

PLANT ECOLOGICAL STRATEGIES: Some Leading Dimensions of Variation Between Species

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■ **Abstract** An important aim of plant ecology is to identify leading dimensions of ecological variation among species and to understand the basis for them. Dimensions that can readily be measured would be especially useful, because they might offer a path towards improved worldwide synthesis across the thousands of field experiments and ecophysiological studies that use just a few species each. Four dimensions are reviewed here. The leaf mass per area–leaf lifespan (LMA-LL) dimension expresses slow turnover of plant parts (at high LMA and long LL), long nutrient residence times, and slow response to favorable growth conditions. The seed mass–seed output (SM-SO) dimension is an important predictor of dispersal to establishment opportunities (seed output) and of establishment success in the face of hazards (seed mass). The LMA-LL and SM-SO dimensions are each underpinned by a single, comprehensible tradeoff, and their consequences are fairly well understood. The leaf size–twig size (LS-TS) spectrum has obvious consequences for the texture of canopies, but the costs and benefits of large versus small leaf and twig size are poorly understood. The height dimension has universally been seen as ecologically important and included in ecological strategy schemes. Nevertheless, height includes several tradeoffs and adaptive elements, which ideally should be treated separately. Each of these four dimensions varies at the scales of climate zones and of site types within landscapes. This variation can be interpreted as adaptation to the physical environment. Each dimension also varies widely among coexisting species. Most likely this within-site variation arises because the ecological opportunities for each species depend strongly on which other species are present, in other words, because the set of species at a site is a stable mixture of strategies.

INTRODUCTION

Plant species all use the same major resources of light, water, CO₂, and mineral nutrients. Ecological differences among vascular land plant species arise from different ways of acquiring the same resource rather than from use of alternative foodstuffs. Leaves, stems, roots, and seeds vary between species in construction,

in lifespan, and in relative allocation. This review discusses four major dimensions of variation across vascular land plant species. The dimensions affect ecological strategy, that is, the manner in which species secure carbon profit during vegetative growth and ensure gene transmission into the future. Every plant ecologist will have his or her own list of traits that are informative about a species, and his or her own ranking among those traits. Nevertheless, three of the traits discussed—leaf mass per area, seed mass, and height—rank near the top of most plant ecologists' lists (Vendramini et al. 2002, Weiher et al. 1999, Westoby 1998, Wilson et al. 1999).

ABOUT ECOLOGICAL STRATEGIES

A variety of ecological strategy schemes have been proposed (see review in Westoby 1998). One type expresses response or distribution in relation to single environmental factors. Examples include increasers and decreaseers in relation to livestock grazing (Dyksterhuis 1949), the requirement for canopy gaps during establishment (Denslow 1980), and reestablishment potential in relation to time since fire or other disturbance (Noble & Slatyer 1980). Raunkiaer's (1934) life-form system involves the location of buds from which regrowth occurs following winter or dry season.

Currently, the International Geosphere-Biosphere Program aims to model vegetation dynamics under future global change. To this end a broad-purpose scheme of plant functional types is seen as essential, and various committees and workshops have been discussing this matter (McIntyre et al. 1999). Among the schemes that have included more than one dimension (Begon et al. 1996, Loehle 2000, Smith & Huston 1989), the best developed is Grime's CSR triangle (Grime 1974, 1977, 1979; Grime et al. 1988). The R (ruderal) dimension expresses response to disturbance, and the S-C (stress tolerator-competitor) dimension expresses capacity to take advantage of favorable growth conditions. The merits of the CSR scheme have been vigorously debated. Nevertheless, the underlying idea is simply that coping with disturbance and adapting to fast versus slow growth opportunities are two major dimensions of ecological variation. This much would have been accepted by most plant ecologists since the 1800s.

Strategy schemes can have different aims. Some have region-specific applications in range or forest management. Some express concepts about the most important factors and opportunities shaping the ecology of plants. Here we wish to focus on a particular role for ecological strategy schemes: their potential for drawing together and organizing the knowledge gained from hundreds of experiments worldwide, each covering one or a few species. Southwood (1977) likened ecology to what chemistry must have been like before the periodic table of the elements was invented. As he put it, "each fact had to be discovered by itself, and each fact remembered in isolation."

To benefit from synthesizing experimental results across different continents and environments, potential indicators of the ecology of species need to be measured easily and consistently worldwide. The conceptual strategy schemes such as

CSR have not met this need. Rather, species are related by comparing performance or distribution in a landscape where they occur together. For this reason attempted syntheses have been forced back to growth-form, life-form, or habitat categorizations in the attempt to make sense of the accumulated experimental literature (e.g., Connell 1983, Crawley 1983, Goldberg 1996, Goldberg & Barton 1992, Gurevitch et al. 1992, Schoener 1983, Vesik & Westoby 2001, Wilson & Agnew 1992). With this in mind, Westoby (1998) previously suggested a “leaf-height-seed” scheme, with the three dimensions readily quantifiable.

Here we put this idea in a different way. Rather than setting up a named three-dimensional strategy scheme, we present a shortlist of dimensions that might be helpful for literature synthesis. At least one of the traits associated with each dimension can be readily quantified. The list need not stop at three, and there need be no requirement for absolute consensus about rankings. Still, if reasonably wide agreement can be achieved about a few traits worth measuring consistently, then we may hope for considerable benefits from using these traits as predictors of ecological behavior.

ABOUT DIMENSIONS OF VARIATION

Criteria for Ranking a Dimension of Variation

ECOLOGICAL SIGNIFICANCE The position of a species along the dimension should be known to have an important influence with regard to how the species makes a living or where it does best. Preferably, there should be solid experimental evidence about this. Often there may be cross-species correlations among traits, such that information about one measurable trait carries with it broader knowledge about the ecology of species.

SPREAD AND CONSISTENCY Species should be spread widely along the dimension (breadth of variation is discussed in “Spread of Species Along the Dimensions,” below). Further, rankings of species along the dimension should be consistent (at least approximately) in the face of within-species variation due to plasticity, acclimation, or ecotypic variation. Traits need not be constant within species. Indeed, it would be surprising if natural selection had not endowed species with some capacity to adjust traits of ecological importance depending on the situation. The consistent-ranking criterion means that plasticity and other variation within species should not be a conceptual problem, though they may cause complications in measurement.

PRACTICALITY FOR LITERATURE SYNTHESIS It should be practical to quantify the dimension in a manner that does not depend on the local context of physical environment or co-occurring species.

Cross-species correlations among traits can arise in different ways. Most straightforward and desirable (for the purpose at hand) is a physically enforced

tradeoff. An example is that seed output per gram of seed produced cannot be increased without a decrease in mass of individual seed. This is a matter of logic. Another example is that longer leaf lifespan seems nearly always to demand a more robust structure and hence greater leaf mass per area.

Trait correlation can also arise because available niches favor it. For example, lifestyles or habitats involving tall stems might tend also to select for larger seed mass. These correlations might be expected to be looser than correlations enforced by a physical tradeoff.

Trait correlations across species arise also by correlated evolutionary divergence of traits at a phylogenetic branch-point deep in the past, with the trait combinations persisting within each of the descendant lineages (Felsenstein 1985, Lord et al. 1995, Prinzing et al. 2001, Wright et al. 2000). These old divergences should not be regarded as a causation that is distinctly separate from present-day ecological selection or from a physically enforced tradeoff, because the evolution of species into present-day opportunities often has a large element of phylogenetic niche conservatism (Harvey & Rambaut 2000, Price 1997, Westoby 1999, Westoby et al. 1995). Only if the traits in question were incapable of responding to selection through millions or tens of millions of years would it be useful to regard the present-day correlation as owing to the old divergence rather than to continuing selection. It makes sense to regard the most recent causative process as the effective cause of a present-day pattern.

