

Least-Cost Input Mixtures of Water and Nitrogen for Photosynthesis

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ABSTRACT: In microeconomics, a standard framework is used for determining the optimal input mix for a two-input production process. Here we adapt this framework for understanding the way plants use water and nitrogen (N) in photosynthesis. The least-cost input mixture for generating a given output depends on the relative cost of procuring and using nitrogen versus water. This way of considering the issue integrates concepts such as water-use efficiency and photosynthetic nitrogen-use efficiency into the more inclusive objective of optimizing the input mix for a given situation. We explore the implications of deploying alternative combinations of leaf nitrogen concentration and stomatal conductance to water, focusing on comparing hypothetical species occurring in low- versus high-humidity habitats. We then present data from sites in both the United States and Australia and show that low-rainfall species operate with substantially higher leaf N concentration per unit leaf area. The extra protein reflected in higher leaf N concentration is associated with a greater drawdown of internal CO₂, such that low-rainfall species achieve higher photosynthetic rates at a given stomatal conductance. This restraint of transpirational water use apparently counterbalances the multiple costs of deploying high-nitrogen leaves.

Keywords: leaf economics, nitrogen-use efficiency, photosynthesis, water-use efficiency.

Water and nitrogen (N) are two of the key resources involved in the process of carbon fixation by plants. The bulk of leaf nitrogen is found in the photosynthetic complex, especially in the protein Rubisco (Lambers et al.

1998). When the stomates are open to allow CO₂ to diffuse into the leaf, water is inevitably lost in transpiration. Also, water is split during photosynthesis, the hydrogen being incorporated in sugar intermediates, and water is the medium in which nutrients and photoassimilates are transported around the plant.

Economic analogies have often been used to describe the way plants operate, with resources such as water, nitrogen, and carbon viewed as currencies that can be acquired, stored, and spent (e.g., Oriens and Solbrig 1977; Mooney and Gulmon 1979; Bloom et al. 1985; Givnish 1986; Chapin 1989; Kikuzawa 1991; Eamus and Prichard 1998). Concepts such as water-use efficiency (WUE) and photosynthetic nitrogen-use efficiency (PNUE) are widely used to describe the ratio of carbon assimilation rate to transpiration rate or to leaf N concentration, respectively (Field et al. 1983; Smith et al. 1997; Lambers et al. 1998). The use of a term such as “efficiency” hints that this ratio should be maximized in order for a plant to operate optimally. However, since there are multiple currencies operating simultaneously, viewing their relationship to carbon gain one at a time is not the best way to frame our understanding of plant ecophysiology. For example, traits or behaviors that increase one efficiency may result in a decrease in another (e.g., PNUE and WUE may trade off; Field et al. 1983).

In this article, we take a standard microeconomics framework for optimizing the mix of two inputs to a production process and show how it can be used to understand the use of water together with nitrogen in photosynthesis. This way of considering the issue integrates concepts such as WUE and PNUE into the more inclusive objective of optimizing the input mix for a given situation. A key component of this framework is the relative cost of procuring (or using) water versus the cost of procuring (or using) nitrogen for photosynthesis. We consider the implications of shifts in these relative costs with site characteristics, focusing on low- versus high-humidity sites. We relate these implications to previously published work that shows that leaves of perennial species from low-rainfall sites have high N concentration per leaf area, and we

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Table 1: Description of the six study sites

	Vegetation type	Soil type (parent material)	Annual rainfall (mm)	Mean annual temperature (°C)	Mean annual 9 A.M. temperature (°C) and relative humidity (%)
Australia (high nutrient): ^a					
High rain	Closed forest	Red-brown clay	1,220	17.5	17.3, 69
Low rain	Low open woodland	Yellow-gray sand	1,220	17.5	17.3, 69
Australia (low nutrient): ^a					
High rain	Open woodland	Light red clay	387	17.5	18.7, 49
Low rain	Open shrub mallee	Loamy red sand	387	17.5	18.7, 49
United States: ^b					
High rain ^c	Montane humid temperate forest	Clay loam ultisols	1,829	12.5	
Low rain ^d	Desert grassland and shrubland; pinyon-juniper woodland	Sandy aridosols	222	13	

Note: Long-term data were available for the high-rainfall U.S. site (Coweeta long-term ecological research [LTER]); only 2000 data were available for the low-rainfall U.S. site (Sevilleta LTER). Since U.S. sites have a particularly distinct growth season, only data for May–October were used in calculating the ratio of low- to high-rainfall site VPD, whereas mean annual 9 A.M. temperature and relative humidity were used for Australian sites.

^a Estimated vapor pressure difference (VPD) ratio (low-rainfall : high-rainfall site) = 1.8.

^b Estimated VPD ratio (low-rainfall : high-rainfall site) = 2.6.

^c May–October mean temperature = 19.7°C; relative humidity = 72%.

^d May–October mean temperature = 22°C; relative humidity = 37%.

assess the evidence for considering this a general pattern. We also explore how the framework can be used to generate testable hypotheses concerning the interplay of water and nitrogen in carbon fixation for coexisting species that have different physiologies and morphologies.

Traits such as photosynthetic capacity, leaf N concentration, specific leaf area (leaf area per mass), dark respiration rate, and leaf life span vary widely between species and also tend to be intercorrelated (Reich et al. 1997, 1998). Describing and understanding the implications of between-species variation in these leaf traits have become increasingly important goals for plant eco(physio)logists since the mid-1980s (Field and Mooney 1986; Schulze et al. 1994; Reich et al. 1997, 1998; Aerts and Chapin 2000; Niinemets 2001; Westoby et al. 2002). Recently, large-scale vegetation models have begun to make use of the general “scaling” relationships between traits that have become apparent from this work (Moorcroft et al. 2001). Identifying the extent to which these scaling relationships shift predictably with environmental factors will increase the quality of information available for use in modeling exercises as well as add to our understanding of plant evolution (Reich et al. 1997; Wright et al. 2001, 2002). This article provides a framework for understanding certain aspects of these patterns, especially how and why resources may be used in different proportions in contrasting environments.

Methods

The economics approach we use in this article is based on the standard framework for understanding the optimiza-

tion of a two-input mix for a production process (e.g., Tisdell 1972; Samuelson and Nordhaus 1995). This will be described in detail in “Optimizing a Two-Input Mix for a Production Process” and “The Relative Costs of Water and Nitrogen in Different Habitats.” In this section, we provide background information regarding the field data presented, which is drawn from previous studies carried out in both Australia and the United States (Reich et al. 1999; Wright et al. 2001).

The four Australian sites (table 1) consisted of two pairs of high- and low-rainfall sites, with one pair on nutrient-rich clay soils and one pair on nutrient-poor sandy soils. They were described in detail by Wright et al. (2001). Total phosphorus (P) concentration of topsoil was used as an index of soil nutrient status since it reflects the underlying geology, which itself largely determines what kind of vegetation may develop on a site in a given rainfall zone in eastern Australia (Beadle 1962). All Australian sites are flat to gently sloping, experience rainfall spread relatively evenly across the year, and have the same mean annual temperature. The two U.S. sites have also been described previously (Reich et al. 1999). The arid New Mexico site consisted of closely situated desert grassland, shrubland, and pinyon-juniper woodland on sandy soils (Sevilleta long-term ecological research [LTER]). The North Carolina site (Coweeta LTER) is montane humid temperate forest on clay loam soil. As for the rainfall-contrasted pairs of Australian sites, these two sites had similar mean annual temperature.

