Research reviews
Biotic and abiotic consequences of differences in leaf structure

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SUMMARY

Both within and between species, leaves of plants display wide ranges in structural features. These features include: gross investments of carbon and nitrogen substrates (e.g. leaf mass per unit area); stomatal density, distribution between adaxial and abaxial surfaces, and aperture; internal and external optical scattering structures; defensive structures, such as trichomes and spines; and defensive compounds, including UV screens, antifeedants, toxins, and silica abrasives. I offer a synthesis of selected publications, including some of my own. A unifying theme is the adaptive value of expressing certain structural features, posed as metabolic costs and benefits, for (1) competitive acquisition and use of abiotic resources (such as water, light and nitrogen) and (2) regulation of biotic interactions, particularly fungal attack and herbivory. Both acclimatory responses in one plant and adaptations over evolutionary time scales are covered where possible. The ubiquity of trade-offs in function is a recurrent theme; this helps to explain diversity in solutions to the same environmental challenges but poses problems for investigators to uncover numerous important trade-offs. I offer some suggestions for research, such as on the need for models that integrate biotic and abiotic effects (these must be highly focused), and some speculations, such as on the intensity of selection pressures for these structures.

Key words: leaf anatomy, leaf morphology, gas exchange, herbivory, leaf nutrients, chemical defence, optimization, trade-off.

INTRODUCTION

Both between and within plants (individuals or species), leaves are diverse in structure. Variations are prominent in, for example, linear dimensions, dissection of the margins, dry mass per unit area, nutrient content, cell size, optical scattering and absorption, stomatal density and apertures, presence or absence of trichomes, and cuticle composition. This diversity is demonstrably under genetic control, including the plastic responses such as leaf size and mass per unit area in response to the light environment. We presume that the differences are largely adaptive, either for acquiring resources (mostly in photosynthesis) or in biotic interactions, such as retarding leaf herbivory. In some cases, the adaptive value of a structural feature can be demonstrated directly, by using some innovative methods. Constraining leaf angle displays can demonstrate the value of leaf angles for photosynthesis (Ehleringer & Hammond, 1987); removing trichomes can demonstrate their effectiveness against herbivory (Kanno, 1996). Many other quantitative benefits (and costs) have been investigated. In this review, I concentrate on the costs, benefits and associated trade-offs for distinct structural features, above the level of genes and biochemistry. Many features, such as trichomes or stomata, show adaptive value for multiple purposes (for an example, see Press, 1999). For example, trichomes can function both in energy balance and in defence, and in defence against both microbes and herbivores. Trade-offs between costs and benefits, particularly as marginal costs and benefits, are expected to be close if function is well optimized by natural selection. Indeed, close balances are often observed. This closeness supports the variability of structures, and it explains partly how very divergent structures can provide adaptation to the same selection pressures in different plant species.
LEAF STRUCTURE AFFECTS RESOURCE ACQUISITION AND USE

The cuticle

The cuticle, present in almost every land plant, is foremost a barrier against water loss as well as against pathogen invasion. The cuticle also offers much protection against a loss of solutes to rain (leaching by throughfall), although some does occur, especially in acid conditions (Pearcy & Baker, 1991). Because leaves flex in the wind and other stresses, the cuticle must be flexible or layered. Abrasion of the cuticle in high wind can increase water loss by transpiration (Grace, 1974; Pitcairn & Grace, 1985). The layer of wax or cutin is commonly rather thin (several μm), except in many xeromorphic plants, where it can reach 60 μm (Ihlenfeldt & Hartmann, 1982). Consequently, the metabolic cost of constructing the cuticle is typically a few percent of total leaf construction cost. (This accounting excludes structuring the cuticle in high wind can increase water loss by transpiration (Grace, 1974; Pitcairn & Grace, 1985). The layer of wax or cutin is commonly rather thin (several μm), except in many xeromorphic plants, where it can reach 60 μm (Ihlenfeldt & Hartmann, 1982). Consequently, the metabolic cost of constructing the cuticle is typically a few percent of total leaf construction cost. (This accounting excludes surface resins, which can make up half the leaf mass and in species such as Larrea tridentata.) The thickness does vary, and so does the corresponding water permeability, by about one hundredfold (Schreiber & Riederer, 1996). This variation is often in acclimation to water regimes (Turner, 1994).

Stomata

These dynamic pores are present at densities of several hundred per square millimetre. Not all plants have them; indeed, Woodward (1998) poses the question, ‘Are stomata necessary?’ All major taxa do possess stomata now, having evolved increasing densities of them though the Upper Carboniferous period. At the least, stomata are required for control of the exchange of CO₂ for water vapour, which is also inherently related to transpirational cooling. Woodward (1998) begins with cooling as a need in full sunlight and notes that cooling is effective even for plants of short stature, poorly coupled to the atmosphere (as defined by Jarvis & McNaughton, 1986). This occurs because the stirred part of the troposphere (the convective boundary layer) typically maintains humidities well below saturation, even in the presence of much evaportranspiration. Much more attention has been given to CO₂-water-vapour exchange, as will be discussed shortly.

As a population, stomata can be described by their areal density or by the fraction of epidermal cells that they represent (stomatal index). They are further described by their distribution of apertures. Although the area-averaged effect of stomatal opening is to confer a conductance that is controlled physiologically, not all stomata are open equally. A typical histogram of apertures is unimodal, but transients in light or humidity can induce broader and even multimodal distributions (Buckley et al., 1997). Aperture responds to at least three major physiological state variables (Tardieu, 1994; Tardieu & Simmoneau, 1998): (1) photosynthetic metabolites, so that conductance keeps pace with need for CO₂ substrate (in the leaf interior; Mott, 1988); (2) hormones or regulators, particularly abscisic acid or ABA (as a water-stress signal), primarily from the roots (Blackman & Davies, 1985; implicating cytokinins; Zhang & Davies, 1990; Tardieu et al., 1993, 1996); and (3) hydraulic linkages. Hydraulic linkage is overall to the bulk water status of the plant but local linkages to the epidermal cells are responsible for stomatal responsiveness to humidity (Haefner et al., 1997). Bunce (1997) describes how the three physiological variables can be linked and how the linkages can be deduced experimentally. It is notable that the upper and lower (adaxial and abaxial) leaf surfaces can differ markedly in stomatal density and in physiological responsiveness (Pospíšilová & Solárová, 1980).

Jones (1998) distinguishes between three major adaptive functions of stomata: optimizing the trade-off in taking up CO₂ while losing water; controlling the risk of dehydration, particularly poising the leaf water potential above the point of catastrophic xylem cavitation (Tyree & Sperry, 1988); and regulating of temperature by transpirational cooling. These functions will be discussed individually here. A uniform framework to explain all these functions simultaneously is not yet available, either mechanistically or evolutionarily (that is, demonstrating the adaptiveness, or cruder optimality, of observed behaviour).