All three criteria for importance are met by leaf mass per area trading off with leaf lifespan (LMA-LL) and by mass of individual seed trading off with seed output per gram of reproductive effort (SM-SO). Height of a species at maturity and the spectrum from small to large leaf size and twig size meet the criteria of broad spread and practical measurement. They are also known to be ecologically significant. However, height is a complex trait with several components, and the costs and benefits of leaf size are poorly understood.

LEAF MASS PER AREA AND LEAF LIFESPAN

Species with higher leaf mass per leaf area (LMA) have thicker laminae, veins that protrude more, higher tissue density, or combinations of these (Niinemets 1999, Pyankov et al. 1999, Shipley 1995, Wilson et al. 1999, Witkowski & Lamont 1991). High-LMA species tend to achieve longer average leaf lifespan in a variety of habitats (Figure 1) (Diemer 1998a,b; Reich et al. 1997; Ryser & Urbas 2000; Williams-Linera 2000; Wright et al. 2002), suggesting that longer leaf lifespans require extra structural strength (Coley 1988, Reich et al. 1991, Wright & Cannon 2001). In short, the LMA-LL spectrum is a trade-off between potential rate of return per leaf mass and duration of return.

Higher LMA protects against wear and tear and also deters herbivory. Under any of several concepts about allocation to defense (Bryant et al. 1983, Coley et al. 1985, Herms & Mattson 1992), species with slower leaf turnover should spend more to discourage herbivores. Thicker, tougher leaves are themselves the

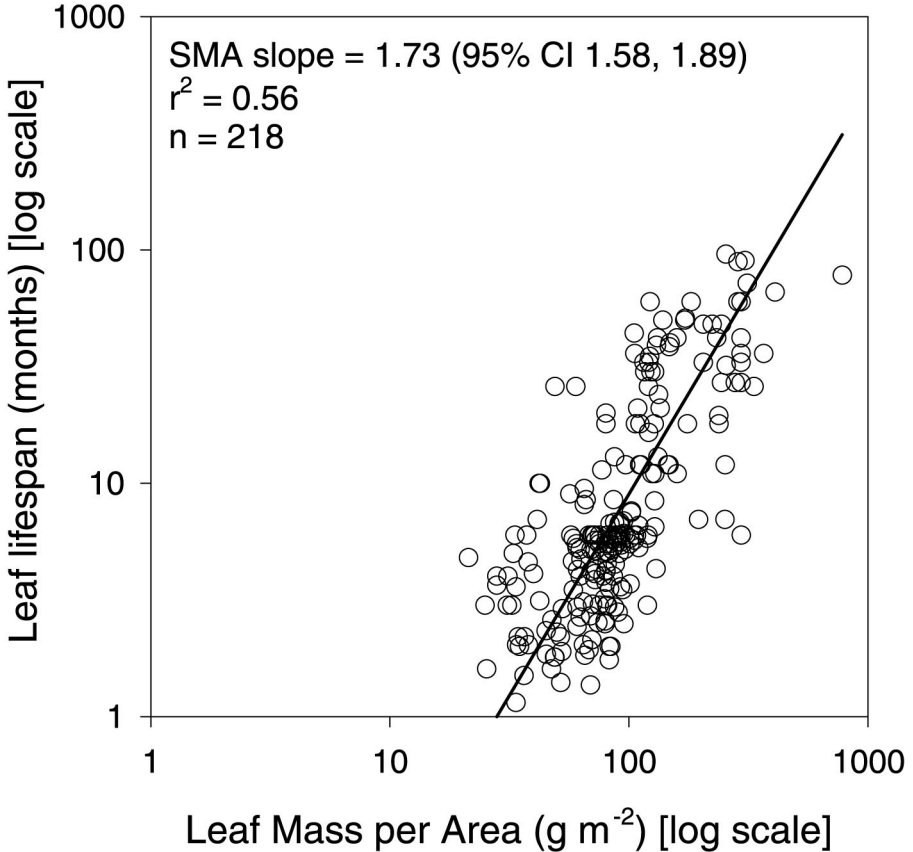


Figure 1 Correlation between leaf lifespan and leaf mass per area across 218 species from several habitats and continents. Regraphed from Reich et al. (1997); data kindly provided by the authors. SMA = Standard Major Axis; CI = confidence interval.

most common and general-purpose form of defense (Coley 1983, Cunningham et al. 1999), but long leaf lifespan may also be correlated with greater relative allocation to tannins, phenols, or other defensive compounds (Coley 1988). Slow leaf turnover should favor strength against wear and tear for the same reason it favors defense against herbivores. For both these reasons, defense against herbivory can be regarded as part of the LMA-LL spectrum.

Leaf Economics and Theory for Leaf Lifespan

A leaf represents an investment on the part of a plant. Kikuzawa's theory for leaf lifespan (Figure 2) can be understood through the curve of cumulative return from the investment. This return is expressed as net dry-mass gain per unit leaf

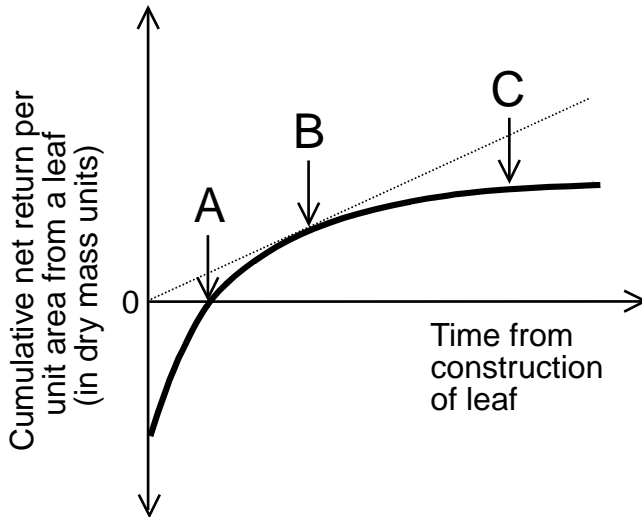


Figure 2 Essentials of existing theory for leaf lifespan (Kikuzawa 1995). Curve shows cumulative dry-mass return from a unit leaf area, net of costs of leaf respiration and of root and stem activity to support the leaf's photosynthesis. Curve is initially negative owing to construction costs (leaf mass per area), then increases through a leaf's lifetime. Payback time for the investment is at A. Net dry-mass return per time per leaf area is the slope of a line from the origin to the curve. It is maximized at the lifespan B. This optimum at B, and also payback time A, shift to longer lifespan if the cumulative dry-mass gain curve is shallower (slow-revenue environments) or if the initial investment is greater (higher leaf mass per area). At C, approximately, the leaf is no longer returning net dry-mass revenue.

area. Construction costs per unit leaf mass vary relatively little between species (Chapin 1989, Poorter & De Jong 1999, Villar & Merino 2001). Cumulative return is initially negative by the amount of LMA, which is dry-mass investment per leaf area, then rises through the lifespan. The slope becomes shallower over time owing to deterioration of the leaf's position within the canopy or of its physiological capacity. Eventually a leaf returns no further net dry-mass gain (at C in Figure 2) when photosynthesis no longer exceeds costs of leaf respiration and of root and stem activity to support the leaf's photosynthesis.

