

LETTER

Balancing the costs of carbon gain and water transport: testing a new theoretical framework for plant functional ecology

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Abstract

A novel framework is presented for the analysis of ecophysiological field measurements and modelling. The hypothesis ‘leaves minimise the summed unit costs of transpiration and carboxylation’ predicts leaf-internal/ambient CO₂ ratios (c_i/c_a) and slopes of maximum carboxylation rate (V_{cmax}) or leaf nitrogen (N_{area}) vs. stomatal conductance. Analysis of data on woody species from contrasting climates (cold-hot, dry-wet) yielded steeper slopes and lower mean c_i/c_a ratios at the dry or cold sites than at the wet or hot sites. High atmospheric vapour pressure deficit implies low c_i/c_a in dry climates. High water viscosity (more costly transport) and low photorespiration (less costly photosynthesis) imply low c_i/c_a in cold climates. Observed site-mean c_i/c_a shifts are predicted quantitatively for temperature contrasts (by photorespiration plus viscosity effects) and approximately for aridity contrasts. The theory explains the dependency of c_i/c_a ratios on temperature and vapour pressure deficit, and observed relationships of leaf $\delta^{13}\text{C}$ and N_{area} to aridity.

Keywords

Aridity, nitrogen, optimality, photosynthesis, plant functional traits, stable isotopes, stomatal conductance, temperature, transpiration, viscosity.

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INTRODUCTION

Optimisation by natural selection is a powerful concept for generating testable hypotheses about organismal traits and their relationships to the environment (Givnish 1986; Mäkelä *et al.* 2002). We explore the consequences of a simple optimality criterion that provides a unifying explanation for the following observations on plants, all strongly supported in the literature:

- The relative conservatism of the ratio between leaf-internal (c_i) and ambient (c_a) mole fractions of CO₂ (Wong *et al.* 1979; Ehleringer & Cerling 1995). The ratio tends to vary by only about $\pm 30\%$ (rates of gas exchange can vary through two orders of magnitude), and to be constant under variation of c_a , light and nutrient supply. This conservatism signifies tight regulation of the balance between carbon gain and water loss. We introduce the symbol $\chi = c_i/c_a$ to simplify the notation later on.

- The decline of χ with vapour pressure deficit (D). Previously assigned various mathematical forms (Leuning 1990; Oren *et al.* 1999; Medlyn *et al.* 2011), this decline is well described by $\chi = \xi/(\xi + \sqrt{D})$ where ξ is a parameter related to the ‘carbon cost of water’ (Medlyn *et al.* 2011). Medlyn *et al.* (2011) refer to this parameter as g_1 .

- The tendency demonstrated in many transect studies for the stable carbon isotope signature ($\delta^{13}\text{C}$) in the leaves of C₃ plants – a proxy for time-averaged values of χ – to become less negative, indicating lower χ , with increasing aridity (Stewart *et al.* 1995; Miller *et al.* 2001; Zheng & Shangquan 2007; Prentice *et al.* 2011).

- The tendency of leaf N per unit area (N_{area}) in all plants to increase from wet to dry climates (Wright *et al.* 2003,

2005), implying that N_{area} increases as χ declines (Prentice *et al.* 2011).

A general microeconomic optimisation criterion concerns investments in two or more resources required to manufacture a product. Here, the product is photosynthate, and the resources are the photosynthetic apparatus (with costs assumed proportional to Rubisco carboxylation capacity, V_{cmax} , at a standard temperature, and approximately proportional to N_{area}) and the transpiration pathway (with costs assumed proportional to the maximal transpiration rate, E). Wright *et al.* (2003) proposed the existence of an optimum rate of investment in transpiration and photosynthetic capacity, dependent on the *ratio* of their costs, which would achieve a given rate of net assimilation at least total cost. This analogy requires that the resources are substitutable, e.g. that plants can compensate for high water costs in dry climates by keeping stomata relatively closed while increasing investment in photosynthetic capacity, maintaining a given level of carbon assimilation at reduced c_i . Wright *et al.* (2001) noted that this form of resource substitution constitutes a widespread, previously overlooked mechanism of drought tolerance in plants.

Wright *et al.* (2003) considered carbon assimilation as proportional to the product of two inputs, conceptualised as water and nitrogen. We extend their reasoning to make quantitative predictions of trade-offs between photosynthetic and water-transport parameters from the standard model of C₃ photosynthesis (Farquhar *et al.* 1980) combined with plant water-relations theory. We use a graphical approach analogous to Wright *et al.* (2003) to analyse field data on photosynthesis, stomatal conductance and leaf traits from species in contrasting climates.

Cowan & Farquhar (1977) introduced an optimisation hypothesis for stomatal behaviour. Their hypothesis is equivalent to maximising $(A - \lambda E)$ where A is net carbon assimilation and λ is an 'exchange rate' between carbon and water. Biochemical properties of leaves, and hydraulic properties of stems, were assumed fixed over the time scale of interest (principally the diurnal cycle), although λ could vary more slowly. The general solution to this optimisation is complex (Arneeth *et al.* 2002; Konrad *et al.* 2008; Katul *et al.* 2010); tractable approximations have been proposed (Katul *et al.* 2010; Medlyn *et al.* 2011). However, as noted in a pioneering analysis by Givnish (1986), the Cowan-Farquhar optimality hypothesis is incomplete because it does not account for the (competing) costs of maintaining both water flow and photosynthetic capacity. Following Wright *et al.* (2003), we propose an optimal balance of investments in both functions. Remarkably, we predict a relationship between χ and D mathematically identical to that of Medlyn *et al.* (2011). But its single parameter (here called ξ) has a subtly different interpretation, based on the *relative* costs of maintaining a transpiration pathway capable of delivering water at a rate E , and leaf proteins capable of delivering photosynthate at a rate V_{cmax} . These costs can be expressed in terms of traits, and are expected to vary across environments. We examine how relationships among V_{cmax} , N_{area} and g_s vary across environments, and provide a coherent, quantitative interpretation of these variations.

