THE EVOLUTION OF PLANT FUNCTIONAL VARIATION: TRAITS, SPECTRA, AND STRATEGIES

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Variation in plant functional traits results from evolutionary and environmental drivers that operate at a variety of different scales, which makes it a challenge to differentiate among them. In this article we describe patterns of functional trait variation and trait correlations within and among habitats in relation to several environmental and trade-off axes. We then ask whether such patterns reflect natural selection and can be considered plant strategies. In so doing we highlight evidence that demonstrates that (1) patterns of trait variation across resource and environmental gradients (light, water, nutrients, and temperature) probably reflect adaptation, (2) plant trait variation typically involves multiple-correlated traits that arise because of inevitable trade-offs among traits and across levels of whole-plant integration and that must be understood from a whole-plant perspective, and (3) such adaptation may be globally generalizable for like conditions; i.e., the set of traits (collections of traits in syndromes) of taxa can be considered as "plant strategies."

Keywords: plant traits, adaptation, fitness, functional groups, selection.

Introduction

What is a plant functional trait? For simplicity, we define this as any attribute that has potentially significant influence on establishment, survival, and fitness, and in this article we will largely focus on those traits related to the ability to acquire, use, and conserve resources. An ecophysiological trait can be considered adaptive if it has a direct and positive impact on fitness in natural environments (Ackerly et al. 2000). This idea seems logical, simple, and straightforward. Nonetheless, despite increased understanding of the diversity of plant functional traits within and among plant species (e.g., figs. 1, 2), identification of the trade-offs among traits that collectively limit and define successful trait syndromes (Reich et al. 1997, 1999), and exploration of the potential for natural selection on ecophysiological traits, our collective ability to directly demonstrate such selection remains extremely limited. However, all is not lost. We have made important strides in (1) characterizing the enormous range of interspecific and inter-population variation in physiological traits, (2) identifying patterns of trait variation across communities and along resource gradients, (3) quantifying the integrated whole-plant determinants of growth and survival in competitive milieus, (4) studying selection in natural populations, and (5) exploring the genetic basis for evolutionary change in ecophysiological traits. Each kind of study contributes to the working hypothesis that genetic differences underpinning functionally important ecophysiological traits determine the outcomes of competitive interactions in complex environments and across

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gradients and that these genetic differences have arisen via natural selection of phenotypes with heritable genetic differences.

In this article we will (1) describe variation in plant functional traits and some approaches for conceptual generalization or simplification, (2) discuss plant functional trait variation and trade-offs in relation to four environmental gradients (light, water, nutrients, and temperature) and evaluate evidence for selection potential and genotypic differentiation in these traits, (3) discuss causation or compromises that lead to correlations and trade-offs among traits and ask whether the evidence supports a theory of a primary plant strategy that can hold across all resource, stress, or other gradients, and (4) finish with a summary of future research opportunities and challenges.

What Are Appropriate Adaptive Contexts for Interpreting Specific Functional Traits?

Historically, plant ecologists have held as a fundamental working hypothesis the idea that a plant whose form and function maximizes its net carbon balance and growth in a given environment is usually going to be successful in such environments. In assessing the relationship of functional variability with plant competition, distribution, production, and survival, an important question is to what extent functional spectra and trait syndromes reflect adaptations. Correlations among species' traits and between these traits and the environments in which they are found can be interpreted in more ways than simply "adaptations" (Rose 1996). First, differences in traits among species that occupy contrasting environments may be the result of divergences in traits among major plant lineages deep in evolutionary time that are passed on to descendent
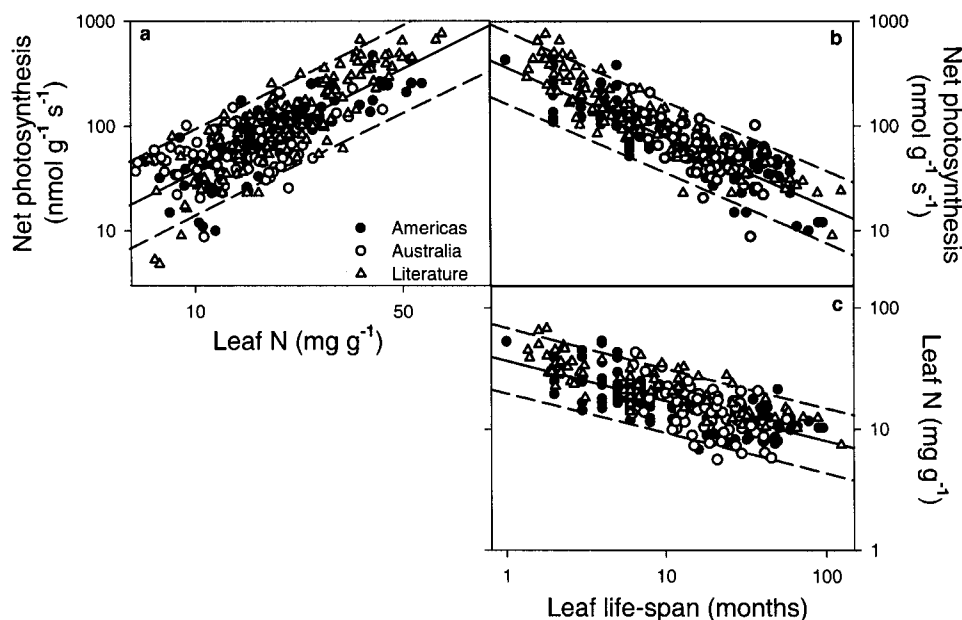
Fig. 1 The relationships between net photosynthetic capacity (nmol g^{-1} s^{-1}), leaf nitrogen concentration (mg g^{-1}), and leaf life span (mo) for species from three independent data sets: 111 species from six sites in the Americas (Reich et al. 1999), filled circles; 79 species from four sites in New South Wales, Australia (Wright et al. 2001, 2002), open circles; and 170 species from a large number of sites and studies from a literature data set (Reich et al. 1997), open triangles. Net photosynthetic capacity and leaf N were measured for young mature leaves, whereas leaf life span was the average longevity of a leaf for that species. The regression line of fit and 95% confidence intervals (for individual points) are shown for the field data from Reich et al. (1999). Redrawn using data from Reich et al. (1997, 1999) and Wright et al. (2001, 2002).

taxa. However, for a heritable trait that has functional consequences (which surely includes all the traits we are discussing in this article), remaining unchanged over evolutionary time unambiguously signals that natural selection is holding it stationary. Indeed, such traits may be predicted to be under stabilizing selection (Ackerly 2003). Moreover, the use of phylogenetically independent contrasts has shown that in most cases, functional trait variation of the type focused on in this article reflects significant patterns of correlated evolutionary change, which lends support to the adaptive interpretation of trait-trait correlations and trait-environment associations (Westoby et al. 1995, 2002; Ackerly 1999; Ackerly and Reich 1999; Wright et al. 2002; fig. 3). Second, biogeographic trait-trait and trait-environment correlations can be the result of plastic responses to the environment rather than representing genotypic differences. In essence, trait differences among taxa may only reflect their distributions, not a genetic basis for the trait value. Common garden, reciprocal transplant, and gradient experiments (highlighted in this article) can help sort this out. Third, populations or genotypes can be preadapted to a given selection factor or environmental condition. When they invade new habitats or geographic areas, or if their environment changes, their survival depends on whether their functional traits are suited to their environment. Thus, current species distributions may reflect ecological sorting processes rather than *in situ* adaptive evolution (Losos 1996). Nevertheless, ecological sorting is likely to reflect past natural selection as populations are likely to track environments for which they are adapted and are more likely to succeed in a new environment if their ancestors have experienced similar environments in the past. In much of this article, we assume that some meaningful fraction of the variability among functional traits does typically arise from adaptive evolution, and we present evidence to assess those claims.

Plant Functional Groups and Axes

Variation among taxa in individual functional traits can be classified using discrete (e.g., functional group) or continuous (e.g., axes or spectra, used interchangeably hereafter) categories. Multiple functional traits may be correlated due to evolutionary or biophysical constraints and trade-offs (Reich et al. 1997) and hence represent meaningful syndromes (used interchangeably with strategies). The concept of strategies has been proposed many times from a variety of perspectives (Grime 1977; Coley et al. 1985; Westoby et al. 2002). The usefulness of classifying plant taxa within differing functional groups or along functional spectra (based on one or multiple traits) has been evaluated frequently (Grime 1979; Pearcy and Ehleringer 1984; Garnier 1992; Lavorel et al. 1997; Diaz et al. 1999; Craine et al. 2002; Ackerly 2003; Reich et al. 2003a). The use of functional groups and syndromes might help us to understand the response of vegetation to historical environmental variability and to predict the response of vegetation to environmental change without requiring detailed information on each and every species. Although some authors have used "functional type" to mean a specific kind of functional group (e.g., those that respond similarly to a global change agent), the terms have been used so variably that we use them interchangeably in this article.
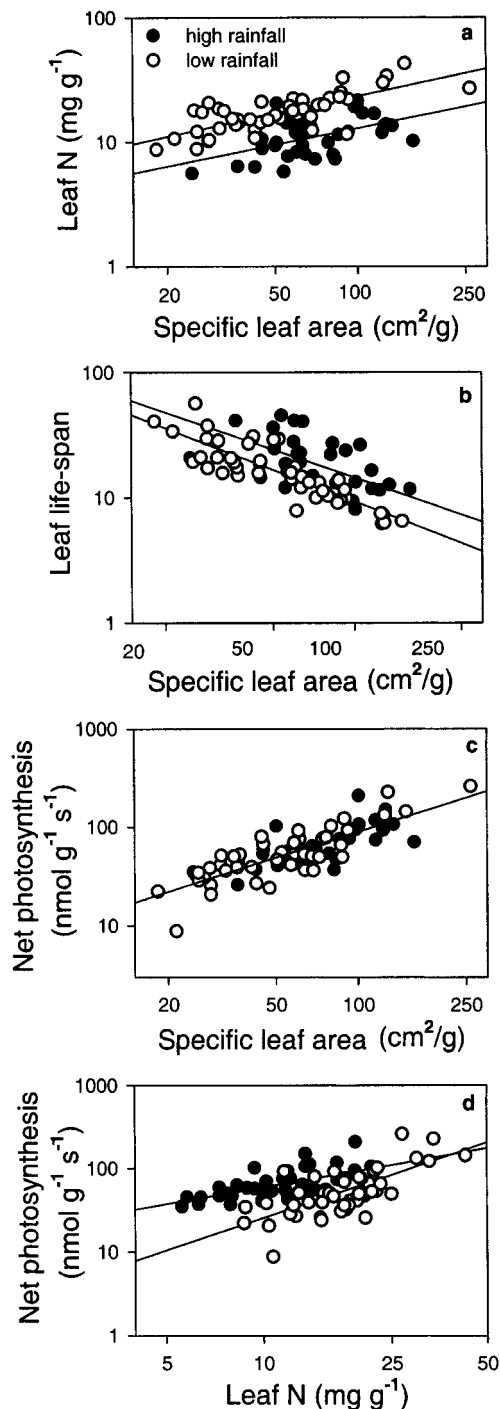
Fig. 2 The relationships of net photosynthetic capacity (nmol g^{-1} s^{-1}), leaf nitrogen concentration (mg g^{-1}), and leaf life span (mo) in relation to specific leaf area (cm^2 g^{-1}) and net photosynthetic capacity versus leaf N for 79 species from two high rainfall (1220 mm annual rainfall, filled circles) and two low rainfall (387 mm annual rainfall, open circles) sites in New South Wales, Australia, with similar mean annual temperature. The two sites at each rainfall level include a low and a high soil phosphorus site, which are pooled. Regression lines are shown for separately low- versus high-rainfall species except where the lines were not significantly different (one common line is used instead). Redrawn using data from Wright et al. (2001, 2002).

