Optimal Stomatal Control in Relation to Leaf Area and Nitrogen Content

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We introduce the simultaneous optimisation of water-use efficiency and nitrogen-use efficiency of canopy photosynthesis. As a vehicle for this idea we consider the optimal leaf area for a plant in which there is no self-shading among leaves. An emergent result is that canopy assimilation over a day is a scaled sum of daily water use and of photosynthetic nitrogen display. The respective scaling factors are the marginal carbon benefits of extra transpiration and extra such nitrogen, respectively. The simple approach successfully predicts that as available water increases, or evaporative demand decreases, the leaf area should increase, with a concomitant reduction in nitrogen per unit leaf area. The changes in stomatal conductance are therefore less than would occur if leaf area were not to change. As irradiance increases, the modelled leaf area decreases, and nitrogen/leaf area increases. As total available nitrogen increases, leaf area also increases. In all the examples examined, the sharing by leaf area and properties per unit leaf area means that predicted changes in either are less than if predicted in isolation. We suggest that were plant density to be included, it too would further share the response, further diminishing the changes required per unit leaf area.

Keywords optimal leaf area, stomatal conductance, optimality theory, resource substitution

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1 Introduction

In this paper, we examine some relationships between total plant leaf area and the properties of leaves, and between photosynthetic capacity per unit leaf area (taken as being related to the amount of nitrogen per unit leaf area), and the transpiration rate per unit area. We integrate earlier work on the optimisation of water use in relation to carbon gain (Cowan 1977, Cowan and Farquhar 1977) with that by Field (1983) on the optimisation of nitrogen allocation within a canopy in relation to canopy carbon gain. We consider the problem of identifying the optimal leaf area for

Table. List of symbols.

Symbol	Name	Units
A	net CO_2 assimilation rate of leaf	mol CO_2 m^{-2}_{leaf} s^{-1}
E	transpiration rate of leaf	mol H_2O m^{-2}_{leaf} s^{-1}
N	leaf functional N content	mol N m^{-2}_{leaf}
g	stomatal conductance to H_2O	mol air m^{-2}_{leaf} s^{-1}
a	leaf area	m^2_{leaf} m^{-2}_{ground}
t	time	s
$_t$ (subscr.)	total for plant	
A_t	net CO_2 assimilation rate of plant	mol CO_2 m^{-2}_{ground} s^{-1}
E_t	transpiration rate of plant	mol H_2O m^{-2}_{ground} s^{-1}
N_t	plant functional N content	mol N m^{-2}_{ground}
T	duration of a day	s
A^+	daily assimilation per unit leaf area	mol C m^{-2}
E^+	daily transpiration per unit leaf area	mol H_2O m^{-2}
λ	invariant value of $(E/A)_N$ in optimal plant	mol H_2O mol^{-1} CO_2
η	invariant value of dN/dA in optimal plant	mol N $mol^{-1} CO_2$ s
ν	invariant value of $(N/A)_E$ in optimal plant	mol N $mol^{-1} CO_2$ s
E_p	potential transpiration rate	mol H_2O m^{-2}_{leaf} s^{-1}
h	effective boundary layer conductance to water vapour	mol air m^{-2}_{leaf} s^{-1}
ε	rate of increase of latent heat with sensible heat of water vapour saturated air	dimensionless
r_b	boundary layer resistance to water vapour	
α	ratio of E_t to E_p, a measure of water availability	m^2 leaf m^{-2} ground
C_i (C_a)	intercellular (ambient) CO_2 mole fraction	mol CO_2 mol^{-1}air
k	carboxylation efficiency	mol air m^{-2}_{leaf} s^{-1}
m	ratio of k to N	mol air mol^{-1} N s^{-1}
A_V	RuBP carboxylation-limited expression for A	mol CO_2 m^{-2}_{leaf} s^{-1}
A_J	RuBP regeneration-limited expression for A	mol CO_2 m^{-2}_{leaf} s^{-1}
V	maximum RuBP carboxylation rate	mol CO_2 m^{-2}_{leaf} s^{-1}
J	potential electron transport rate	mol e^- m^{-2}_{leaf} s^{-1}
J_m	maximum potential electron transport rate	mol e^- m^{-2}_{leaf} s^{-1}
I_2	useful irradiance absorbed by PSII	mol photons m^{-2}_{leaf} s^{-1}
f	fraction of leaf absorbed light unavailable for CO_2 assimilation	unitless
θ	colimitation factor relating J to J_m and I_2	unitless
Γ	CO_2 compensation point	mol CO_2 mol^{-1}air
K'	effective Michaelis-Menten constant for Rubisco	mol mol^{-1}air
χ	marginal cost of assimilation in terms of X	mol CO_2 mol^{-1} X s^{-1}
X	additional limiting resource, e.g. phosphorus	mol X m^{-2} leaf
X_t	total X	mol X $plant^{-1}$

a plant that can add leaves indefinitely without causing self-shading. After obtaining some general optimisation results, we apply them to a simple model of photosynthesis and transpiration and seek general ecophysiological implications. We show that the simple model leads to relationships between leaf properties (e.g. nitrogen concentration, intercellular [CO_2]) and environmental factors (e.g. rainfall, irradiance, nitrogen availability) that are broadly predictive of those observed in the field. A more rigorously structured treatment of the equations underlying the linked optimisation of canopy nitrogen allocation, water use and carbon dioxide gain is given in the accompanying paper (Buckley et al. 2002).