MATERIALS AND METHODS

Data

Data were field measurements on all abundant woody dicots (trees if present, and shrubs) at four sites in eastern Australia (Table 1). Latitude ranges from 18°S to 42°S; mean annual temperatures (MAT) from 10.4 and 22.6 °C; longitude over 5° (coastal to interior) and mean annual precipitation (MAP) from 396 to 1133 mm. The sites were paired as follows. A 'cold' high-latitude site in Tasmania was contrasted with a 'hot' low-latitude site in Queensland. The Queensland site has higher rainfall but similar climatic moisture index $MI = P/E_q$, where P is MAP and E_q is equilibrium evapotranspiration (calculated as in Gallego-Sala *et al.* 2010. See Appendix S1 for definitions of hydroclimatic variables). At intermediate latitudes, in New South Wales, a 'wet' coastal site was contrasted with a 'dry' inland site. These sites have intermedi-

ate temperature (MAT 17 to 18°C) between the cold and hot sites; but the wet site has a much higher MI , and the dry site a much lower MI , than either the cold or the hot site.

Net photosynthesis (A_{sat}) and stomatal conductance (g_s) were measured simultaneously in the field at saturating light intensity (800 to 1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$, depending on the ambient light intensity) and temperatures close to ambient, using either a LiCor 6400 (Tasmania, Queensland) or a CIRAS-1 PP (New South Wales) infra-red gas analysis system. Measurements were made on freshly cut, sun-exposed branches. Fieldwork was scheduled so that ambient temperatures were similar regardless of site. CO₂ concentration, vapour pressure deficit and measurement temperatures were held within narrow ranges (388–402 ppm, 1.8–2.1 kPa, 23.0–27.0 °C). Four to seven replicate measurements per species were made, on different individuals. Leaf samples were analysed for specific leaf area (SLA), N by mass (converted to N_{area} using SLA) and $\delta^{13}\text{C}$. Carboxylation capacity at 25 °C ($V_{\text{cmax}}[25]$) was calculated using the Farquhar *et al.* (1980) model, assuming that A_{sat} is Rubisco-limited (Kattge *et al.* 2009) and applying the temperature dependency of V_{cmax} from Bernacchi *et al.* (2003, 2009). Day respiration was estimated by $R_d = 0.01 V_{\text{cmax}}$. $V_{\text{cmax}}[25]$ is expected to be more closely related to nitrogen investment than V_{cmax} at ambient temperature, but the differences were slight because measurement temperatures were close (within $\pm 2^\circ$) to 25 °C.

MI (Table 1) is used as an (inverse) index of general climatic aridity. Note that lower P and/or higher E_q both imply increasing limitation on ecosystem-level evapotranspiration, E_a , which in turn is a principal driver of D on large spatial and temporal scales (McNaughton & Jarvis 1991; Raupach 2000). An alternative measure of climatic aridity is the Cramer-Prentice α (Table 1), a standardised estimate of E_a/E_q (Gallego-Sala *et al.* 2010). α is related to MI by the Budyko framework for water vs. energy controls of catchment water balance (Wang *et al.* 2012). For quantitative analysis of aridity effects on χ , we use $\Delta E = E_q - E_a = E_q (1 - \alpha)$ as a proxy for the long-term effective value of D . Appendix S1 explains the rationale for our choice of hydroclimatic variables, and the relationships among them.

Graphical and statistical analyses

All species sampled were included except two C₄ species (*Atriplex stipitata* and *Triodia scariosa*) and two species of *Exocarpus* (*E. aphyllus* and *E. cupressiformis*). The latter are

Table 1 Site locations and climates: mean annual precipitation (MAP); mean annual temperature (MAT); and moisture index (MI), Cramer-Prentice α , equilibrium evapotranspiration (E_q) and incident photosynthetically active radiation during the growing season (PAR_0) all based on annual mean climate values and calculated as in Gallego-Sala *et al.* (2010). Primary data (monthly means of precipitation, temperature and incident shortwave radiation) were obtained from ANU climatologies at 0.05° resolution (M. Hutchinson, personal communication 2012) for 1970–2010

Sites	Location	MAP (mm)	MAT(° C)	MI	α	E_q (mm)	PAR_0 (mol m ⁻²)
'cold'	42.387°S 147.048°E	540	10.4	0.68	0.72	799	9484
'hot'	18.295°S 145.492°E	1066	21.6	0.70	0.64	1515	13869
'wet'	33.680°S 151.148°E	1133	17.3	1.00	0.92	1138	11604
'dry'	32.976°S 146.156°E	396	17.9	0.31	0.36	1289	11487

leafless, with photosynthetic stems, and were extreme outliers in the relationship between $V_{\text{cmax}}[25]$ and N_{area} . The analysis included 14 species from the cold site, 17 from the hot site, and 35 each from the wet and the dry site (Table 2). Twenty-six species were classified as N-fixers based on available information. This category consists mainly of Fabaceae but also includes two actinorhizal *Allocasuarina* species and one cycad (*Macrozamia communis*), which has a cyanobacterial symbiont.

Relationships examined (within and across sites) were $V_{\text{cmax}}[25]$ vs. N_{area} , V_{cmax} and N_{area} vs. g_s , the normalised values $V_{\text{cmax}}/A_{\text{sat}}$ and $N_{\text{area}}/A_{\text{sat}}$ vs. g_s/A_{sat} (the rationale for these comparisons is described below), $\delta^{13}\text{C}$ vs. χ , N_{area} vs. $\delta^{13}\text{C}$, and N_{area} and $\delta^{13}\text{C}$ vs. MI. All g_s values are given as conductances to CO_2 . Statistical analyses were carried out using SMATR, which fits standardised major axis slopes – suitable when the choice of the ‘x’ or ‘y’ variable is not predetermined (Warton *et al.* 2006). Non-significant intercepts were set to zero.

Hypothesis and approach

We hypothesised that plants minimise $\text{Cost} = a.E/A + b.V_{\text{cmax}}/A$ where a is the (carbon) cost of maintaining the transpiration stream required to support assimilation at a rate A under normal daytime conditions, and b is the cost of maintaining photosynthetic proteins at the level required to support assimilation at the same rate. V_{cmax} , E and A here are molar flux densities (mol CO_2 or H_2O per unit leaf area and time). Note that whereas both E and A can vary rapidly (minutes), Cost expresses the maintenance requirements for the *capacities* for maximum rates of transpiration and photosynthesis. These vary much less rapidly (weeks to months).