For this exercise we arbitrarily define four kinds of groupings. The first and most traditional grouping is based on discrete, typically qualitative individual traits (table 1). These include many strongly related to ancestry (e.g., monocot or dicot; annual or perennial; C$_3$ or C$_4$ photosynthesis). The second group is based on where a taxon lies along a continuum of quantitative values for a shared trait such as leaf life span, seed size, net photosynthetic capacity (A$_{max}$), or others. The third group is based on suites or syndromes of coordinated quantitative traits (Poorter et al. 1990; Reich et al. 1997, 1998b; Craine et al. 2001, 2002; Westoby et al. 2002). The fourth group uses post hoc classification schemes that attempt to group plant species based on their responses to specific environmental factors (Lavorel et al. 1997). This last grouping is based on integrated whole-plant behavior and outcomes and includes traditional classifications of shade tolerance, drought tolerance, and the like as well as theoretical concepts such as the C-S-R triangle (Grime 1977).

Whole genera or families or even larger clades often belong to the discrete qualitative groups (table 1). In other words, differences between these qualitative groups often arose at a phylogenetic branch point deep in the past (Sinha and Kellog 1996), with the trait combinations persisting into present-day species within each of the descendant lineages. However, even old divergences should not be regarded as a cause of current traits that are distinctly separate from present-day ecological selection or from a physically enforced trade-off because the evolution of species into present-day opportunities often has a large element of phylogenetic niche conservatism about it (Westoby et al. 1995; Westoby 1999). Only if the traits in question were incapable of responding to selection through millions or tens of millions of years would it be useful to regard the present-day correlation as the result of the old divergence rather than as due to continuing selection. Early arriving plant species on oceanic islands have been known to radiate from the herb functional group that their clade occupies on main lands into woody growth forms (Givnish 1998), presumably because the woody plant niche is not occupied by other competing clades. Such occasional wide divergences support the idea that phylogenetically conservative traits are maintained by continuing selection rather than being constrained by deep history.

Within each functional group there is typically a wide spectrum of variation in continuous traits, yet there is often a difference on average among groups. For instance, among angiosperms, woody shrubs typically have slightly lower leaf %N (fig. 4) than trees, followed in increasing order by herbaceous monocots, herbaceous dicots, and woody climbers. These differences are probably an outcome of selection. The difference on average among functional groups for a given continuous trait suggests that there is greater selection for low %N in certain groups, but within each group the selective pressure to have any specific level of that trait is weak (in the example, %N). In contrast, the coordination and linkages among many important traits due to biophysical constraints and selection (Reich et al. 1997) has apparently led to the occurrence of syndromes of traits that are evident within both closely or distantly related taxa. In the next several sections we focus on providing examples of some such evidence for four different kinds of environmental factors.
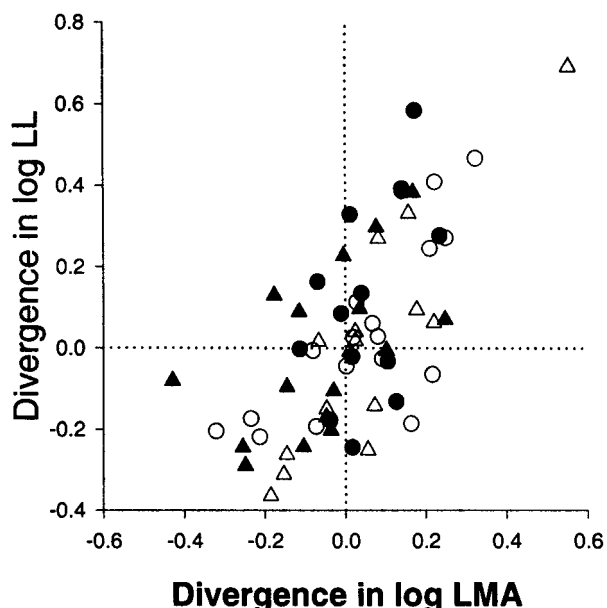
Fig. 3 Evolutionary divergences in leaf life span (LL) and leaf mass per area (LMA) using phylogenetically independent contrasts for species from the four New South Wales sites described in fig. 2. LMA is the inverse of specific leaf area. Filled symbols, high rainfall species; open symbols, low-rainfall species; circles, species at P-rich sites; triangles, species at P-poor sites. From Wright et al. (2002).

Traits, Trade-offs, and Evidence for Selection: Light, Water, Nutrients, Temperature

How are functional traits arrayed along environmental and/or trade-off axes? What is the nature of physiological trade-offs between traits of interest? Are there direct empirical studies linking trait variation to carbon gain, growth, or some element of fitness? In the following sections we will highlight examples of studies assessing functional variation and whether it can be related to selection processes, focusing in turn on each of the four major environmental gradients important for terrestrial plants. Because we cannot hope to be comprehensive, we use our own research and selected work of others as examples. For each factor we summarize findings about trait variation, correlation, and trade-offs in relation to specific environmental gradients and then ask whether there are studies that provide evidence that such patterns reflect evolution by natural selection.

A common theme regarding multiple traits and their trade-offs and integrated whole-plant consequences runs through each of these following sections. Published evidence increas-

ingly demonstrates that variation in plant functional traits is highly constrained by convergent evolution and biophysics with all taxa having traits that fall at some location on a universal trade-off spectrum (Reich et al. 1997). Correlated traits related to interception (e.g., specific leaf area [SLA]), uptake (e.g., A_{max}), use (e.g., respiration [R_d]), and turnover (e.g., tissue life span) of resources form this fundamental spectrum of variation. At one end of the spectrum, taxa can be characterized as having fast tissue turnover and high potential for resource capture and rapid short-term growth, whereas at the other end of the spectrum, species have slower tissue turnover and traits that enhance resource conservation (Grime 1977; Grime et al. 1997; Chapin 1980; Reich et al. 1992, 1997, 1999). In the sections that follow, we focus our attention on plants with "nonintuitive" strategies. It is generally believed that we understand that selection is for high growth rate under high near-optimal environmental conditions (high light, high water, high nutrients, optimal temperatures) and high competitive pressures. Yet the majority of taxa do not have the "high growth rate" syndrome. Therefore, we focus on asking how functional variation leads to success for these taxa.

Light Gradients and Shade Tolerance

It has long been hypothesized that competition in shade favors plants whose morphological and physiological traits maximize their net rate of carbon gain there (Givnish 1988). More generally, until recently it was thought (Kitajima 1994; Kobe et al. 1995; Walters and Reich 1996, 2000b; Reich et al. 1998a, 1998c) that the shade-tolerant plant strategy would employ the same set of traits thought to be employed phenotypically by plants when growing in darker rather than lighter microhabitats: thinner or less dense leaves, more leaf area deployed per unit plant mass, and lower respiration rates.

The seedling establishment and survival phase is considered the key bottleneck in the life-history dynamics of understory-tolerant trees. As a result, many researchers have focused on the seedling stage as the life-history stage in which shade-tolerance traits are of greatest importance and selective pressures are greatest. We rely on classifications of shade tolerance by authors, often observational and anecdotal but sometimes based on measures of light microhabitat distributions (Lusk and Reich 2000) or survival responses to low light (Pacala et al. 1994; Walters and Reich 1996).

Traits of Taxa Arrayed along Shade-Tolerance Continuum

In a review of traits related to shade tolerance, Walters and Reich (1999) assessed a number of long-held hypotheses using data for seedlings of broadleaf evergreen tropical and temperate deciduous woody taxa. Shade tolerance was defined by

Table 1

Different Kinds of Functional Groupings

| Basis	Trait (examples)
Qualitative, discrete trait	Dicot/monocot, woody/not, N-fixer/not, C3/C4, conifer/angiosperm
Relative value of quantitative, continuous trait	SLA, A_{max}, leaf life span, height, seed mass, hydraulic conductance
Quantitative, suite of continuous traits	Leaf-trait syndrome, Corner's rule syndrome
Qualitative or quantitative; integrated response	Shade tolerance, drought tolerance, C-S-R scheme, PFTs for prediction
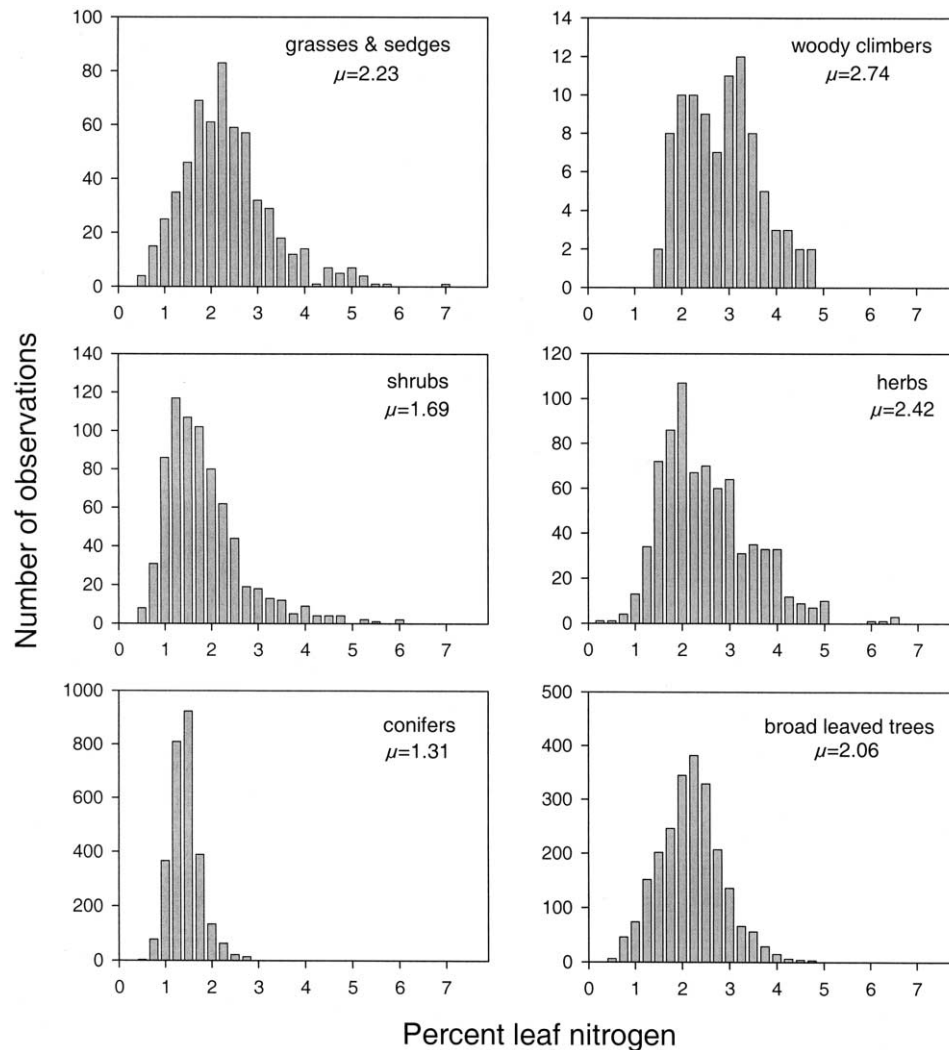
Fig. 4 Frequency distribution of % leaf N among functional groups for plants grouped in evergreen conifer trees and five angiosperm groups: broad-leaved trees, shrubs, woody climbers, herbs, and grasses and sedges. From a literature compendium (J. Oleksyn and P. Reich, unpublished data).

researchers as the ability to survive in deep shade, and species were sorted into three tolerance classes. Traits were measured in conditions typical of closed forest understory (0%–4% of open-sky light) and tree-fall gap light environments (4%–12% of open-sky light), and all contrasts were made for comparable light environments. Among others, the following hypotheses were assessed: (1) shade-tolerant species would have low light-saturated photosynthetic rates but as a trade-off have higher photosynthetic carbon gain in deep shade than intolerants due to higher quantum yield and/or lower light compensation point; (2) shade-tolerant species would have thinner (or less dense) leaves (higher SLA) than intolerants to ensure greater light interception per gram leaf; (3) shade-tolerant species would have whole-plant biomass distribution that enhanced leaf area per gram plant (i.e., a high leaf area ratio [LAR]) and also to enhance light interception; and (4) shade-tolerant taxa would have traits that maximized resource retention, such as low respiration rates and extended leaf longevity. Although

the study did not expressly examine it, a shade-tolerant strategy may also be predicted to include both the capacity to take advantage of sunflecks through, for example, rapid induction of photosynthesis (Pearcy et al. 1994) and limited investment in mechanisms of xanthophyll-mediated energy dissipation.