Early verbal formulations (Chabot & Hicks 1982, and more recently Niinemets 2001, Poorter 1994, Williams et al. 1989) were to the effect that leaf lifespan needed to be long enough to pay back the initial investment costs (point A in Figure 2). This is true, but plainly lifespans need to be longer than the payback time if plants are to grow. In Kikuzawa's model (Kikuzawa 1991, 1995; Kikuzawa & Ackerly 1999), revenue per unit time per unit leaf area is maximized. Replacing an old leaf with a new leaf becomes justified when the current return on an old leaf (marginal return) falls below the expected rate of return averaged over the life of

a new leaf (point B in Figure 2). Optimizing per unit leaf area assumes (in effect) that new leaves can be produced only by closing down old leaves. At point B in Figure 2 leaves are closed down while still producing net dry-mass revenue. However, plants do generate new leaves without closing down the same area of old leaves. Longer lifespans (point C rather than B in Figure 2) would be favored if leaves were only discarded when their net revenue had deteriorated to zero. A shoot carbon budget model (Ackerly 1999) favored keeping leaves this long to maximize extension growth. However, building new leaves demands nitrogen as well as photosynthate, and some of this nitrogen is reallocated from old leaves prior to leaf fall (Aerts & Chapin 2000). This should favor closing down old leaves sooner, somewhere between points B and C in Figure 2.

In environments where revenue accrues more slowly, the curve in Figure 2 is shallower, and points A and B are both shifted to longer lifespan. In species with higher LMA the curve starts more negative, and similarly points A and B are both shifted to longer lifespan. Thus, although point A (payback) does not predict the correct lifespan, it predicts the same direction of lifespan response to alternative curves as does point B (maximum return per leaf area). However, point C (no further return) does not predict longer lifespan in response to slower revenue accrual or higher LMA. The pace at which the cumulative net return curve flattens is what decides lifespan if this depends on the point of no further return.

Correlates, Costs, and Benefits

Species with low LMA tend also to have higher photosynthetic capacity per unit leaf mass, A_{mass} (Field & Mooney 1986, Niinemets 1999, Reich et al. 1997, Wright et al. 2001). As well as having more light-capture area deployed per mass, low-LMA species generally have higher leaf N concentrations (Diemer 1998a,b; Field & Mooney 1986; Reich et al. 1997) and shorter diffusion paths from stomata to chloroplasts (Parkhurst 1994). Leaf N reflects the concentration of Rubisco and other photosynthetic proteins (Lambers et al. 1998). Leaf N is more similar across species per unit leaf area than per unit leaf mass (Reich et al. 1997). Probably the lower N_{mass} in leaves of high-LMA species is partly a forced tradeoff (because a greater concentration of fibers, cell walls, etc. leaves less room for N-rich mesophyll) and partly reflects evolutionary coordination between N allocation and LMA and leaf lifespan.

Variation in LMA and leaf lifespan among coexisting species is 3- to 50-fold, strikingly greater than the 2- to 3-fold shifts between habitat types (Table 1). What are the relative advantages or disadvantages to species at different positions along the LMA–LL spectrum, and why is there not a clear advantage at some particular LMA–LL compromise in a given habitat?

Low LMA, high photosynthetic capacity, and generally faster turnover of plant parts permit flexible response to the spatial patchiness of light and soil resources (Grime 1994), giving short-term advantages over high-LMA species. However, high-LMA–long-LL species have longer-term advantages. Longer mean residence time of nutrients (Aerts & Chapin 2000, Eckstein et al. 1999, Escudero et al.

TABLE 1 Summary of three dimensions of ecological variation between species discussed here. (The height dimension is not included in this table.)^a

| | LMA-LL | SM-SO | LS-TS |
|---|--|---|--|
| Basis of relationship | Presumed that greater engineering strength of leaf is required for longer LL. There are several parallel LMA-LL relationships, for example ~40% shorter LL for a given LMA was achieved at low rainfall (Wright et al. 2002). | SO = (mass allocated to reproduction)/(SM plus accessory mass per live seed). Because SM varies much more widely than mass allocated to reproduction per unit canopy area or leaf area and because accessory mass is closely correlated with SM, SM is the dominant influence on SO. | Presumed owing to requirements of mechanical support, hydraulic conductance, and leaf spacing. Possibly also large leaves require large meristems, which cannot be accommodated in very thin twigs. |
| Slope of relationship (standardized major axis on log-log scales) | LL increases faster than LMA. Across all available data log-log slope 1.73, 95% confidence intervals 1.6–1.9 (Reich et al. 1997); within-site slope 1.3 common to 4 sites, 95% confidence intervals 1.1–1.6 (Wright et al. 2002). | Seed output versus seed mass log-log slope approx. -1 (Henery & Westoby 2001). | Leaf area versus twig cross-section log-log slopes 1.01 (deciduous angiosperms), 1.14 (evergreen angiosperms), 1.44 (gymnosperms) (Brouat et al. 1998), 1.69–2.05 at 3 sites (Westoby & Wright in press 2002). |
| Other correlated traits | Mass-based leaf N (N-mass), leaf diffusive conductance G(s), and net photosynthetic capacity A(max) all negatively correlated with LMA and LL (Reich et al. 1999) LL correlated with tissue density (Ryser 1996, Ryser & Urbas 2000, Schlapfer & Ryser 1996). | Correlates of SM include dispersal mode ($r^2 \approx 0.29$) (Leishman et al. 1995), height or growth form ($r^2 \approx 0.20$) (Leishman et al. 1995, Levin 1974, Mazer 1989, Metcalfe & Grubb 1995), leaf size (Cornelissen 1999), relative growth rate, LMA (Reich et al. 1998), seedling size (Grime & Jeffrey 1965). Smaller, rounded seeds are likely to have persistent soil seed banks in England (Hodkinson et al. 1998, Thompson et al. 1993), Argentina (Funes et al. 1999), and New Zealand (Moles et al. 2000) but not in Australia (Leishman & Westoby 1998). | LS with height $r^2 = 0.29$ (gymnosperms included), with seed mass 0.26, with infructescence size 0.79 (gymnosperms excluded) (Cornelissen 1999). Relationship between LS and LMA seems complex (see text). |

(Continued)

TABLE 1 (Continued)

| | LMA-LL | SM-SO | LS-TS |
|---|--|---|--|
| Variation across sites, between species within sites, and within species. | ~50-fold variation in LMA (12–560 g m ⁻² (Fonseca et al. 2000, Niinemets 1999), > 100-fold variation in LL (Eckstein et al. 1999, Reich et al. 1997). Between-species variation in LL is much larger than within-species (factor of >200 compared with 2, respectively) (Eckstein et al. 1999). LMA variation among coexisting species is greater than between habitats, e.g., 3- to 50-fold versus 2- to 3-fold (Reich et al. 1999). | Within temperate zone differences between communities account for only ~4% of variation in seed mass between species (Leishman et al. 1995). Differences between the tropics and the temperate are somewhat larger (Lord et al. 1997). Species establishing in deep shade tend to have larger seeds. Range within sites 4–5 orders of magnitude (log ₁₀ units). Central 66% of species (± 1 SD) spans ~2 log ₁₀ units (mean of 7 floras) (Leishman et al. 2000, Lord et al. 1995). Within species ± 1 SD (66% of seeds) spans ~4-fold (median of 39 species) (Michaels et al. 1988). | 6 classes defined by Raunkiaer (1934) from leptophyll (<25 mm ²) to megaphyll (>164,000 m ²), spanning 5 orders of magnitude. Range among coexisting species 2.5–5 orders of magnitude (Ackerly & Reich 1999, Brouat et al. 1998, Cornelissen 1999, Fonseca et al. 2000, Niinemets & Kull 1994, Westoby & Wright 2002, White 1983a,b). |

^aLMA, leaf mass per area (g m⁻²) = 1/SLA, specific leaf area; LL, leaf lifespan or leaf longevity; tissue density = dry mass/volume; SM, seed mass; SO, seed output (numbers of viable seeds), per area occupied or per leaf area or per plant mass; LS, leaf size, either leaf area or leaf width (refers to green surfaces, hence leaflets within compound leaves) TS, twig size (diameter or cross-sectional area) at base of current year's growth.