Previous analyses have often focused on predicting g_s , but it is conceptually simpler to predict χ . The two are related by Fick’s law, $g_s = (A/c_a)/(1 - \chi)$. $a.E/A$ and $b.V_{\text{cmax}}/A$ represent the ‘unit costs’ of transpiration and carboxylation respectively. They respond in opposite ways to a change in χ , leading as we will show to the existence of a minimum in Cost that depends on the relative magnitudes of a and b .

THEORETICAL ANALYSIS

Principles

A value of χ that satisfies the optimisation criterion (χ_o) must satisfy the following:

$$a.\partial(E/A)/\partial\chi + b.(V_{\text{cmax}}/A)/\partial\chi = 0 \quad (1)$$

Given that $E = 1.6g_sD$ and $A = g_s c_a(1 - \chi)$, and assuming that $A \gg R_d$ (day respiration) and $c_i \gg \Gamma^*$ (the photorespiratory compensation point), it is shown below that the optimum is obtained for $\chi = \chi_o$ where

$$\chi_o = \xi/(\xi + \sqrt{D}) \quad (2)$$

and $\xi = \sqrt{(bK/1.6a)}$, where K is the Michaelis–Menten coefficient for Rubisco-limited photosynthesis at a $p\text{O}_2$ of 21 kPa.

By applying Fick’s law to both transpiration and assimilation, we obtain

$$E/A = 1.6(D/c_a)/(1 - \chi) \quad (3)$$

and from Farquhar *et al.* (1980) for Rubisco-limited photosynthesis,

$$V_{\text{cmax}}/A = (\chi + K/c_a)/\chi \quad (4)$$

The derivatives are

$$\partial(E/A)/\partial\chi = 1.6(D/c_a)/(1 - \chi)^2 \quad (5)$$

and

$$\partial(V_{\text{cmax}}/A)/\partial\chi = -K/\chi^2 c_a. \quad (6)$$

Therefore, if eqn (1) holds then

$$1.6(aD/c_a)/(1 - \chi)^2 = bK/\chi^2 c_a \quad (7)$$

which on re-arrangement yields eqn (2). The turning point is a minimum, as both second derivatives are positive.

This simple derivation, to our knowledge, has not been published before. Relaxing the assumption that $c_i \gg \Gamma^*$ yields a small correction to eqn (2):

$$\chi_o = \Gamma^*/c_a + (1 - \Gamma^*/c_a)\xi/(\xi + \sqrt{D}) \quad (8)$$

where $\xi = \sqrt{[b(K + \Gamma^*)/1.6a]}$. This solution should be more accurate than eqn (2) at low c_i . For simplicity, however, we use eqn (2) henceforward.

The interpretation of costs

Various predictions follow from eqn (2) by equating the cost of photosynthesis with the respiration required to maintain carboxylation capacity, and the cost of transpiration with the respiration required to maintain the transpiration pathway, over a timeframe of months to years and potentially including more and less favourable periods for growth. For simplicity we consider only these maintenance costs. We do not consider root costs, assumed to be common to both functions.

We can then express b as the ratio of total (24-h) leaf maintenance respiration to V_{cmax} . This is probably a relatively conservative quantity (Reich *et al.* 1998) but it will be several times larger than the ratio R_d/V_{cmax} measured during daytime, because mitochondrial respiration continues in the dark, and is partly inhibited in the light.

We can also relate the carbon cost of transpiration to E . Neglecting capacitance and gravitational effects, E equals the rate of flow of water through the stem according to Darcy’s law (Whitehead 1998):

$$E = v_H \Delta\Psi k_s \rho_w / \eta h \quad (9)$$

where v_H is the Huber value (the ratio of sapwood area to the leaf area it supplies), $\Delta\Psi$ (Pa) the typical daytime water potential difference between the soil and the leaf, k_s (m^2) sapwood permeability (a wood property independent of the properties of water: see Reid *et al.* 2005 for definitions), ρ_w (mol m^{-3}) the density of water, η (Pa s) the viscosity of water, and h (m) the mean path length (approximately the mean