Consider a set of leaves with a fixed total amount of nitrogen available to be shared among them (N_t) (strictly we consider only the nitrogen available for photosynthetic machinery). Consider also that there is a fixed supply of water to be transpired by the set of leaves at a total rate (E_t), and total leaf area per unit ground area (a). The nitrogen per unit area, N, is given from

$$N \cdot a = N_t \tag{1}$$

and the transpiration rate per unit area, E, is given from

$$E \cdot a = E_t \tag{2}$$

The idea is to maximise the total assimilation rate, $a \cdot A(N,E)$, where A is the assimilation rate per unit leaf area, and $A(N,E)$ denotes that assimilation rate is a function of both the nitrogen content and the transpiration rate (or, in more familiar terms, the stomatal conductance).

Variation over Time

More realistically, A and E are integrals over time, t. We limit our discussion to a single day ($t = 0$ to T) to preclude nitrogen movement among leaves. We seek to find the leaf area for which the maximum total amount of carbon is assimilated by the set of leaves over the period of interest, for example a day. The solution needed is the maximum value of aA integrated over the day, and will occur when the derivative of this integral with respect to a is zero, provided that the extremum is a maximum. Therefore we seek the solution of

$$\frac{d}{da}\left[a\int_0^T A\left(\frac{N_t}{a},\frac{E_t}{a},t\right)dt\right]=0 \tag{3}$$

Thus

$$\int_0^T A dt + a\frac{d}{da}\int_0^T A\,dt = 0 \tag{4}$$

and denoting the daily integrals with a superscripted plus sign ($^+$),

$$\int_0^T A\,dt = A^+ \tag{5}$$

and

$$\int_0^T E\,dt = E^+ \tag{6}$$

We rewrite Eq 4 as

$$A^+ + a\left(\frac{\partial A^+}{\partial N}\frac{dN}{da}+\frac{\partial A^+}{\partial E^+}\frac{dE^+}{da}\right)=0 \tag{7}$$

However, the direct dependence on area, a, can be eliminated by noting that:

$$\frac{dE^+}{da}=\frac{d}{da}\left(\frac{E_t}{a}\right)=-\frac{E_t}{a^2}=-\frac{E^+}{a} \tag{8}$$

and, similarly, that

$$\frac{dN}{da}=-\frac{N}{a} \tag{9}$$

so that Eq 7 becomes

$$A^+ = \frac{\partial A^+}{\partial N}N + \frac{\partial A^+}{\partial E^+}E^+ \tag{10}$$

Equation 10 says that there is an extremum in aA^+ when A^+ is homogeneous in N and E^+. Note, from Eq 7 above, that the first partial derivative in Eq 10 is evaluated at constant E^+, and that the second is evaluated at constant N.

As an aside we note that this may be rewritten as

$$\frac{\partial \ln A^+}{\partial \ln N}+\frac{\partial \ln A^+}{\partial \ln E^+}=1 \tag{11}$$

which is a result reminiscent of metabolic control analysis of photosynthetic CO_2 fixation (Giersch et al. 1990). It shows that at the optimum, the relative resource limitations sum to unity.

From earlier theoretical work on optimisation, the partial derivatives in Eq 10 should be constant for a given set of values for E_t and N_t. That is, in an optimal canopy, the effect of moving a tiny element of daily transpiration, E^+, from one place to another, without changing N, is zero, and the marginal gain of A^+, $(\partial A^+/\partial E^+)_N$, is *everywhere* the same (Cowan and Farquhar 1977) at $1/\lambda$. Within the optimal canopy the effect of movement of an infinitesimal element of nitrogen from one place to another is also zero, and the sensitivity of A^+ to N, at constant E^+, $(\partial A^+/\partial N)_{E^+}$ is *everywhere* the same, at $1/\nu$ (in Buckley et al. 2002, it is shown that if $(\partial A^+/\partial E^+)_N$ is not in fact invariant, the criterion for optimal nitrogen use is replaced by invariance of $1/\eta$). The marginal N cost of A^+ was discussed by Field (1983) and by Farquhar (1989).