1992) permits a progressively greater share of nitrogen pools in a habitat to be sequestered (Aerts & van der Peijl 1993). Further, slow decomposition of high-LMA litter may restrict opportunities for potentially fast-growing competitors (Berendse 1994, Cornelissen et al. 1999). Second, over time high-LMA–long-LL species accumulate greater total leaf mass than low-LMA species (Bond 1989, Midgley & Bond 1991). Despite the offsetting effect of less leaf area per unit leaf mass, high-LMA species tend to generate a larger total leaf area as well (Gower et al. 1993, Haggard & Ewel 1995, Reich et al. 1992). Combining their lower photosynthetic capacity per leaf area (Reich et al. 1999) with this greater accumulation of leaf area may result in above-ground net primary production similar to or higher than that of low-LMA species (Bond 1989, Gower et al. 1993, Haggard & Ewel 1995, Matyssek 1986, Midgley & Bond 1991, Reich et al. 1992).

The slope of LL-LMA relationships among coexisting species has been significantly steeper than 1.0 in several datasets (evaluated using Standard Major Axis “model 2” slope fitting from Diemer 1998b, Reich et al. 1999, Wright et al. 2002).

That is, species with twice the leaf mass per area typically had more than twice the leaf lifespan. Would this not lead to runaway selection for ever-increasing LMA and leaf lifespan? Not necessarily. The revenue stream generated by a leaf unavoidably diminishes in value as time passes ("time-discounting") (Westoby et al. 2000) for a combination of reasons. Leaves suffer damage from herbivores and pathogens (Coley & Barone 1996, Landsberg & Gillieson 1995, Lowman & Box 1983, Showalter et al. 1986) and are colonized by epiphylls (Clark et al. 1992, Coley et al. 1993). Their light-interception position deteriorates owing to over-shading by leaves produced subsequently, by competitors and by the plant itself (Ackerly & Bazzaz 1995, Hikosaka 1996, Kitajima et al. 1997, Koike 1988). A given export rate of photosynthate from the leaf becomes less valuable, because if obtained earlier it could have been reinvested sooner (Harper 1989). Taking all these factors together, there may be no clear-cut advantage to either long leaf lifespan or low-LMA strategies among coexisting species, in terms of fitness value of carbon gain over the lifetime of a unit of leaf mass (Westoby et al. 2000).

Leaf Mass per Area: Leaf Lifespan Tradeoff in Different Environments

Greater leaf mass per area represents greater cost to the plant. If it were possible to achieve the same leaf lifespan for lower LMA, plants would be selected to do so. In our view, the underlying reason why leaf lifespan and LMA are correlated is that long leaf lifespan nearly always requires leaves to be strong in an engineering sense. Depth and material strength are the two main influences on the strength of a horizontal beam (Vogel 1988), and both of these are reflected in LMA.

Within the overall LMA-LL correlation shown in Figure 1, there are seemingly a number of parallel relationships. Shifts in the LMA required to achieve a given leaf lifespan could arise from two causes. First, the wear and tear on a leaf might be more severe in some environments than others. Second, leaf tissue might be softer in some environments than others, such that a greater lamina depth is required to achieve a given overall structural strength. It has recently been shown how differences between rainfall environments can be traced to this second cause (Wright & Westoby 2002a, Wright et al. 2002). Average LMA is well known to be higher at low rainfall, owing to thicker leaves, denser tissue, or both (Cunningham et al. 1999, Fonseca et al. 2000, Mooney et al. 1978, Niinemets 2001, Schulze et al. 1998, Specht & Specht 1989). It has now been shown that this does not achieve longer leaf lifespan [two rainfall comparisons in Australia (Wright et al. 2002a) and one in the United States (Reich et al. 1999)]. That is, a shift to higher LMA is required at low rainfall to achieve a given leaf lifespan. Surprisingly, the higher-LMA leaves at low rainfall did not show greater structural strength. Rather, low-rainfall species tended to be built from softer tissue (Wright & Westoby 2002a). Low-rainfall species had higher leaf N per mass and per area (Wright et al. 2001). This was associated with stronger drawdown of internal CO₂ concentrations, leading to economy of transpiration, but was associated also with softer

tissue, requiring higher LMA for a given overall leaf strength and leaf lifespan (Wright & Westoby 2002a).

Species characteristic of shaded understory usually have longer leaf lifespan in association with lower LMA than species from well-lit habitats (Bongers & Popma 1990, Hladik & Miquel 1990, King 1994, Lusk & Contreras 1999, Suehiro & Kameyama 1992, Valladares et al. 2000, Xu et al. 1990; but see Williams et al. 1989). Similarly, within species, individuals or leaves growing in shade often have longer leaf lifespan and lower LMA (Miyaji et al. 1997, Reich et al. 2002, Steinke 1988). The low wind, high humidity, and reduced risk of wilting that characterize dense-shade environments may make it possible to achieve longer leaf lifespan without physical reinforcement expressed as a cost in increased LMA (see also Bongers & Popma 1990). Slow revenue has been proposed to explain the increased leaf lifespan in shade (Figure 2) but does not explain decreasing LMA at the same time as increasing leaf lifespan. The most plausible explanation for increased leaf lifespan in conjunction with lower LMA is that there are a number of separate but parallel LMA-LL relationships (as shown for rainfall in Figure 3). The shift to humid, low-wind, low-radiation conditions of shaded understory is a shift toward the upper left in Figures 1 and 3, but within shaded

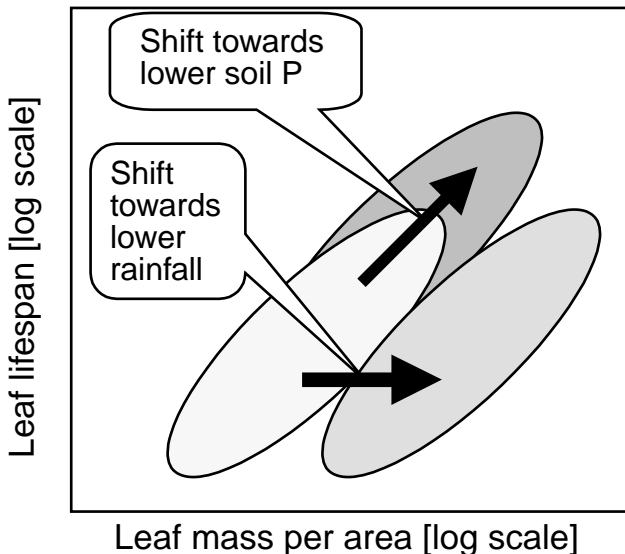


Figure 3 Schematic of leaf lifespan: leaf mass per area (LMA) relationships observed by Wright et al. (2002). Each oval cloud represents the scatter of species in a given habitat. Species occurring at lower soil P tend to have higher LMA, and leaf lifespan is also higher, corresponding to the same LMA-LL relationship observed across species within habitat. Species occurring at lower rainfall also tend to higher LMA but have shifted to a parallel relationship achieving shorter leaf lifespan for a given LMA.

understorey there would still be a positive relationship between LMA and leaf lifespan.

Species occurring on nutrient-poor soils shift toward higher average LMA and longer leaf lifespan than species on more fertile soils (Chapin 1980, Monk 1966, Reich et al. 1992). It has recently been shown (Figure 3) that the shift toward higher leaf lifespan and LMA on low-nutrient soils occurs along the same LMA-LL relationship as on higher nutrients, rather than shifting to a different parallel LMA-LL relationship, as at low rainfall and deep shade. Most likely there is stronger selection in nutrient-poor habitats to extend nutrient retention (Aerts & van der Peijl 1993), favoring extended leaf lifespan, which is in turn made possible by higher LMA.