Table 2 Species analysed

Sites	Genus_species	Family	Nitrogen-fixing species
'Cold'	<i>Acacia dealbata</i>	Mimosaceae	Yes
	<i>Aotus ericoides</i>	Fabaceae	Yes
	<i>Banksia marginata</i>	Proteaceae	No
	<i>Bossiaea cinerea</i>	Fabaceae	Yes
	<i>Cassinia aculeata</i>	Asteraceae	No
	<i>Daviesia latifolia</i>	Fabaceae	Yes
	<i>Epacris impressa</i>	Epacridaceae	No
	<i>Eucalyptus pauciflora</i>	Myrtaceae	No
	<i>Eucalyptus rubida</i>	Myrtaceae	No
	<i>Eucalyptus tenuiramis</i>	Myrtaceae	No
	<i>Leucopogon ericoides</i>	Epacridaceae	No
	<i>Leucopogon virgatus</i>	Epacridaceae	No
	<i>Persoonia juniperina</i>	Proteaceae	No
	<i>Pultenaea juniperina</i>	Fabaceae	Yes
'Hot'	<i>Acacia flavescens</i>	Mimosaceae	Yes
	<i>Acacia leptostachya</i>	Mimosaceae	Yes
	<i>Allocasuarina torulosa</i>	Casuarinaceae	Yes
	<i>Bursaria incana</i>	Pittosporaceae	No
	<i>Corymbia citriodora</i>	Myrtaceae	No
	<i>Corymbia intermedia</i>	Myrtaceae	No
	<i>Corymbia trachyphloia</i>	Myrtaceae	No
	<i>Eucalyptus portuensis</i>	Myrtaceae	No
	<i>Gastrolobium grandiflorum</i>	Fabaceae	Yes
	<i>Grevillea glauca</i>	Proteaceae	No
	<i>Grevillea parallela</i>	Proteaceae	No
	<i>Lophostemon suaveolens</i>	Myrtaceae	No
	<i>Persoonia falcata</i>	Proteaceae	No
	<i>Petalostigma pubescens</i>	Picrodendraceae	No
<i>Planchonia careya</i>	Lecythidaceae	No	
<i>Pogonolobus reticulatus</i>	Rubiaceae	No	
<i>Xylomelum scottianum</i>	Proteaceae	No	
'Wet'	<i>Acacia floribunda</i>	Fabaceae	Yes
	<i>Astrotricha floccosa</i>	Araliaceae	No
	<i>Correa reflexa</i>	Rutaceae	No
	<i>Dodonaea triquetra</i>	Sapindaceae	No
	<i>Eucalyptus paniculata</i>	Myrtaceae	No
	<i>Eucalyptus umbra</i>	Myrtaceae	No
	<i>Lasiopetalum ferrugineum</i>	Malvaceae	No
	<i>Leptospermum polygalifolium</i>	Myrtaceae	No
	<i>Lomatia silaifolia</i>	Proteaceae	No
	<i>Macrozamia communis</i>	Zamiaceae	Yes
	<i>Persoonia linearis</i>	Proteaceae	No
	<i>Pomaderris ferruginea</i>	Rhamnaceae	No
	<i>Pultenaea daphnoides</i>	Fabaceae	Yes
	<i>Pultenaea flexilis</i>	Fabaceae	Yes
<i>Syncarpia glomulifera</i>	Myrtaceae	No	
<i>Synoum glandulosum</i>	Meliaceae	No	
<i>Xylomelum pyriforme</i>	Proteaceae	No	
<i>Allocasuarina sp</i>	Casuarinaceae	Yes	
<i>Acacia suaveolens</i>	Fabaceae	Yes	
<i>Banksia marginata</i>	Proteaceae	No	
<i>Boronia ledifolia</i>	Rutaceae	No	
<i>Corymbia gummifera</i>	Myrtaceae	No	
<i>Eriostemon australasius</i>	Rutaceae	No	
<i>Eucalyptus haemostoma</i>	Myrtaceae	No	
<i>Gompholobium glabratum</i>	Fabaceae	Yes	

Table 2 (continued)

Sites	Genus_species	Family	Nitrogen-fixing species	
'Wet'	<i>Grevillea buxifolia</i>	Proteaceae	No	
	<i>Grevillea speciosa</i>	Proteaceae	No	
	<i>Hakea dactyloides</i>	Proteaceae	No	
	<i>Hakea teretifolia</i>	Proteaceae	No	
	<i>Hibbertia bracteata</i>	Dilleniaceae	No	
	<i>Lambertia formosa</i>	Proteaceae	No	
	<i>Leptospermum trinervium</i>	Myrtaceae	No	
	<i>Persoonia levis</i>	Proteaceae	No	
	<i>Phyllota phyllicoides</i>	Fabaceae	Yes	
	<i>Pimelea linifolia</i>	Thymelaeaceae	No	
	'Dry'	<i>Acacia doratoxylon</i>	Fabaceae	Yes
		<i>Acacia oswaldii</i>	Fabaceae	Yes
		<i>Callitris glaucophylla</i>	Cupressaceae	No
		<i>Dodonaea viscosa ssp angustissima</i>	Sapindaceae	No
<i>Dodonaea viscosa ssp cuneata</i>		Sapindaceae	No	
<i>Dodonaea viscosa ssp spatulata</i>		Sapindaceae	No	
<i>Eremophila mitchelli</i>		Myoporaceae	No	
<i>Eucalyptus intertexta</i>		Myrtaceae	No	
<i>Geijera parviflora</i>		Rutaceae	No	
<i>Hakea tephrosperma</i>		Proteaceae	No	
<i>Pimelea microcephala</i>		Thymelaeaceae	No	
<i>Senna artemisioides var 1lft</i>		Fabaceae	Yes	
<i>Senna artemisioides var 3lft</i>		Fabaceae	Yes	
<i>Solanum ferocissimum</i>		Solanaceae	No	
<i>Spartothamnella puberula</i>	Lamiaceae	No		
<i>Acacia colletioides</i>	Fabaceae	Yes		
<i>Acacia havilandiorum</i>	Fabaceae	Yes		
<i>Acacia wilhelmiana</i>	Fabaceae	Yes		
<i>Bertya cunninghamii</i>	Euphorbiaceae	No		
<i>Beyeria opaca</i>	Euphorbiaceae	No		
<i>Brachychiton populneus</i>	Malvaceae	No		
<i>Cassinia laevis</i>	Asteraceae	No		
<i>Eremophila deserti</i>	Myoporaceae	No		
<i>Eremophila glabra</i>	Myoporaceae	No		
<i>Eucalyptus dumosa</i>	Myrtaceae	No		
<i>Eucalyptus socialis</i>	Myrtaceae	No		
<i>Eutaxia microphylla</i>	Fabaceae	Yes		
<i>Grevillea anethifolia</i>	Proteaceae	No		
<i>Melaleuca uncinata</i>	Myrtaceae	No		
<i>Micromyrtus sessilis</i>	Myrtaceae	No		
<i>Olearia decurrens</i>	Asteraceae	No		
<i>Olearia pimelioides</i>	Asteraceae	No		
<i>Philotheca difformis</i>	Rutaceae	No		
<i>Santalum acuminatum</i>	Santalaceae	No		
<i>Bossiaea walkeri</i>	Fabaceae	Yes		

Two C₄ species (*Atriplex stipitata* and *Triodia scariosa*) and two species of *Exocarpus* (*E. aphyllus* and *E. cupressiformis*) were excluded from the analysis.

foliage height). The Huber value enters here because Darcy's law describes total water flow through a stem of given area, whereas transpiration is expressed as the water flow per unit leaf area. The leaf-specific maintenance respiration cost of the sapwood, assuming a paraboloid stem, is

$$R_s = v_H r_s h \rho_s / 2 \quad (10)$$

where r_s is the sapwood specific respiration rate (s⁻¹) and ρ_s (mol m⁻³) sapwood density. The maintenance cost of sapwood per unit transpiration is given by the following:

$$a = R_s/E = r_s h^2 \rho_s \eta / 2 \Delta \Psi k_s \rho_w \quad (11)$$

This expression does not allow for the effect of the tapering of xylem elements, which would result in k_s decreasing with height and potentially reduce the dependence of a on height from quadratic to linear: see Becker *et al.* (2000), McCulloh *et al.* (2003, 2009).