When finite nitrogen and water supplies are optimally used, the following relations hold throughout the plant:

$$\frac{\partial A^+}{\partial N}=1/\nu \tag{12a}$$

and

$$\frac{\partial A^+}{\partial E^+} = 1/\lambda \tag{12b}$$

Note that the partial derivatives in Eq 12 represent potentially variable physiological properties, and the imposed constants ν and λ represent the optimal values of those properties. Applying Eq 12 to Eq 10 we obtain

$$A^+ = N/\nu + E^+/\lambda \tag{12c}$$

This identifies a local property of optimized gas exchange. It is easily summed over the total leaf area, a, to relate the resource constraints (E_t and N_t) to the total carbon gain of the plant ($A^+{}_t$):

$$A^+{}_t = N_t/\nu + E^+{}_t/\lambda \tag{12d}$$

Thus

$$\int_0^T aAdt = \frac{N_t}{\nu} + \frac{\int_0^T aEdt}{\lambda} \tag{12e}$$

Equation 12d appears to be linear in N_t and E_t^+. However, this expression describes a physiological relationship that holds only at the optimum. As the resource supplies (N_t and E_t^+) vary, so will the values of ν and λ. This is clarified by noting that $\nu = \nu(N_t, E_t^+)$ and $\lambda = \lambda(N_t, E_t^+)$. We further note that the result could be simply extended to include some other limiting resource, X, such as phosphorus, so that

$$A^+ = N/\nu + E^+/\lambda + X/\chi \tag{13}$$

where is the marginal cost of assimilation (at constant N and E^+) in terms of X. Eq 13 may appear inconsistent with Eq 12c, but, as before, the invariant marginal costs (ν, λ, and χ) each depend on all three resource supplies ($\nu = \nu(N_t, E_t^+, X_t)$ and so forth), so the values of ν and λ that apply to Eqs 12c and 13 are not the same. Presumably, when phosphorus is limiting, the marginal costs ν and λ become greater than when phosphorus is plentiful.

2 Transpiration and Diffusion of Carbon Dioxide

To find how Eqs 12 and 13 translate into specific dependence on leaf area, we need expressions for the diffusional exchange of water vapour and carbon dioxide, considered in this section, and of the biochemistry of photosynthesis, considered in subsequent sections.

The transpiration rate per unit leaf area, E, has a rectangular hyperbolic dependence on stomatal conductance to the diffusion of water vapour, g, with a maximum rate, E_p, the potential transpiration rate per unit leaf area. Thus:

$$aE = a\frac{gE_p}{g+h} = E_t \tag{14}$$

where

$$h = 1/((\varepsilon + 1.1)r_b) \tag{15}$$

r_b is the boundary layer resistance to water vapour and ε is the rate of increase of latent heat of water vapour saturated air with increase in sensible heat (Cowan 1977). (Note the accompanying paper, Buckley et al. 2002, identifies g with total conductance to CO_2).

We introduce α, which can be regarded as the ratio of the supply of water to the plant roots to the evaporative power of the atmosphere, as

$$\alpha = E_t/E_p \tag{16}$$

Note that α has the units of leaf area per unit ground area. It represents the leaf area that would be required to match a total transpiration rate of E_t were the stomatal conductance infinite. Rearranging Eq 14 using Eq 16, we have

$$g = \frac{\alpha h}{a - \alpha} \tag{17}$$

We describe the rate of diffusion of CO_2 from the atmosphere to the intercellular spaces, with C_a and C_i representing the CO_2 mole fractions outside and inside the leaf, respectively, by:

$$A = \frac{C_a - C_i}{1.6/g + 1.37r_b} \tag{18}$$

3 Application to a Simple Model of Photosynthesis

We now combine the above equations of optimisation and diffusion with one of the biochemistry of photosynthesis. For our initial exploration of what the optimisation of canopy carbon accumulation means explicitly in terms of dependence on a, we start with the simplest case. We consider steady conditions with no temporal (or spatial) variation in environment (and no self-shading).

We also start with the most simplified description of the biochemistry of rate of assimilation by a leaf, equivalent to a linear dependence of A on C_i, the intercellular [CO_2].

$$A = k(C_i - \Gamma) \tag{19}$$

Γ is the compensation point, and k is the carboxylation efficiency, here taken as proportional to the nitrogen content per unit area (N):

$$k = m \cdot N = mN_t / a \tag{20}$$

Solving Eqs 18 and 19, we obtain

$$A = \frac{C_a - \Gamma}{1/k + 1.6/g + 1.37 r_b} \tag{21}$$

Combining the condition for optimal leaf area (Eq 3) and the expansion of A into its responses to E and N (Eq 10), we have

$$\frac{d(aA)}{da} = A - \left.\frac{\partial A}{\partial E}\right)_N E - \left.\frac{\partial A}{\partial N}\right)_E N$$

It is simple to substitute Eqs 17, 20 and 21 (for example, into Eq A7 of the Appendix) and find that this result is always negative, i.e. that there is no optimum. More succinctly one can use Eqs 17, 20 and 21 to find the total assimilation rate per unit ground area:

$$A_t = aA = \frac{C_a - \Gamma}{\dfrac{1}{mN_t} + 1.6(1/\alpha - 1/a)((\varepsilon + 1.1)r_b) + 1.37 r_b / a} = \frac{C_a - \Gamma}{\dfrac{1}{mN_t} + \dfrac{1.6}{\alpha h} - [1.6(\varepsilon + 1.1) - 1.37] r_b / a} \tag{22}$$

Since the term in square brackets is always positive, aA decreases as a increases. This means, for this simple model, that the maximum total assimilation rate, aA, occurs with minimum area, and hence with the maximum conductance and the greatest nitrogen/area. To transpire all the available supply of water with a finite g, a must be greater than α (see Eq 17), and so the maximum aA occurs when a is infinitesimally greater than α.