Optimization of assimilation rate/transpiration rate (A/E) by stomata. Stomata cost almost nothing to develop. Similarly, they cost little metabolic energy to operate (Assmann & Zeiger, 1987). Consequently, the costs and benefits in their operation are almost wholly those of resource use (water, CO₂, nutrients) that they modulate. The most important trade-off is that of photosynthetic CO₂ gain against water loss, or A against E. Cowan & Farquhar (1977) proposed an optimization principle, that stomata should maintain a constant ratio of the marginal increase in CO₂ gain to marginal increase in transpiration:

\[ \frac{\partial A}{\partial E} = \text{constant}. \]

Eqn 1

The basis of this principle is that there is a metabolic cost (proportional to E) of maintaining the magnitude of E required for a given A: the cost of constructing and maintaining roots and other tissue. In an exceptional combination of theory and experiment, Givnish (1986) showed how the constant could be evaluated for particular plants and growth conditions. He included the effects of water stress, not just water use, and extended the theory to allocation of root and shoot.

How do stomata (or conductance per leaf area,
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$g_s$ regulate both $A$ and $E$. We must specify the micrometeorological environment: flux densities of photosynthetically active radiation PAR, near-infrared (NIR) and thermal infrared (TIR); air temperature, humidity, $CO_2$ concentration, and windspeed; and the resistance of any canopy boundary layer between the leaf and our point of measuring the micrometeorological variables. Three major processes then must be modelled: leaf assimilation, leaf energy balance, and stomatal response to the leaf environment. The equations can be formulated to a very good level of accuracy, although the simultaneous solution is mathematically challenging (Collatz et al., 1991; V. P. Gutschick, unpublished). A simpler, partly qualitative viewpoint can be taken, to show that increasing $g_s$ increases $A$ but decreases water-use efficiency (WUE): WUE $= A/E$. Consider first the transport of water vapour, through the conductance of the stomata ($g_s$) and the conductance of the boundary layers (leaf and canopy taken together, with total conductance $g_m$). The total conductance is $g_m = 1/(1/g_s + 1/g_b)$, using the addition of series resistances (1/conductance). Clearly, stomata control only part of this conductance, a point to which we must return. The transpiration rate is simply this total conductance multiplied by the difference in water vapour `concentration’ from leaf interior to stirred air outside the boundary layers: $E = g_m (e_{\text{leaf}} - e_{\text{air}})/P$. This formula incorporates the total air pressure, $P$, so that $E$ is formulated in terms of the water-vapour mole fraction. Conductance is used in the familiar molar units (mol m$^{-2}$ s$^{-1}$), which are less dependent on temperature and pressure than the old velocity units (m s$^{-1}$; see Jones (1992), pp. 54–55). Next, consider the transport of CO$_2$, through similar physical paths, followed by its biochemical reaction in mesophyll cells. The physical-path conductance of CO$_2$ from its partial pressure in free air ($C_a$) to that in the substomatal cavity ($C_s$) is very similar to that for water vapour: $g_m = 1/(1.6/g_s + 1.37/g_b)$; the factors 1.6 and 1.37 account for the lower diffusibility of CO$_2$ than of water vapour. The reaction rate, which is simply $A$, can be approximated (from full enzyme kinetics, as in Farquhar et al. (1980)) as being proportional to the CO$_2$ mole fraction in the substomatal cavity, $C_s/P$, yielding $A = g_m C_s/P$ in units of mol m$^{-2}$ s$^{-1}$ (commonly quoted in micromoles, not moles). Empirically and enzyme-kinetically, $g_s$ is simply the slope of $A$ against $C_s/P$, which is fairly constant over modest ranges of $C_s$.

With these definitions, we obtain

$$A = g_m C_s = g_m (C_a - C_s)$$

Eqn 2a

Solving for $C_s$ and expressing $A$ in terms of free-air CO$_2$ level and the conductances, we have:

$$C_s = C_a g_m / (g_m + g_b)$$

Eqn 2b

$$A = C_a g_m g_{\text{leaf}} / (g_m + g_b) = C_a g_m / (1 + g_{\text{leaf}} / g_b)$$

Eqn 2c

We thus obtain an expression for instantaneous water-use efficiency of the leaf:

$$WUE = A/E = \frac{C_a g_m' (e_{\text{leaf}} - e_{\text{air}})}{1 + g_m'/g_m}$$

$$= \frac{C_a g_m' e_{\text{leaf}} - e_{\text{air}}}{g_m' + g_m / g_m}$$

Eqn 2d

In the final formula, the first factor is dependent mostly on the external environment: $C_a/(e_{\text{leaf}} - e_{\text{air}})$. (Of course, leaf-interior vapour pressure is a function of leaf temperature, which is affected by the water-vapour conductance, a complication that we dismiss for now and that has an equally complex resolution in theory and experiment.) The second factor is almost a constant, having a narrow range from 0.62 to 0.72. The final factor expresses the physiological control of WUE by the factor $g_m'/g_m$. Physical conductance and biochemical capacity act in completely different ways. In any environment with boundary layers fixed by leaf dimensions and windspeed, a higher stomatal conductance increases $g_m$ and confers both high $A$ (Eqn 2c) and low WUE (Eqn 2d). The trade-off is so sharp that most plants control $g_s$ so as to keep $C_s / C_a$ in a very narrow range, c. 0.7 for plants with the $C_3$ pathway (Bell, 1982; Wong et al., 1985).

Stomata have somewhat different leverage over $A$ and WUE than in this simple model, because there are biophysical feedbacks: (1) an increase in $g_s$ leads to decreased leaf temperature, which flattens the rate of decrease of WUE; (2) within the leaf and canopy boundary resistances, increased $g_s$ humidifies the air, similarly flattening the drop of WUE (an equivalent statement is that stomatal control is diluted by the boundary-layer resistance, as is apparent in the formula for $g_m$ already described); (3) losses of water to soil evaporation or to competitors decrease $g_s$ increases. This last feedback arises from two effects; (a) a more humid canopy decreases the gradient in water-vapour pressure from soil to canopy air, and (b) in the long term, high $g_s$ confers higher $A$ and faster growth. The canopy closes earlier and suppresses soil evaporation (analogous results were reported as a function of crop planting density by Richards (1991)). In certain sets of conditions, WUE can even rise with modest increases in $g_s$; a case in a field experiment is reported by Meinzer et al. (1997). In general, these feedbacks dilute the control of both $A$ and $E$ or WUE by stomata, for the canopy as a whole. For individual leaves, and especially for individual plants competing with the group, many feedbacks such as changes in canopy humidification do not apply, and stomatal control retains much value.