Leaf-to-air vapor pressure differences (VPDs) were estimated for each site from site temperature and relative humidity data following Jones (1983; assuming 100% va-

por saturation inside leaves). The estimated VPD ratio (table 1) between Australian low- and high-rainfall sites was 1.8 (using mean annual 9 A.M. relative humidity and temperature), while the estimated VPD ratio for U.S. sites was 2.6 (using data from the May–October growing season only).

We studied 11–23 perennial species at each site, including broadleaf, needle-leaf and leafless, stem-photosynthesizing shrubs and trees, perennial forbs, perennial grasses, and N-fixing and non-N-fixing species, with both angiosperms and gymnosperms represented. Species at Australian sites were chosen randomly from previously compiled species lists. Species at U.S. sites were selected to provide a spread of leaf traits.

Standard methods were followed for measuring leaf traits (e.g., Bassow and Bazzaz 1997; Reich et al. 1998, 1999; Eamus et al. 1999). Measurements were made on young to medium-aged, fully expanded, outer-canopy leaves, for which leaf traits are relatively stable, before age-related decline in nutrient contents and photosynthetic capacity (Reich et al. 1991). Leaf-area-based photosynthetic capacity (A_{area}), dark respiration rate ($R_{\text{d-area}}$), and stomatal conductance for water vapor (g_s) were measured using portable photosynthesis systems operated in differential mode (CIRAS-1, Portable Photosynthesis Systems, Herts, United Kingdom, for Australian data; LCA-2, ADC, Hoddesdon, United Kingdom, for U.S. data) from mid-morning to late morning (8 A.M. to 12 P.M.) at saturating or near-saturating light conditions and at relatively non-limiting VPDs and temperatures. Measurements were made in situ (U.S. data) or immediately after detaching branches (Dang et al. 1997; Reich et al. 1998; Mitchell et al. 1999). The $R_{\text{d-area}}$ was measured at 25°C. Projected leaf area was determined with image analysis software. Kjeldahl N content was determined for oven-dried leaves. An average of 6.2 samples was taken for Australian species, all from different individuals; at least 10 samples from several individuals were taken for U.S. species.

Individual measurements were averaged for each species-site combination, since we were primarily interested in cross-species log-log “scaling” relationships between traits and in differences in those scaling relationships between sites. All variables were deemed normal following log transformation (Shapiro-Wilk test, $\alpha = 0.05$). Standardized major axis (SMA) slope-fitting techniques (Warton and Weber 2002) were considered most appropriate for investigating bivariate relationships, since X as well as Y variables had variation associated with them because of both measurement error and species sampling; hence, it was inappropriate to minimize sums of squares in the Y dimension only (Sokal and Rohlf 1995). Standard multiple regression was used for testing the three-way relationship between leaf N concentration (N_{area}), ambient-to-internal

CO_2 drawdown ($c_a - c_i$), and stomatal conductance to water vapor (g_s).

Optimizing a Two-Input Mix for a Production Process

General Case

The “production function” of a production process indicates the maximum output possible given various combinations of inputs. The common two-input case is described in standard microeconomics texts (e.g., Tisdell 1972; Samuelson and Nordhaus 1995). Imagine a production process in which the amount of output (P) is proportional to the levels of the two inputs applied ($P \propto I_1 I_2$). On a graph with axes I_1 and I_2 , a given level of production is represented by a concave curve, which may or may not be a strict hyperbola (P_1 in fig. 1). Such a curve is known as an “equiproduct curve,” isoquant or isocline; it describes a continuous spectrum of alternative input mixtures that each give rise to the same rate of production. It implies that the two inputs are to a large degree substitutable for one another. Land and labor could be the two inputs, for example. Increasing the level of one

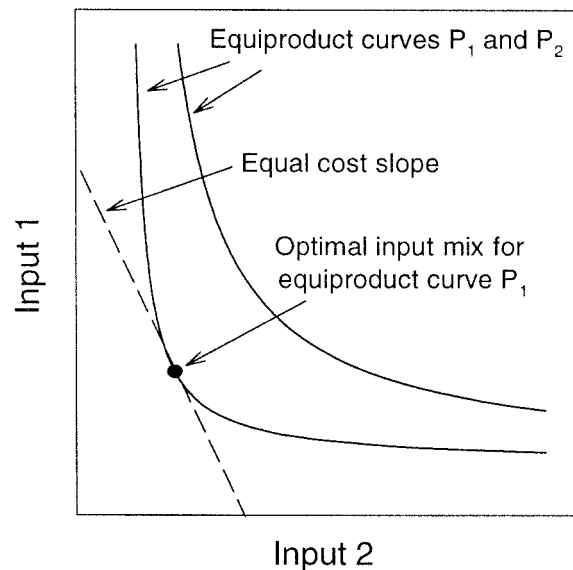


Figure 1: Standard microeconomics treatment (e.g., Samuelson and Nordhaus 1995) for the optimization of a production process in which the rate of production is proportional to the levels of the two inputs (I_1 , I_2) applied to the process. Each equiproduct curve describes a continuous spectrum of alternative input mixtures that each give rise to the same rate of production. The equal-cost slope indicates the ratio of unit-costs (or substitutability) of the two inputs. The optimal input mixture for a given rate of production is where the slope of the equiproduct curve is equal to that of the equal-cost slope.

input at a fixed level of the other results in increased total production, resulting in a shift to a higher equiproduct curve (P_2 in fig. 1). In fact, there is an infinite number of nested equiproduct curves within the graph space. The challenge for a firm is to identify the least-cost combination of inputs that results in a desired level of production. Finding this optimal solution is in fact quite simple: it depends on the relative cost of the two inputs. Specifically, the ratio of the unit-costs of the two inputs gives the equal-cost slope (fig. 1). Any point along a given equal-cost slope describes an input mixture with the same total cost. The location on any equiproduct curve that has the same slope as (is tangential to) the equal-cost line identifies the input mixture that produces a given output with least cost or, equivalently, that produces the greatest output from a given total cost. Naturally, if the unit-cost of one input changes, the equal-cost slope changes also, and a different combination of inputs would then be optimal for a desired level of production.

Applying the Framework to the Interplay of Water and Nitrogen in Carbon Fixation

Choice of Axes. In this section, we show how the two-input production framework can be applied to the use of water and nitrogen in carbon fixation. Its assumptions and implications apply during what we will call “active” photosynthesis, that is, during periods of the day or year when light, water, and temperature are relatively nonlimiting. The framework does not seek to explain diurnal stomatal behavior, as modeled previously by Cowan (1982) and Farquhar and Sharkey (1982), among others.