In this simplest of cases, the optimisation depends only on subtle differences in the effects of the boundary layer resistance on A and E. In the next section we see strong effects when, at non-saturating light intensity, the capacity for photosynthesis is no longer linearly proportional to nitrogen concentration.

4 Extension Using a Biochemical Model of Photosynthesis

We first extend the treatment to use Rubisco kinetics (Farquhar et al. 1980) with

$$A = A_V = \frac{V(C_i - \Gamma)}{C_i + K'} \tag{23}$$

where V is the maximum velocity, and K' is the effective Michaelis Menten constant for carboxylation, taking into account oxygen inhibition. When V is made proportional to N, we obtain the same result as in the previous section. That is, that aA_V increases as a decreases to its lower bound, α (see Eq A8 in the Appendix and Fig. 1).

Of course, at large values of A, the system will become electron transport rate (J) limited, because of insufficient absorbed irradiance, I.

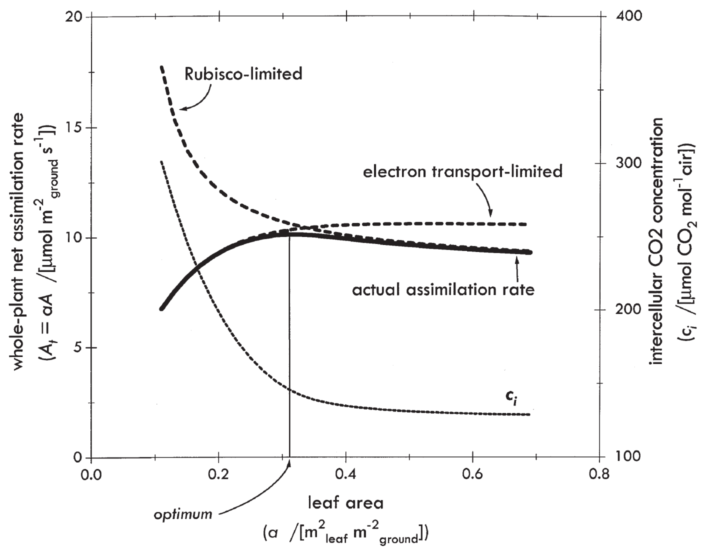

Fig. 1. The products aA_V (Rubisco-limited whole plant assimilation rate) and aA_J (electron transport-limited rate) are plotted versus leaf area, a. The actual value of total assimilation rate is the minimum of aA_V and aA_J (solid line). Its maximum value, which therefore defines the optimal leaf area, a, occurs when aA_J is limiting, but near to where aA_V and aA_J intersect, corresponding to co-limitation by Rubisco and electron transport. The parameter α, which is a measure of rainfall (see Eq 16 in the text) = 0.05. C_a = 360 µmol/mol.

We replace Eq 23 by

$$A = A_J = \frac{J(C_i - \Gamma)}{4(C_i + 2\Gamma)} \tag{24}$$

and take the maximum rate of electron transport, J_m, as being proportional to N, in the expression of Farquhar and Wong (1984)

$$\theta J^2 - (J_m + I_2) + J_m I_2 = 0 \tag{25}$$

where I_2 is the irradiance effectively absorbed by photosystem II

$$I_2 = (1 - f)I/2 \tag{26}$$

and f represents losses. Now we obtain the opposite result, and aA_J generally decreases as a decreases (see final paragraph in the Appendix and Fig.1). Fundamentally this occurs because A (= A_J) is no longer proportional to N.

Combining Eqs 23 and 24 as

$$A = \min\{A_V, A_J\} \tag{27}$$

we find that aA has a maximum on the $a\,A_J$ locus, but typically near the "breakpoint" where $A_J = A_V$. Fig. 1 plots aA_V and aA_J vs. a for $\alpha = 0.1$, with I = 1000 µmol m^{-2}s^{-1} and shows such a result. von Caemmerer and Farquhar (1981) noted that in terms of optimal water use efficiency, stomatal conductance should often adjust so that photosynthesis is working at this transition.

At first sight, when the calculations are tested, it appears that the homogeneity condition (Eqs 10 to 12) does not apply, but this is because Eq 27 is not continuously differentiable at the breakpoint. If Eq 27 is smoothed by hyperbolic minimization, say,

$$0.99A^2 - (A_V + A_J) + A_V A_J = 0 \tag{28}$$

(shown as the smooth curve of actual assimilation rate in Fig. (1)), then the homogeneity condition holds at the optimum.