What does the evidence show? Although as expected, the tolerant species had lower light-saturated net photosynthetic rates (especially on a mass basis) than the other two groups (Walters and Reich 1999; subset of data shown in table 2), this was not associated with a trade-off that led to traits that enhance carbon gain in low light. Neither the quantum yield nor the light compensation point differed significantly between tolerant, intermediate, and intolerant groups in either the tropical or temperate taxa (table 2). Hence, there is no evidence that shade-tolerant species actually gain more energy than intolerants via photosynthesis in either low or very low light conditions.

Another older assumption still common among ecologists

Table 2

Summary of Mean Values of Leaf and Whole-Plant Traits for Seedlings Grown at 0%–4% of Full Light for Numerous Tree Species Characterized as Intolerant and Tolerant in Tropical Evergreen and Temperate Deciduous Biomes

	Tropical evergreen		Winter deciduous	
	Intolerant	Tolerant	Intolerant	Tolerant
LCP (μmol m^{-2} s^{-1})	5.4 a	6.6 a	10.7 z	11.5 z
A$_{max}$ (nmol g^{-1} s^{-1})	178 a	78 b	153 z	118 y
R$_d$-leaf (nmol g^{-1} s^{-1})	14.8 a	6.7 b	20.2 z	8.5 y
SLA (cm^2 g^{-1})	52.5	26.1	52.3 z	37.5 y
LMR (g g^{-1})	0.48 a	0.49 a	0.56	0.35
LAR (cm^2 g^{-1})	23.9 a	14.1 b	33.5 a	13.7 b
Leaf life span (mo)	8	28	na	na
RGR (mg g^{-1} d^{-1})	10.3 a	5.3 b	14.7 z	8.7 y

Note. The intermediate tolerance group is omitted. Values at 4%–12% light are also not shown here but indicate similar differences among intolerants and tolerants for each biome as those shown at 0%–4% light. Contrast between tolerance groups shown for each biome separately; means without a common letter within a row are significantly different ($P < 0.05$). LCP, light compensation point; A$_{max}$, net photosynthetic capacity; R$_d$-leaf, leaf respiration; SLA, specific leaf area; LMR, leaf mass ratio (total leaf mass/whole-plant mass); LAR, leaf area ratio (total leaf area/whole-plant mass); RGR, relative growth rate. From a literature compendium, Walters and Reich (1999).

unfamiliar with the subfield is that leaves of shade-tolerant taxa have higher SLA than those that are less tolerant. This pattern would match the idea that all plants phenotypically develop higher SLA when grown in increased shade. These ideas about genotypic and phenotypic light responses arose from the notion that producing a greater surface area per gram leaf should lead to greater light interception and hence carbon gain, and therefore should be advantageous and selected for in increasingly shaded conditions. Although it has been clearly demonstrated in numerous studies that almost all taxa typically produce leaves of higher SLA when grown in deeper shade, the evidence does not support the idea that tolerant species also have higher SLA leaves than intolerants. In fact, the opposite is true: shade-tolerant species have low SLA leaves (table 2; Veneklaas and Poorter 1998).

At the whole-plant scale, it has been presumed that shade-tolerant species have greater leaf area display per gram plant (i.e., to increase light interception) than intolerants, due to both greater SLA (refuted above) and a higher fraction of whole-plant biomass distributed to foliage. The evidence also fails to support the latter idea (table 2). The data show either similar leaf mass fraction for tolerants as intolerants (tropical evergreens; Walters and Reich 1999) or the opposite of the hypothesis: lower LMR for tolerants than intolerants (tropical evergreens [Veneklaas and Poorter 1998], temperate deciduous [Walters and Reich 1999]). Of interest, even the phenotypic response of taxa to increasing shade (i.e., the paradigm that any genotype will shift biomass allocation toward leaves when growing in deep shade) has recently been shown to be overemphasized because of the failure of researchers to account for plant size in such comparisons (Reich 2002). By default, if shade-tolerant plants have neither a greater fraction of their

biomass in foliage nor a greater surface area per gram leaf, it is impossible for them to have a greater leaf area display per gram plant (LAR), which refutes this hypothesis as well (table 2). However, differences in canopy architecture among species along shade-tolerance gradients could lead to greater interception per unit leaf area. Given the set of traits associated with shade tolerance, it should not be surprising (but would be to most ecologists) that tolerant species have on average lower growth rates than intolerant species even when growing at comparable light levels in deep shade (table 2).

In contrast to the lack of support for the hypothesized higher carbon uptake efficiency at low light and higher potential light interception efficiency (i.e., higher LAR) of shade-tolerant species, their hypothesized tendency to conserve resources has been supported. On average, shade-tolerant species have lower leaf, stem, and root respiration rates than intolerants under comparable conditions both in experiments (Walters et al. 1993; Reich et al. 1998c; Walters and Reich 2000b; Valladares et al. 2000; Kaelke et al. 2001) and in natural settings (Lusk and Reich 2000). For instance, when shade tolerance is defined by either the average or the lowest light levels at which a taxa is distributed in a forest understory, those found in deeper shade have lower respiration rates (fig. 5; Lusk and Reich 2000). After exposure to experimental gap treatments, tropical understory plants, including species from the genus *Barringtonia*, which is commonly found in shaded understory environments, exhibited higher levels of photoinhibition and were slower to recover than species that usually inhabit high solar radiation environments (Lovelock et al. 1994). The results indicate that the shade-tolerant understory species have a decreased capacity to dissipate excess light energy, presumably through xanthophyll-mediated processes.

Within functional groups not markedly constrained in their leaf lifetime, shade-tolerant species have longer leaf life span than sympatric intolerants, including for temperate evergreen conifers (Lusk and Contreras 1999), moist tropical forests (Coley 1988), and tropical rain forest species (Williams et al. 1989; Reich et al. 2003b). It has also been hypothesized that shade-tolerant species maintain higher carbohydrate concentrations (another resource-conservation strategy) than intolerants, but the limited evidence to assess this idea is mixed (Kobe 1997; Kruger and Reich 1997; DeLucia et al. 1998; Kaelke et al. 2001).

Although many of the comparisons above compare distantly related taxa, the similarity of patterns in temperate and tropical woody systems suggests they are common. Unfortunately, there are few comprehensive studies that examine variation in shade tolerance among species within genera or populations within species. Among those that do, support is consistent but somewhat variable. For instance, in studies of six to seven sympatric shrub species in the *Piper* genera, the more shade-tolerant species had longer leaf life span, lower %N, lower SLA (at comparable light levels), and lower A$_{max}$ than the intolerants (Chazdon and Field 1987; Williams et al. 1989), which indicates that related taxa varying in shade tolerance align themselves along the more general multidimensional leaf trade-off surface characterized by Reich et al. (1997). However, in a study of 16 *Psychotria* species, Valladares et al. (2000) found that the shade-tolerant species had on average only slightly longer leaf lifespan and lower A$_{max}$, R$_d$, and relative growth rate (RGR)
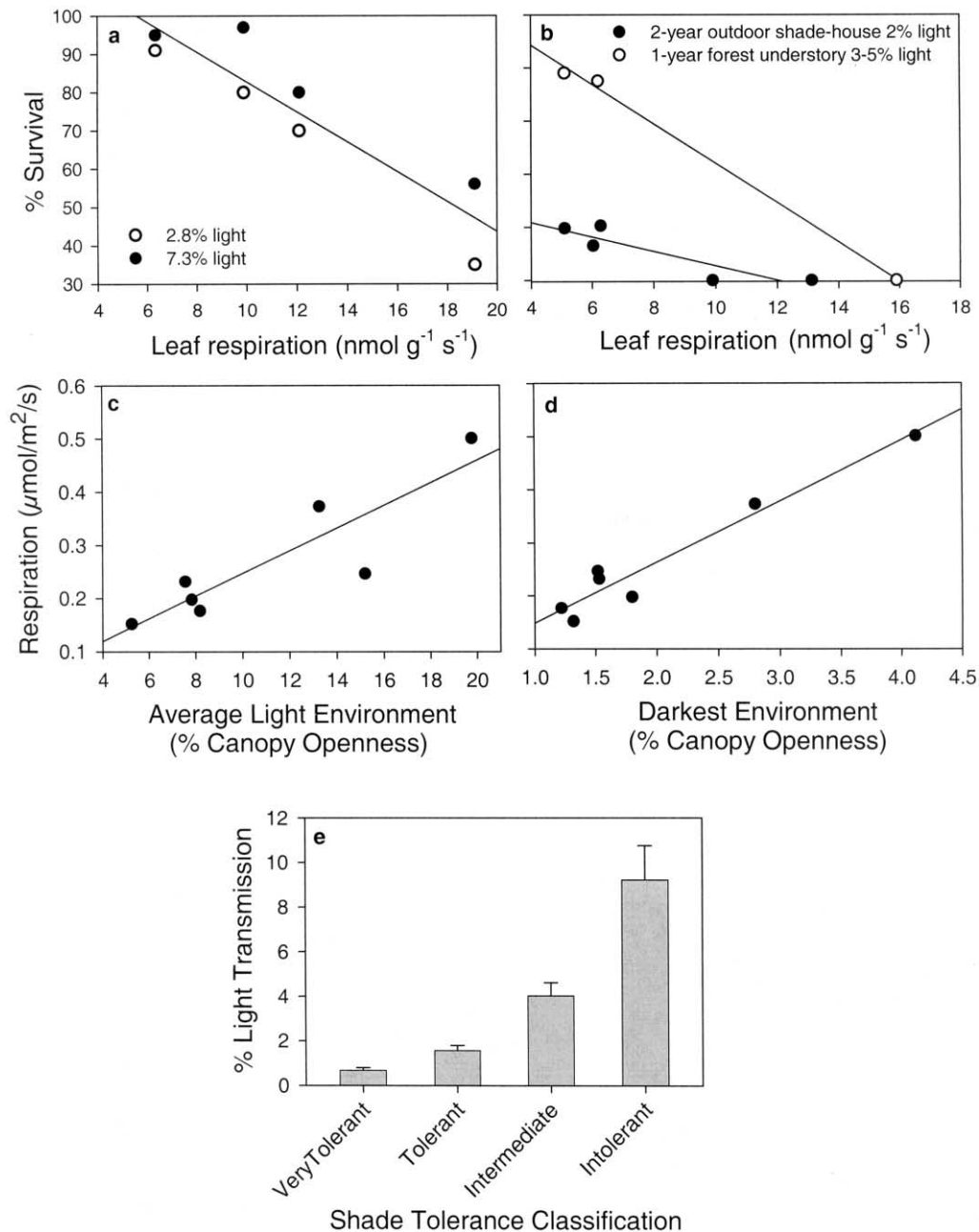
Fig. 5 *a*, *b*, Survival at low light versus leaf respiration (from three experiments, Walters and Reich 1996, 2000*a*, 2000*b* and Kaelke et al. 2001) for seedlings of six woody broadleaved species in temperate North America. *a*, First-year survival in a greenhouse experiment of four species at both 2.8% and 7.3% of full light in relation to average respiration rates at these light levels (Walters and Reich 2000*a*, 2000*b*). *b*, First-year survival and respiration in a field experiment in forest understory at 3%–5% of full light (Kaelke et al. 2001) and 2-yr survivorship at 2% light in an outdoor shade-house experiment (Walters and Reich 1996) in relation to respiration rates measured in complementary experiments (Reich et al. 1998; Lusk and Reich 2000). *c*, *d*, Leaf dark respiration in relation to the median and the lowest light levels in which species were found in a native forest understory (from Lusk and Reich 2000) for seven such species (including four from the upper panels). *e*, Percentage light transmission by stands of forest trees differing in shade tolerance (data from Canham and Burbank 1994 and J. Oleksyn and P. Reich, unpublished data) for a total of 23 species of temperate trees in North America and Europe.

than the gap-demanding species, in contrast with much larger variation in these traits among species within each group.