Discussions of the value of stomatal control in balancing the instantaneous rates of carbon (C) gain
and water loss are incomplete. Much more general models can be constructed. If we consider only water: (1) water costs can vary with soil water status (more root mass is needed as this declines); (2) water availability rates can be constrained by the decrease in water potential that threatens to cause xylem cavitation; (3) the rate of water use, and thus WUE, can be less relevant than constraints on total water availability (water volume in the potential rooting volume). Consider the change from conditions of unlimited water bearing a cost of acquisition (root function) to a limitation in volume. The value or weighting of WUE then increases relative to A. Models with varied degrees of inclusiveness and complexity exist, predicting varied optimal programmes for stomatal control (Berninger et al., 1996; Haxeltine & Prentice, 1996; Santrucek & Sage, 1996). Many predicted (and observed) changes in stomatal conductance, from both aperture control and stomatal density development, apply over the span of leaf development time, not just as a response to the immediate environment. In a viewpoint covering the longest time spans, we must consider the evolution of developmental controls over stomatal density and physiological controls over aperture. Robinson (1994) argues that plant families or taxa that evolved earlier were constrained, and therefore did not develop as 'efficient' stomatal control. A precise definition of efficiency must be developed to clarify Robinson's point fully. One must also ask in what trade-offs these older taxa excel, so that they are not extinguished by modern taxa.

We should also consider other resources, such as N, as changing the cost–benefit structure for stomatal control. The simple arguments already discussed assumed that mesophyll conductance, or some other measure of photosynthetic capacity or investment, was given a priori. The relative values and availabilities of water and N must actually be balanced, so that \( g_e \) and \( g_m \) (or leaf N content) are optimized together. This will be discussed further in a later section.

For stomata to (nearly) optimize \( A/E \), they must respond appropriately to environmental signals. To respond to \( A \), they must respond to a photosynthetic metabolite. This metabolite must be near or in the guard cells (Jarvis & Davies, 1998). No metabolite has yet been identified, although it has been demonstrated that stomata respond to internal \( \text{CO}_2 \) partial pressure in the leaf (Mott, 1988). Stomata must also respond to \( E \) or to the atmospheric humidity (absolute or relative) that helps to determine \( E \). Empirically, the response of \( g_e \) to the full set of environmental conditions, including humidity, is often well approximated by the Ball–Berry model (Ball et al., 1987), but not always (Jarvis & Davies, 1998; Dewar, 1995):

\[
g_e = \frac{mAh_s}{C_s} + b \quad \text{Eqn 3}
\]

(\( h_s \) and \( C_s \) are, respectively, the relative humidity and the \( \text{CO}_2 \) concentration at the leaf surface, beneath any leaf boundary layer; the slope \( m \) and the intercept \( b \) are both measures of commitments to use water and to favour assimilation over water-use efficiency). Stomata that respond according to this form do decrease \( g_e \) as evaporative demand (closely proportional to \( 1 - h_s \)) rises. The apparent response to humidity actually derives from a direct, mechanistic response of \( g_e \) to transpiration rate (Mott & Parkinson, 1991) and, more specifically, to epidermal transpiration rate (Saliendra et al., 1995; Haefner et al., 1997). However, as leaf temperature rises, the resupply of water is also activated, such that the net response of \( g_e \) is close to a response in \( (e_{\text{leaf}} - e_{\text{air}}) \) (a temperature function closely paralleling \( e_{\text{leaf}} \)); thus, a response to \( e_{\text{air}}/e_{\text{leaf}} \), or relative humidity. Haefner et al. (1997) demonstrated the realism of the full hydraulic model, not only for bulk leaf conductance but also for its patchy behaviour and for its transient behaviour, opposite in direction to the final response.

**Regulation of leaf water potential by stomata.** Stomatal conductance and transpiration increase together, and the water potential decrease from soil to leaf, \( \psi_l = \psi_s + \Delta \psi \), increases with \( E \). Models of varying complexity and inclusiveness show how \( \psi_l \) responds to \( g_e \) (Jones, 1992, especially p. 158 et sqq.). Many of these models are used to argue that \( g_e \) can be set to maintain \( \psi_l \) above the point of catastrophic xylem cavitation (Tyree & Sperry, 1988), which is very expensive in lost function in leaf and stem. (Partial cavitation, as is often observed in field conditions (Meinzer et al., 1997) might nevertheless be within the optimal behaviour.) However, stomata do not respond directly to bulk \( \psi_l \) but to particular combinations of epidermal and guard-cell water potentials (Haefner et al., 1997). A specific structural (hydraulic) linkage enforces this form of response. Leaves also respond to ABA (Tardieu & Simmoneau, 1998) as a signal of root or soil water status; perhaps the ultimate response is more directly to soil mechanical strength (Tardieu, 1994; Masle, 1998) than to water potential alone, with the former as a better indicator of future prospects of water extraction. The resultant combination of response to hydraulic signals and to ABA can result in \( \psi_h \) that is stable, or at least kept above a ‘floor’ value, in many plants called isohydric (Saliendra et al., 1995; Tardieu & Simmoneau, 1998).

Stomatal regulation in response to both \( A/E \) and water status can be joined via mechanistic responses of \( g_e \) to photosynthetic metabolite(s), transpiration and ABA, as already noted.

**Regulation of leaf temperature by stomata.** Leaf temperature affects all manner of resource use. Increasing temperature (\( T \)), up to an optimum, is desirable for activating \( \text{CO}_2 \) assimilation and in-
creasing the photosynthetic N-use efficiency. It can also affect photosynthetic transport and organ development. Extremes are to be avoided. At high $T$, thermal damage can occur; stomata do open at high $T$, perhaps adaptively to limit $T$. Low $T$ can lead to chilling and freezing injuries; in some plants, chilling alone is not damaging, but it is when combined with high light levels (Ball et al., 1991, 1997).