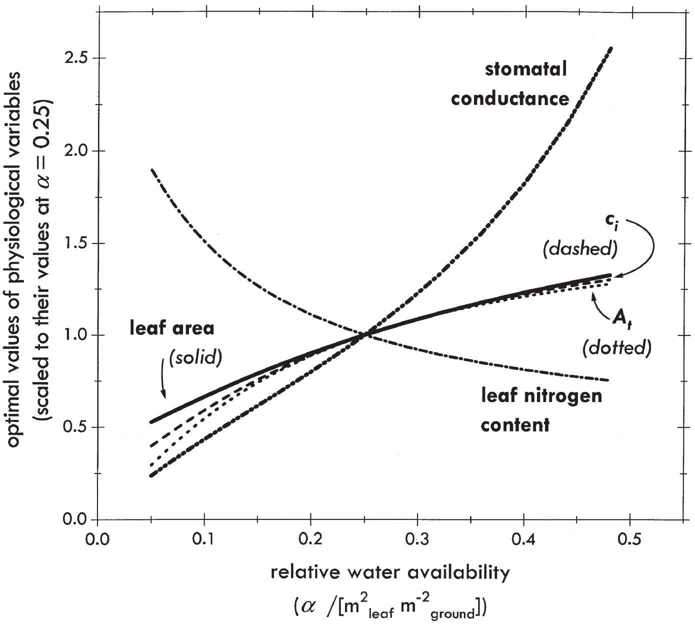

Fig. 2. Stomatal conductance, g, leaf area, a, assimilation rate per unit leaf area, A, intercellular (CO_2), $C_{i,}$ and leaf nitrogen concentration, N, are shown as they relate to α, which is a measure of rainfall (see Eq 16 in the text). N declines in a saturating fashion with rainfall; leaf area, assimilation rate and C_i increase in a saturating manner; and stomatal conductance increases with rainfall, but with slightly positive curvature. The values of parameters are scaled to their values at $\alpha = 0.25$, which are $g = 0.55$ mol $m^{-2}s^{-1}$, $a = 0.51$ m^2 leaf/m^2 ground, $A = 19.1$ µmol $m^{-2}s^{-1}$, and $C_i = 226$ µmol/mol. The nitrogen content is that giving a Rubisco capacity of $V = 400$ µmol m^{-2}leaf s^{-1}, and an electron transport capacity of $J_m = 2.1 \cdot 400$ µmol m^{-2} leaf s^{-1}. Also, $C_a = 360$ µmol/mol.

4.1 How Does the Optimisation Change with Different Water Supply/Aridity

While the optimisation condition of homogeneity (Eqs 10 to 12) is general enough to include diurnal variation in the environment, we restrict our exploration at this stage to a static environment representing a day's duration. While drought is a stochastic phenomenon, the average period between rainfalls is usually considerably greater than a day in most places of interest, so that λ can be taken as a constant here.

We now examine how the simple model, incorporating leaf biochemistry (Eqs 23 to 28), but with no diurnal variation in light intensity or other variables, or effects of evaporative cooling on photosynthesis, predicts response to change in α, the supply of water relative to demand.

Using numerical computation we see that as α increases, so too do a, g, A and C_i, in the example chosen (see Fig. 2). As α changes from 0.05 to 0.3, a factor of 6, equivalent to a 6-fold increase in total transpiration, E_t, the conductance g and area a share the required increase, becoming 3.3 times and 2.9 times their respective initial values. For $\alpha > 0.3$, modelled stomatal conductance increases more than leaf area. In practice, numbers of plants per unit area also increase with increasing α, and so the sharing will be three-way, diminishing still further the changes required at the individual leaf level.

Our simple analysis suggests that as conditions become more arid, there should be both a smaller stomatal conductance and less leaf area with greater nitrogen per unit area. The associated decline in intercellular CO_2 concentration means