As shown above, the traits of shade-tolerant species do not support hypotheses and optimality theory that suggest that shade-tolerant species should be characterized by high SLA

leaves, high allocation of biomass to leaves rather than roots, and high LAR. In fact, shade-tolerant plants have the opposite set of traits when measured in common environments (Walters and Reich 1999). Although this may seem counterintuitive at first thought, it makes sense when viewed from a whole-plant,

multiple-trait "syndrome" standpoint. A whole-plant shade-tolerance strategy involves maintenance of captured resources rather than high resource gain, so traits known to promote resource conservation should be selected for. These include low mass-based respiration rates and extended leaf life span, which are coordinated with low %N, low SLA, and low mass-based A_{max} in multidimensional trait space (Reich et al. 1997, 1998b; Wright et al. 2001, 2002).

Relationship of Shade-Tolerance Traits to Fitness Components

Do the seedling traits identified as common to shade-tolerant species enhance their fitness? In addition to vegetative physiology and morphology (table 1), seed characteristics have long been considered relevant to shade tolerance. Survivorship data show that seed resources "buy time" in terms of extended survival for species that may or may not otherwise be physiologically tolerant of deep shade (Walters and Reich 1996, 2000a). Once seed resources are exhausted, however, whole-plant carbon balance (measured by whole-plant RGR) is directly related to the balance between total carbon costs (largely respiration of leaves, stems, and roots, plus tissue turnover) and total carbon uptake from photosynthesis (Saverimuttu and Westoby 1996; Walters and Reich 2000b). Overall, seed size may be modestly related to shade tolerance (Grubb and Metcalfe 1996) since seed size is strongly related to seedling life span during cotyledon phase but not at all related at true leaf stage (Westoby et al. 2002).

What is the role of vegetative physiology in relation to growth and survival in shade? The preponderance of evidence suggests that tolerant species do not consistently have greater carbon balances or seedling growth rates in low light than do intolerant species (Walters et al. 1993; Kitajima 1994; Pacala et al. 1994; Kobe et al. 1995; Walters and Reich 1996, 1999; Reich et al. 1998a). Instead, there appears to be a trade-off between carbon gain (and growth) potential and low-light survival (Walters et al. 1993; Kitajima 1994; Pacala et al. 1994; Kobe et al. 1995; Walters and Reich 2000a). Hence, shade tolerance is associated with biomass and energy conservation traits that maximize survival (fig. 5) but that can only occur at a trade-off with traits that enhance growth potential (Coley 1988; Walters et al. 1993; Kitajima 1994; Kobe 1997). As part of this trade-off, tolerant species always have lower carbon gain and growth potential at high light than intolerants and never win the early race for canopy dominance under such conditions (Walters et al. 1993; Kitajima 1994; Kruger and Reich 1997).

The trade-off between carbon gain potential at high light and survival at low light probably results (Walters and Reich 1999) from selection in low light for energy conservation traits and against unused carbon gain capacity. For example, the high growth potentials of intolerant species require high whole-plant respiration rates (Walters et al. 1993; Reich et al. 1998c; Tjoelker et al. 1999), a characteristic likely to be disadvantageous in very low light (fig. 5) because a given amount of energy (i.e., respiration) consumes a greater proportion of total growth or storage when carbon gain and growth rates are low. Similarly, there is nothing to be gained by having rapid leaf turnover if new leaves in higher light environments on a shoot are not required in order to maintain a given level of light interception in the face of self and neighbor shading. Therefore, in shaded conditions, unrealized carbon gain potential due to severe light limitations should be trimmed by selection for low respiration rates and extended leaf life span.

Additionally, high growth potential in low light might also increase the risk of damage and death. The leaf traits required for high carbon gain and growth potential (e.g., higher N and SLA and lower fiber, tannins, and toughness; Reich et al. 1991; Lambers and Poorter 1992) also increase the probability of leaf loss to herbivores and/or mechanical damage (Coley 1988; Braker and Chazdon 1993; Edenius et al. 1993). In high light, intolerant species can outgrow tolerant species despite incurring greater rates of herbivory (Coley 1988). In contrast, in low light in which growth and carbon gain are strongly constrained, greater herbivory rates on intolerant species might lead to lower growth and survival for intolerant than for tolerant species. Hence, selection for protection from herbivores (and mechanical damage) should trim excess growth capacity in shade because these traits, such as higher structural carbon and lower nitrogen, should be reflected in lower SLA and A_{max} (and hence lower respiration and tissue turnover).

In summary, there is evidence demonstrating a syndrome of traits associated with shade tolerance. Although lower tissue and whole-plant respiration rates appear to be one of the critical traits associated with shade adaptation (fig. 5), they are part of a larger resource-conservation syndrome that also includes low A_{max}, low tissue N, low SLA, and a low distribution of biomass to leaves as well as traits that enhance storage and protection from herbivores, pathogens, and mechanical damage. Functional variability vis-à-vis light gradients seems to represent a case of selection of multiple traits that align along a multidimensional trade-off surface that has in all likelihood arisen by convergent selection for perennial plants in distinct floras and biogeographic realms. Additionally, as adults, shade-tolerant species, due to physiological shade tolerance of their leaves, carry large canopies that densely shade the understory (Reich et al. 1992; Canham et al. 1994; fig. 5) to levels that intolerant species cannot survive while their own offspring can.

Although it is likely that the trait differences demonstrated among tolerant versus intolerant species resulted from selection, the evidence is indirect. Unfortunately, to our knowledge, there is a paucity of data that directly examines genetic variation in plant functional traits among individuals within populations that can be related to variation in irradiance (Nicotra et al. 1997), and no studies of phenotypic selection in shade were listed in the review by Arntz and Delph (2001) of evidence for the evolution of leaf physiological traits.

Plant Traits Related to Water Availability

Leaf traits. Broad differences in leaf traits of species from low- and high-rainfall habitats were recognized early on by plant ecologists (Schimper 1903; Maximov 1929; Shields 1950). Even within species, populations in drier environments have been shown to have greater leaf-level water use efficiency (Comstock and Ehlreinger 1992; Zhang et al. 1993). In general, many perennial species from arid regions have thick leaves with thick cuticles and small, thick-walled cells, features that
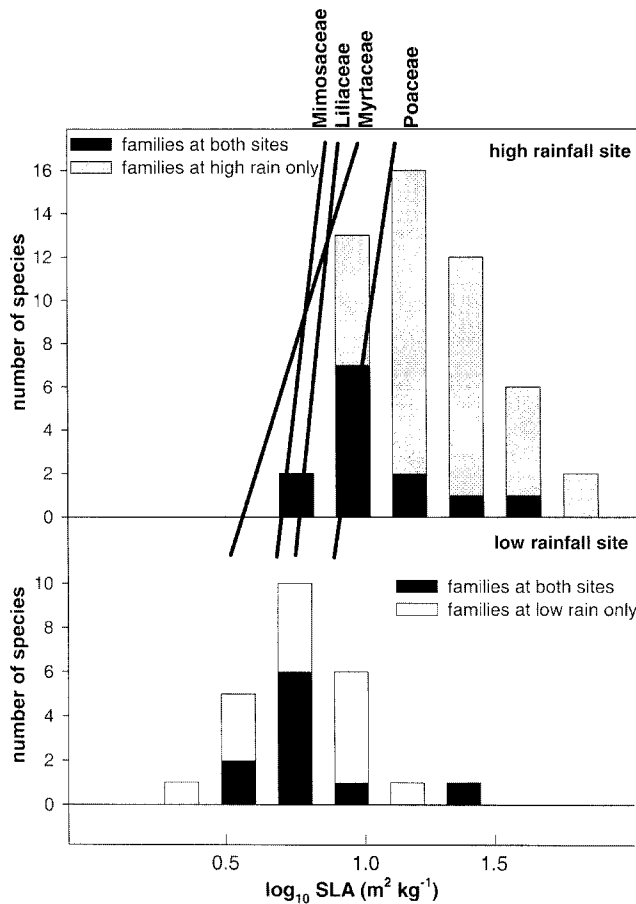
Fig. 6 Frequency distribution of specific leaf area ($m^2\ kg^{-1}$) for species at a low-rainfall and a high-rainfall site in New South Wales, Australia. Data also show differences for families present at only one site or at both and additionally show differences across sites within four families. From Westoby et al. (1998).

are thought to be adaptations to water stress (Maximov 1929; Cunningham et al. 1999; Niinemets 2001). These features contribute to the well-documented trend of generally lower SLA of such species (Specht and Specht 1989; Cunningham et al. 1999; Fonseca et al. 2000; fig. 6).

The typically low SLA of species growing in dry areas (and on nutrient-poor soils) has been associated with an increased leaf life span in habitats where rapid growth is not possible and slow tissue turnover is therefore favored (Grime 1977; Grubb 1986; Reich et al. 1992, 1999; Chapin et al. 1993; Turner 1994). However, recent evidence suggests that relationship between SLA and leaf life span may differ across rainfall gradients. The first evidence of this was presented by Reich et al. (1999), who found that species at the driest of six sites in the Americas (New Mexico) had shorter leaf life span and higher leaf N at a given SLA. A series of studies looking at leaf traits of woody perennials in southeastern Australia (Wright et al. 2001, 2002, 2003) generalized this result across a large number of species and identified links between a number of leaf traits that apparently underlie this pattern.

Leaf traits of ca. 80 species were characterized from four sites: a relatively fertile and an infertile site within each of two rainfall zones (annual rainfall 390 mm and 1200 mm), all sites having similar mean annual temperature. Similar to results from previous multispecies comparisons (Reich et al. 1999), SLA, mass-based A_{max} (A_{mass}), R_{d-mass}, leaf N_{mass}, and P_{mass} tended to be positively correlated with common slopes fitted across sites (Wright et al. 2001; fig. 1). But species from drier sites differed in several important respects (fig. 2). They had (1) higher N and P (but lower leaf life span) at a given SLA, (2) lower A_{max} at a given leaf N or P, (3) higher R_{d-mass} at a given SLA or A_{mass}, and (4) lower stomatal conductance to water (G_s) at a given area-based photosynthetic rate, A_{area}.

These trends were interpreted as a water-conservation strategy in species from dry habitats that involves trade-offs between water use efficiency and N use efficiency (Wright et al. 2003). By investing heavily in photosynthetic enzymes, a larger drawdown of internal CO_2 concentration was achieved (i.e., c_i [intercellular CO_2 concentration] was lower) and a given photosynthetic rate was possible at a lower stomatal conductance to water or CO_2. However, water use during active photosynthesis was similar for species from the drier and wetter habitats because the savings achieved via lower c_i were counterbalanced by the lower leaf-to-air vapor pressure difference (VPD) at drier sites, transpiration being (largely) a product of conductance and VPD. Thus, the apparent benefit of the strategy was that dry-site species reduced water loss at a given A_{area} down to similar levels as species from higher humidity habitats. The cost of high leaf N was reflected in higher R_{d-mass} (at comparable temperatures) and, presumably, in additional costs incurred by N acquisition and in increased herbivory risk.