Both stomatal conductance and leaf geometry affect leaf $T$. At steady state, leaf $T$ adjusts to balance the energy fluxes per unit leaf area:

$$0 = Q_{SW}^+ + Q_{TIR}^+ - Q_{TIR}^- - Q_b - Q_{ec}$$

Eqn 4

($Q_{SW}$ is the net rate of absorption of shortwave radiant energy, which depends on spectral absorptivity and leaf display angle). The influx of thermal infrared radiant energy ($Q_{TIR}$) is almost independent of leaf structure or of display angle, depending only on surrounding temperatures and the nearly invariant leaf thermal absorptivity. The next three terms for energy losses all depend on leaf $T$, increasing (mostly nonlinearly) with $T$. Thermal infrared losses ($Q_{TIR}$) increase as the fourth power of $T$ but are essentially independent of leaf structure, display angle or physiology. Evaporative cooling ($Q_b$) is simply the molar transpiration rate times the heat of vaporization of water. This cooling rate responds to stomatal conductance (a component of total conductance $g_s$; see the discussion around Eqs 2a–2d) and to $T$ (because internal vapour pressure in the leaf rises exponentially with $T$). Convective and conductive cooling to air ($Q_{ec}$) increases linearly with $T$. As stomatal conductance increases, $Q_b$ increases. This affords stomata a modest control of $T$, over a range in the order of 10°C, depending on, for example, windspeed. I use the term ‘modest’ because transpiration changes less than proportionally with $g_s$, because stomatal resistance is diluted in boundary-layer resistance and there is a negative feedback (increasing $g_s$ also decreases the vapour-pressure deficit, $e_{leaf} - e_{air}$ in Eqn 2a). Empirically, there is little evidence of a direct response to $T$ under normal environmental conditions, as expressed in the general success of the Ball–Berry and related models; in these models, the only effects of $T$ are on $A$. The adaptive reasons are not clear.

**Acclimation of stomatal density and control programme to long-term environmental conditions.** Stomatal density decreases as atmospheric CO$_2$ concentration rises; the stomatal index decreases even more regularly (Morison, 1998). This decrease is arguably very adaptive (Kurschner et al., 1998), given a link to stomatal conductance (note that the conductance contribution of individual stomata can also change, e.g., if the size or maximal aperture changes). Simply, assimilation is enhanced without cost, or the $E$ to support a given $A$ decreases. This developmental response is seen over evolutionary time as well as in the lifetime of single plants (Wagner et al., 1996). Of course, it is variable with leaf position in the canopy; Poole et al. (1996) caution that this must be accounted for in interpreting data, especially palaeontological. The response of stomatal density seems to be independent of life form (e.g., herb or tree) but dependent on exposure and on initial stomatal density (Beerling & Kelly, 1997).

Changes in other environmental variables such as humidity or PAR flux density over the duration of a leaf’s growth also affect the stomatal density as well as the stomatal control programme (the short-term responsiveness of $g_s$ to environmental variables such as radiative fluxes and humidity, as is expressed in Eqn 3) (Bunce, 1998). The control programme (expressed, e.g., as magnitudes of slope $m$ and of intercept $b$ in Eqn 3) acclimates at elevated [CO$_2$]. A significant part of the acclimation might be to altered water status (Morison, 1998). Typically, the acclimation preserves the ratio of internal to ambient CO$_2$ partial pressures, $C_i/C_a$ (Morison, 1998). We can rewrite Eqn 2d, for water-use efficiency, using $A$ as in the far right-hand side of Eqn 2a, to obtain

$$WUE = \frac{k_m C_a (1 - C_i/C_a)}{g_{ba} (e_{leaf} - e_{air})}$$

Eqn 5

Given that $g_{ba}/g_{ba}$ varies little (see previously), we see that as ambient CO$_2$ pressure $C_a$ rises at constant $C_i/C_a$, there is an increase in WUE (and in water status).

**Trichomes**

These leaf hairs function in defence (see later), but also affect gas exchange and temperature. In many plants, trichomes decrease the absorption of shortwave radiation by leaves and keep them cooler (Ehleringer, 1981; Baldocchi et al., 1983). The silversword plant on Mt Haleakala, Hawaii, is an exception: it uses partly focused light reflected from trichomes to keep its apical meristem very much warmer than ambient air, to aid its development (Melcher et al., 1994). The principal cost of pubescence to alter leaf $T$ is decreased light interception. This might be a negligible cost in high-light (light-saturated) environments, or even a benefit, from the avoidance of photoinhibition (see Press (1999) for a further discussion of leaf pubescence).

Trichomes also keep water droplets off the leaf surface and the stomata (Brewer & Smith, 1997), which helps to maintain leaf gas exchange (Smith & McClean, 1989; Brewer & Smith, 1995). In calcicole species, trichomes act as sinks for excess calcium that would otherwise cause stress to the plants and result in stomatal closure (De Silva et al., 1996).
Overall leaf size, shape and display

Leaves range widely in linear dimensions, from millimetres to nearly 1 m; they also vary in shape, from nearly circular with entire margins to deeply lobed or serrated margins. A highly dissected leaf margin decreases the effective size of the leaf. Small size or dissection thus increases the boundary-layer conductance, which is proportional to √[windspeed/ (linear dimension)]. The fractional control of A and E by stomata is kept higher than in large or entire leaves. Also, heat transport is facilitated, so that leaf temperatures are held close to air temperature. This can bear a cost, in that it decreases leaf cooling and WUE gains at high transpiration rates. As a benefit, leaves suffer less extremes of temperatures, neither high T in high sun and low transpiration, nor low T at night under radiative cooling (radiation frosts are a hazard; Leuning, 1988). All these effects are modulated by leaf position within the canopy, of course. Deeper in the canopy, wind penetration is decreased, as is radiative input both in shortwave and thermal radiation. As a result, the trade-offs vary with position and so can the leaf shape.

Size as linear dimension and thickness affects the efficiency of resource use. Larger, thicker petioles are demanded for broader and thicker leaves. ‘Sun’ leaves are thicker than shade leaves, for example. Costs of petioles actually make sun plants less effective than shade plants of the same size, for intercepting PAR (Sims & Pearcy, 1994). Why, then, does sun architecture occur? Vallardes & Pearcy (1998) propose that shade plants would be more damaged by photoinhibition, from high PAR interception on leaves of limited electron-transport capacity. Niklas (1992) argues that in one species of plant, petiole investment is excessive for light interception, summed over the day. I suggest that the architecture might be closer to optimal if one were to account for sunlight interception being more valuable early and late in the day, when vapour-pressure differences are smaller and WUE is larger.

Compound leaves require a higher investment in support (rachis plus petioles) than do simple leaves of the same area. Givnish (1978) argues that compound leaves are nevertheless a cheap disposable structure in seasonally dry tropics. They decrease water loss from (absent) branches in the dry season. Niinemets (1998a) also notes that petioles in compound leaves are low in N content and are therefore cheaper to construct in terms of the most limiting resource.