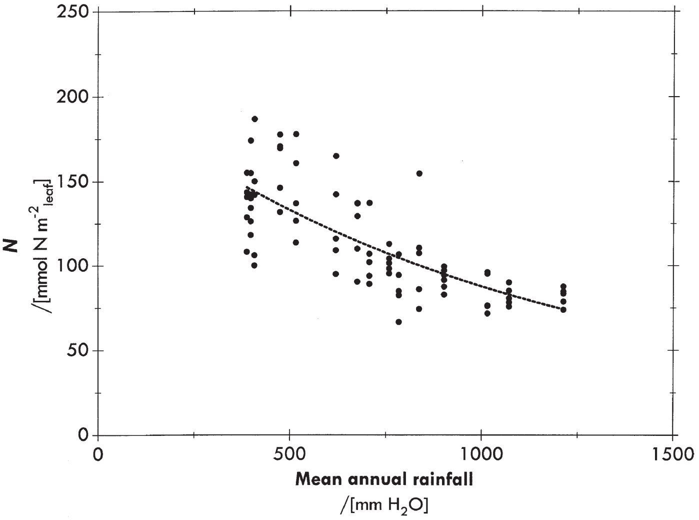

Fig. 3. Nitrogen per unit leaf area of *Eucalyptus dichromophloia* leaves collected along the Northern Australia Tropical Transect *vs*. mean annual rainfall at collection site. These data form part of a larger unpublished study by Miller, Williams and Farquhar. Details of collection are as those described for carbon isotope discrimination by Miller et al. (2001). The dotted line has the form $N = N_0 \exp(-kr)$, where r (mm) is rainfall, and N_0 = 196 mmol N m^{-2}, and $k = 8 \cdot 10^{-4}$/mm.

less carbon isotope discrimination and this result is in accord with observations of several authors (eg Stewart et al. 1995, Buchmann et al. 1998), including those working at the drier end of the North Australia Tropical Transect (NATT) (Schulze et al. 1998 and Miller et al. 2001). The NATT data also show the same sense of curvature in C_i or discrimination as seen in Fig. 2. B. Lamont et al. (personal communication) observed the same pattern in *Hakea* species along a rainfall gradient in Western Australia, and in other members of the Proteaceae along a rainfall gradient in the Cape of South Africa. W. Stock (personal communication) examined two species of *Ptilotus* along a rainfall gradient from Perth, W. Australia (834 mm) to Kalgoorlie (278 mm). He found that carbon isotope discrimination decreased and nitrogen per unit leaf area increased as rainfall diminished.

The increase in N with decreasing water availability was also observed among diverse Eucalypt species by Mooney et al.(1978), and has also been seen among Eucalypts on the NAT Transect (Schulze et al. 1998, Miller, Williams and Farquhar, unpublished data) and among other perennial species in eastern Australia (Wright et al. 2001).

Fig. 3 shows a subset of the unpublished data of Miller et al. The data are of sun-exposed leaves from the upper parts of *Eucalyptus dichromophloia* trees, collected near the middle range of the NAT Transect (see Miller et al. 2001 for details), and plotted against mean annual rainfall at the collection site. The nitrogen concentration (expressed per unit leaf area, but not as a mass fraction) decreases with increasing rainfall. There is a hint that the slope flattens at high rainfall, and this is clearly evident when data for all *Eucalyptus* species in the study are synthesised (Miller et al. unpublished).

The model shows the same curvature (see Fig. 2). In the model it occurs because N_t is constrained, and so N is proportional to $1/a$. It turns out that a increases reasonably linearly with α, giving the positive curvature seen in N. The same curvature is seen in data on *Hakea* and other members of the Proteaceae (B.B. Lamont, P.K. Groom and R.M. Cowling, personal communication). The same shape occurs in the data on leaf mass per unit area in the above references, as

N/mass changes less, and is also seen in the plot by Roderick et al. (2000). The latter authors draw attention to the need to consider soil acidity in assessing rainfall gradients, and obviously the present treatment is blind to those effects.

It is important to note, also, that it is only the nitrogen associated with photosynthesis that is included in our model. Nitrogen that does not increase photosynthesis directly (for example, N in chlorophyll, light-harvesting complexes, and lignin) introduces an inhomogeneity in the relationship between A and N. Inclusion of light-harvesting inhomogeneities would favor higher leaf areas, as the relative nitrogen cost of light-harvesting is lower in thin leaves (Evans 1998), but nitrogen overhead that does not necessarily scale with photosynthetic capacity, such as that required for manufacturing epidermal and vascular tissue, would favour lower leaf areas. It is thus not certain, *a priori*, what effect inclusion of other nitrogen inhomogeneities would have on the results of this analysis.

The modelling above relates to the ratio, α, of water supply, E_t, to potential evaporation, E_p, and so can be interpreted in terms of humidity, or of thermal radiation, as well as rainfall. So, as humidity decreases, or thermal radiation increases, the result is the same as rainfall decreasing, i.e. a decrease of total leaf area (a) – we say nothing about the size of individual leaves but do use a particular value of r_b for computations – and a concomitant increase in N per unit leaf area (N).

4.2 How Does the Optimisation Change with Changing Irradiance?

The model predicts that as irradiance decreases, leaf area, a, increases and nitrogen per unit leaf area, N, decreases concomitantly. For the same parameter values as above, and with α set at 0.3, a is 0.37 at 2000 µmol m^{-2}s^{-1}, 0.44 at 1500, 0.59 at 1000, 1.04 at 500, and 2.50 at 200. In the calculations α is constant, but in practice thermal radiation and irradiance are correlated. Introducing such a correlation merely reinforces the pattern above. The prediction is in line with observations of decreases in N and photosynthetic capacity as growth irradiance is reduced (e.g. von Caemmerer and Farquhar 1984, Evans 1998).