It is as yet unproven to what extent these findings generalize to other aridity gradients, but there is abundant indirect evidence that they may. High N_{area} of low-rainfall perennials has been commonly reported or is implied by their typically low SLA in combination with their similar or sometimes higher N_{mass} (Killingbeck and Whitford 1996; Cunningham et al. 1999). High N_{area} may also maximize use of the typically high irradiance in such places (Cunningham et al. 1999; Roderick et al. 2000; Niinemets 2001). Wright et al. (2001) found lower c_i at a given stomatal conductance in low-rainfall species and related this back to their high N_{area}. Consistent with this are findings from smaller data sets demonstrating a negative relationship between N_{area} and c_i (implied from the carbon isotope ratio of leaf tissue) presented by Hanba et al. (1999; temperate forest trees in Japan) and Anderson et al. (1996; 14 *Eucalyptus* species grown in a common garden). In addition, data from Wright et al. (2001) combined with those from Reich et al. (1997) show c_i decreasing with increasing N_{area} at a given G_s ($P < 0.001$, $n = 210$; CO_2 drawdown estimated from A_{area} and G_s; data not shown), which suggests the existence of a broadscale pattern. In several studies, carbon isotope discrimination has been determined in species occurring along aridity gradients, which gives additional insight into trends in c_i with precipitation. Stewart et al. (1995) studied 348 species from 12 Australian plant communities; their results imply a linear trend of decreasing c_i with decreasing rainfall. Within *Eucalyptus* species only, results from Miller et al. (2001) imply a similar trend in terms of the cross-species mean. By contrast, Schulze et al. (1998) found decreasing c_i at the driest end of the gradient only (multiple genera and growth forms studied

along the same broad transect [the Northern Australian Tropical Transect] as used by Miller et al. [2001]), as did Warren et al. (2001) in a literature review of carbon discrimination in conifers. Miller et al. (2001) also found that c_i was lower in typically xeric species than in co-occurring typically mesic species; however, within individual species, c_i dropped with rainfall within only five of 13 species.

Research examining genotypic differences in carbon and water vapor exchange traits among individuals within populations (Kalisz and Teeri 1986; Geber and Dawson 1990; Donovan and Ehleringer 1994; Dudley 1996b, 1997) and studies of phenotypic selection in relation to site moisture conditions (Lechowicz and Blais 1988; Dudley 1996a) are more abundant than for any other factor. A variety of traits have been shown to differ among individuals occupying drier versus wetter microhabitats with heritability almost always demonstrated but varying widely (Arntz and Delph 2001). Selection on water use efficiency has received considerable attention. Such studies have relied on either gas exchange or isotopic approaches and have generally shown that individuals vary in water use efficiency (or some other trait) and that selection on the trait in question occurs. However, in most such studies, there is in fact no way of knowing whether the trait that is hypothetically selected on is merely correlated with other tissue or whole-plant attributes that are actually responsible for fitness because none of these studies have been able to evaluate the determinants of fitness from a time-integrated and whole-plant perspective.

Hydraulic conductance and resistance to cavitation. A general trade-off between efficiency and safety in the hydraulic transport of water is becoming increasingly well established across diverse taxa (Sperry et al. 1993; Sperry 1995; Sobrado 1997; Hacke et al. 2001). Interspecific competition and water stress are thought to be critical selection agents that influence the form and function of the water transport systems of plants, which results in this efficiency-safety trade-off. Hydraulic conductance is associated with photosynthesis in rainforest species (Brodribb and Feild 2000) and in other plant systems as well (Cochard et al. 1997; Linton et al. 1998; Comstock 2000; Tausend et al. 2000), which indicates coordination between the photosynthetic apparatus and hydraulic architecture. This coupling diminishes, however, in stressful environments that experience large variation in diurnal water potential (T. J. Brodribb, personal communication). Hydraulic conductance is also correlated with plant growth (Shumway et al. 1993; Vander Willigen and Pammenter 1998). Under optimal environmental conditions in highly competitive systems and in the absence of water stress, hydraulic conductance is maximized, presumably to maximize gas exchange and growth. In xeric conditions, survival depends on the ability to withstand extreme xylem tension, which can lead to embolism, loss of xylem function, and ultimately to plant death. Indeed, seedling mortality has been correlated with extensive cavitation (Williams et al. 1997). Under xeric conditions, resistance to cavitation appears to be maximized at the expense of efficiency in water transport.

Among riparian and upland species in the Sonoran Desert, resistance to cavitation corresponded to distribution, providing support for the long-held notion that water stress is an important selective force in shaping xylem function. Upland
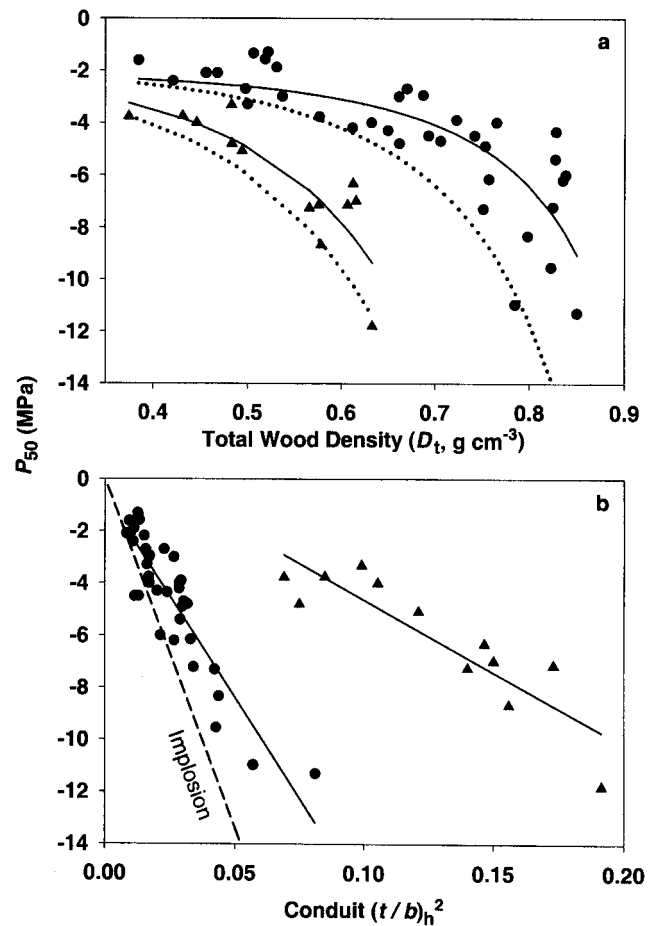

Fig. 7 *a*, Cavitation resistance (P_{50}) versus wood density (D_t) for woody angiosperm (circles) and conifer stems (triangles) from several sites in North America. The dotted lines suggest a boundary below which data are excluded because of conduit implosion. *b*, P_{50} versus the ratio squared $(t/b)_h^2$ of conduit thickness (t) and double-wall span (*b*) for angiosperm vessels (circles) and conifer tracheids (triangles). Crosses and dashed line show the implosion limit based on estimates for angiosperm and conifer species (data extend off scale). Data above the limit indicate a safety factor from implosion. Angiosperm vessels exhibit a lower estimated safety factor than conifer tracheids. From Hacke et al. (2001).

desert species showed significantly greater resistance to cavitation than riparian species, and a weak trade-off was apparent between hydraulic conductance and vulnerability to xylem cavitation (Pockman and Sperry 2000).

Wood density and xylem wall reinforcement has been shown to correlate with cavitation resistance (Hacke et al. 2001). These traits are thought to provide support against implosion by tension in the xylem. These relationships, however, vary between angiosperms and conifers due to contrasting xylem anatomy (fig. 7). In general, for a given wood density, conifers have greater resistance to cavitation but lower maximum conducting efficiency of their xylem. This may cause conifers to be less competitive in optimal environments but may contribute to their success in resource-limited habitats and in achieving massive height growth. New evidence is emerging that the

pore apertures of pit membranes, which form the border between xylem conduits, are also correlated with resistance to cavitation and correspond well to species distributions. For example, riparian species tend to have larger pit membrane apertures than xeric species (U. G. Hacke, personal communication).

Variation among closely related species in leaf form and function (Siso et al. 2001; Corcuera et al. 2002) and xylem structure and hydraulic architecture (Villar-Salvador et al. 1997; Cavender-Bares and Holbrook 2001) have been shown to be related to habitat gradients in water availability. In a study of 17 sympatric oak species in Florida, conductivity (Max. K_s) and whole-shoot transpiration per unit sapwood area increased, while the ratio of sapwood area to leaf area (Huber value) decreased with increasing soil water availability of the species' native habitats (fig. 8a–8d; Cavender-Bares and Holbrook 2001). Maximum hydraulic conductance (Max. K_s) was significantly correlated with radial growth rate (fig. 9a). There was also an increase in xylem embolism in species in wet habitats relative to those from xeric habitats, which gives rise to a trade-off between growth rate and cavitation resistance (fig. 9b).

Sobrado (1997) found in the seasonal tropics that drought deciduous species maximized hydraulic conductivity in the short term at the expense of seasonal occurrence of embolism. Evergreen species had reduced water transport capacity but maintained relatively constant hydraulic conductivity during the wet and dry seasons. A similar trade-off has been shown in temperate systems, which results from increased resistance in evergreen trees to freezing-induced xylem cavitation (Davis et al. 1999).

As mentioned earlier, selection for certain traits may have been strong either within lineages or among environmental gradients or both, and each results in functional variability. As a result, when these data are analyzed using the method of independent contrasts, the significance of the correlations between hydraulic conductance and soil moisture, as well as whole shoot transpiration and soil moisture, actually increase (fig. 8e, 8f). Independent contrasts allow the components of hydraulic properties that are conserved at the lineage level to be factored out. By comparing correlation coefficients between species pairwise trait differences versus the phylogenetic distance between them to a null model (methods described in Cavender-Bares and Wilczek 2003), we found mean vessel diameter and Huber values among oaks to be significantly conserved ($P = 0.02$ and $P = 0.01$, respectively). These aspects of hydraulic architecture are likely to constrain species-level variation in hydraulic conductance to some degree. Thus, interspecific variation in hydraulic conductance appears to covary with habitat despite genetic heritage that leads to conservation of other aspects of hydraulic architecture. This may help explain why both red and white oaks can occupy the same
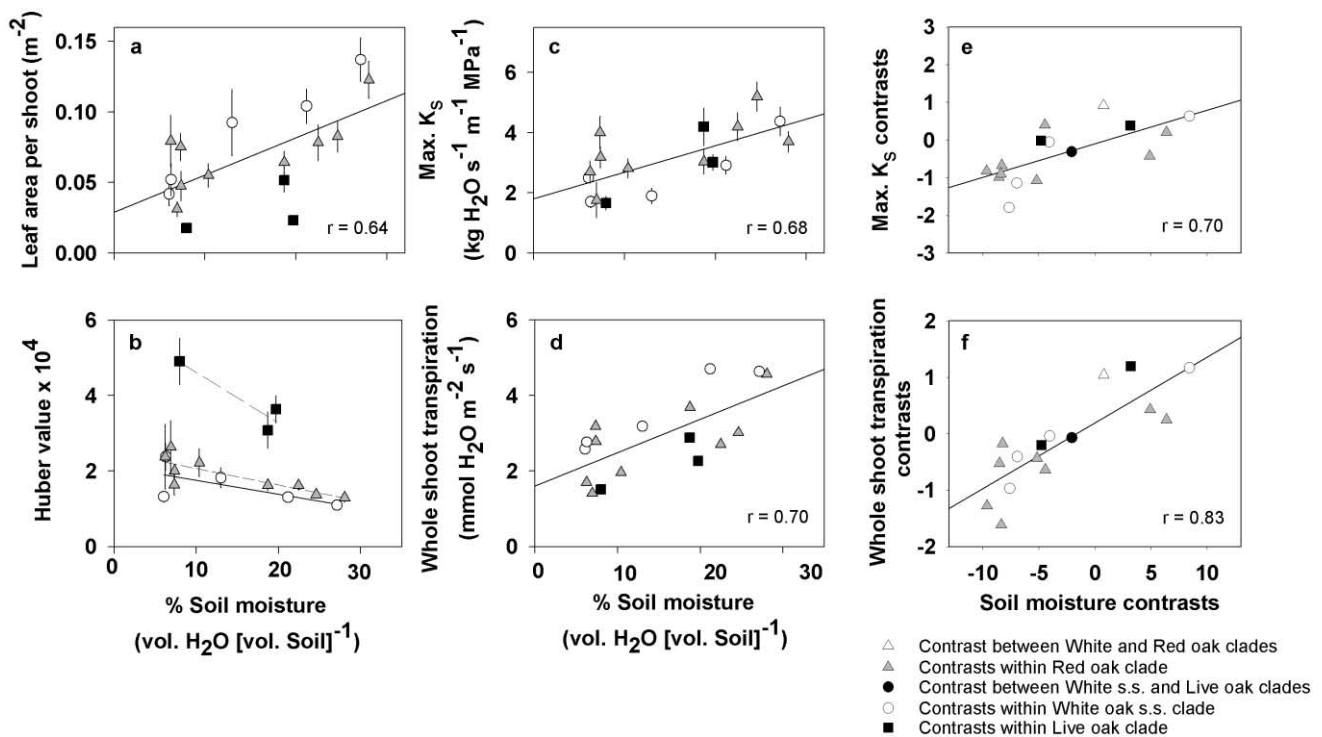

