not shown) and all 2510 observations. The slopes of the relations did not differ significantly among organ types, but at all common tissue N concentrations, R was lower in leaves than in roots or stems (Fig. 3), similar to the analyses using all individual observations.

DISCUSSION

In aggregate, the analyses above indicate that R–N scaling relationships were consistently observed regardless of whether the analyses were made using all data, using species-site averages, or using species averages for only those species with multiple organ data. No consistent differences in organ-specific R–N slopes emerged from the analyses. Although for all data pooled there was a significantly greater R–N slope for leaves than for roots

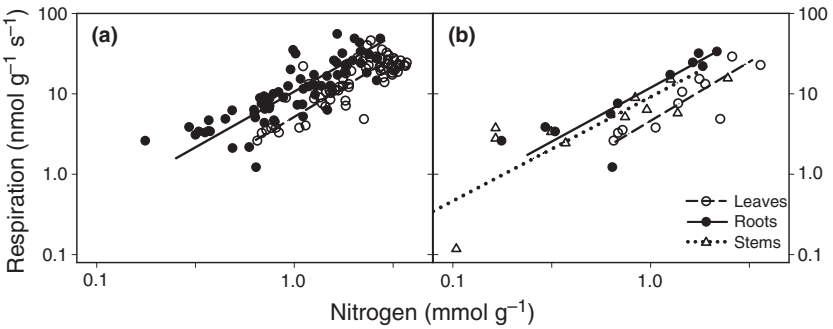

Figure 3 Mass-based dark respiration (nmol g^{-1} s^{-1}) in relation to tissue nitrogen concentration (mmol g^{-1}). Both are expressed on a logarithmic ($base_{10}$) basis. Data (left panel) are shown using species averages for only those species (n = 67) with data for both leaves (open circles) and roots (closed circles). Relationships (all values on a log $base_{10}$ basis): for leaves, respiration = 0.716 + 1.477*N ($P < 0.001$, $R^2 = 0.69$), for roots, respiration = 1.028 + 1.388*N ($P < 0.001$, $R^2 = 0.69$). Data (right panel) are shown using species averages for only those species (n = 11) with data for leaves (open circles), roots (closed circles) and stems (triangles). Relationships (all values on a log $base_{10}$ basis): for leaves, respiration = 0.665 + 1.469*N ($P < 0.001$, $R^2 = 0.74$); for roots, respiration = 1.075 + 1.341*N ($P < 0.001$, $R^2 = 0.72$); for stems, respiration = 0.961 + 1.293*N ($P = 0.003$, $R^2 = 0.64$). Scales are identical among panels; hence slopes may be compared among panels.

or woody stems (Table 1), this was not consistently true within the three broad plant groups (Table 1) and was also not significant using species-site averages (data not shown) or using species averages for only species with multiple organ data (Fig. 3). Similarly, differences in scaling slope among plant groups depended on the particular relationship examined. Given that several other factors, including substrate availability (Amthor 2000; Cannell & Thornley 2000; Atkin & Tjoelker 2003; Tjoelker *et al.* 2008), also influence R it may not be surprising that one single scaling exponent does not occur in all cases.

By contrast, a clear difference among organs emerged in the intercept and/or overall position (elevation) of their R–N relationships (Table 1; Figs 1–3). At a given tissue N concentration, leaf R was consistently lower than stem R or root R. This was evident when considering each individual plant group alone (Fig. 2), as well as across the pooled data set (Fig. 2) or the data set with common species (Fig. 3), hence this appears to be a general trend. We view the much more comparable R–N scaling in roots and stems as further evidence that leaves are behaving differently. Given that stems and roots, which differ so greatly in structure and function, nonetheless show generally comparable R–N relationships, the consistently lower R per N of leaves in these analyses should be viewed as robust evidence that this is a general phenomenon. These differences were substantial; e.g. for all taxa pooled (and spanning most of the common range of N among organs), at a tissue N of 0.5 mmol g^{-1}, mean R of leaves, root and stems was 1.6, 3.8 and 4.2 nmol g^{-1} s^{-1}, respectively, and at a tissue N of 2.5 mmol g^{-1}, mean R of leaves, roots and stems was 22.2, 33.2 and 36.4 nmol g^{-1} s^{-1}, respectively (equations given in Table 1). Similar contrasts emerge from the data sets using averages for species with measures of both leaves and roots (Fig. 3); at a tissue N of 1 mmol g^{-1}, mean R of leaves was 5.2 nmol g^{-1} s^{-1} in contrast to 10.7 nmol g^{-1} s^{-1} for roots.