Key implications of the theory

Equation (2) describes a dependence of χ_o on aridity through D . Other things being equal, a drier atmosphere implies a lower χ_o – because high D increases water flow through the plant, with no benefit in carbon gain. At very high D some plants show a decline in water flow, but this is necessarily accompanied by a further reduction in χ . Thus, we predict that χ should increase with MI, if temperature is held constant. (Temperature effects are considered below.) Equation (11) further suggests how plants in dry environments might counter this direct effect of aridity by lowering a , thereby increasing ξ . These include reduced height, and maintaining a constant $\Delta \Psi$ even at low soil water potential; both of which can be considered adaptations to drought.

Equations (2) and (11) also imply responses of ξ to temperature. K in eqn (2) increases steeply with temperature (Bernacchi *et al.* 2009), from 196 ppm at 10 °C to 1094 ppm at 30 °C. Other things being equal, this effect should lead to increased χ_o at higher temperature. Among the terms contributing to a , it is unlikely that the specific respiration rate of sapwood (r_s) over the growing season would be greater in a warmer environment, because of the ubiquitous thermal acclimation of basal respiration rates (Atkin & Tjoelker 2003). The term in eqn (11) expected to change most steeply with temperature is the viscosity of water (η) (Roderick & Berry 2001), 1.31 mPa s at 10 °C but only 0.798 mPa s at 30 °C. This response should increase ξ , and thereby increase χ_o , with increasing temperature. Thus, the temperature dependencies of both K and η lead to the prediction that χ should increase with temperature, if MI is held constant.

Graphical representations of data

Using N_{area} as an index of investment in photosynthetic capacity and g_s for water transport, Wright *et al.* (2003) observed that isopleths of A in $N_{\text{area}}-g_s$ space would be hyperbolas; and that for any pair of cost values for water and N, the least-cost investment strategy would be where the tangent to the curve has a slope equal to the ratio of these costs. This prediction was supported by field measurements from sites differing in aridity. Within a site, different species showed widely ranging values of N_{area} and g_s that nevertheless fell around a line corresponding to proportionality. The slope of this line was greater in drier sites, as expected when investment in water becomes more costly relative to investment in N.

The analogous representation in the Farquhar *et al.* (1980) model framework is in $V_{\text{cmax}}-g_s$ space. Using the eqn for Rubisco-limited photosynthesis together with Fick's law, it can be shown that the constant of proportionality between V_{cmax} and

g_s is a function only of χ , c_a and K ; and that for any given value of K , if both V_{cmax} and g_s are normalised by A (hereafter V and G), then the relationship between them collapses to a single hyperbola (see Appendix S2). The optimality theory above predicts steeper slopes of V_{cmax} with respect to g_s , and higher values of V (with correspondingly lower values of G) as the costs of transpiration increase relative to those of photosynthesis.

Sensitivity coefficients

Sensitivity coefficients (S) for χ_o with respect to different variables can be obtained by differentiation of eqn (2). Sensitivity coefficients represent the ratio of fractional change in one variable (here χ_o) to fractional change in another variable (x): $S = (x/\chi_o) \partial \chi_o / \partial x$. For an increment Δx with respect to a reference value x , the increment $\Delta \chi_o$ with respect to the corresponding reference value χ_o can be approximated by

$$\Delta \chi_o \approx S(\chi_o/x) \Delta x \quad (12)$$

The sensitivity coefficients are $-(1 - \chi_o)/2$ for a and D , and $(1 - \chi_o)/2$ for b and K . This approach makes it possible to predict effects of relative changes in factors affecting any of the terms influencing χ_o , without knowing their absolute values.

EMPIRICAL RESULTS

Approximate proportionality between V_{cmax} [25] and N_{area} can be seen in Fig. 1. The relationship across all sites is weaker than in some studies (e.g. Kattge *et al.* 2009) because the data include species from a wider range of environments. Niinemets *et al.* (2009) showed a comparable scatter. In pairwise comparisons, the slope of the $V_{\text{cmax}}-N_{\text{area}}$ relationship at the dry site is shallower ($P < 0.05$) than the slopes at all of the other sites. Thus, more N is required to support a given V_{cmax} at the dry site. The slope at the hot site is also shallower ($P < 0.05$) than the slope at the cold site. Other pairwise differences are non-significant.

Some N-fixing species have exceptionally high N_{area} for a given V_{cmax} , but others do not. The overall slope (across all sites) for N-fixers is slightly greater than that for non-N-fixers ($P < 0.05$), but the data do not suggest a general pattern of 'luxury consumption' or storage of N by N-fixers.

Within each site, species also show approximate proportionality between V_{cmax} and g_s , but the slopes vary between sites. The cold site shows a steeper slope than the warm site (Fig. 2a: $P < 0.01$), and the dry site shows a steeper slope than the wet site (Fig. 2b: $P < 0.01$). There was no significant difference between the slopes of the cold and the dry site, or the hot and the wet site. These findings agree with our predictions that χ should increase towards both warmer and wetter climates. Results obtained using V_{cmax} [25] instead of V_{cmax} were closely similar and all the statistical statements applying to the one variable also apply to the other.