Photosynthesis follows Fick’s law for diffusion of gases (Lambers et al. 1998): $A_{\text{area}} = g_c(c_a - c_i)$, where A_{area} is photosynthetic capacity expressed per unit leaf area, g_c is stomatal conductance to CO_2 , c_a is ambient CO_2 , and c_i is the CO_2 concentration inside a leaf. This expression has the same form as for the two-input production process. That is, production is proportional to both of two quantities, a stomatal conductance and a CO_2 concentration difference.

The rate of water loss from a leaf during photosynthesis (transpiration) is largely a function of the leaf-to-air difference in water vapor pressure (VPD) and of stomatal (and boundary layer) conductance (Lambers et al. 1998). Stomatal conductance to water, g_s , is proportional to g_c , the two measures being interconverted via the molar diffusion ratio between CO_2 and water (Farquhar and Sharkey 1982). Since the partial pressure of water vapor inside leaves is close to saturation, VPD is particularly affected by the humidity of the surrounding air and by leaf temperature (Jones 1983). Thus, all else being equal, lower stomatal conductance translates into a lower transpiration

rate. At a given g_s and leaf temperature, transpiration is higher in lower-humidity (higher VPD) habitats.

The first axis in interpreting photosynthesis as a two-input production process is water use, as represented by g_s . In “The Relative Costs of Water and Nitrogen in Different Habitats,” this will be extended for understanding production in different humidity habitats by incorporating VPD in the axis.

The extent to which internal CO_2 concentration (c_i) is drawn down relative to ambient CO_2 (c_a) can be understood as a balance between stomatal conductance and photosynthetic capacity (Ehleringer 1995; van den Boogaard et al. 1995; Lambers et al. 1998). The higher the conductance, the less drawdown at a given photosynthetic capacity. The higher the photosynthetic capacity, the greater the drawdown at a given conductance. Leaf nitrogen largely consists of photosynthetic enzymes, and a substantial proportion of variation in photosynthetic capacity among species is explained by leaf nitrogen concentration (Field and Mooney 1986; Reich et al. 1997). Thus, at a given g_c (or g_s) per leaf area, one would expect that higher leaf N per area (N_{area}) should generally translate into a larger drawdown of internal CO_2 (and thus higher A_{area}). The second axis in interpreting photosynthesis as a two-input production process is thus nitrogen use, as represented by N_{area} . In “Comparisons with Field Data” and “An Alternative Calculation of the Cost of Nitrogen,” we will examine evidence for the link between $c_a - c_i$ and N_{area} and briefly discuss alternative formulations for including leaf nitrogen in the framework.

Reformulation of Fick’s Law. If Fick’s law is reformulated by assuming that $c_a - c_i$ is correlated with N_{area} (at a given stomatal conductance) and that g_c is proportional to g_s , we have a new expression, $A_{\text{area}} \propto N_{\text{area}} g_s$, describing carbon gain in terms of the interplay between nitrogen and water. In this treatment, the product is carbon fixation and the inputs are water and nitrogen. The A_{area} equiproduct curves can then be drawn on axes of nitrogen (N_{area}) and water use (g_s), each curve describing a continuous spectrum of alternative input mixtures that give rise to the same rate of carbon fixation, A_{area} . For simplicity, we will assume that the equiproduct curves are strictly hyperbolic (fig. 2), although it is sufficient to assume that the equiproduct curves are only concave (Tisdell 1972). In this framework, the least-cost input mixture for generating a given output (A_{area}) depends on the relative expense for procuring and using nitrogen versus procuring and using water. As described previously, the ratio of these expenses defines the steepness of the equal-cost slopes, and the location on any equiproduct (equal- A_{area}) curve that is tangential to an equal-cost line identifies the input mixture that produces a given output with least cost or, equiva-

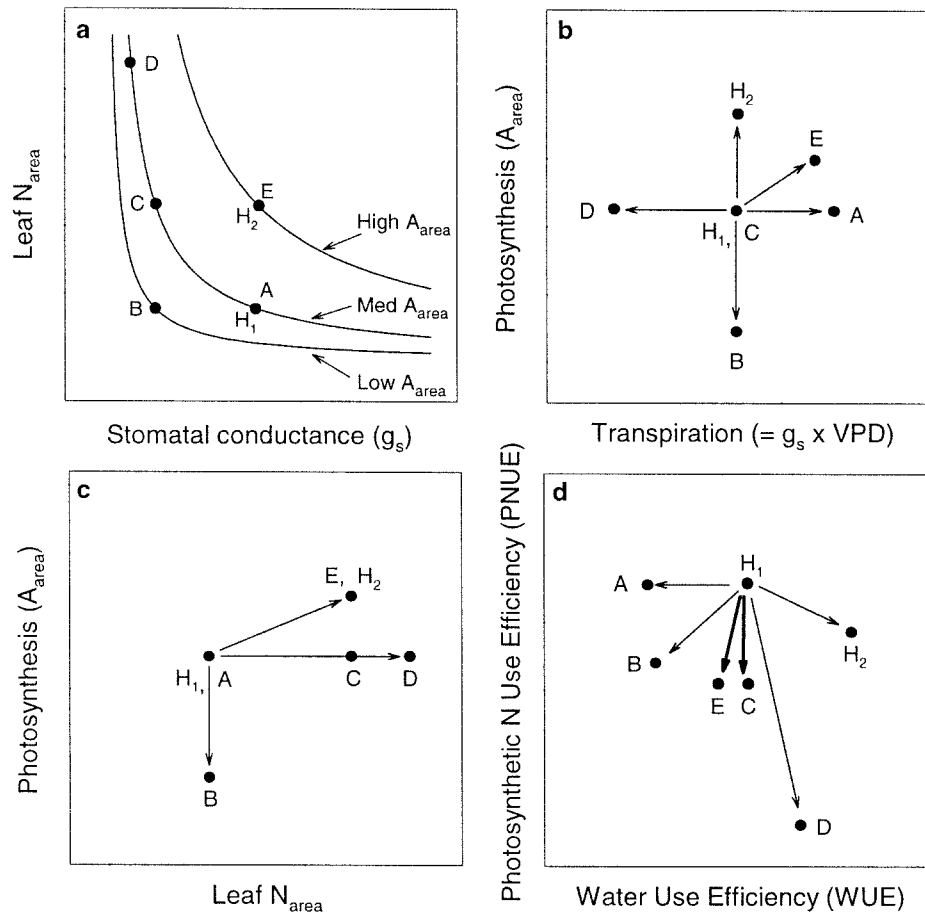


Figure 2: Understanding the use of water and nitrogen in photosynthesis as a two-input production process. *a*, Leaf nitrogen per area (N_{area}) and water (via stomatal conductance, g_s) are the two inputs; the equiproduct curves represent different levels of photosynthesis per unit leaf area (A_{area}). *A–E* denote possible leaf strategies or input mixtures for species occurring in a low-humidity habitat; these are contrasted with a hypothetical species occurring in a high-humidity habitat (H_1). H_2 represents a second possible input mix for a species in the high-humidity habitat (see text). *b–d*, Trends in transpiration, N_{area} , A_{area} , photosynthetic nitrogen-use efficiency (PNUE), and water-use efficiency (WUE) corresponding to the hypothetical strategy shifts in *a*. The observed shifts in leaf traits between sites (fig. 3) best fitted shift types *C* and *E*.

lently, that produces the greatest output from a given cost. This way of considering the issue allows the use of water and nitrogen in photosynthesis to be considered simultaneously; that is, it integrates concepts such as water-use efficiency and photosynthetic nitrogen-use efficiency into the more inclusive objective of optimizing the input mix for a given situation.