Fig. 8 Mean soil moisture of Florida oak species' habitats in relation to (a) whole-shoot leaf area, (b) Huber value (ratio of sapwood area to supported leaf area), (c) maximum hydraulic conductance per unit sapwood area, and (d) whole-shoot transpiration rate per unit sapwood area. Symbols represent three oak lineages (red oaks, gray triangles; white oaks s.s., white circles; and live oaks, black squares). a, b, d, e, Adapted from Cavender-Bares and Holbrook (2001). e, f, Standardized independent contrasts for Max. K_s (e) and whole-shoot transpiration (f) in relation to soil moisture of species' habitats; contrasts are standardized by branch length distances following methods of Ackerly and Reich (1999). Symbols represent contrasts within or across the three lineages, as indicated.
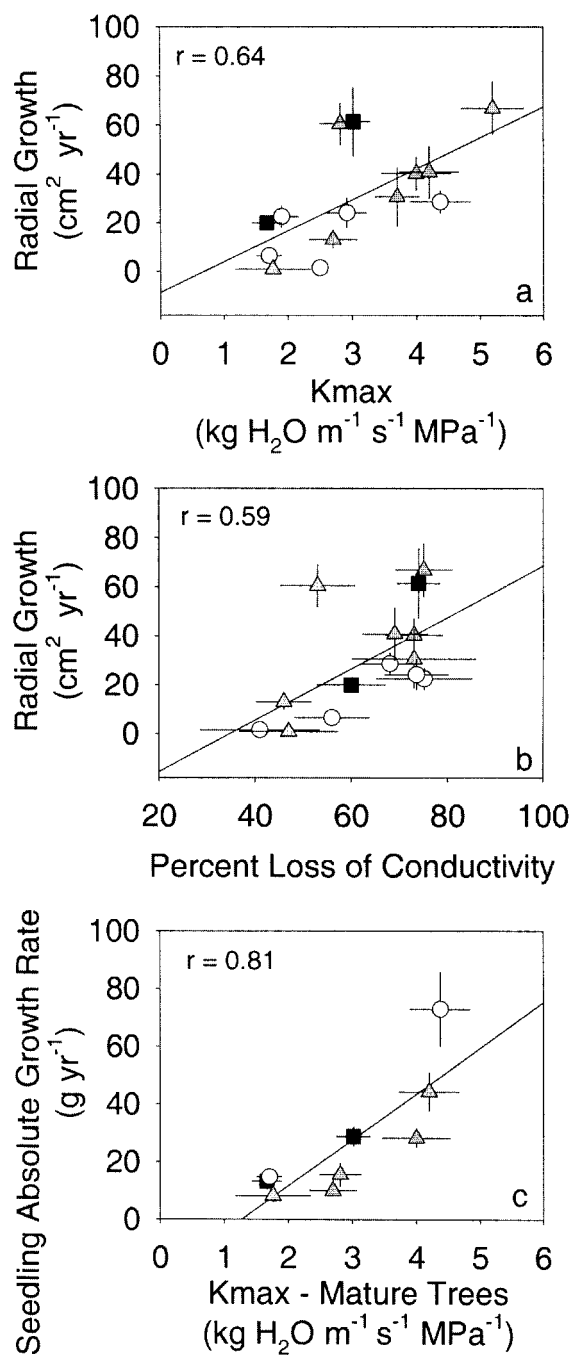
Fig. 9 Species means of mature Florida oak trees for annual radial growth increments (averaged for 10 yr) in relation to (*a*) species means for Max. K$_s$ and (*b*) native embolism (percent loss of conductivity). *c*, Seedling absolute growth rates (biomass after 1 yr of growth in a common garden) in relation to Max. K$_s$ of mature trees. Symbols represent three oak lineages as in fig. 8.

hydraulic properties and the selection forces within species habitats.

An argument can be made that plasticity may also contribute to these trait correlations because they were measured for species across their natural distributions in the field. This is an important consideration in all of the studies discussed here. However, in a common garden, where environmental variation was minimized, J. Cavender-Bares, F. A. Bazzaz, and K. Kitajima (unpublished data) found that the whole-plant transpiration was still highly significantly correlated with soil moisture in habitat of origin. Moreover, absolute growth rate of seedlings grown in a common garden for one year was significantly correlated with maximum hydraulic conductance of mature trees (fig. 9*c*), which indicates that functional traits measured at the species level indicate genetic differentiation rather than merely plastic response to environmental variation.

Plant traits and strategies vis-à-vis nutrient availability. Understanding plant strategies for different nutrient supply regimes involves understanding how traits affect the acquisition, allocation, and loss of a limiting nutrient. Although differences in traits such as SLA or leaf longevity across nutrient gradients have been hypothesized for many years (Beadle 1966; Monk 1966; Chapin 1980), strong evidence regarding relationships between traits and nutrient availability is rare in part due to the greater difficulty of quantifying nutrient availability compared to irradiance or moisture. However, we mention several such studies.

First, Fonseca et al. (2000) found decreasing SLA and leaf width with decreasing soil P content across three levels of soil P (a total of 13 sites) in eastern Australia, which held rainfall constant across P groups. Cunningham et al. (1999) found similar responses using phylogenetically independent contrasts in the same region, and Wright and Westoby (1999) found lower SLA in species from low-P sites when grown with species from high P sites in a common environment. Second, in Minnesota, Craine et al. (2001) measured a few leaf and root traits, such as tissue density, leaf angle, and growth, for 76 species grown under similar conditions and constructed a composite axis from high- to low-tissue-density species. In general, the relative abundance of species along a long-term experimental N supply gradient was associated with their scores on the tissue density axis (fig. 10) such that mean traits (PLA scores) varied markedly with N addition rate. Data that directly examine genetic differences in functional traits across nutrient gradients (other than as part of a multifactor gradient) are extremely scarce, as are studies that assess phenotypic selection across such gradients.

Here we describe the series of traits that are associated with the accumulation and maintenance of biomass in perennial herbaceous plants under low N, based largely on studies on an outwash sand plain in Minnesota (Wedin and Tilman 1990; Craine et al. 2002), and how strategies are likely to have been shaped by competition at low N supply. We choose to emphasize biomass accumulation as a representation of the ability to persist in such resource-poor environments. As opposed to light, species differences in tolerance of low N supply has not been separated from their differences in N acquisition potential, both of which affect competitive outcomes. Although competition for N at low supplies has been demonstrated as being important for assemblage composition (Wedin and Tilman

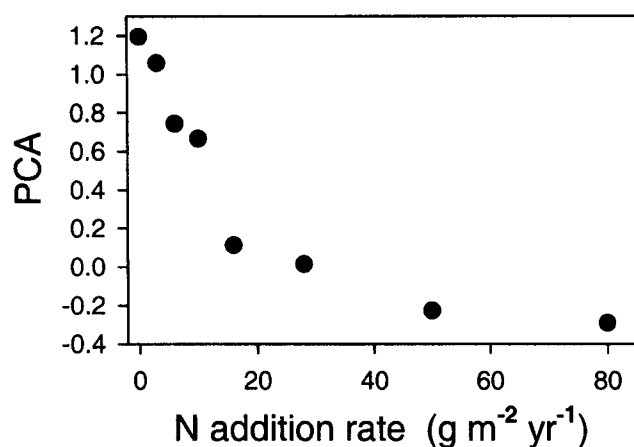habitats even though they differ significantly in various aspects of their wood anatomy. By using independent contrasts, the correlations between hydraulic conductance and soil moisture increase, which provides evidence for a functional link between

Fig. 10 The relationship between a long-term experimental N addition gradient and the mean scores of the species present on a multiple tissue density axis (based on PCA axis scores for the species in a nearby common garden), both in central Minnesota. From Craine et al. (2001).

1993), it still remains to be shown that tolerance for low N supplies in the absence of competition is an important factor for the fitness of plants. We leave open the possibility that this may be important and do not narrowly describe those species that are common at low N supplies as good competitors for N at low N supply as we referred to low-light-tolerant species. As such, we refer to traits that are beneficial at low N supplies as "low-N" traits and the species that possess them as "low-N" species rather than signifying whether the traits are associated with competition or tolerance.

At low N supply, for plants to grow large, they must acquire as much N as possible, allocate it in a manner that maximizes biomass accumulation, and lose as little as possible. A root in soil that has low N supply generally can take up N faster than it is supplied, and plant roots cannot increase uptake by increasing specific rates of uptake or surface area (Smethurst and Comerford 1993; Leadley et al. 1997). As such, at low N supply, the functional unit of uptake is root length. Producing length efficiently means producing roots that have low diameter, low tissue density, and low N_{mass}.

For a given amount of N acquired, two keys to the accumulation of high biomass are extended tissue longevity and high C : N ratios (Chapin 1980). Extended tissue longevity decreases losses and allows biomass to accumulate despite moderate or low productivity (Aerts 1990; Reich et al. 1992). High C : N ratios maximize the amount of biomass per unit of N. Short-term studies that examine relative production rates show species with high RGR as seedlings produce more biomass (Cornelissen et al. 1996; Aerts and Chapin 2000). However, low-RGR species accumulate more biomass long term (over 3–5 yr or more for herbaceous species; Tilman 1988; Craine et al. 2002). To produce long-lived leaves, tissue density should be high and leaves must have low nutrient concentrations and low photosynthetic rates (all relative to their local flora) in order to be an adaptive strategy (Reich et al. 1997), and these patterns are true for herbaceous perennials (Craine et al. 2002). Although data are still limited, the relationships

among root traits appear to parallel those of the leaves. Taxa successful at low N have long-lived roots (Weaver and Zink 1946; Reich et al. 2001; Craine et al. 2002) that have high tissue density, high structural fractions (Hendricks et al. 2000), and low N concentrations (Reich et al. 2001; Craine et al. 2002). Low-N species maintained greater biomass than high-N species more by producing tissues with lower N concentrations and greater longevity (Ryser and Urbas 2000; Craine et al. 2002), rather than by acquiring more N per unit tissue. Moreover, plants that produce high biomass in low N availability conditions do not necessarily allocate their biomass above- and belowground differently (Aerts and Chapin 2000; Reich 2002). Instead, in vegetation where the ratio of root longevity to leaf longevity is relatively high, biomass accumulates disproportionately belowground. In grasslands in Minnesota, the high fraction of biomass that is belowground in low-N species appears to be more of a consequence of relative greater longevity of roots than leaves, which allows more biomass to accumulate belowground than aboveground (Craine et al. 2002) and more root biomass to accumulate in grasslands than forests, despite lower root production (Reich et al. 2001).

It is well known that plant species can affect the N cycle (Wedin and Tilman 1990), although the full sets of traits associated with plant-mediated changes in ecosystem N supply and the mechanisms by which it happens are still under investigation. For example, for 28 non-N_2-fixing grassland species grown in monoculture for five years on sandy soils, the primary axis of variation among species was associated with the degree to which species increased microbial immobilization and hence decreased net N mineralization (Craine et al. 2002), the portion of the total internal ecosystem N supply that becomes available to plants or is more likely to be lost. The species that decreased mineralization the most had the low-N tolerance suite of linked ecophysiological and whole-plant traits. They produced and maintained large amounts of biomass, had tough, long-lived leaves and roots with low metabolic rates, high C : N ratios, and high root : shoot ratios. Some of these differences in traits and their effects on N cycling were similar in nearby comparisons of naturally established woody patches versus patches of these same herbaceous species: oaks had lower C : N ratios, shorter-lived roots, a lower root : shoot ratio, a lower root standing biomass, and higher N detrital production and net N mineralization rates (Reich et al. 2001).