Leaf display angle presents a richness of trade-offs in leaf function. Angles that favour high light interception (normal to the sun, and perhaps actively tracking the sun) favour high efficiencies in using nutrients and N, but low efficiencies in using light (much light is intercepted at irradiances far exceeding the light-saturation point of the leaf) and in using water. An extensive discussion, pointing to the abundant detail in the literature, has been given elsewhere (Gutschick, 1997). Several interesting phenomena can be summarized here. One is that the optimal leaf angle varies with depth in the canopy (Loomis & Williams, 1969; Duncan, 1971; Niinemets, 1998b) and with the relative importance of WUE over assimilation and growth rate (plants can change solar tracking modes with changes in water status (Forseth & Ehleringer, 1983; Reed & Travis, 1987)). Superior light-use efficiency is achieved with leaves that are more erect. Crops have been bred for this trait (Trenbath & Angus, 1975), which apparently gives up the stronger shading of competitors afforded by more planophile leaves. Canopies as a whole show different (higher) light-use efficiencies than individual leaves (Monteith, 1994).

Finally, it is inadequate to characterize a leaf's light interception and light-use (or N-use) efficiency on the basis of the total of direct and diffuse interception. The distribution between direct and diffuse light is important, both for single leaves (fine leaves that give diffuse solar shadows or penumbras are beneficial; Gutschick, 1991) and for whole canopies (Leuning et al., 1998).

Mesophyll structure, particularly total mass and nitrogen investments

The development of the palisade layer(s) of cells, as number and length, is most responsive to light levels. Sun leaves are markedly thicker and can have additional palisade layers compared with shade leaves (Nobel & Hartsock, 1981; Thompson et al., 1988). In terms of resource use, development of the mesophyll (palisade plus spongy mesophyll) represents foremost the investment in N and in total construction costs. Therefore, the remaining discussion will focus on N and on total dry mass per leaf area.

Nitrogen is allocated to leaves increasingly as the opportunity for photosynthesis increases, especially with increasing PAR flux density. The declining investment in old leaves can be reversed (Johnston et al., 1969). This is clearly adaptive, at least for plants in which fast growth is valuable, and the patterns along the gradient of microenvironments in a canopy have been so analysed (Hirose & Werger, 1987); for a first-principles derivation of the optimum investment in overall mass, see Gutschick & Wiegel (1988). Accompanying the increasing mass of N per leaf area in high sunlight is an increasing partitioning to carboxylation enzymes at the expense of light-capturing chlorophyll complexes (Cowan, 1986; Evans, 1989), another clearly adaptive pattern. In general, the patterns tend to maximize canopy photosynthetic rate per total mass or per total mass of N. These rates per mass are much more directly
related to relative growth rate than are rates per leaf area (Gutschick, 1987).

To maintain an optimal distribution of N between leaves, N in old leaves that have been overtopped must be moved to new leaves. Such resorption and remobilization of N is widely observed, whereas the fraction reabsorbed is moderate, as it is for most nutrients (one-half or less, on a mass basis; Vitousek, 1982), notably less than the optimality models predict. A fundamental limitation on the remobilization of all nutrients is that enough of the biochemical and phloem-transport systems must be maintained to catabolize cell contents and to export nutrients in low-molecular-mass compounds.

The distribution of N investment, or total mass per leaf area, between different leaves on a plant is only part of the pattern. What sets the absolute magnitude of N per leaf area, N_s, or the related fractional content of N, f_s? There are substantial differences in N_s or f_s between plants in similar microenvironments (say, trees compared with grasses in the same geographic location). One determinant is certainly functional balance between root and shoot. Strong photosynthetic function of N in the shoot, as in high light, dilutes N, whereas strong root function in acquiring N increases f_s. A ‘passive’ balance sets f_s in this accounting (Gutschick, 1993; Gutschick & Kay, 1995). Rate limitations on the uptake of N (or P) lead to low f_s. High [CO_2] increases shoot function and leads similarly to low f_s, as is widely observed, both in current experiments and in comparisons of leaves from earlier centuries with present-day leaves (Peñuelas & Matamala, 1990). Low-N soils often lead to thick or sclerophyllous leaves, which not only have low f_s but great thickness, or dry mass per unit area, and long leaf lifetimes. Givnish (1979) explained the combined pattern. He demonstrated, for example, that greater rates of increase of lifetime A occur at greater leaf thickness; only with great thickness does the marginal benefit equal the marginal cost of constructing the leaf and supporting its function. This pattern should nevertheless be re-examined in the light of recent findings showing that construction costs do not vary systematically with leaf structure (Poorter & Villar, 1997).

The optimum for average mass (or N) per leaf area in the whole canopy is rather broad and flat. Consequently, even substantial deviations from the optimum bear little cost in photosynthetic performance. Gutschick &Wiegel (1988) proposed that canopies develop with a mass per unit area that is well below the optimum. The extra leaf area developable per unit mass can decrease light availability to competing plants. The hypothesis has not been tested yet. The optimum mass per leaf unit area increases with leaf area index; indeed, canopies do follow this trend. A broadly related hypothesis is that leaves absorb excess light (by having higher PAR absorptivity than is optimal) to deprive competing plants of light. Conversely, plants with decreased chlorophyll levels were proposed as being superior in photosynthesis (Gutschick, 1984); field tests bore this out in soybean (Pettigrew et al., 1989).

A second determinant is niche differentiation between life forms, such as trees versus grasses. Trees commonly have low A per leaf area (Wullschleger, 1993) (the exceptions cited by Nelson (1984) remain exceptions). Their strategy of development and of N use in particular differs from that of grasses. In regions with seasonal leafing-out, established trees use N that was reabsorbed to the trunk (Ryan & Bormann, 1982) for an early leaf flush that establishes a superior claim to light interception. However, young trees are often outcompeted by grasses. It remains puzzling to me why juvenile tree foliage is not programmed developmentally to attain high N_s and A. Certainly, such plasticity is possible, at least in shape, and might extend to N_s. Developmental plasticity can have little or no cost (J. Schmitt, pers. comm.). One possibility is that grasses are always superior in A per unit mass, given their very low investment in supporting structures. (A similar argument can be made for vines.) Thus, the competition for A per unit mass is lost, and trees, committed to a woody structural base, however modest at first, must express superiority in other resource use or later in time.

A third determinant is the trade-off between the instantaneous photosynthetic N-use efficiency (PNUE) and WUE. High N content, absolute or as a mass fraction, can confer high WUE. It increases the mesophyll conductance and decreases g_s/g_m, which increases WUE (see Eqn 2d). However, assimilation per mass of leaf is a modestly declining function of mass per unit area (Gutschick & Wiegel, 1988), at all magnitudes of mass per unit area. Thus, assimilation per unit mass of N declines similarly. Furthermore, if high g_s decreases C_s, the carboxylation rate per mass of Rubisco enzyme declines, also decreasing A per mass of N in the whole leaf. The magnitude of N_s that is optimal depends on the relative costs and benefits of water and N. High N availability favours high WUE and low PNUE. Such trade-offs are seen in different shrub species (Field et al., 1983), but their generality is questionable (Meinzer et al., 1992, Poorter & Farquhar, 1994).