Comparing Water and Nitrogen Use in Species Operating in Different Humidity Habitats. Consider as a reference point a hypothetical species occurring at a high-rainfall site that typically operates with some given combination of g_s with N_{area} (point H_1 in fig. 2*a–d*). Now compare this with a second hypothetical species, species *A*, which has the same combination of g_s with N_{area} but occurs in a low-rainfall

habitat with lower ambient water vapor pressure (higher leaf-to-air VPD). Expenditure of water by *A* during active photosynthesis would be higher (since transpiration = $g_s \times \text{VPD}$), but its photosynthetic rate would be the same. Thus, the two species (points H_1 and *A*) lie at the same position in figure 2*a* but are separated when transpiration (fig. 2*b*) or water-use efficiency (WUE; fig. 2*d*) are considered. Specifically, the WUE of the low-rainfall species would be lower than that of the species with similar leaf traits occurring in the more humid habitat. Since the photosynthetic rate and N_{area} were the same for the two species, their photosynthetic nitrogen-use efficiency (PNUE) would be the same (fig. 2*c*, 2*d*).

Alternative leaf strategies for species in low-humidity environments are illustrated by *B–E* in figure 2*a*. A species

at *B* is operating with the same N_{area} but lower g_s than the high-rainfall species H_1 . Specifically, g_s is decreased sufficiently to counter the transpiration increase that would otherwise result from lower atmospheric humidity. This would decrease A_{area} because of the lower conductance for CO_2 . Thus, point *B* lies on a lower A_{area} equiproduct curve than H_1 in figure 2*a* and has both lower A_{area} at a given transpiration rate (WUE; fig. 2*b*, 2*d*) and lower A_{area} at a given N_{area} (PNUE; fig. 2*c*, 2*d*).

A species at *C* is operating with lower g_s to counter the effect of lower atmospheric humidity on transpiration (as did *B*) but with leaf N higher to draw down internal CO_2 concentration (widen $c_a - c_i$) and sustain output A_{area} despite the lower stomatal conductance. In option *C*, PNUE is lower for a species than for the species operating at high humidity, but WUE is similar (fig. 2*b*–2*d*).

At *D*, species at low humidity might seek to increase WUE, driven by selection to use less water during active photosynthesis. To accomplish this, they would need to reduce g_s by a still greater margin than in the shift from H_1 to *C*, sufficient not only to offset the effect of lower humidity but also to reduce transpiration rate still further. To maintain photosynthetic rate so that the reduced water use did in fact lead to increased WUE, leaf N would need to be higher by a considerably larger margin to achieve similar output A_{area} despite the low g_s . Photosynthetic nitrogen-use efficiency would be considerably lower for such a species at *D*, achieving higher WUE at low rainfall (fig. 2*d*).

Finally, at *E*, species at low humidity might operate at higher leaf N but at similar g_s to those from higher humidity (H_1). The transpiration rate would be higher for these species because of the lower humidity, while the wider differential between c_a and c_i would also increase output A_{area} . In figure 2*d*, it can be seen that one cost of achieving similar or somewhat lower WUE at low humidity as at high humidity is a decrease in PNUE.

Comparisons with Field Data

Over the three contrasts of high- versus low-rainfall sites, dry-site species averaged 2.4 times higher leaf N concentration per area (N_{area}), or 1.7 the leaf nitrogen at a given specific leaf area (SLA; fig. 3*a*–3*c*). Higher N_{area} was associated with wider differentials between internal and external CO_2 concentrations (higher $c_a - c_i$) at a given stomatal conductance ($p < .005$ in each of the three data sets; table 2), suggesting that the nitrogen difference represented a difference in photosynthetic enzyme content. This result is consistent with 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) as well as from a larger data set consisting of species from around the globe; data from this study combined with those from Reich et al. (1997) show c_i decreasing with increasing N_{area} at a given g_s ($p < .001$, $n = 210$; CO_2 drawdown estimated from A_{area} and g_s ; data not shown).

Associated with the steeper CO_2 gradients, dry-site species had higher photosynthetic rates (A_{area}) at a given g_s (fig. 3*d*–3*f*). Dry-site species had similar mean g_s to the high-rainfall species in two of three data sets and thus somewhat higher photosynthetic capacities (fig. 3*d*, 3*f*); in the third data set, dry-site species had lower mean g_s and thus similar A_{area} to high-rainfall species (fig. 3*e*). Common to all data sets, the proportional shift in mean A_{area} between high- and low-rainfall species was only 0.5–0.6 as great as the proportional change in N_{area} ; that is, the average PNUE at drier sites was lower.

Leaf N per area is equal to leaf N on a mass basis (N_{mass}) divided by SLA. Nevertheless, the negative relationships between N_{area} and SLA depicted in figure 3 are not artifacts caused by leaf area appearing as the numerator in one term and as the denominator in the other. The N_{mass} is not constant but tends to be correlated with SLA (Field and Mooney 1986; Reich et al. 1997). Further, both N_{mass} and SLA vary considerably more widely among species than within species (Bassow and Bazzaz 1997; Wright et al. 2001). The key point in figures 3*a*–3*c* is that the shifts between high- and low-rainfall species in terms of N_{area} cannot be interpreted as resulting only from the generally lower SLA at low rainfall. By viewing the traits two at a time, we find that it is clear that they are also shifted toward higher N_{area} at a given SLA. Similarly, the shifts in A_{area} - g_s relationships are best seen in a two-dimensional graph space rather than, for example, in terms of the ratio of A_{area} to g_s . Both g_s and the drawdown of internal CO_2 contribute to A_{area} .