Long-term competition for nutrients requires that competitively superior plants be able to lower the availability of nutrients while still growing at this low availability (Tilman 1988). Plants can lower the availability by either decreasing the supply (e.g., increasing microbial immobilization), preempting the supply from reaching competitors, or both. Plants with high litter C : N increase microbial immobilization and therefore lower net mineralization. The high C : N, low mineralization suite of traits has been linked to lower soil solution concentrations and long-term competitive superiority for nutrients when they are at low supply (Wedin and Tilman 1993). However, competition for nutrients is likely to involve supply preemption as well as or instead of supply reduction. Preempting the supply from reaching the roots of other plants means having more root length than competitors. If compe-

tition for nutrients is symmetric, the higher the fraction of root length that an individual has, the higher the fraction of the N supply that it preempts, and therefore the higher the fraction of the N supply that it acquires. In that sense, although resource economics can constrain production, the additional root length production will always lead to greater N acquisition in the face of competition. Consequently, competition for N at low supplies should select for plants with thin roots that live a long time, and with high $C : N$ ratios to allow production of more roots for a given amount of N.

The low-N strategy discussed here corresponds generally to strategies and trait relationships discussed previously (Grime 1977; Chapin 1980; Berendse et al. 1987; Tilman 1988; Poorter et al. 1990; Tilman and Wedin 1991; Grime et al. 1997; Reich et al. 1997; Aerts and Chapin 2000). It incorporates the toughness, longevity, and low rates of activity first emphasized by Grime (1977) and Chapin (1980) and quantified by Coley (1988) and Reich et al. (1991, 1992, 1997) while also incorporating the feedbacks to N availability of Wedin and Tilman (1990). For example, species that have low nutrient concentrations were found by Grime et al. (1997) to better sustain yield under limiting supplies of nutrients, and they had long leaf longevity and low decomposition rates.

Temperature gradients. There have been many ecophysiological studies examining genetic variation in functional traits among populations from different temperature origins but few with large sample sizes. Those that exist do suggest some commonalities and some differences with syndromes of plants adapted to resources such as nutrients, light, and water. For example, common garden studies of 26 and 18 populations of *Alnus sinuata* and *Betula papyrifera*, respectively, suggest that genetic differences in A_{max} were inversely related to growing season length, and thus leaf life span, in these deciduous tree species (Benowicz et al. 2000), which is consistent with the broad convergent patterns found among species and biomes (Reich et al. 1997, 1999).

In their native settings, populations of pines and spruces in northern Europe that live in increasingly cold habitats are characterized by longer needle life span, shorter and more scleromorphic needles, smaller seeds, lower growth rates (fig. 11), and lower needle N concentrations (Langlet 1936; Reich et al. 1996; Oleksyn et al. 2003). These are all traits associated with the resource-conservation strategy in general and in particular for low nutrient supply. In addition to temperature, colder climates, including those in northern Europe, are generally characterized by lower nutrient and moisture availability, so it is impossible to deduce separately the role of temperature from those of the resources per se.

When grown in common gardens, pine and spruce populations originating from colder environments are characterized by sets of traits that ostensibly improve the ability to obtain and conserve nutrients and maintain quasi-homeostatic metabolic rates (Reich et al. 1996; Oleksyn et al. 1998), all deemed important in the low temperature and low nutrient supply rates of such native habitats. These include higher tissue nutrient concentrations under common garden conditions, which play a role in the maintenance of higher R_d at any given temperature and are important hypothetically in the maintenance of sufficiently high R_d in cold temperatures (fig. 11). Cold-origin populations in common gardens also have lower plant growth rate (Oleksyn et al. 1992, 2000a, 2001), higher biomass allocation to roots (Oleksyn et al. 1992, 1998, 1999), and lower mean nonstructural needle carbohydrate concentrations (Oleksyn et al. 2000b; Vucetich et al. 2000). Additionally, populations from colder habitats appear to retranslocate a greater fraction of N and P from senescing tissues (Oleksyn et al. 2003), which conserves nutrients. Studies at common garden sites indicated that nutrient resorption is under partial genetic control (Oleksyn et al. 2003) and that this potentially adaptive strategy may contribute to higher nutrient conservation in plants from cold habitats. Enhanced resorption of N and P from senescing needles of northern populations has perhaps evolved as a genetic adaptation to low rates of organic matter decomposition and availability of nutrients observed to occur at colder soil temperatures (Chapin 1987; Heal and Block 1987; Oleksyn et al. 2003). Most of the nutrient conservation strategies listed above, together with higher cold hardiness of high-latitude populations of Scots pine (Repo et al. 2001), can increase their survival success in nutrient-poor soils and in cold environments. The evidence of that can be seen in recently published survival data from the most comprehensive Scots pine provenance experiment series established in the mid-1970s in Russia (Shutyaev and Giertych 2000).

A General Theory or Primary Strategy of Functional Variation?

Evidence for a General Theory of Functional Strategies

As described above, correlated leaf traits such as leaf life span, SLA, leaf N, leaf diffusive conductance, A_{max}, and R_d form a fundamental spectrum of variation among plant species (Field and Mooney 1986; Reich et al. 1991, 1992, 1997, 1998b, 1999; Mulkey et al. 1995; Diemer 1998a, 1998b; Eamus et al. 1999; Niinemets 1999; Ryser and Urbas 2000). At one end of the spectrum, species (typically characteristic of high-resource habitats or the high-metabolism strategy) can be characterized as having fast tissue turnover and high potential for resource capture and rapid short-term growth, whereas at the other end of the spectrum, species have slower tissue turnover and traits that enhance nutrient conservation (Chapin 1980; Grime 1977; Poorter et al. 1990; Poorter and Garnier 1999). To be capable of a rapid growth rate, plants must have tissues capable of high rates of resource extraction (e.g., high A_{max}), a capacity that requires tissues with fine structure (e.g., SLA; Reich et al. 1997) that are rich in N compounds critical to metabolism and C exchange and that is associated with rapid tissue turnover. In contrast, the resource-conservation strategy relies on retention of C and N in long-lived, structurally robust tissues (Coley et al. 1985; Reich et al. 1991) that respire at low levels (Lusk and Reich 2000) and thus must have low concentrations of key N-rich metabolites and enzymes (Reich et al. 1998b, 1998c; Walters and Reich 1999). The multiple-trait trade-off relationships identified above and interpreted as evidence of coordinated plant physiological strategies have been shown to reflect significant patterns of correlated evolutionary change based on several kinds of tests using independent contrasts (Ackerly and Reich 1999; Fonseca et al. 2000; Wright et al. 2002; figs. 4, 5).

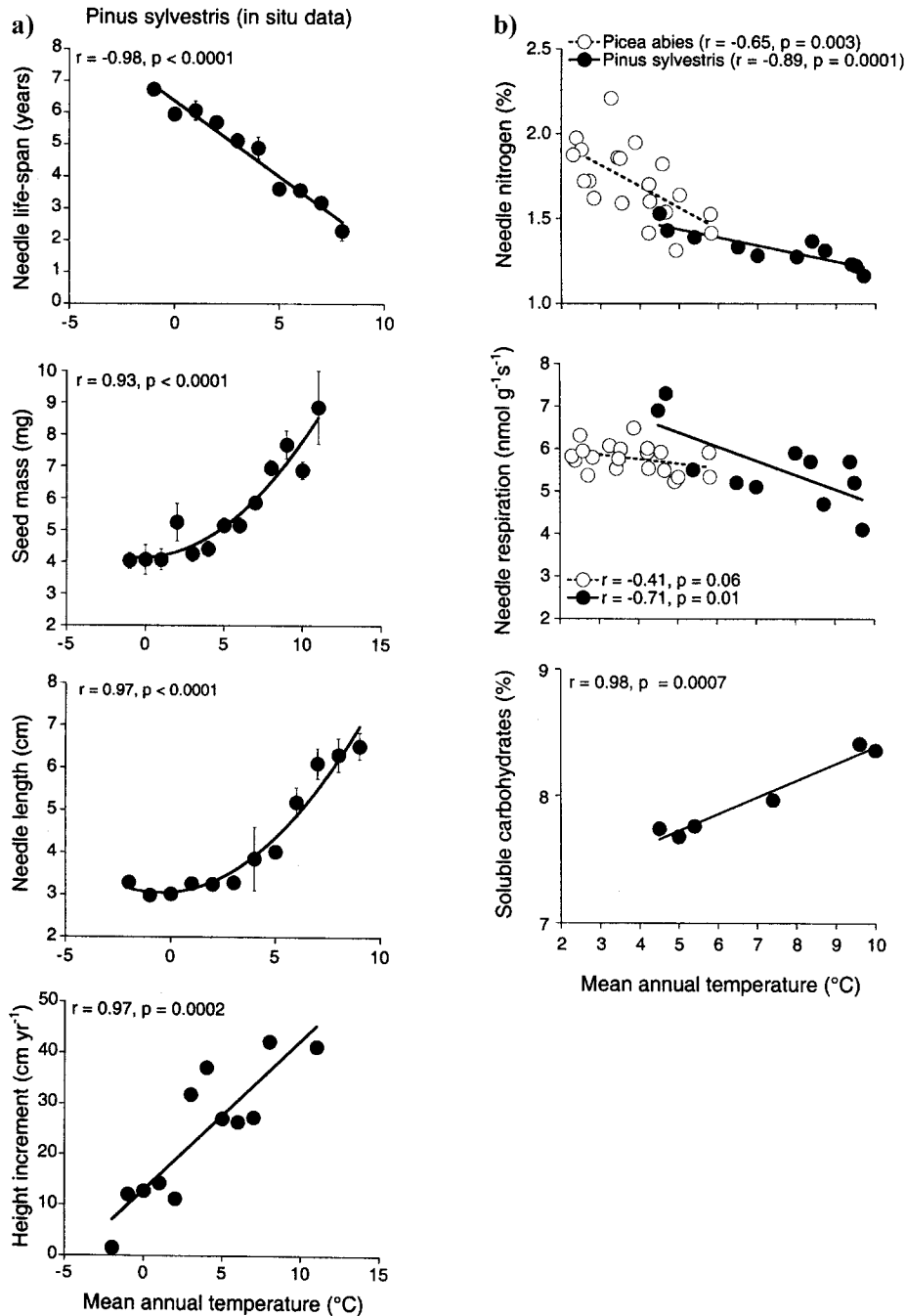It is as yet unclear how thoroughly this apparently coor-

Fig. 11 *a*, Needle longevity, seed mass, needle length, and growth rate of European Scots pine populations along native temperature gradients. *b*, Needle %N, dark respiration, and carbohydrate concentrations in a common garden in central Europe for Picea and Pinus populations of differing temperature at the site of origin. From Oleksyn et al. (1998, 2000*b*), Reich et al. (1996), and J. Oleksyn and P. Reich (unpublished data).

dinated set of leaf traits relates to root traits. Evidence is generally supportive but incomplete (Reich et al. 1998*a*, 1998*c*; Wright and Westoby 1999; Craine et al. 2001, 2002). The leaf-trait syndrome is also associated with important whole-plant and stand characteristics (Lambers and Poorter 1992; Reich et al. 1992, 1997; Craine et al. 2002), some of which can influence important environmental factors such as resource

availability and microclimate, which creates complex potential feedback interactions at an ecological scale.

The question of whether shortages of different resources (or other environmental factors) select for similar traits could be considered the "stress debate." Some authors have argued that particular suites of traits are adaptive in the face of many different resource stresses (Grime 1977, 1989; Chapin et al.

1993); others have emphasized that different suites of traits are advantageous according to the most limiting resource in question (Grubb 1998). We do not intend to fully enter this debate here but mention that evidence supports both perspectives to some extent (see Fonseca et al. 2000). For instance, the "low metabolic rate, low tissue turnover, low %N syndrome" is associated with plants adapted to low light, nutrient, and moisture conditions (Chapin 1980; Reich et al. 1991, 1992; Walters and Reich 1999; Wright et al. 2001, 2002; Craine et al. 2002) and with plants adapted to cold temperatures (Reich et al. 1996; Oleksyn et al. 1998). Thus, we conclude that a single multiple trait axis does exist that represents a general trade-off strategy continuum for plant functional traits. Recognizing this can help us achieve synthesis across the global range of terrestrial ecosystems. However, plants do not have the same sets of traits for each of these conditions (Reich et al. 1999; Wright et al. 2001, 2002), and identification of whether these trait syndromes vary with environment in predictable, patterned ways is an important current and future activity.