Kranz anatomy

The specialization of leaf cells into mesophyll and bundle sheath is of most marked value in allowing the C_4 path of photosynthesis. Numerous articles have reviewed the advantages of C_4 photosynthesis in the efficiencies of using water, N, light, and even C substrates themselves (see, e.g., Ehleringer & Monson (1993), who also present the arguments that the pathway evolved in response to low [CO_2] in the
Miocene epoch). The assimilation rates of C₄ plants are far less sensitive to ambient [CO₂] than those of C₃ plants, because C₄ plants have a CO₂-concentrating biochemical pump. The relative performances of the two pathways in the currently increasing CO₂ levels are of intense interest. I still regard it as difficult to explain why C₄ plants have not replaced C₃ plants even more extensively. A common argument is that C₃ plants are more down-regulated by low temperatures. However, some C₄ plants function well at low T; if this can evolve in a few families, why has it not done so in all the families in which the C₄ path evolved independently? (This topic is also discussed by Press, 1999.)

**Joint ‘optimization’ of nitrogen content and leaf lifetime**

A variety of arguments have been developed to relate these traits. One early argument is that leaves with high N content per unit mass have high costs of construction and should require longer lifetimes to pay these costs back. A more careful analysis of payback rates, and field measurement, shows the reverse: high-N leaves are short-lived (Williams et al., 1989; Reich et al., 1997). At the other extreme, evergreens have long lifetimes that are commonly correlated with low Nₑ. However, this trait need not simply optimize PNUE evaluated over the whole life cycle. Jonasson (1989) found that, in five shrub species over widely different locations, leaf lifetimes were not markedly long, nor was the efficiency of reabsorbing N from senescing leaves high. He proposed that evergreenness was an adaptation to low rates of N supply from soil.

Extensive reviews have been presented by Garnier & Aronson (1998) and by Grime et al. (1997); and for a discussion of nutrient utility as affected by both leaf lifetime and nutrient resorption see Eckstein et al. (1999).

**Leaf optical structure, relevant to PAR absorption**

Many structures within the leaf, particularly the cell walls, scatter light (Fukshansky, 1991). The combined scattering and absorption of light lead to a steep gradient of total flux density with depth in the leaf. Thus, the photosynthetic rate also varies steeply with depth. However, novel leaf-sectioning experiments reveal that photosynthesis does not fall off with the same profile as light (Nishio et al., 1993). This is true in particular at high light flux densities. At low light, photosynthesis does follow the light absorption profile, so that no light is wasted in excess absorption and the quantum yield reaches its limiting value near 0.05 mol CO₂ mol⁻¹ photons. The adaptive value of the manner in which light absorption (pigment concentration) and enzyme capacity are distributed across the leaf thickness has been investigated several times (Gutschick, 1984; Parkhurst, 1994). Modelling demonstrates that the exact shape of these profiles is not critical, but having an appreciable gradient allows a high actual quantum yield in high light. Interestingly, the whole-leaf rate of photosynthesis is not strongly altered by the distribution of stomatal conductance between top and bottom surfaces, even though CO₂ is constrained to enter the leaf at the surface with the lowest light level (Gutschick, 1984).

More details of leaf optical structure and the effects on leaf performance are given by Evans (1999) and Han et al. (1999).

**Leaf optical structure for UV protection**

Ultraviolet B and C flux is damaging to DNA in all cells, including plant cells. Leaves deploy UV-absorbing compounds (especially flavonoids) in the epidermis and throughout the mesophyll. As one might expect, the degree of protection is greatest in sun leaves most exposed to UV, and in longest-lived leaves having the greatest time-integrated dose (Day et al., 1993). The cost of UV screens is currently being assessed. The demand for screening varies with depth in the leaf and also laterally, because plant cells both scatter and focus radiation. Consequently, screening is being investigated as a fully three-dimensional phenomenon (Alenius et al., 1995).

**Leaf structure affects interactions with herbivores and pathogens**

**Mechanical defences**

*Waxy cuticle.* This is the primary defence against microbial and viral invasion, as well as a barrier to water and solute loss (Hadley, 1980). Thickness is quite variable, as already noted; chemical composition and fine mechanical structure are perhaps more important in functions such as providing a barrier against water loss (Kerstiens, 1996). Fungi had a key role in the evolution of cuticle properties (Taylor & Osborn, 1996). Penetrating the cuticle remains a key step in the fungal invasion of leaves (Mendgen et al., 1996). Fungi can degrade the cuticle (Commenil et al., 1998; Sugui et al., 1998), but leaves can detect the products (Schweizer et al., 1996) and initiate other defences such as the hypersensitive reaction.

*Trichomes.* These leaf ‘hairs’ may be extensions of single epidermal cells. They may also themselves be multicellular (Esau, 1965). Trichomes occur in almost every plant family (Johnson, 1975) and commonly have a defensive value (Levin, 1973) because they impede herbivores mechanically (including making attachment difficult) or irritate them.
Trichomes can also secrete defensive compounds, as discussed later. Other functions of trichomes are known: (1) acquiring resources (leaf trichomes hold water and absorb both water and nutrients in some bromeliads (Raven et al., 1992), while root trichomes are commonly known as root hairs, performing the same function); (2) limiting the interception of UV radiation or of total radiation and hence limiting leaf temperatures (Ehleringer, 1981; Baldocchi et al., 1983); and (3) excreting excess salt, as in mangroves and many other species in diverse biomes.

Trichomes can deter feeding by small invertebrates (Letourneau, 1997). Kanno (1996) established this for soybeans attacked by false melon beetles. In addition to correlating the extent of herbivory with hairiness, he manipulated hairiness by shaving leaves. Finally, he showed that trichomes were responsible, rather than solvent-extractable chemical defences, by applying the latter in reciprocal treatments. In other plant–herbivore systems, the protection afforded by trichomes is less marked. Gannon & Bach (1996) found that the development of bean beetle larvae on soybeans was variously retarded or accelerated by trichome density, according to the model of tuberville et al. (1996). They tested a model of trade-offs of defence costs against benefits. This model focuses on net growth potential, and it predicts the highest levels of defence at an intermediate availability of resources. The model held for variations in availability of light, but less closely for water. Overall, trichomes seem to have modest defensive value (quantitative, not absolute) and modest cost. They are clearly not required, given that many plants have few or no leaf trichomes, yet they survive. Plants have other methods of defence or avoidance of leaf herbivory to use in various combinations, as we shall see later. The defences are effective, in that leaf herbivory is estimated at only 5–20% in some representative ecosystems (Golley, 1981; Schowalter et al., 1981). The costs overall can be substantial, particularly for perennials. Tropical forests seem to suffer higher herbivory rates than do temperate forests, especially in young leaves and understory leaves, and more in seasonally dry forests than in wet forests (Coley & Barone, 1996).