The trait shift toward higher N_{area} in species occurring at lower rainfall constitutes a shift upward in terms of the two-input framework in figure 2*a*. Of the possible upward shifts, alternatives *C* and *E* were those mainly observed. The average shift between species in the Australian low-nutrient rainfall contrast can be characterized as a shift from H_1 to *C*; on average, low-rainfall species had higher N_{area} , lower g_s , and similar A_{area} to high-rainfall species (fig. 3*b*, 3*e*; fig. 4*b*). Photosynthetic nitrogen-use efficiency was lower for species operating at low humidity, but their WUE was similar (the shift toward lower g_s counterbalanced the difference in ambient water vapor pressure). By contrast, the average shift between species in the Australian high-nutrient and U.S. contrasts consisted of higher A_{area} and N_{area} but similar g_s in low-rainfall species (shift from H_1 to *E*). However, since A_{area} increased proportionally less

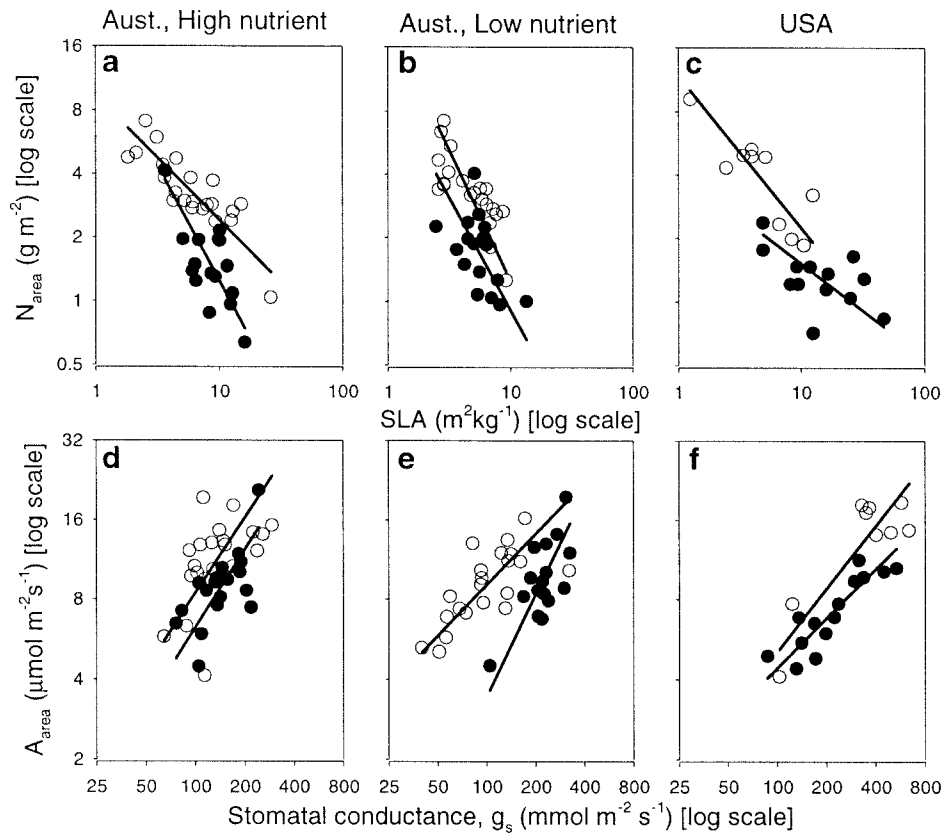


Figure 3: Relationships between leaf N_{area} and specific leaf area (SLA; *a-c*) and between net photosynthetic rate (A_{area}) and stomatal conductance (g_s ; *d-f*) for three sets of perennial plant species contrasted on rainfall (*filled circles*, high-rainfall species; *open circles*, low-rainfall species). Fitted slopes are standardized major axes (SMAs) fitted through the species data for each site. SMA descriptions (slope, 95% confidence intervals, and correlation r): N_{area} versus SLA: *a*, high rain (HR) -1.09 ($-1.59, -0.74$), $r = -0.68$; low rain (LR) -0.59 ($-0.75, -0.47$), $r = -0.85$; *b*, HR -1.07 ($-1.67, -0.68$), $r = -0.54$; LR -0.89 ($-1.19, -0.67$), $r = -0.79$; *c*, HR -0.45 ($-0.76, -0.26$), $r = -0.54$; LR -0.72 ($-1.10, -0.48$), $r = -0.85$. A_{area} versus g_s : *d*, HR 0.98 ($0.66, 1.45$), $r = 0.66$; LR 0.95 ($0.65, 1.37$), $r = 0.54$; *e*, HR 1.28 ($0.87, 1.87$), $r = 0.71$; LR 0.64 ($0.46, 0.89$), $r = 0.72$; *f*, HR 0.62 ($0.46, 0.83$), $r = 0.88$; LR 0.79 ($0.51, 1.23$), $r = 0.86$.

than N_{area} and estimated transpiration, both PNUE and WUE were on average lower for the low-rainfall species in these data sets (*E* in fig. 2*d*).

It is important to note that these observations—that dry-site species use as much or more water in transpiration and achieve photosynthetic rates as least as high—apply during photosynthesis occurring under relatively nonlimiting conditions. This is not to say that dry-site species fix as much carbon and use as much water considered over 12 mo, since arid environments have shorter periods during which soil water supports active growth. The data presented here apply to perennial species that persist year-round in low-rainfall habitats, in contrast to annual or ephemeral species that may complete their rapid life cycle while water is freely available.

The Relative Costs of Water and Nitrogen in Different Habitats

In a habitat with a given typical humidity, between-species variation in g_s contributes directly to variation in transpiration rate. However, to compare the relative costs of nitrogen and water between habitats differing in humidity, the g_s axis in figure 2*a* would have to be rescaled by leaf-to-air VPD to represent actual water loss to transpiration ($g_s \times \text{VPD}$). On the rescaled graph, what was a single equal- A_{area} hyperbola in $N_{\text{area}}-g_s$ graph space expands to become a family of nested hyperbolas, each corresponding to a different VPD (but all with the same A_{area}). In a nested set of hyperbolas such as these, the tangent at any given X value is steeper as one shifts to successively higher hyperbolas (this property also applies to the nested set of

Table 2: Multiple regressions of dependent variable CO₂ drawdown ($c_a - c_i$) on leaf N per area (N_{area}) and stomatal conductance, g_s , by data set

Data set	Coefficients		Whole model		Total df	<i>p</i>
	β	<i>p</i>	<i>F</i>	<i>r</i> ²		
NSW high nutrient:						
log N_{area}	.23	.001	11.1	.37	40	<.001
log g_s	-.35	.003				
Constant	2.79	<.001				
NSW low nutrient:						
log N_{area}	.28	<.001	59.9	.77	37	<.001
log g_s	-.51	<.001				
Constant	3.07	<.001				
United States:						
log N_{area}	.22	.004	13.7	.59	21	<.001
log g_s	-.38	<.001				
Constant	2.77	<.001				
All data:						
log N_{area}	.25	<.001	100.9	.67	100	<.001
log g_s	-.49	<.001				
Constant	3.06	<.001				

Note: NSW = New South Wales. Data shown are the *F* statistic, explanatory power, degrees of freedom, and significance of the whole model and the parameter estimates (β) and significance of the individual terms in each model. All variables were log₁₀ transformed before analysis. The significance of N_{area} in each model demonstrates that higher leaf N per area was associated with greater drawdown of internal CO₂ (i.e., $c_a - c_i$ was higher) at a given stomatal conductance (g_s).

hyperbolas shown in fig. 2a, in which the hyperbolas differed in their respective A_{area} .