LMA-Related Leaf Traits that Have Been Suggested as Alternative Strategy Indices

Historically, LMA first attracted attention as a significant descriptor of plant strategies because of its relationship to potential relative growth rate, potRGR. PotRGR is the exponential growth rate (dry mass gain per mass per time) measured on fast-growing seedlings given plentiful water and nutrients. PotRGR has been seen as a bioassay of responsiveness to favorable conditions (Grime & Hunt 1975, Lambers & Poorter 1992). PotRGR is made up of net assimilation rate \times leaf mass fraction \times specific leaf area (SLA). Hence, LMA ($= 1/\text{SLA}$) necessarily influences potRGR. Indeed, in most comparative studies SLA ($= 1/\text{LMA}$) has been the largest of the three sources of variation between species in potRGR (Lambers & Poorter 1992, Wright & Westoby 1999, and references therein). It has now become apparent that high LMA, long leaf lifespan, slow turnover of plant parts, and long nutrient residence times are associated with adaptation to slow-growth situations in a more fundamental way than is slow seedling potRGR (Aerts & van der Peijl 1993, Chapin 1980, Cunningham et al. 1999, Poorter & Garnier 1999).

LMA is made up of lamina depth multiplied by tissue density (Witkowski & Lamont 1991). Both components, or measures closely related to them, have been advocated as better indices of plant strategies than LMA. Leaf volume is made up of solid (cell walls), liquid (cell contents), and gas (intercellular space). Roderick et al. (1999a,b, 2000) argued that liquid volume of leaves should be considered fundamental, because the metabolically active components are in liquid phase. Further, because light capture is area-based while gas exchange is volume-based (Charles-Edwards 1978), the surface area-to-volume ratio of leaves should be considered a fundamental descriptor of leaf structure and function. In effect, this argues that leaf thickness is more informative than LMA or SLA. Dry mass/fresh mass (dry matter content) approximates tissue density for leaves with little intercellular space and has been used in several studies (e.g., Ryser 1996, Wright & Westoby 1999). Wilson et al. (1999) found dry matter content more tightly correlated than LMA with a "primary axis of specialization" that Grime et al. (1997) identified by ordination of 67 traits among 43 British herbaceous species, corresponding to

the C-S axis of the CSR scheme, but Vendramini et al. (2002) found the reverse in Argentina.

In our view, LMA remains the most useful single indicator of leaf strategy, although thickness, dry matter content, and volume components should also be measured where possible (Garnier et al. 1997, Niinemets 1999). First, LMA is the construction cost of a unit leaf area, a fundamental quantity in leaf economics. Second, a leaf's physical strength depends on both its thickness and its tissue density. Third, LMA generally appears to be correlated as least as strongly with traits such as leaf lifespan, residence time of nutrients, and photosynthetic capacity as are alternative indicators (Niinemets 1999, Ryser 1996, Ryser & Urbas 2000, Schlapfer & Ryser 1996, Vendramini et al. 2002, Wright et al. 2002). Fourth, internal volumes are much harder to measure than mass and area. Most workers would be unwilling to shift to expressing traits on a volume rather than a mass basis, except for species without internal gas volume, where the two are interchangeable.

SEED MASS AND SEED OUTPUT

The mass of an individual seed ranges 5–6 orders of magnitude across species, even within communities (Figure 4). This is much larger than within-species variation (Table 1). Within-species variation occurs mainly within individuals rather than among plants or populations (Obeso 1998, Vaughton & Ramsey 1998), indicating environmental effects during development more than genetic differences between mothers.

Vegetation can be thought of as species competing to occupy patches. Under this “sessile dynamics” theoretical tradition (Fagerström & Westoby 1997), the ground available is imagined as a set of patches. The abundance of each species is represented by the proportion of patches it occupies. For species to persist in these patch-occupancy models, they need to colonize vacant patches at least as rapidly as they vacate patches by the death of individuals. A crucial parameter in the criteria for invasion and coexistence is the chance that a vacated patch will be reached by one or more seeds from a patch already occupied by the species. Seed output per occupied patch (or per unit area) is a central quantity for understanding the differences in potential colonization ability between species within communities of sessile, patch-occupying species.

Several studies have found seed output negatively correlated with seed mass, sometimes after adjusting for plant size (Greene & Johnson 1994 across 17 woody species, Jakobsson & Eriksson 2000 across 72 seminatural grassland species, Shipley & Dion 1992 across 57 herbaceous angiosperms, Turnbull et al. 1999 across 7 annuals in limestone grassland, Werner & Platt 1976 across 6 *Solidago* species). In a study that expressed seed output per square meter occupied, log seed mass could predict about three fourths of the variation between species in log seed output across 47 woody evergreen species (Henery & Westoby 2001), and slope was -1 , i.e., directly inversely proportional. By definition, seed output per square meter is equal to mass devoted to reproduction per square meter

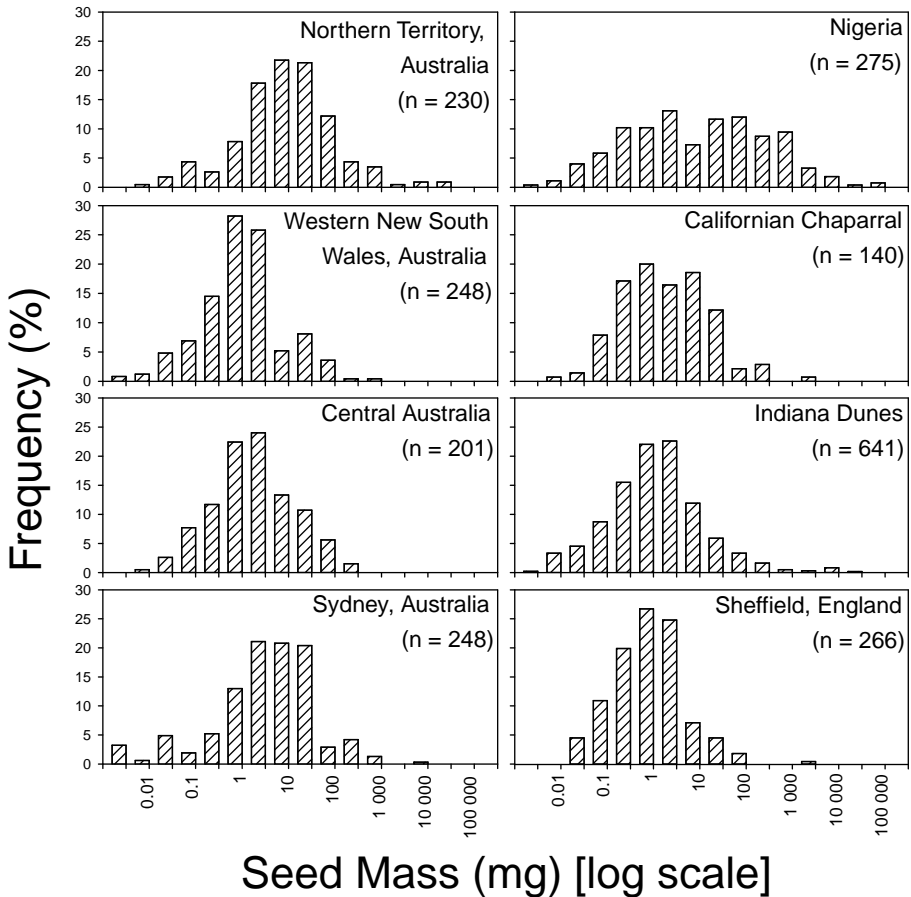


Figure 4 Cross-species frequency distributions of individual seed mass for several locations (Leishman et al. 2000). Two bars per order of magnitude of seed mass.

divided by (seed mass + accessory costs per seed), where accessory costs include fruit structures, dispersal structures, and early aborted seeds. The influence of these different components on seed output must depend on how widely each varies and on any cross-correlations between them. In Henery & Westoby's (2001) dataset, seed mass varied across three orders of magnitude, but reproductive production varied across only one (even allowing for limited sampling during a single season); hence, seed mass accounted for three fourths of the variation in output. Accessory costs varied in proportion to seed mass and so did not change the -1 slope.