Spines. Plants have a variety of sharp structures for defence: spines, which are modified leaves or stipules; thorns, which are modified branches; and prickles, such as sand burrs, which are epidermal growths. Here discussion will be limited to spines, but the cost–benefit analyses apply quite directly to thorns and prickles. Spines deter large herbivores, primarily mammals. Mammals have two basic methods of eating leaves: wholesale, with branches (pruning), and selectively, for leaves alone (picking). The formidable spines of Acacia tortilis in East Africa seem to protect neighbouring true leaves from pruning by goats, but not from picking (Gowda, 1996). They preserve not the leaves themselves but the potential to regenerate leaves from meristems. Also preserved are carbohydrate and nutrient re-
serves in the branch tissues. These are smaller but critical benefits. The cost of these spines was more than repaid by the shoot biomass saved. An attractive prospect is constructing and testing a model for the whole life cycle, to assess deferred benefits and costs such as these.

**Tough tissues.** Within leaves, the tissues with the highest mechanical resistance or toughness include the large veins. Toughness is conferred by thick cell walls and lignification in xylem vessels and in non-conducting fibre cells. Choong (1996) found quantitative relations of cell-wall volumetric content and fibre content to toughness in *Castanopsis fissa*. Toughness protected older leaves, whereas younger leaves had more protection by phenolic compounds. (The protective value of lower N content in old leaves was not evaluated.)

**Abrasives.** The most widespread abrasive compound is silica, effectively restricted to the grasses and some minor taxa such as *Equisetum*. The silica in grasses is hydrated, that is, opal (Baker, 1960). Its abrasiveness (Esau, 1965) limits herbivory on grasses, which otherwise are highly attractive for their absence of woody tissue and of toxins. One of the most remarkable hypotheses, being examined (Kaiser, 1998) is that the widespread replacement of other vegetation by grasses in the Miocene era drove the extinction of North American horses, which had lower rates of tooth growth than horses on other continents.

**Stomatal design.** Does the distribution of stomata, or their individual structure, help to decrease the risk of fungal entry into leaves? I once speculated that the distribution of stomata favouring abaxial over adaxial surfaces might be so protective (Gutschick, 1984). However, the macroevolution of plants seems not to favour a particular pattern of adaxial:abaxial ratio in stomatal density (Beerling & Kelly, 1996). It seems that the structure of individual stomata is more important in deterring fungal invasion. The topography of stomata can induce fungi to form (or not to form) appressoria, the hyphae that are specialized to penetrate other cells (Read et al., 1997). Protection can be offered by a thick wax layer (Rubiales & Niks, 1996) or by waxy plugs that bear a cost of decreased photosynthesis (Brodribb & Hill, 1997).

**Other structures, and overall architecture.** A number of plant species have small structures (domatida) that harbour mites, which in turn can clean away fungal spores (O’Dowd & Willson, 1989). More generally, grasses protect their meristems from most grazing animals by their position at or below soil level. That is, aboveground, grasses are almost all leaf. In addition, the bunchgrass growth habit allows the rapid recovery of tissue growth after grazing; carbohydrates are mobilized rapidly from roots (Richards & Caldwell, 1985). Clonal growth is another way of protecting a sufficient number of meristems.

**Chemical defences**

**Classes of compound.** Chemical classifications of defensive compounds are readily found in both the introductory literature (Salisbury & Ross, 1992) and the specialist literature (Rosenthal & Berenbaum, 1991). In addition to chemical structure, an important distinction (Feeny, 1975) is between the **quantitative** defences present in large quantities and the high-potency **qualitative** defences. In the former group, tannins and resins have high metabolic costs, both for the producing leaf and for the herbivore that detoxifies the compounds. The latter group includes cardiac glycosides (Boppre, 1978) and insect hormones or analogues (Slama, 1980, 1987; Bowers, 1991). These toxins are present at levels <1% in dry mass but are highly effective at deterring herbivory (digitoxin) or at killing herbivores (insect juvenile hormones such as juvabione, which prevent normal metamorphosis). The potent chemicals trade off their high effectiveness against (1) limited range (e.g., cardiac glycosides, unlike tannins, do not affect invertebrates) and (2) a negligible cost to the herbivore once a biochemical adaptation evolves to avert the defence. It is well known that some insects can even turn the glycosides into protectants for themselves against their own predators (Boppre, 1978; Holzinger & Wink, 1996). Tannins act broadly against both invertebrates and vertebrates but require large investments of C.

More traditional categorizations by mode of action resolve the antifeedants, the toxins, the anti-digestants and the phytohormones. One antifeedant shared by several plant species is 2,4-dihydroxy-7-methoxy-1,4-benzoazxin-3,1 (DIMBOA) (Barry et al., 1991); resistance to corn borers, for example, is quantitatively related to DIMBOA concentration. Potent toxins that are effective against almost all herbivores (Rosenthal & Janzen, 1979) include alkaloids, glucosinolates and cardiac glycosides. These first two classes of chemical protectants are most common in crop plants and their relatives (Letourneau, 1997). As with all defences, they can be overcome by some herbivore species or races. Herbivores must expend both energy and nutrients in detoxifying plant protectants (Foley, 1992), which gives the chemicals a remanent value as defences even against capable herbivores.

The energetic and N costs of N-based defences are significant. However, as N availability to plants rises, these costs are diluted in a larger flux of metabolic energy. One might hypothesize that defences are most supportable at high N, given this dilution of costs and the greater benefit of defence (plants are more at risk at high N content because they are
nutrionally more attractive to herbivores). The null hypothesis, by contrast, is that high-N plants are more damaged than low-N plants. Letourneau (1997) has reanalysed 135 published studies that purported to demonstrate that high N is correlated with high herbivory. She found very mixed correlation in true field conditions (not in pots or glasshouses). One alternative to high N attracting herbivores is that some insects are ‘powerful’ rather than discriminating feeders, and can consume more of low-N leaves to extract sufficient protein (Slansky & Feeny, 1977; Moran & Hamilton, 1980; Feeny, 1991; Woodward et al., 1991). One can also compare different genotypes under the same conditions to estimate whether the cost of defence is significant.