Why should leaves have lower R at a common N than stems or roots, given the common perception of leaves as engines of metabolic activity? One possibility is simply that in leaves a smaller proportion of total N is found in respiration-related 'metabolic' components than in roots or stems. Much of the N in roots and stems is involved in metabolically expensive functions such as conversion and storage of non-structural carbohydrates, and solute and nutrient uptake, assimilation and transport (Cannell & Thornley 2000; Comas & Eissenstat 2004; Bouma 2005; Lambers & Ribas-Carbo 2005). In contrast, leaf N is involved in both respiratory and photosynthetic activities. All green leaves fix atmospheric CO_2 and as a result a high proportion of leaf nitrogen (*c.* 50–75%) is distributed in the photosynthetic machinery, in Calvin-cycle enzymes, pigment–protein complexes and electron transport components (Terashima & Evans 1988; Evans & Seemann 1989; Makino & Osmond 1991) in the chloroplasts, none of which engage in TCA-cycle (Krebs cycle) respiratory metabolism in the mitochondria, but which do incur considerable respiratory costs for their construction, maintenance and turnover. Whether leaves might rely more heavily than roots or stems in the inefficient alternative respiratory pathway is unknown (Lambers & Ribas-Carbo 2005). Additionally, N can be present in a number of non-respiratory structures and compounds in leaves, stems and

roots, including chemical defences and structural components, but it is not clear whether relative allocation of N to such compounds varies consistently among the three organs across diverse species.

A complementary explanation for the lower R at a common N in leaves than in stems or roots might involve additional intra-leaf energy sources that could lower net R per unit N, as proposed by Cannell & Thornley (2000). The ATP, C compounds and reducing equivalents produced in the light by photosynthesis may supply at least part of the energy required for growth, protein turnover and phloem loading in leaves without consuming C substrates (Cannell & Thornley 2000) and thus offset respiratory costs (via reduced demand for adenylates), because once produced in the chloroplast they may be used by leaves in either the light or the dark. As a result, the generally high respiratory cost that would otherwise be associated with the large allocation of N to photosynthetic processes in leaves may be in fact offset, resulting in the smaller flux of respiratory CO_2 per unit N compared with that in fine roots or woody stems. In the two complementary explanations for lower R per unit N in leaves than roots or stems, N-rich leaf tissues are either employed in non-respiratory activities (e.g. in photosynthetic activities) or produce metabolically critical compounds during photosynthesis that would otherwise need to be synthesized in the dark at an energy cost, or both.

The slopes of the specific tissue-level R–N scaling relationships presented in this paper (all > 1) differ from the isometric scaling (slopes *c.* 1) of whole-plant respiration and whole-plant nitrogen reported by Reich *et al.* (2006). How can these seemingly contradictory results be explained and reconciled? First, we can conclude that this difference between 'per plant' and 'per g tissue' relationships is not an artefact of different sets of study species or conditions, as individuals from the Reich *et al.* (2006) study included in the current data set (n = 966 observations) also had slopes > 1 for leaves, stems and roots on a per g tissue basis, and also had lower R at a common N in leaves than in roots or stems (data not shown). Perhaps this latter difference (in R per N) between leaves, stems and roots can help to explain the isometric scaling of whole-plant respiration and whole-plant nitrogen (Reich *et al.* 2006), as follows.

As a general rule, specific whole-plant nitrogen concentration (nitrogen per unit plant dry mass) decreases with plant size both (i) due to the increasing proportion of biomass that is found in nitrogen-poorer roots and stems rather than in nitrogen richer leaves, and (ii) due to intrinsic decreases in the nitrogen concentration of roots and stems with increases in plant size (Machado & Reich 2006; Reich *et al.* 2006). Any decline in nitrogen concentration of roots (or stems) with increasing size would lead to lower total plant root (or stem) respiration per unit nitrogen content because of the positive (> 1) scaling slopes of the log–log relations shown in Table 1. If biomass distribution among leaves, stems and roots was invariant with plant size, organ-specific declines in nitrogen concentrations in increasingly larger plants would alone reduce aggregate whole-plant respiration per total nitrogen content in larger plants, resulting in less than isometric scaling (< 1 scaling slopes) of total plant respiration to total plant nitrogen. However, the increasing fraction of total biomass that is roots and stems, rather than leaves, in increasingly larger plants, offsets the nitrogen concentration-based decline in respiration, because roots and stem have greater respiration rates per unit nitrogen than foliage (Figs 1–3). Given that the aims of both the present study at the per g tissue scale and the earlier whole-plant scale report (Reich *et al.* 2006) were to identify general respiration–nitrogen scaling patterns across diverse biotic and environmental sources of variation, they integrated (and thus standardized across or obscured) many other important drivers of respiration (e.g. temperature, species, carbohydrate status, etc.). Hence, despite what has been learned about respiration physiology at tissue and whole-plant scales from these and other studies (e.g. Amthor 2000; Burton *et al.* 2002; Atkinson *et al.* 2007; Tjoelker *et al.* 2008), there is clearly much more to learn about complexities, nuances and generalities of respiration–nitrogen relations.