The plots for N_{area} vs. g_s (Fig. 2c, d) show a similar pattern of differences between sites to the plots for V_{cmax} vs. g_s , with one anomaly: the $N_{\text{area}}-g_s$ slopes between the dry and wet sites

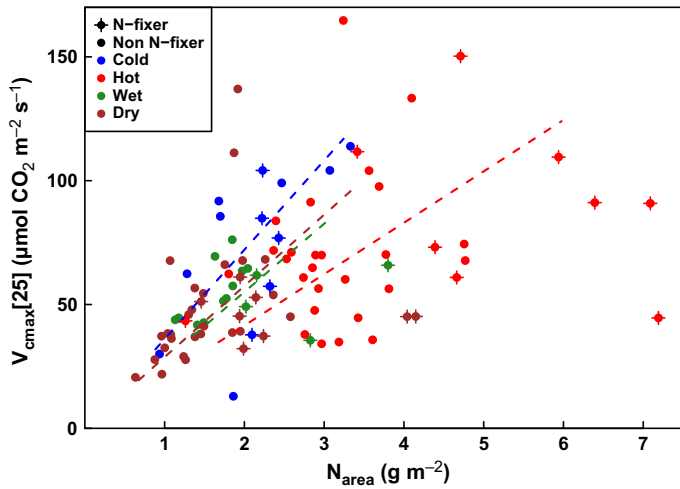


Fig. 1 Relationships between carboxylation capacity at 25 °C ($V_{\text{cmax}}[25]$) and nitrogen per unit leaf area (N_{area}), colour-coded by sites: cold = blue, hot = red, wet = green, dry = brown. N-fixing species are identified by crosses.

differ about threefold, while the $V_{\text{cmax}}-g_s$ slopes differ only about twofold. In pairwise comparisons, the pattern of differences is the same for N_{area} as for V_{cmax} , except that the $N_{\text{area}}-g_s$ relationship is shallower ($P < 0.05$) at the dry site than at the cold site. This difference is to be expected, given the lower ratio of V_{cmax} to N_{area} at the dry site (Fig. 1).

The same data after normalisation by A collapse on to a single hyperbola (Fig. 3). Equation (Appendix S2.2) is exact – the scatter is due to small variations in measurement temperatures affecting K . This curve is analogous to the equiproduction functions in Wright *et al.* (2003). Different positions along the curve correspond to different χ values, or equivalently, different combinations of V_{cmax} and g_s that yield the same assimilation rate. The species-mean values for each site are separated as our hypothesis predicts. The cold and dry sites both have higher mean values of V_{cmax}/A , and lower mean values of g_s/A , than the other two sites. The same contrasts are shown in the measured χ values (Fig. 3, inset). On average, species at the dry and cold sites have lower χ than species at the wet and hot sites.

To compare these differences with predictions of the change in χ_o between sites we applied eqn (12), summing the estimated effects of increments above and below the mid-point of temperature (for the cold-hot comparison) or ΔE (for the dry-wet comparison) (Appendix S3). Moving from the wet site to the dry site yielded $\Delta\chi_o \approx -0.186$. The observed difference between mean χ values is -0.155 . This is only 17% less than the prediction, but the difference is significant ($P < 0.002$), suggesting that some mitigation mechanism (e.g. lower stature) may be allowing plants at the dry site to maintain more open stomata than they could otherwise.

For the cold-hot comparison, moving from the hot site to the cold site yielded $\Delta\chi_o \approx -0.112$ from the temperature effect on K , and -0.034 from the temperature effect on η . In other words, the predicted effect of temperature on χ due to Rubisco kinetics is three times larger than the effect of viscosity.

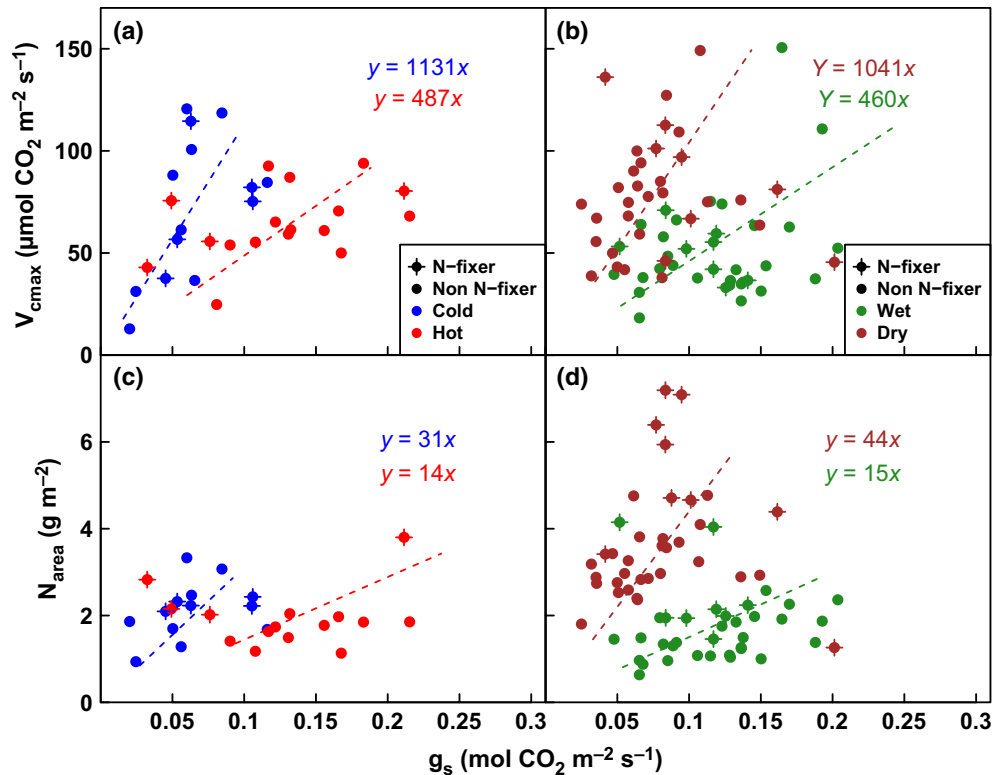


Fig. 2 Relationships between carboxylation capacity (V_{cmax}) and stomatal conductance to CO₂ (g_s) in (a) cold vs. hot sites and (b) wet vs. dry sites; (c), (d) corresponding relationships between nitrogen per unit leaf area (N_{area}) and g_s . Colours are as in Fig. 1. N-fixing species are identified by crosses.