Two hyperbolas in an equal- A_{area} , varying-VPD family are shown in figure 5a, allowing comparison of the hypothetical species H_1 with strategy *C* once more. Whereas H_1 and *C* lie on the same equal- A_{area} hyperbola when portrayed in $N_{\text{area}}-g_s$ graph space (fig. 2a), point *C* lies directly above H_1 when viewed in terms of N_{area} and transpiration, with both strategies having the same A_{area} and transpiration rate but with *C* on a hyperbola of higher VPD (lower atmospheric humidity) than for H_1 . With *C* on a higher hyperbola but at the same X value, the tangent at *C* is steeper than that at H_1 (see appendix), implying a steeper equal-cost slope at low humidity if *C* represents the optimal input mix of N and water for that particular A_{area} . A steeper equal-cost slope at low humidity would imply an increase in the relative cost of water to N in that habitat or, equally, a decrease in the cost of N relative to water. This could be because water was harder to obtain or, equally, because nitrogen was somehow cheaper.

This shifting of point *C* to being above point H_1 when transpiration rather than conductance is considered can be related back to the observed N_{area} and g_s data (fig. 4b) by imagining the cloud of low-rainfall points shifted to

the right by the estimated mean VPD difference between sites (1.8; table 1). By contrast, right shifting the clouds of low-rainfall points by the VPD difference in the other two contrasts (fig. 4a, 4c) results in the “average” low- and high-rainfall species lining up such that they lie approximately along a line intersecting with the origin. This leads to a different conclusion for these contrasts regarding the relative costs of water and nitrogen in low- and high-rainfall sites. One property of the nested hyperbolas described above is that the tangents have equal slope at points where a line from the origin intersects with each hyperbola, since the slope depends only on the ratio of *Y* and *X* values at a given point (see appendix). In other words, in the Australian high-nutrient and U.S. contrasts, the average high-rainfall species (H_1) and low-rainfall species (*E*) had a similar N_{area}/g_s ratio and lay on their respective hyperbolas at points with similar tangents (fig. 5b), implying similar equal-cost slopes in the high- and low-humidity habitats. In summary, the average type of strategy shift observed in two of the three sets of contrasts did not connote a change in the relative cost of water versus nitrogen at low rainfall, whereas in one contrast it did: water appeared to be relatively more expensive than nitrogen at low rainfall.

Implications for Coexisting Species

If species in low-humidity environments can operate at higher leaf N, it may be asked why species at higher humidity should not also operate at higher leaf N at a given g_s , increasing their photosynthetic rate without decreasing water expenditure. This hypothetical shift is indicated as from H_1 to H_2 in figures 2a–2d, and it does not require rescaling by site VPD to compare relative costs because the two strategies coexist. Since the tangents of equiproduct hyperbolas steepen with increasing A_{area} at a given g_s (as described in “The Relative Costs of Water and Nitrogen in Different Habitats” and the appendix), if the tangent of the equiproduct curve at H_1 is equal to the equal-cost slope for that habitat (i.e., the input mix is optimal), then the tangent at H_2 , having a different slope, must describe a less cost-effective input mix for the greater A_{area} achieved at H_2 . For that particular A_{area} , the optimal input mix would in fact entail higher N_{area} than at H_1 and also higher water expenditure but lower N_{area} than at H_2 .

If the relative costs of water and N were set by site characteristics, such as N availability, rainfall, and soil water-holding capacity (Bloom et al. 1985), and if coexisting species all had optimal combinations of N_{area} and g_s (in terms of the model presented in “Optimizing a Two-Input Mix for a Production Process”), then each species would be expected to lie on its respective equal- A_{area} hyperbola at the point with the tangent equal to the equal-slope line

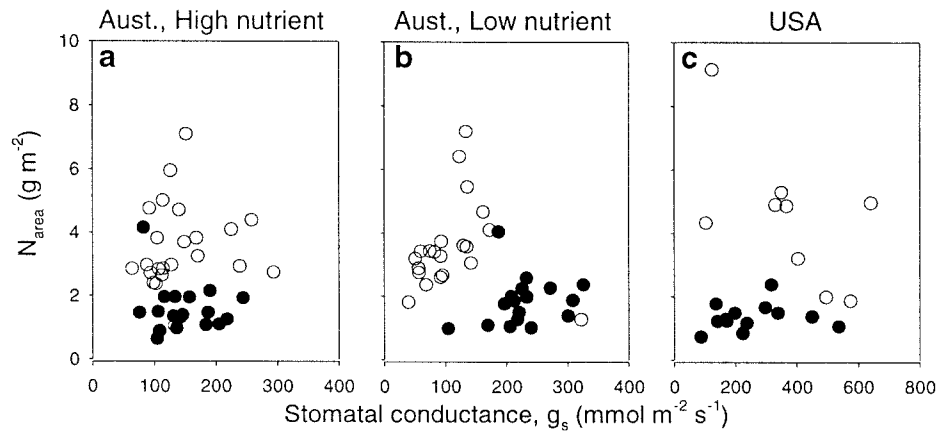


Figure 4: Observed combinations of N_{area} and stomatal conductance, g_s , for the study species; symbols as for figure 3

for that habitat. That is, the ratio of N_{area} to stomatal conductance would be the same for each species. On the other hand, contrasting physiologies or morphologies could potentially confer different relative costs of N and water. There could be “preference” or adaptation for a particular N source (e.g., Raven and Sprent 1993), presence or absence of mycorrhizae, shallow versus deep rooting, C_3 versus C_4 versus CAM physiology, and so on. If it were relatively cheaper for one species to obtain and maintain a given N_{area} , then the equal-cost slope would be steeper for that species and the optimal mix for its A_{area} would entail higher N_{area} and lower g_s , indicating lower PNUE and higher WUE than for the other species in the habitat. For example, nitrogen-fixing species typically operate at high leaf N. Where this is combined with low g_s , it should be interpreted as N being cheap relative to water, with the high leaf N serving to economize on water use. However, where high leaf N is combined with high g_s , this should not be interpreted as a shift in the relative costs of nitrogen and water.

Observed $N_{\text{area}}-g_s$ trait combinations for the six sites are shown in figures 4a–4c. Within four of six sites, the majority of species have similar N_{area}/g_s ratios (suggesting that the relative cost of inputs is largely set by site properties), whereas there is considerable scatter for species at the Australian high-nutrient dry site (fig. 4a) and clearly no typical N_{area}/g_s ratio at the dry U.S. site (New Mexico; fig. 4c). This scatter may be due to widely varying relative costs of the inputs among species at these sites, although in the case of the New Mexico data it may also reflect the fact that the “site” was actually a composite of closely situated desert grassland, shrubland, and pinyon-juniper woodland. Although all were on sandy soils, it is possible that

the relative costs of nitrogen and water differed between the subsites.

In summary, the framework presented in this article can suggest testable hypotheses concerning the interplay of water and nitrogen in carbon fixation, both for coexisting species and those from different habitats and for those with different physiologies and morphologies. In addition, using this framework, we may be better able to understand previously reported patterns such as evidence of a negative relationship between PNUE and WUE, found both across woody species (Field et al. 1983; DeLucia and Schlesinger 1991) and among wheat cultivars (van den Boogaard et al. 1995, 1997).