Strategies of Functional Variation and Trait Correlation: Causation, Coordination, Compromise

Consider sets of traits that show similar slope relationships in many habitat types (figs. 1, 2; Reich et al. 1997, 1999; Wright et al. 2001). Some of these trait correlations can be understood as largely causal (i.e., linked by physiological mechanisms). In leaves, for example, a high concentration of photosynthetic enzymes (reflected in leaf N) and bioenergetic molecules (reflected in leaf P) are required for high A_{max}. Proteins must be continuously turned over, hence high protein content leads to a high R_d. Phloem loading of photosynthates continues on into the dark period, which provides a causal link between A_{max} and leaf R_d in addition to the link via leaf N. Another example of direct, physically enforced causation is that seed output per gram of seed produced cannot be increased without a decrease in mass of individual seed. Another example is that longer leaf life span seems nearly always to demand a more robust structure and hence greater leaf-mass per area. These causations can extend to clusters of three or more traits. For example, high mass-based A_{max} requires both high %N and high SLA (Reich et al. 1997, 1999).

Spectra of variation underpinned by these causal trade-offs represent conflicting costs and benefits. It is not possible to have higher protein concentration without incurring higher R_d, and it is not possible to produce more seeds from a given expenditure without each seed being smaller. Any given strategy along the strategy-spectrum, therefore, represents a compromise. A species should evolve to the best compromise given the physical habitat and other competing strategies. Most (all?) functional traits influence key currencies (e.g., water, C, N), and the best compromise should depend on their relative costs, i.e., on the exchange rate between the currencies (Wright et al. 2003).

Traits interconnected causally in this way typically are correlated fairly tightly. For example, seed output per square meter of leaf area against seed mass $r^2 = 0.75$ across 3.5 orders of magnitude (Henery and Westoby 2001), leaf life span against SLA r^2 in range 0.71–0.84 across ca. 1.5 orders of magnitude

of leaf life span within each of six vegetation types (Reich et al. 1999), leaf size against twig size $r^2 = 0.86$ across deciduous angiosperms spanning 2 orders of magnitude (Brouat et al. 1998). Of course, these correlations appear tighter when the species studied span a wider range of the traits: in studies in which species spread along only a subset of the total range of each axis, the scatter typically appears larger relative to the correlation.

For spectra of variation that are of interest in the context of understanding functional differences between species, there is not a single best compromise. Rather, species have evolved to different compromises. SLA and leaf life span vary by 1–2 orders of magnitude across species, whereas leaf size and seed size vary by 6 orders of magnitude or more. Most strikingly, much of this variation is between species operating interspersed at a site (figs. 2, 4). There is, of course, variation across climate or soil environmental gradients also (figs. 4, 5).

A second way traits can come to be correlated across species is by coordination (Westoby 1998; Ackerly and Reich 1999; Shipley and Lechowicz 2000). Directionality is a key difference between causality and coordination. In causal links, one variable is (at least in large part) cause and the other is effect. In coordination, the relationship is reciprocal, or else due to common causation from a third variable. In reality some, maybe most, trait associations may be an uneven mix of causality and coordination. Coordination arises because particular trait values function more successfully as a combination rather than because one trait drives another mechanically or physiologically. For example, both life histories involving tall stems and habitats favoring tall stems tend to favor larger seed mass. Similarly, there are tendencies for seeds having different morphological adaptations for dispersal to be of different sizes. Relationships arising by coordination are often quite loose. At least in the temperate zone (Westoby et al. 2002), most seeds above ca. 100 mg are adapted for dispersal by vertebrates, most seeds below ca. 0.05 mg are morphologically unassisted, although wind moves them easily. In between, relationships between seed mass and dispersal morphology are very weak indeed.

Sometimes a pair of traits can be correlated in one direction within habitat but in the opposite direction across habitats. A case in point seems to be the relationship between leaf size and SLA. Grubb (1998) and (Shipley 1995) found that among species with similar ecology and operating in a similar light climate, those with larger leaves tended to have lower SLA. They suggested this was a requirement for mechanical support. But across sites, both SLA and leaf size tend to decline toward lower rainfall and lower soil nutrient (Fonseca 2000). Similar to Grubb and to Shipley, Niinemets (2001) found lower SLA in larger-leaved species, but in these cases the pattern seemed to be driven largely by the differences between canopy and shaded species. In data sets spanning a range of habitats, within-habitat and between-habitat patterns are liable to cancel out, which leaves little or no overall relationship between leaf size and SLA (Ackerly and Reich 1999; Fonseca 2000).

What are the consequences of these correlation patterns among quantitative traits for the idea of functional types or syndromes? First, for traits that are tightly correlated, either worldwide or conditionally within habitat, one can say that syndromes exist. If one knew one of the traits, one could ap-

proximately predict the other. The spectra of variation describe combinations of traits, not just one at a time. Second, the variation is in reality continuous rather than being made up of "types" in the sense of discrete categories. This is beginning to be recognized by the latest models for vegetation dynamics under global change. However, these models still proceed by chopping continuous variation in traits such as SLA into categories for computing convenience. Given that variation in some of the most important quantitative traits is in fact known to be continuous, a high priority for future modeling should be to develop ways of expressing these traits as continuous variation. Third, some of the main spectra of variation are substantially independent of each other. Indeed, they have been identified as priorities precisely because they express different aspects of a plant's ecology. "Substantially independent" does not mean here that no correlation can be detected. For example, plant canopy height at maturity and seed mass had r^2 between 0.17 and 0.30 in five temperate floras (Leishman et al. 1995). These relationships were statistically significant, but still, they mean that 70%–83% of the variation in seed mass occurs among species at a given height. For this sort of relationship, it would not be helpful to speak of syndromes uniting seed mass with plant height. Most of the variation in dispersal and seed establishment ecology (as indicated by seed mass) occurs within height categories rather than being correlated with height.

Summary

We have presented evidence for adaptive variation in plant functional traits in relation to environmental gradients and to strategies of resource capture and survival. It is clear that much remains to be done. Ackerly et al. (2000) noted several areas that may be particularly promising for future research vis-à-vis the evolution of plant ecophysiological traits. One involves comparative studies of ecophysiological variation in distantly or closely related species that allow hypothesis testing about adaptive significance of traits. A second involves identifying genotypic variation in traits related to fitness. A third takes the holistic perspective that views the plant as an integrated system and therefore addresses the interactions among traits that influence survival, growth, and reproduction and how these might lead to diversification of suites of traits in contrasting environments and/or for contrasting strategies. All of these kinds of studies are valuable, but almost every study is, almost unavoidably, limited in either genetic information or in the details of the explicit linkages between traits and fitness components. We present several examples.

Across broad environmental gradients, increasing numbers of broad interspecific (Reich et al. 1997; Fonseca et al. 2000; Shipley and Lechowicz 2000; Wright et al. 2001; Ackerly 2003) and narrow intragenus or intraspecific studies (Sandquist and Ehleringer 1997; Oleksyn et al. 1998, 2003; Ackerly and Donoghue 1998; Cavender-Bares and Holbrook 2001; Miller et al. 2001) have shown strong evidence for a genetic basis for variation among populations or species that is at the very least consistent with general hypotheses about the adaptive value of the trait(s) in question and/or the trade-offs between traits (and hence the selection process). However, most of these studies lack any other genetic information and do not

directly assess whether the trait or traits in question actually enhance any fitness component.

In contrast, in studies that are strong in terms of characterizing genetic trait variation within populations, there is often evidence that a trait that varies across an environmental or "habitat strategy" gradient is related to fitness (Farris and Lechowicz 1990; Geber and Dawson 1990, 1997; Dudley 1996a, 1996b), but the physiological integration at the plant scale is missing, and the actual means by which a trait confers a fitness component is often murky. Yet additional contrast is provided by consideration of studies that examine trait variation within an experimental or observational context that simultaneously assesses plant performance relevant to fitness (carbon balance, growth, survival, or, less often, reproduction). These studies are often strong in terms of characterizing the ecophysiological mechanisms and links between traits and fitness components (Wedin and Tilman 1990; Pacala et al. 1994; Walters and Reich 1996, 2000b). However, these typically involve far less taxa than the indirect, multiple trait studies mentioned above and often examine taxa without consideration of ancestry (but see Saverimuttu and Westoby 1996; Henery and Westoby 2001). Together, all three types of studies provide evidence for coordinated variability in functional traits among taxa and for their consequences vis-à-vis plant success in varying environments or competitive contexts.

We emphasize the idea that selection probably occurs across "strategies" within habitats as much as across environments. Although this may be implicit, it is rarely (if ever) explicitly stated. There is certainly strong empirical evidence for the wide spread among species within habitats in their position along multitrait dimensional space (i.e., in their strategies). There is not direct experimental demonstration that this wide spread of syndromes arises from frequency-dependent interaction between species rather than from use of different site-determined microhabitats. That is not because of laziness, it is because the decisive experiment is almost impossible in practice (Westoby et al. 2002), and since site-determined microhabitats are always influenced by interactions among species, even separately defining each is exceedingly difficult.

Of course, it is much more difficult to discern selection across "strategies" because these are difficult to identify and quantify in contrast with environmental gradients. This may be part of the reason for criticism of schemes such as the C-S-R plan. Not only are they hard to quantify as functional groups or axes in the first place, but, because of the difficulty of quantification, they are difficult to use in tests of selection processes or of functional variability in general. In contrast, functional groups based on single or suites of traits or on quantitative schemes such as leaf-height-seed (Westoby 1998) could be used in experimental tests. Regardless, we argue that functional variation has evolved in relationship to plant strategies (which fall on continuous multidimensional axes) as well as in relationship to environments and that the two are related but not identical. We argue further that selection for functional traits is roughly equally as strong across strategies within a site as across local, regional, or continental environmental gradients. Thus, there may be as wide or wider a spectrum of successful strategies within a site than the mean strategy differences among sites along major resource gradients (figs. 1, 2). Let us compare the relationships between pairs of leaf traits for arid

versus humid sites in figure 2. The spread of traits (i.e., the two-dimensional trade-off surface) within a site is typically similar to or larger than the mean distance across two-dimensional trade-off surfaces for sites marked by resource differences.

Why should this be so? Perhaps this results from heterogeneity of selection pressures and ecological sorting opportunities within sites. Selection for drought tolerance features along an increasingly arid gradient (or a cold one, dry one, etc.) may act somewhat similarly on all individuals to some extent (Etterson and Shaw 2001). In contrast, within a site there are species functionally well suited to all possible (highly multivariable) combinations of resource availability, competitive milieu, and disturbance regimes. In essence, within any site there is great heterogeneity in time and space in resources, competition and disturbance, which effectively makes up a large number of potential niches, so no single factor is acting to drive selection or sorting similarly among all taxa.

In conclusion, a variety of approaches have helped us collectively learn more about the role of functional traits in evolution, the constraints on functional trait variability, and the process of selection. However, due to the technical difficulties involved, studies that are satisfactorily robust from both evo-lutionary biology and physiological ecology perspectives are rare if not nonexistent. To cite one of the reviewers of this article, "The difficulty is, of course, that both evolutionary biology and physiological ecology are technically very demanding, and it is difficult to do both well. The evolutionary biologists, to get the large sample sizes necessary to estimate evolutionary parameters, do relatively simple measures, which is unsatisfying to the physiological ecologist. Equally, the small sample sizes and lack of evolutionary context in the more complex functional studies done by the physiological ecologist frustrate the evolutionary biologist." We believe that this succinctly describes one of the main challenges for the field in the coming decade: to organize and conduct studies that continue the work of attempting to bridge this difficult gap.

Acknowledgments

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