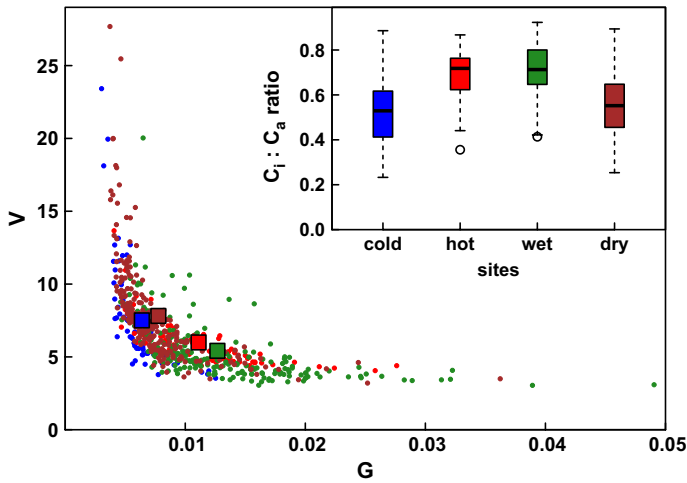


Fig. 3 Demonstration of the ‘unit production’ function, which represents a trade-off between carboxylation capacity ($V = V_{\text{cmax}}/A$) and transpiration ($G = g_s/A$). Colours as Fig. 1. Large squares denote values of V and G averaged over all species within each of the four sites. The inset shows box-and-whisker plots (mean, upper and lower quartiles, and minimum and maximum values) for the measured c_i/c_a values, similarly averaged over all species within each of the sites.

However, neither effect alone is sufficient to explain the observed difference between mean χ values (-0.154). The predicted effect via K is significantly ($P < 0.05$) smaller than this observed difference. However, the sum of predicted effects via K and η combined (-0.146) is statistically indistinguishable from the observed difference.

Our hypothesis further predicts that $\delta^{13}\text{C}$ (because of its relation to time-averaged χ) and N_{area} (because of its relation to $V_{\text{cmax}}[25]$) should covary, and each should be related to temperature and water availability. Fig. 4a, b show relationships of $\delta^{13}\text{C}$ to χ , and N_{area} to $\delta^{13}\text{C}$, in the complete data set. The slope for N_{area} vs. $\delta^{13}\text{C}$ is slightly steeper ($P < 0.05$) for N-fixers. The slope for $\delta^{13}\text{C}$ vs. χ is indistinguishable between N-fixers and non-N-fixers. Both N_{area} and $\delta^{13}\text{C}$ values at each site show systematic shifts, in the expected direction, with MI (Figs 4c, d). N_{area} shows a slightly steeper increase ($P < 0.01$) with MI in N-fixers, while the response of $\delta^{13}\text{C}$ is indistinguishable between N-fixers and non-N-fixers.

Multiple regressions using mean annual precipitation and temperature as predictors of N_{area} and $\delta^{13}\text{C}$ showed significant additional effects of temperature ($P < 0.001$; data not shown). However, in multiple regressions using MI and mean annual temperature as predictors, N_{area} showed no significant additional effect of temperature, while $\delta^{13}\text{C}$

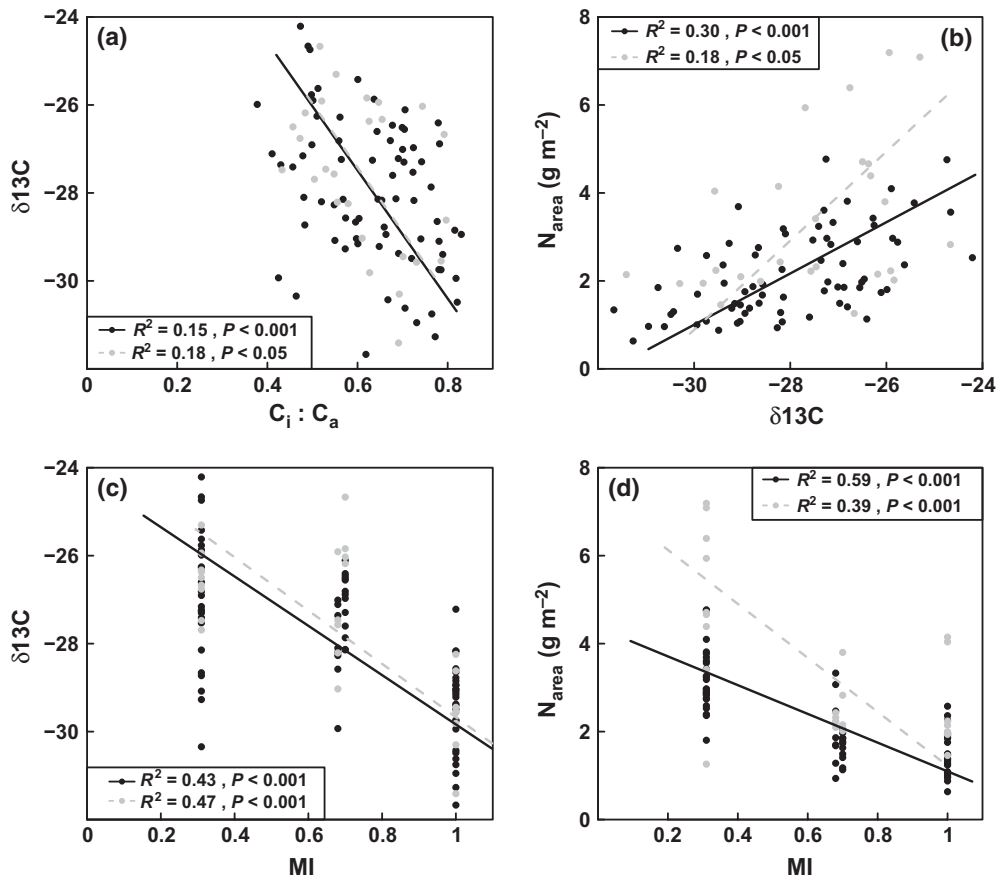


Fig. 4 Relationships between (a) $\delta^{13}\text{C}$ and c_i/c_a , (b) N_{area} and $\delta^{13}\text{C}$, (c) $\delta^{13}\text{C}$ and (d) N_{area} on the climatic moisture index (MI). Separate regressions are shown for N-fixing species (grey) and others (black).

showed a barely significant additional effects of temperature ($P < 0.05$). These findings suggest that MI adequately captures the response of N_{area} and the major part of the response of $\delta^{13}\text{C}$ to climate, including both temperature and water availability effects.