An Alternative Calculation of the Cost of Nitrogen

Alternatively, the N_{area} axis in the input-mix treatment could be rescaled to show N uptake requirement per time per leaf area. Assuming steady-state conditions, the annual N uptake requirement per unit leaf area (N_{req}) would be equal to the rate of N loss per leaf area, which could be estimated as litterfall N_{area} divided by average leaf life span. Litterfall N_{area} and leaf life span are in fact known for the Australian species described in this study (Wright et al. 2002; Wright and Westoby 2003). However, patterns of $N_{\text{req}}-g_s$ combinations (not shown) were very similar to patterns of $N_{\text{area}}-g_s$ combinations, especially with regard to the shift between rainfall zones. This was because green-leaf N_{area} and N_{req} were well correlated across species ($r = 0.73$, $p < .001$, $n = 64$), so that high- and low-rainfall species were separated similarly in N_{req} and in N_{area} .

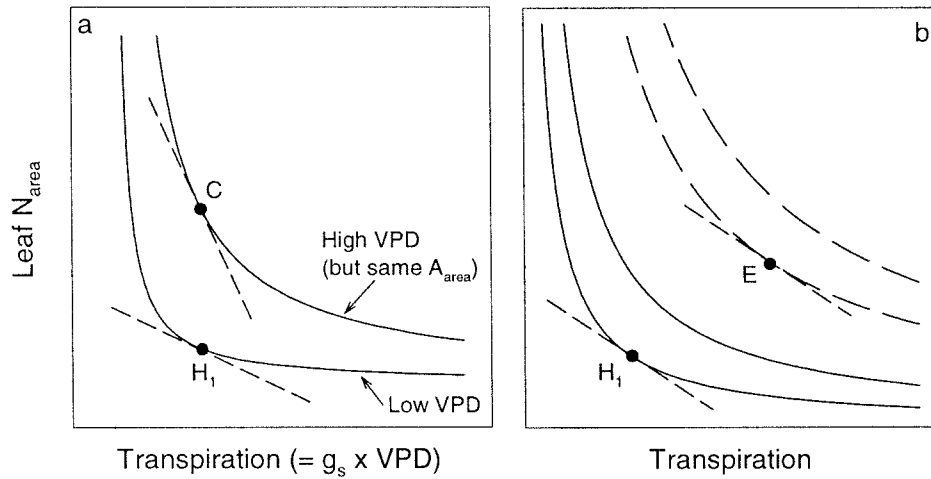


Figure 5: With the X-axis of figure 2a rescaled by vapor pressure difference (VPD) to represent actual water use (transpiration), families of equal A_{area} hyperbolas can be plotted, each hyperbola within a family corresponding to a different VPD. *a*, Two hyperbolas differing in VPD in a family of equal A_{area} hyperbolas. Point C is now directly above H_1 ; thus, the tangent at C is steeper, implying that water is relatively more expensive than nitrogen at low humidity in that scenario. *b*, Two hyperbolas differing in VPD in each of two different A_{area} families. *Solid lines*, low A_{area} hyperbolas; *dashed lines*, high A_{area} hyperbolas; higher VPD hyperbola in each family lies to the upper right of the lower VPD hyperbola. Hypothetical species E and H_1 lie along a line from the origin at points with equal tangents on their respective hyperbolas, implying that the relative cost of water and nitrogen does not differ from high to low humidity.

Generality of the Patterns

We found that species inhabiting arid environments were shifted toward substantially higher N_{area} but also higher N_{area} at a given SLA (leaf thickness or tissue density). It had previously been known that dry-site species have generally lower SLA than species from wetter sites (Mooney et al. 1978; Specht and Specht 1989; Pierce et al. 1994; Schulze et al. 1998; Cunningham et al. 1999; Fonseca et al. 2000) yet similar average N per leaf mass (Killingbeck and Whitford 1996), contrary to predictions that N per mass should be lower at low rainfall (Mooney and Gulmon 1979). Together, those results indicate a general trend for dry-site species to have higher N_{area} (see also Pierce et al. 1994; Schulze et al. 1998). Here the high N_{area} has been confirmed and generalized, and it was shown that it allows dry-site species to achieve higher A_{area} at a given stomatal conductance while achieving A_{area} during active photosynthesis at least as high as for wetter-site species.

From Fick's law, it follows that higher A_{area} at a given stomatal conductance requires a larger drawdown of internal CO_2 , c_i . Time-averaged CO_2 drawdown can be estimated via carbon isotope discrimination (Farquhar et al. 1989). With this method, there have been several reports of decreasing c_i with increasing site aridity, as found here, not only within species (Ehleringer 1995) but also within a genus (*Eucalyptus*; Miller et al. 2001), among both angiosperm and coniferous trees (Schulze et al. 1998; Warren

et al. 2001) and in terms of community means (data from 348 species from 12 sites in northern Australia; Stewart et al. 1995). In some of these studies (Schulze et al. 1998; Warren et al. 2001), the decrease has only become noticeable at the driest end of the rainfall gradient. Still, taken together, there is substantial evidence in support of the general nature of the broad trends reported here for low-compared with high-rainfall perennial species.

Costs and Benefits of High N_{area} at Low Rainfall

Constructing low SLA leaves with high leaf N_{area} must carry significant costs. In general, the construction cost per gram of leaf does not vary systematically with SLA (Chapin 1989; Poorter and De Jong 1999; Villar and Merino 2001). This implies that the (generally) lower SLA leaves of dry-site species are more expensive to build per unit leaf area than leaves of high-rainfall species. Constructing leaves with high N_{area} may incur additional costs. One cost would be the respiratory cost of maintaining high leaf-protein contents (Penning de Vries 1975; Ryan 1995; Amthor 2000; Cannell and Thornley 2000), reflected in an increase in dark respiration with N_{area} at all sites (fig. 6a–6c). Presumably, there would also be costs in acquiring the extra nitrogen (extra root growth or support for root symbionts) and perhaps in increased desirability to insect herbivores (Mooney and Gulmon 1979). Among the Australian spe-

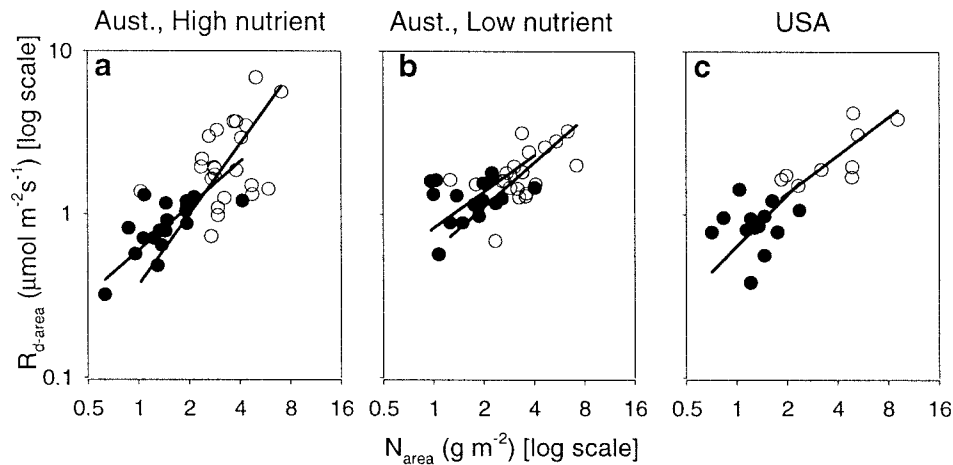


Figure 6: Relationships between dark respiration ($R_{d\text{-area}}$) and leaf N_{area} for the three sets of species from high- and low-rainfall sites. Symbols as for figure 3. Fitted slopes are standardized major axes (SMA). SMA descriptions (slope, 95% confidence intervals, and correlation r): *a*, HR 0.91 (0.62, 1.33), $r = 0.68$; LR 1.44 (0.96, 2.16), $r = 0.40$; *b*, HR 0.74 (0.45, 1.24), $r = 0.27$; LR 0.94 (0.61, 1.36), $r = 0.51$; *c*, HR 1.06 (0.59, 1.91), $r = 0.08$; LR 0.78 (0.46, 1.31), $r = 0.79$.