Hoffland et al. (1996) found that radish cultivars that were more protected against a fungus had to bear significant costs of more cell wall in leaves (but less wall and more protein in roots). Darrow & Bowers (1997) found no apparent cost (as decreased growth rate) for more potent defences, namely the iridioid (1997) found no apparent cost (as decreased growth wall and more protein in roots). Darrow & Bowers (1997) found no apparent cost (as decreased growth rate) for more potent defences, namely the iridioid glycosides, in Plantago species that were better protected against lepidopteran insects. Costs of defence can be decreased by the defences’ being inducible, as in systemic acquired resistance to fungi, with chitinase to break down fungal cell walls (Enkerli et al., 1993). Infrequent expression of defences also decreases the selection pressure on insects to overcome defences, which could be more important than saving metabolic costs.

**Consequences of differences in leaf structure**

**Nutritional unattractiveness from low nutrient content.** This topic has been discussed, in part, already. In general, low N content in leaves makes them unattractive to herbivores (Fox & Macauley, 1977; McNeil & Southwood, 1978). At very low N contents, in sclerophyllous leaves, herbivory is limited to those animals that have evolved special digestive strategies (i.e. leaf fermentation in the gut; Cork, 1996). These strategies allow the herbivore to extract sufficient N from quantities of leaf matter that would otherwise exceed intake capacity. Fermentation also decreases the passive loss of N in faeces.

**Balancing defence costs and benefits.** Theories of optimal defence have been predicated on several grounds, such as the balance of photosynthetic C supplies relative to N supplies (Bryant et al., 1983). Assuming that secondary metabolism is plastic and scales up or down adaptively, high N availability favours the use of C supplies for growth relative to the production of C-based defences (i.e. tannins). As Herms & Mattson (1992) review in detail, the premises of plasticity and adaptiveness merit testing, as do the predictions of shifts in defence with nutrient status. The authors also present a wide-ranging discussion of complementary theories of defences, such as environmental constraint models (Bryant et al., 1985), which postulate that other stresses such as drought might militate against growth, making the diversion of C to defence free from additional costs. The broadest framework is the model in which growth is traded off against differentiation (structural and metabolic) (Loomis, 1932, 1953). It should be noted that evidence for all the theories remains mixed at present.

A general premise is that the more valuable leaves should be better protected (e.g. by spines and chemicals). The comparative adjective ‘more’ requires elaboration. The youngest leaves on any one plant commonly have the highest photosynthetic rate (per mass as well as per area). Harper (1989) argues cogently that the earliest productivity of leaves (as exported photosynlate) is the most valuable and the most important to defend. The argument applies primarily in exponential growth, in which reinvestment of photosynthe in the ability to make more photosynthe is a critical determinant of final reproductive biomass and thus of fitness. Indeed, higher investments in defensive alkaloids can be found in younger leaves (Iwasa et al., 1996). However, older leaves can contain more tannins, which cannot be retranslocated to younger leaves (Oleksyn et al., 1997). Another sense of ‘more valuable’ arises in comparing plants of different nutritional status. Leaves of low-N plants in tropical forests have more tannins than leaves of trees in adjacent open areas (disturbed sites of high N) (Coley et al., 1985). Are the low-N leaves more...
valuable to the low-N tree than high-N leaves are to the high-N tree? Or are high-N leaves better protected with N-based alkaloids that are cheaper for them to make? It is critical to make the proper comparison. A second consideration here is that some defences compromise other defences. Letourneau (1997, Table 1) gives some intriguing examples, such as trichomes hindering predators of mites as well as herbivorous mites themselves. Another example is an alkaloid, tomatine, decreasing the effectiveness of parasites of a leaf herbivore. These second-order interactions make it more challenging to assess costs and benefits. Reviews by Pasteels et al. (1983) and Gauld & Gaston (1994) are informative.

CONCLUSIONS

Many aspects of leaf structure have been studied for their adaptive value in permitting efficient resource use and in defence against herbivory. Within limited spheres (limited ranges of species to compare, or a limited range of environments), the studies are very enlightening about how leaf structure is moulded in many details (i.e. thickness, nutrient content and hairiness). Some larger challenges remain. First, some analyses must be joined. There are traits such as stomatal conductance that affect the use of light and water, and also N. Similarly, trichomes affect both defence and the use of resources such as light. Costs and benefits must be assessed for all these resources, in a single metabolic ‘currency’ or, better, a currency of ultimate Darwinian fitness. Economic analogies for multiple resource inputs do exist that are promising (Bloom et al., 1985), but implementation is very difficult. I have attempted to use such a framework for evaluating the optimum in gs and root:shoot ratio jointly, given specified availabilities of water and N. Problems arise from the beginning: for example, root investment is a resource use, but gs is a modulator of resource-use efficiency, not a resource. The effect of gs on leaf temperature, which also modulates performance, is further removed. More general frameworks, such as those in Gutschick (1987), only propose the existence of objective functions (goals) and of numerical searches for an optimum. Numerical values, however, are less informative and extensible than are true formalisms, such as equations for marginal gains.

Second, we must explain why different solutions exist for the same challenges: for example, different combinations of leaf N, stomatal conductance and leaf lifetime occur in coexisting plants. One general approach to explaining this fact is that multiple solutions are very nearly equally close to optimal. A second approach is that the different combinations represent evolutionarily stable strategies (Maynard Smith & Price, 1973) in a game-theory analysis of competition. Tilman (1982) elaborated some specific behaviour in resource use alone, called resource partitioning, but greater generality is demanded. A third approach is to consider that selection pressures to evolve various traits and combinations of traits are much decreased by ubiquitous trade-offs, and very many in number, such that they all dilute each other. Regarding trade-offs, consider dry mass per leaf area. Gains in light-use efficiency are compromised by, or traded off against, losses in N-use efficiency. There are also trade-offs in time; WUE is more valuable in one growth stage, PNUE in another. This is the analogue of alternating selection in genetics. Trade-offs are so common and so closely matched that the theoretical optimum for this trait, and many others, is very broad. The concept of dilution arises from population genetics theory. To eliminate variant phenotypes, variant genotypes must be eliminated. Strong selection pressure can do so, over a certain number of generations, or weak selection over many generations. However, there cannot be a large number of strong selection pressures. Each strong selection requires a large number of ‘genetic deaths’ (a large proportion of propagules dying); many strong selection pressures eliminate the entire population or species. One can readily think of hundreds or perhaps thousands of selection pressures on a comparable number of traits. One concludes that most of the net selection pressures, after trade-offs are accounted for, are very weak or are multimodal. The challenge of explaining leaf structure then is largely inverted, to demonstrate that trade-offs are closely balanced and net selection pressure is weak, for all traits showing variability.

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