In practice, of course, as a becomes larger, self-shading becomes more important. Such effects on canopy gas exchange are dealt with numerically in Buckley et al. (2002). An analytical approach to the optimisation equations required when self-shading occurs will be developed elsewhere.

4.3 How Does the Optimisation Change with Changing Nitrogen Availability?

The model predicts that as total nitrogen increases, leaf area, a, increases. The model is parameterised such that nitrogen per unit leaf area, N, is represented by maximum Rubisco activity, V. In the examples above, the latter was set at $100/a$ µmol m^{-2}s^{-1}. For the same parameter values as above ($I = 1000$, $\alpha = 0.3$), a is 0.31 (the minimum) at $V = 25/a$ µmol m^{-2}s^{-1}, 0.39 at $50/a$, 0.59 at $100/a$, 0.72 at $150/a$, and 0.84 at $V = 200/a$. This means that the eight-fold increase in total nitrogen, N_t, is accompanied by only a 2.7-fold increase in Rubisco/leaf area, and a 3-fold increase in leaf area, a. Assimilation rate per unit leaf area A, increases by only 57%, from 22.8 to 30 µmol m^{-2}s^{-1}, because of the constraint on total transpiration, and hence on conductance and intercellular (CO_2). The result is in accord with physiological experience of what happens when nitrogen availability is increased to plants. Masle (1982) and Evans (1983) showed how leaf area in wheat increased with additional available nitrogen, for example. Of course in the present simulation water use is constrained to a fixed rate, and we are unaware of papers where nitrogen effects on leaf area were so constrained. However, the result highlights the essential linkage between the optimization of nitrogen and water use. In fact, Buckley et al. (2002) show that it is not possible to identify optimal values for leaf nitrogen content for leaves within a canopy unless the response of stomatal conductance to a hypothetical perturbation in N is known. One obvious solution to this dilemma is to constrain stomatal behavior by optimising both water and nitrogen use simultaneously, as we have done here.

5 Discussion

The simplifications involved in the modelling are numerous. Only transpiration, photosynthesis, and the nitrogen associated with photosynthesis are considered. There is no self shading, or consideration of other nitrogen costs, or of leaf longevity. The optimisation has been written in terms of the "benefit" of carbon assimilation. In practice, there are costs in terms of the carbon required to construct a leaf, and these need to be paid back over the lifetime of the leaf (Givnish 1986). See also Reich et al. (1997) for interesting data relating leaf properties to longevity.

Even the treatment of photosynthesis is simplified with no distinction being made between the [CO_2] intercellular spaces and that at the sites of carboxylation. Such a treatment would more realistically penalise high N concentrations. The N costs of light harvesting are also ignored, and the N within the leaf is assumed to be distributed in such a way that potential electron transport rate, J, is always homogeneous in N and I (Eq 25). In practice, this may be impossible even in theory for leaves that receive solar beam light from different angles over the day, and scattered light in varying quantities and directions over the day. In Buckley et al. (2002) we also explore a counter-example, by including the overhead N cost for light capture and assuming uniform distribution of all other N within a leaf (Badeck 1995). This represents a limiting, non-optimal scenario (Farquhar 1989).

Despite these simplifications, the treatment developed in the present study manages to predict several features relating to aridity, irradiance and nitrogen availability that are in accord with observations. These are summarised below.

6 Summary

An equation is developed for the simultaneous optimisation of nitrogen and water use by leaves of a non-self-shading plant over a short period of time, such as a day. The result is that total assimilation is a scaled linear sum of total nitrogen and total transpiration (see Eq 12). The result applies when environmental conditions vary diurnally, but, again, with no self-shading.

This somewhat general description of the optimisation of CO_2 assimilation with respect to water use and the display of nitrogen is then explored for ecophysiological insight. It is applied to a simple model of the environment, where there is no variation in time or space (and no self-shading), and assessed using a biochemical model of photosynthesis. The analysis suggests that as conditions become more arid, there should be (1) a smaller stomatal conductance, (2) less leaf area per plant, (3) greater nitrogen per unit leaf area, and (4) less carbon isotope discrimination. These predictions are in accord with observations of several authors. Similarly, the simple model also predicts the commonly observed decrease in nitrogen per unit leaf area, and in photosynthetic capacity, as growth irradiance is reduced, and the increase in leaf area as available nitrogen increases.

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Appendix. Dependence of canopy assimilation rate on leaf area for temporally and spatially constant environmental conditions, using a biochemical model of photosynthesis.