DISCUSSION

The predictability of environmental trends in leaf traits

The optimality hypothesis presented here provides a unifying explanation for the relative constancy of χ under a range of conditions, its quantitative variation with temperature and water availability, and the emergent responses of N_{area} and $\delta^{13}\text{C}$ to climate.

Our theoretical analysis and empirical results support the prediction of Wright *et al.* (2003) that high V_{cmax} and N_{area} in arid environments represent an adaptation to drought. Large investment in photosynthetic capacity allows a given assimilation rate to be maintained with lower stomatal conductance and reduced water loss. Reduced χ towards dry environments is predicted by eqn (2). The observed reduction in mean χ across species is slightly smaller than predicted, suggesting involvement of plant-level mechanisms that could lower the cost of transpiration as described by eqn (11).

The data also support our prediction of reduced χ in cold climates. The dependence of χ on K follows from the expression for ξ in eqn (2). Equation (11) also predicts an increase in a due to the greater viscosity of colder water. The predicted enzymatic effect is about threefold larger than the viscosity effect, but both are needed to explain the data.

It might have been expected that the increase in temperature from the cold to the hot site would be accompanied by increased D . But the two sites have similar MI values, and the change in χ is opposite to what would be predicted from increased D . From eqn (2), increased D with temperature should cause a *reduction* in χ from the cold to the hot site. We observe an increase.

A ‘trade-off’ or ‘complementarity’ between the marginal nitrogen and water use efficiencies of photosynthesis ($\partial A/\partial N$, approximately proportional to $\partial A/\partial V_{\text{cmax}}$, and $\partial A/\partial E$) is inevitable even for an individual plant over a short period, because of their opposite responses to χ (Field 1983; Farquhar *et al.* 2002). Palmroth *et al.* (2013) demonstrated this trade-off for *Pinus taeda* leaves grown under ambient and elevated c_a . They showed that leaves have higher efficiencies at high c_a , but that for each value of c_a they are disposed along a gradient characterised by a negative relationship between marginal nitrogen and water use efficiencies. Our analyses further show that the preferred χ values shift in a predictable way along this gradient.

The proportionality between V_{cmax} and N_{area} is not constant. In particular, more N is apparently required to support a given level of V_{cmax} in the dry climate. Prentice *et al.* (2011) found that the increase of N_{area} with aridity along the North East China Transect was steeper than expected given only the modest observed increase in PAR (photosynthetically active radiation) along the transect, and observed changes in $\delta^{13}\text{C}$. A requirement for extra N could arise due to greater investment in structural N in the thicker (low SLA) leaves characteristic of

arid sites, and/or to reduced mesophyll conductance (Niinemets *et al.* 1998) under drought conditions (Zhou *et al.* 2013). Low mesophyll conductance would mean that the standard gas-exchange measurement of V_{cmax} yields an underestimate of Rubisco activity. We do not have data to distinguish these possibilities. However, our finding of elevated V_{cmax} with disproportionately elevated N in the dry environment is consistent with the idea that wild plants compensate for the decline in apparent V_{cmax} – shown in drying experiments (Manzoni *et al.* 2011; Zhou *et al.* 2013) – by further increasing their investment in leaf N.

Optimisation criteria

Medlyn *et al.* (2011) showed that the Cowan-Farquhar optimality criterion is well approximated for *electron transport-limited photosynthesis* by eqn (2), but with $\xi = \sqrt{(3\Gamma^*/1.6\lambda)}$. Equation (2) is independent of c_a . The same criterion applied to Rubisco-limited photosynthesis (Katul *et al.* 2010) yields a related function, including the same dependence on \sqrt{D} (apparently a robust prediction from different approaches), but with an additional dependence on c_a (Medlyn *et al.* 2013). Our approach provides an alternative derivation of the formula of Medlyn *et al.* (2011), extending its applicability to Rubisco-limited photosynthesis.

It cannot be assumed *a priori* that any plant- or leaf-level property is optimised, not least because the optimisation criterion is unknown. Alternative criteria could be supposed to be consistent with maximising reproductive fitness. However, our results show that the hypothesis proposed by Wright *et al.* (2003) can be applied in a standard ecophysiological modelling framework, yielding a robust, consistent and quantitative biological interpretation of a range of observed trait relationships.

Towards a comprehensive approach to trait data analysis and vegetation modelling

The present generation of large-scale vegetation models treats ecophysiological properties of plants simplistically (Prentice & Cwiling 2013). Models neglect the diversity of trait combinations that co-exist (Wright *et al.* 2004; Maire *et al.* 2012). For example, values of V_{cmax} are usually imputed to a plant functional type (PFT), as a single value or a single-valued function of environmental variables (Haxeltine & Prentice 1996). A new theoretical framework is needed to assimilate into models the information now available on the variation, interrelationships and environmental dependencies of plant traits. Our hypothesis provides an essential element, by predicting environmental influences on the covariation of g_s and V_{cmax} . It provides a way to link the key model variables V_{cmax} , N_{area} and χ , and suggests analyses to investigate whether the relationships among them vary as predicted with wood hydraulic properties and environmental variables.

The value of χ predicted by eqn (2) is independent of actual values of V_{cmax} or g_s . However, V_{cmax} and the Huber value (v_H) are necessarily linked (Katul *et al.* 2003) due to the steady-state flow constraint, eqn (9). It seems likely that different species range along a spectrum from low carboxylation capacity and small Huber values (and/or poorly conductive

sapwood), to high carboxylation capacity and large Huber values (and/or highly conductive sapwood), while always satisfying the optimisation criterion. This idea is supported by large variation among species in Huber values, and in xylem hydraulic properties (Gleason *et al.* 2012). Large, co-ordinated variations in V_{cmax} , g_s and A are seen within sites (Fig. 2) and may represent a spectrum of plant hydraulics, which could be modelled as continuous variation within PFTs.

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STATEMENT OF AUTHORSHIP

ICP developed the theoretical analysis and wrote the first draft; ND carried out the graphical and statistical analyses; SMG and IJW provided field and laboratory measurements; all authors contributed to the interpretation of the results and the final manuscript.

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