cies described in this study, we have also found a negative relationship between leaf nitrogen concentration and leaf tissue toughness, which was linked with 40% shorter leaf life span at a given SLA for low-rainfall species (Wright and Westoby 2002), apparently another significant cost to their high N_{area} strategy.

On the other hand, deploying high N_{area} leaves in low-rainfall habitats must have substantial benefits. One hypothesis for higher N_{area} in arid-zone species has been that they will often be exposed to higher light intensities and might be expected to develop higher leaf protein in order to exploit the higher light successfully (Mooney et al. 1978; Cunningham et al. 1999; Roderick et al. 2000; Niinemets 2001). This idea is not inconsistent with our results or model, although, on average, dry-site species showed a greater proportional increase in N_{area} than in A_{area} (2.4 vs. 1.3) and thus had lower average PNUE. However, it seems that the major benefit of a high N_{area} strategy in low-rainfall species is that it permits lower stomatal conductance for a given photosynthetic rate and thus restraint of transpirational water use. By considering the three-part interplay of water, nitrogen, and carbon in terms of optimizing the input mix for a production process, we may be better able to understand the implications of shifts in leaf-trait strategies such as these.

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Appendix

Here we explain two relevant properties of nested sets of hyperbolas as used in the two-input optimization framework. Production P is proportional to the levels of the two inputs applied ($P \propto I_1 I_2$). On a graph with axes I_1 and I_2 , a given level of production is represented by a hyperbola. The first property is that, at a given I_1 value (e.g., g_s or $g_s \times \text{VPD}$), the tangent of each successive hyperbola is more steeply negative as I_2 (N_{area}) increases. The second property is that points on successive hyperbolas with the same ratio of I_2 to I_1 have the same tangent and are connected to each other by a straight line that passes through the origin. Third, these properties apply whether the nested hyperbolas each represent a different level of A_{area} in N_{area}, g_s graph space (e.g., fig. 2*a*); different VPD levels but the same A_{area} in $N_{\text{area}}, g_s \times \text{VPD}$ graph space (fig. 5*a*); or different VPD, different A_{area} hyperbolas in $N_{\text{area}}, g_s \times \text{VPD}$ space (fig. 5*b*).

Taking the first case (fig. 2*a*), we make the assumption that A_{area} is directly proportional to the product of N_{area} and g_s : $A_{\text{area}} \propto N_{\text{area}} g_s$:

$$\therefore A_{\text{area}} = k N_{\text{area}} g_s, \quad (\text{A1})$$

where k is constant.

$$\begin{aligned} \therefore N_{\text{area}} &= \frac{A_{\text{area}}}{kg_s}, \\ \therefore \frac{dN_{\text{area}}}{dg_s} &= -\frac{A_{\text{area}}}{kg_s^2}. \end{aligned} \quad (\text{A2})$$

Thus, at any given g_s value, the tangent on successive A_{area} hyperbolas steepens negatively in direct proportion to the increase in A_{area} (e.g., a shift from H_1 to H_2 in fig. 2a). This is the first property of relevance.

Substituting (A1) into (A2), the equation of the slope of a hyperbola on axes of N_{area} and g_s reduces to

$$\frac{dN_{\text{area}}}{dg_s} = -\frac{N_{\text{area}}}{g_s}. \quad (\text{A3})$$

That is, points on successive A_{area} hyperbolas with the same ratio of N_{area} to g_s have the same tangent ($-N_{\text{area}}/g_s$). The equation of a straight line that passes through the origin is $N_{\text{area}} = bg_s$, where b is the slope of the line. That is, $b = N_{\text{area}}/g_s$, and the points on successive A_{area} hyperbolas with equal slope lie along this line (with their tangents = $-b$). This is the second property of relevance.

Incorporating Site VPD in the Expression

Transpiration (T) is the product of stomatal conductance and leaf-to-air vapor pressure difference; that is, $T = g_s \times \text{VPD}$. For simplicity, we shall simply use V here rather than VPD. Equation (A1) expands to

$$A_{\text{area}} = \frac{kN_{\text{area}}T}{V}, \quad (\text{A4})$$

where k again is a constant. Similar to the derivation in equations (A1)–(A3),

$$\frac{dN_{\text{area}}}{dT} = -\frac{N_{\text{area}}}{T}. \quad (\text{A5})$$

Equations (A4) and (A5) are the general equations for comparing slopes of the different types of hyperbolas described in this article. Comparing coexisting species with the same site VPD, transpiration T is directly proportional to g_s ; hence, equations (A1) and (A3) are just reduced forms of equations (A4) and (A5).

In the section “The Relative Costs of Water and Nitrogen in Different Habitats,” we described rescaling the g_s axis in the two-input treatment such that a given equal- A_{area} hyperbola would expand to become a nested set of hyperbolas, each differing in its site VPD but all representing the same A_{area} . Such a nested set is described by a reduced form of equation (A4), where A_{area} is constant. Multiplying

through by V gives an equation with the same form as equation (A1). That is, while equation (A1) described a nested set of hyperbolas, each with different A_{area} , the same geometrical properties apply to a nested set of hyperbolas, each with different VPD and viewed in $N_{\text{area}}, g_s \times \text{VPD}$ graph space (i.e., N_{area}, T graph space). That is, the tangents of successive hyperbolas steepen negatively in direct proportion to increasing VPD. Points on successive hyperbolas with the same ratio of N_{area} to transpiration have the same tangent.

Finally, consider hyperbolas differing in both A_{area} and VPD in N_{area}, T graph space. The tangent- N_{area}/T in equation (A5) applies irrespective of the value of either A_{area} or VPD. Hence, points H_1 and E in figure 5b, having the same $N_{\text{area}}/\text{transpiration}$ ratio (they lie along a line from the origin), have the same tangent. This is the third property of relevance. It suggested that the relative cost of water and nitrogen did not differ between low- and high-humidity sites in two of the three sets of contrasts. By contrast, in the third contrast, water appeared to be relatively more expensive at low rainfall (point C lay directly above H_1 in N_{area}, T graph space; fig. 5a).

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