The large output advantage of small-seeded over large-seeded species must be counterbalanced at some stage of the life cycle. The most obvious influence of seed mass is on the initial size of the seedling and on the provisions available during

early seedling life. Therefore, it is logical to expect the countervailing advantage to be principally at seedling establishment phase. Strong evidence supports this.

Under sufficiently favorable conditions, 100% of viable seeds make seedlings, no matter how small. Hence, it must be under different kinds of hazards that the advantage of larger seeds becomes apparent. A substantial body of manipulative experiments (Table 2) shows clearly that larger-seeded species usually perform better under hazards during seedling establishment. Further, in four of the six experiments where larger-seeded species did not perform significantly better, the reason is understood. Three in deep shade are discussed below. In a field drought experiment (Leishman & Westoby 1994) conditions were particularly harsh, so that survival was low even in watered treatments.

The benefit of larger seed size applies across many different hazards (Table 2). That is, larger seed size might initially evolve in a lineage owing to one type

TABLE 2 Between-species experiments that have tested the proposition that seedlings from species having larger seeds perform better than seedlings from species having smaller seeds, under various hazards*

| Hazard | Larger-seeded species performed better | Larger-seeded species did not perform significantly better |
|---|---|---|
| Competition from established vegetation | Gross (1984), Bakker (1989), Reader (1993), Ryser (1993), Burke & Grime (1996), Eriksson & Eriksson (1997), George & Bazzaz (1999; first year) | Thompson & Baster (1992), George & Bazzaz (1999; second year) |
| Competition from other seedlings | Leishman (1999), Turnbull et al. (1999) | |
| Deep shade | Grime & Jeffrey (1965), Leishman & Westoby (1994a), Osunkoya et al. (1994), Saverimuttu & Westoby (1996b; cotyledon-phase), Walters & Reich (2000; early phase) | Augspurger (1984), Saverimuttu & Westoby (1996b; first-leaf phase); Walters & Reich (2000; later phase) |
| Defoliation | Armstrong & Westoby (1993), Harms & Dalling (1997) | |
| Mineral nutrient shortage | Jurado & Westoby (1992), Milberg et al. (1998) | |
| Depth under soil or litter | Gulmon (1992), Jurado & Westoby (1992), Jurik et al. (1994), Seiwa & Kikuzawa (1996) | |
| Soil drought | Leishman & Westoby (1994b; glasshouse) | Leishman & Westoby (1994b; field) |

*Updated from Westoby et al. (1996). Studies were included only if they covered at least five species, with seed mass spanning at least one order of magnitude

of advantage but having evolved, would be functional also in relation to other hazards.

Many studies (reviewed in Leishman et al. 2000) have shown that initial seedling size is positively related to seed size across species as well as within species. Seedlings from larger-seeded species also tend to have greater reserves relative to the autotrophic functioning parts of the seedling, and therefore can support respiration longer under carbon deficit. This has been called the "larger-seed-later-deployment" interpretation (Ganade & Westoby 1999, Kidson & Westoby 2000, Leishman et al. 2000) or "cotyledon functional morphology hypothesis" (Garwood 1995, Hladik & Miquel 1990, Kitajima 1996a,b). For competition from established vegetation, depth under soil or litter, and soil drought, better seedling survival might be attributable to larger initial size of the seedling. In most deep shade experiments, for defoliation and for mineral nutrients there is no resource gradient away from the soil surface and consequently no built-in advantage to a larger initial seedling that reaches further away from the surface. Advantages of larger seed mass owing to greater reserves (as distinct from owing to larger initial seedling size) apply during cotyledon phase but not later during seedling life. This has been directly demonstrated under deep shade (Saverimuttu & Westoby 1996, Walters & Reich 1999) and can account for all three cases in which larger seed mass was not associated with better survival under deep shade (Table 2).

There are some consistent shifts in mean log seed size between different environments, though not so many as might be expected from the experimental results. Many studies have shown that species establishing in closed or shaded environments tend to have larger seeds than those in open environments [e.g., Baker 1972, Foster 1986, Foster & Janson 1985, Grubb & Metcalfe 1996 (genera within families but not species within genera), Hewitt 1998, Hodkinson et al. 1998 (angiosperms but not gymnosperms)], Mazer 1989, Metcalfe & Grubb 1995, Salisbury 1942, Thompson & Hodkinson 1998]. Evidence about nutrient-poor versus nutrient-rich soils is contradictory. Westoby et al. (1990) found little effect comparing sclerophyll woodland on low-nutrient soils with temperate rainforest on higher-nutrient soils in Australia. Parolin (2000) found larger seeds in nutrient-poor environments among 58 Central American floodplain species. It has been suggested that species in drought-prone environments are likely to have larger seeds than those in moist environments (Baker 1972, Rockwood 1985, Salisbury 1942). However, the correlation Baker found was mainly caused by a tendency for herbaceous species in flood-prone habitats to have small seeds (Westoby et al. 1992), and Mazer (1989) failed to find a relationship between aridity and seed mass. Seed mass tends to be greater toward low latitudes (Baker 1972, Levin 1974, Lord et al. 1997), and this is only in part a correlate of shifts in growth form, dispersal mode, and shading. No relationship with altitude has been found (e.g., Rockwood 1985).

Despite some shifts in the mean between habitats, especially shaded versus open, it is striking that the spread of seed mass between species within a habitat is very wide (>95% of all variation is within rather than between temperate zone floras) (Table 1 and Figure 4).

LEAF-SIZE–TWIG-SIZE SPECTRUM

Corner (1949) pointed out two cross-species patterns. The thicker the plant axis (stem), the larger the individual appendages (leaves, inflorescences, fruits). The more closely spaced the ramification (branching), the thinner the ultimate axes and the smaller the appendages. Halle et al. (1978) called these patterns Corner's Rules (White 1983a,b), and recent work has confirmed and quantified them (Ackerly & Donoghue 1998, Brouat et al. 1998, Cornelissen 1999).

Twig cross-sectional area is expected to be coordinated with the total leaf area supported on the twig, for both hydraulic and mechanical reasons. However, a given total leaf area might logically be made up of many small or of few large leaves. Hence, coordination of twig cross-sectional area with transpiration demand from the leaves or with requirement for mechanical support does not, in itself, force a correlation between the size of twigs and the size of individual leaves. Presumably, when twigs are closer together, then leaves should be smaller because otherwise they would overlap wastefully. Perhaps also they might damage each other by thrashing together in the wind.

Although the leaf-size–twig-size spectrum is apparent all around us, and quantifications of it are accumulating, its adaptive significance is far from clear. Theory about leaf size has been developed by Parkhurst & Loucks (1972), Givnish & Vermeij (1976), and Givnish (1978, 1979, 1984). Larger leaves have thicker boundary layers of still air. Consequently their convective heat loss is slower, and they tend to be heated above air temperature by a wider margin. This may be a disadvantage, increasing respiration rates more than photosynthesis rates. This effect will be more important for leaves under stronger radiation and where water is in short supply (because transpiration also sheds heat). Givnish (1978, 1979, 1984, 1987) expressed the costs of slow convective heat loss in terms of the carbon expenditure in the root system that would be needed to supply the leaf with sufficient water for cooling by transpiration. These costs were balanced against photosynthetic carbon gain in assessing optimal leaf size. As rainfall decreased, increasing water acquisition costs were expected to favor smaller leaves. Under low soil nutrient, Givnish invoked a flatter response to temperature of mass-based photosynthesis, dropping optimal temperature for net carbon gain and favoring smaller leaves.