Not surprisingly, given the uncertainties in our collective understanding of respiration and the inevitable lag between fundamental research and model development, the capacity of C-cycle models (at ecosystem or global scales) to simulate R is highly uncertain (Cannell & Thornley 2000; Cox *et al.* 2000; King *et al.* 2006; Houghton 2007). In many cases, variation in N is either directly or indirectly represented in the model logic and algorithms that represent respiration processes (Aber *et al.* 1996; Cox *et al.* 2000; Sitch *et al.* 2003; King *et al.* 2006). In some instances, the role of N is indirect, for example played out by surrogates such as photosynthetic capacity and assumed invariance of respiration–photosynthetic capacity ratios, whereas in others respiration may be estimated by tissue N concentrations and thermal regimes (Cox *et al.* 2000; Sitch *et al.* 2003; O. Atkin, personal communication). Dynamic global vegetation models simulate carbon metabolism and are widely used in global C-cycle research. Several such models (e.g. Cox *et al.* 2000; Sitch *et al.* 2003) directly estimate R from tissue N concentration and use the same R–N relationship for leaves, stems and roots for want of better information. Given our findings, this approach seems inappropriate given the observation of lower R per N for leaves than roots. Models that rely on simulating R from N in some fashion, which includes most C-cycle models, can benefit from the findings presented in our paper.

In summary, for the relations examined by observations, taxa and organs pooled, segregated or organized in several ways (Table 1, Figs 1–3); there were consistent and strong

R–N relations among diverse plant organs that vary widely in size, structural composition, growth rate and function. For these 15 tests in Table 1, the mean R^2 = 0.65 and the mean slope = 1.34, with the 95% CI of the mean ranging from 1.24 to 1.44. The generally consistent slopes of the tissue-level R–N scaling for leaves, stems and roots indicates the centrality of this relationship across diverse higher land plants and suggests that constraints on leaf design that allow broad generalizations about resource economics of leaves (Field & Mooney 1986; Reich *et al.* 1997; Wright *et al.* 2004) have parallels for stems and roots. Additionally, the evidence of lower R at any given N in leaves than in roots or stems demonstrates a fundamental and important difference in C-flux physiology between these organs. Simple R–N scaling relations as documented herein, especially when coupled with those that account for adaptation and acclimation of respiration to temperature (Lee *et al.* 2005; King *et al.* 2006; Tjoelker *et al.* 2008) offer promise for global C-cycle modelling (Cox *et al.* 2000; King *et al.* 2006; O. Atkin, personal communication), by providing biologically based means for predicting respiration rates for higher plant organs across the diverse range of plant types, ecosystems and biomes on the planet.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Table S1 Data sources, including the number of sites, the number of species studied, the numbers of observations and the plant module (organ) studied.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/full/10.1111/j.1461-0248.2008.01185.x.

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Supplemental Table 1. Data sources, including the number of sites, the number of species studied, the numbers of observations, and the plant module (organ) studied. The total represent the unique numbers of sites and species combinations, as there was some overlap among sources.

Source	Number of sites	Number of species	Number of observations	Organ
Atkinson et al. 2007	1	4	8	root
Bosc et al. 2003	1	1	10	stem
Burton et al. 2002	7	11	175	root
Comas & Eissenstat 2004	1	10	10	root
Dames 2003	1	1	8	stem
Kitajima et al. 1997	1	6	6	leaf
Lee et al. 2005	1	3	108	leaf
Lusk & Reich 2000	2	11	221	leaf
Lusk et al. 2003; Wright et al. 2004	3	18	23	leaf
Machado & Reich 2006	1	3	314	leaf, root, stem
Maier et al. 1998	1	1	36	stem
Mitchell et al. 1999	1	14	14	leaf
Miyazawa et al. 1998	1	4	4	leaf
Mooney et al. 1983	1	5	5	leaf
Pregitzer et al. 1998	2	1	144	root
Pruyn et al. 2002	2	1	30	stem
Pruyn et al. 2005	2	2	12	stem
Reich et al. 1998a	6	66	68	leaf
Reich et al. 1998b	1	9	438	leaf, root, stem
Reich et al. 2003	1	34	126	leaf, root
Reich et al. 2006	1	1	42	leaf, root, stem
Ryan et al. 1996	1	1	86	leaf, root
Tjoelker et al. 2001	1	5	46	leaf
Tjoelker et al. 2005	1	36	66	leaf, root
Tjoelker et al. unpublished	3	1	354	leaf
Vose & Ryan 2002	1	1	41	leaf, stem
Wright et al. 2001, 2004; Wright & Westoby 2004	4	73	78	leaf
Wright et al. 2004†	2	37	37	leaf
Total§	51	360	2510	

†Include data from Veneklaas *et al* (unpublished, n=25) and Lee *et al* (unpublished, n=12)

§These totals include some duplicate sites and species duplicated across studies. The total number of unique sites was 47 and total number of species sampled was 287.

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