We seek the condition that the following expression is zero, in order to find where a has a value leading to maximum aA.

$$\frac{d(aA)}{da} = A + a\frac{\partial A}{\partial N}\frac{dN}{da} + a\frac{\partial A}{\partial E}\frac{dE}{da} = A + a\frac{\partial A}{\partial N}\frac{d(N_t / a)}{da} + a\frac{\partial A}{\partial E}\frac{d(E_t / a)}{da} = A - \frac{\partial A}{\partial N}N - \frac{\partial A}{\partial E}E \qquad \text{(A1)}$$

We first note that the second term on the right hand side of Eq A1 is

$$\left.\frac{\partial A}{\partial N}\right)_E \equiv \left.\frac{\partial A}{\partial N}\right)_g$$

To obtain the latter term:

$$\left.\frac{\partial A}{\partial N}\right)_g = \left.\frac{\partial A}{\partial N}\right)_{C_i} + \left.\frac{\partial A}{\partial C_i}\right)_N \left.\frac{\partial C_i}{\partial A}\right)_g \left.\frac{\partial A}{\partial N}\right)_g = \frac{\left.\frac{\partial A}{\partial N}\right)_{C_i}}{1 - \left.\frac{\partial A}{\partial C_i}\right)_N \left.\frac{\partial C_i}{\partial A}\right)_g} \qquad \text{(A2)}$$

and, in turn, the last term on the denominator of Eq A2 is

$$\left.\frac{\partial C_i}{\partial A}\right)_g = -\left(1.37 r_b + 1.6/g\right) \qquad \text{(A3)}$$

Substituting Eq A3 into Eq A2 we now have the second term in Eq A1. The last term in Eq A1 is

$$\frac{\partial A}{\partial E}E = \frac{\partial A / \partial g}{\partial E / \partial g}E \qquad \text{(A4)}$$

In order to evaluate Eq A4 we first note that Eq 14 implies that

$$\frac{E}{\partial E / \partial g} = g\left(1 + g/h\right) \qquad \text{(A5)}$$

To complete the evaluation of Eq A4 we now evaluate $\frac{\partial A}{\partial g}$. Ignoring temperature effects as g changes (see Buckley et al. 2002 for what would be required)

$$\frac{\partial A}{\partial g} = \frac{\partial A}{\partial C_i}\frac{dC_i}{dg} = \frac{\partial A}{\partial C_i}\left(\frac{\partial C_i}{\partial g} + \frac{\partial C_i}{\partial A}\frac{\partial A}{\partial g}\right) = \frac{\frac{\partial A}{\partial C_i}\frac{dC_i}{dg}}{1 - \frac{\partial A}{\partial C_i}\frac{\partial C_i}{\partial A}} = \frac{\frac{\partial A}{\partial C_i}\frac{1.6A}{g^2}}{1 + \frac{\partial A}{\partial C_i}\cdot\left(1.37 r_b + 1.6/g\right)} \qquad \text{(A6)}$$

Equations A6 and A5 together form the last term in Eq A1. So that by substituting Eq A3 into Eq A2 as the second term in Eq A1, we obtain

$$\frac{d(aA)}{da}=A-\frac{\left.\frac{\partial A}{\partial N}\right)_{C_i}}{1+\left.\frac{\partial A}{\partial C_i}\right)_N(1.37r_b+1.6/g)}N-\frac{\frac{\partial A}{\partial C_i}\frac{1.6A}{g}(1+g/h)}{1+\frac{\partial A}{\partial C_i}\left(1.37r_b+1.6/g\right)}=A\left[1-\frac{\left.\frac{\partial A}{\partial N}\right)_{C_i}\frac{N}{A}+\frac{\partial A}{\partial C_i}(1.6/g+1.6/h)}{1+\left.\frac{\partial A}{\partial C_i}\right)_N\left(1.6/g+1.37r_b\right)}\right] \quad (A7)$$

We need to evaluate $\left.\frac{\partial A}{\partial N}\right)_{C_i} N$ under both Rubisco and electron transport limited conditions.

Consider first the Rubisco-limited rate, as given by Eq 23 in the main text:
In this case

$$\left.\frac{\partial A_V}{\partial N}\right)_{C_i} N = A_V \quad (A8)$$

and because, from Eq 15, $1.6/h > 1.37r_\mathrm{b}$, the second (large) term in the brackets on the right hand side of Eq A7 is always greater than 1.
Thus aA_V decreases with a (that is $\frac{d(aA_V)}{da}<0$), and only becomes zero when A is zero, so that the homogeneity condition is not met.
See text after Eq 23.

In the electron-transport limited condition (A_J; see Eq 24) it is clear that

$$\left.\frac{\partial A_J}{\partial N}\right)_{C_i}\frac{N}{A}=\frac{\partial A_J}{\partial J}\frac{dJ}{dN}\frac{N}{A}<1$$

because it is J_m that is linear in N, and not J, except at very low capacities (large a).
This means that aA_J generally increases with a

(that is, $\frac{d(aA)}{da}$ is generally > 0 but becoming zero and reversing slightly at large a).

See text after Eq 28.

In summary, the homogeneity condition (Eq 12) occurs in the branch $A = A_\mathrm{J}$, but usually near the "breakpoint" where $A_\mathrm{J} = A_\mathrm{V}$.