Empirically, leaf size tends to decrease toward dry, sunny, or nutrient-poor habitats (Givnish 1984, 1986, 1987; Hall & Swaine 1981; Raunkiaer 1934; Schimper 1903; Shields 1950; Walter 1973; Webb 1968), as expected under Givnish's treatment. It is widely held that closely ramified branching is better suited to strong light environments (Cornelissen 1993, Givnish 1984, Horn 1971, Kempf & Pickett 1981). A substantial paleobotanical literature uses fossil leaf sizes to estimate past precipitation (Gregory-Wodzicki 2000, Jacobs 1999, Wiemann et al. 1998, Wilf et al. 1998, Wolfe 1995).

Other potential costs and benefits of a position high or low along the leaf-size–twig-size spectrum remain little investigated. Leaf-size–twig-size is well correlated with the size of infructescences and weakly with mass of individual seeds

(Cornelissen 1999). These relationships also occur ontogenetically and between genders in dioecious species (Bond & Midgley 1988, Midgley & Bond 1989), suggesting that under some circumstances selection for larger fruits or flowers could drive selection on leaf size. Smaller-leaved species may suffer less herbivory during leaf expansion, because the duration of expansion is shorter (Moles & Westoby 2000). Ritchie & Olff (1999) modeled coexistence of species that forage at different scales. Species that could orient their foraging accurately into small patches required higher resource concentrations to support their populations. Therefore, fine-scale foraging species were superior in local resource concentrations but unable to occupy most of the space available, and a series of coarser-scale species could coexist. One of their datasets used leaf width as an indicator of foraging scale. Given that leaf size is correlated with twig size and degree of ramification, it could be argued that leaf size acts as a surrogate for something to do with the scale of twig or branch systems, which conceivably reflect the natural scale of foraging for light (Cornelissen 1993, Givnish 1984, Horn 1971, Kempf & Pickett 1981). However, Bragg & Westoby (2002) did not find support for this idea. Although smaller-leaved species were positioned in higher light relative to their height, the light patches in question were several-fold larger than whole plants.

Surprisingly, the dry-mass economics of deploying leaf area as few large versus many small leaves seem to have been little investigated. Dry-mass gain per shoot mass can be partitioned into dry-mass gain/leaf area \times leaf area/shoot mass. Given that leaf area ratio (leaf area per plant mass) has proved to be the largest source of variation in seedling growth between species (Poorter & van der Werf 1998), it would not be surprising if leaf area per shoot mass were important in the economy of branch systems. We have found a substantial tendency for larger-leaved species to have higher leaf mass fraction beyond 10 mm² twig cross-section, but this was counterbalanced by larger-leaved species having lower leaf area per leaf mass (higher LMA) (M. Pickup, A. Basden, M. Westoby, unpublished data). It is already clear that this second pattern is not a universal rule. Grubb (1998) and Shipley (1995) found that among species with similar ecology those with larger leaves tend to have higher LMA. They suggested this was a requirement for mechanical support. Niinemets (1996, 1998; Niinemets & Kull 1994), however, found lower LMA in larger-leaved species; this pattern may occur within a vegetation type when species are differentiated mainly along a shade-tolerance spectrum. Using data from several habitats, Ackerly & Reich (1999) found LMA and leaf size negatively correlated, but this consisted almost entirely of the difference between angiosperms and conifers; there was little correlation within either clade. Across sites, SLA and leaf size both tend to decline towards lower rainfall and lower soil nutrient (Ackerly et al. 2002, Fonseca et al. 2000). In datasets spanning a range of habitats, within-habitat and between-habitat patterns are liable to cancel each other out, leaving little or no overall relationship between leaf size and LMA (Ackerly et al. 2002, Fonseca et al. 2000, Wilson et al. 1999). In summary, if larger-leaved species turn out consistently to have higher leaf mass fractions in their shoots, this will not always be counterbalanced by higher LMA. Higher leaf

mass fraction may deliver a substantial leaf area per shoot mass advantage to large leaf size and large twig size in some comparisons.

POTENTIAL CANOPY HEIGHT

Potential or maximum canopy height can range from ~ 1 cm to >50 m, four orders of magnitude. Sometimes this full range can be found at a single site. Here we consider self-supporting species only. The height-parasites, climbers and epiphytes, are important in some vegetation types. Their strategies testify to the advantage of height but do not really have characteristic heights of their own.

The benefit of supporting oneself at a height cannot be understood by considering a single strategy in isolation (Iwasa et al. 1985). At any moment in the successional process, being taller than neighbors confers competitive advantage through prior access to light. However, height incurs costs from past investment in stems and support structures, from continuing maintenance costs for the stems and vasculature, and from disadvantages in the transport of water to height. In the absence of competition, a single strategy could maximize productivity per leaf area by minimizing the costs associated with height and growing close to the ground. However, plants using this strategy would be open to invasion by plants using a strategy that diverted some resources to nonproductive tissues such as stem and grew slightly taller. Plants using that strategy in turn would be open to invasion by plants using a third strategy that grew slightly taller still, and so forth. Height is the classic case of a strategy that needs to be understood in the context of game theory (Kawecki 1993).

Height is the one quantitative trait that has been adopted by virtually everyone doing comparative plant ecology (e.g., Bugmann 1996, Chapin et al. 1996, Grime et al. 1988, Hubbell & Foster 1986, Keddy 1989, Weiher et al. 1999, Westoby 1998, Wilson et al. 1999). Nevertheless, unlike the LMA-LL and seed mass–seed output spectra, ideas about canopy height strategies include several trade-offs (Givnish 1995). The upper limit on height, the pace at which species grow upward (which may decide relative height advantage at different times after disturbance), and the duration over which stems persist at their upper height, have costs and benefits that are at least partly separate. If the costs and benefits could be elucidated, and if easily measurable key traits could be identified, these components would ideally be separated out.

Some studies have considered the biomass cost for supporting a unit of leaf area at a given height. In herbaceous vegetation taller species have lower leaf area ratios (leaf area per aboveground biomass) owing to lower leaf mass fraction or higher SLA or both. Although shorter species intercept less light per unit leaf area, they are not necessarily inferior with regard to light interception per aboveground biomass (Anten & Hirose 1999, Hirose & Werger 1995).

A weakness of considering light interception per unit biomass is that biomass of stems and branches accumulates over time. Accumulated biomass is not in the

same units as current photosynthesis for assessing the budget at a particular stage of growth. The argument can be improved in two possible directions. One is to express stem and branch biomass as current costs. The other is to consider the time-dynamics of competition for height and light.

Along the current-budget direction, Givnish (1988, 1995) used allocation equations from Whittaker & Woodwell (1968) to estimate current growth of non-leaf tissues. Allocation to non-leaf increased with the height of the tree. Taken together with leaf respiration and with leaf construction costs amortized over the season, these costs can be balanced against current photosynthesis. Through this reasoning a maximum height can be estimated as the height at which costs fully consume all current photosynthesis.

This respiration hypothesis for the upper limit to plant height has been contrasted with a hydraulic-limitation hypothesis (Gower et al. 1996, Ryan & Yoder 1997), leading to a recent outburst of debate (Becker et al. 2000a,b; Bond & Ryan 2000; Mencuccini & Magnani 2000). In reality, arguments about single limiting factors for plant height are unlikely to be profitable, at least for thinking about differences between species. First, species are not expected to evolve to grow as tall as is physiologically possible. It is the density and height of shading by competitors that determines how much benefit can accrue from height growth. Second, natural selection shapes strategies in such a way that no single capability of the plant is limiting. Rather, strategies are characterized by coordination of different capabilities and quantities. Sapwood cross-sectional area is coordinated with total leaf area, the ratio of the two being adjusted to evaporative climate (Mencuccini & Grace 1995, Schafer et al. 2000). Stomatal conductance (and hence assimilation and transpiration) are coordinated with vascular conductance (Hubbard et al. 2001, Magnani et al. 2000, Nardini & Salleo 2000, Sperry 2000) and with the cavitation risk of the vasculature (Whitehead 1998). Constrictions in vessels to lower branches can ensure that sufficient water flow is directed to upper branches (Hacke & Sperry 2001). Vessel tapering can be coordinated with height to buffer the effect that height would otherwise have on conductance of the vascular pathway (Becker et al. 2000a, West et al. 1999). Similarly, vessel length (frequency of cross-walls) is modulated according to height within a tree to balance conductance against cavitation risk (Comstock & Sperry 2000). Pore diameters between vessels control air-seeding of embolisms from one vessel to another and the linkage between xylem pressure and xylem conductance (Sperry 1995, Tyree 1999). If one of these traits were consistently limiting relative to another, then alternative genotypes or species strategies would be favored that reallocated their efforts, because this could relieve the limitation without equivalent disadvantage elsewhere. This is the principle of equalization of marginal returns on alternative expenditures, familiar to economists and evolutionary ecologists (e.g., Venable 1996) but yet to be fully assimilated into physiological thinking. A species' strategies are expected to evolve to the point at which many factors are limiting simultaneously, or no single factor is limiting, depending how one likes to think about it.

Whereas some aspects of height strategy may be understood via the costs and benefits of height at a point in time, other aspects need to be considered over

cycles of disturbance and growth. Disturbances open the canopy, daylight becomes available near the ground, and a race upwards for the light ensues. Races are restarted when a new disturbance destroys the accumulated stem height. Winning strategies are not only those that eventually result in the tallest plants. Any species that is near the lead at some stage during the race may make sufficient carbon profit to ensure that it runs also in subsequent races (which is the criterion for a viable strategy). Entry in subsequent races may occur via vegetative regeneration, via a stored seed bank, or via dispersal to other locations, but the prerequisite for any of these is sufficient carbon accumulation at some stage during the race for light. Within a race series having some typical race duration, one finds successful height strategies that have been designed by natural selection to be among the leaders early in a race, and other successful strategies that join the leaders at various later stages. Among tree species, those with faster growth usually have lower wood densities, associated with less strength and decay resistance (Loehle 1988, 1996). Toward the later stages of height races, tree species with very persistent stems reach the lead because faster-growing species are disintegrating above them, rather than by overtaking the faster-growing species.

SPREAD OF SPECIES ALONG THE DIMENSIONS

For each of the dimensions discussed, species traits tend to shift along climatic gradients and between sites in a landscape, as briefly outlined above. However, a striking feature is the wide spread of traits among species growing interspersed within a single vegetation type.

The fact that assemblage averages shift in response to physical conditions of the site indicates that the species sifted into a site are drawn selectively from the regional flora ["filtered" (Diaz et al. 1998)] with regard to the value of the trait. However, if one compares two sites with different assemblage means, the site with lower mean will include some species with a higher trait value than the assemblage mean of the other site. Further, the spread of trait values seems at least as wide in harsh as in favorable habitats. This contradicts the idea that physical properties of the two sites determine in a simple way what trait values are permitted. Something spreads out the frequency distribution across species within a site into a broad mixture, at the same time that physical properties of the site somehow position the whole frequency distribution. In principle, three sources might contribute to the wide spread within sites: (a) a broad frequency distribution of physical conditions across microsites within each site, (b) continuing immigration from sites with different physical conditions, and (c) some game-theoretic or frequency-dependent process. Data are not available to partition the contributions of these three forces to spreading out the within-site frequency distributions, but we think it likely that game-theoretic processes are the most important. The field experiment to test for a frequency-dependent process is simple in principle. One needs to selectively remove species from a particular band of, for instance, seed mass, then show that recolonization is drawn selectively from that same band of species more than from among the seed

masses left behind. The difficulty is that the processes to be measured are only expected to operate consistently over several generations (which for woody vegetation would mean tens to hundreds of years), over several cycles of disturbance (because using different times since disturbance is one of the main forms of game-theoretical interaction), and over a large enough area of space for realistic population dynamics within all of the species involved (which would mean hectares up to square kilometers for each replicate). This experiment, which would be the natural next step in terms of research logic, is unfortunately nearly unachievable in practice.

The qualitative conditions for coexistence of a broad mixture of strategies for a trait are reasonably well understood. Evolutionarily stable strategy-mixture theory developed by Geritz for seed mass (Fagerström & Westoby 1997; Geritz 1995, 1998; Geritz et al. 1999; Rees & Westoby 1997) illustrates the principles. Species at one end of the spectrum of the trait need to be competitively superior, but at the same time unable to sequester all the space available. In Geritz's models large-seed strategies defeat smaller-seed strategies in seedling competition for space. Hence, strategy mixtures can always be invaded by a larger seed mass, up to the size at which seed output is so low that the population can no longer have a positive rate of increase, even though the strategy is never outcompeted. At the same time, plants using strategies with smaller seeds and higher seed output from each occupied patch are able to persist, because their seeds reach some establishment opportunities that are not reached by any larger seed. In other words, the broad spread of strategies is made possible by a colonization-competition tradeoff (Chesson 2000, Pacala 1997). The specific assumptions of this model are probably not met in most vegetation types (Leishman 2001), but the point is that game-theoretic processes with this general structure are the most likely forces generating broad strategy mixtures within assemblages.

For the LMA-LL and leaf size-twig size dimensions, ESS models have yet to be developed, but appropriate spectra have been suggested. For LMA-LL, a model by Aerts & van der Peijl (1993) is underpinned by a spectrum of time-since-disturbance. Low LMA species grow faster during early succession, but high LMA species have longer nutrient retention times, and over time they take over an increasing proportion of the nutrient pool. For leaf size-twig size, the model by Ritchie & Olff (1999) discussed above is underpinned by an assumption that high-value resources occur in small patches, and species exploiting these small patches are therefore unable to occupy the whole environment.

There have been ESS treatments of height (Givnish 1982, King 1991, Makela 1985, Sakai 1995), of the shading relationship between strategies as affected by SLA or leaf angle (Hikosaka & Hirose 1997, Schieving & Poorter 1999), and of the pace of height growth as affected by allocation between roots and shoots and between stem and foliage (Givnish 1995, Sakai 1991, Vincent & Vincent 1996). All of these treatments predict a single winning strategy. This illustrates that the observed wide spread within sites on these dimensions is not inevitable.

The ESS treatment of Iwasa et al. (1985) accounts for a mixture of height strategies. This shows that provided the costs of maintaining leaves at a given

height rise with height in an accelerating manner, leaves should be spread through a continuous range of heights. It can easily be imagined that this strategy mixture could be made up of many species of different heights, though Iwasa et al. left open the possibility of a single species with a deep canopy.

CONCLUSION AND SOME FUTURE DIRECTIONS

In comparing ecology to chemistry before the periodic table, Southwood (1977) pointed both to the disorganized condition of ecological knowledge and to the hope for integration via an agreed-upon ecological strategy scheme. Actually, ecological strategy schemes are unlikely to look like a periodic table (Steffen 1996). A closer analogy might be personality schemes as used in psychology (Atkinson et al. 1990). Personality schemes have spectra such as introvert to extrovert, analytical to emotional. Key issues in personality scheme research have been about the number of spectra that convey different, useful information (consensus is approximately 5) and about the meaning of particular spectra and their predictive power for what people will do in different situations.

Similarly in ecology, the need is to identify leading dimensions of variation that seem useful. The list can be open-ended: There is no need to decide in advance on a scheme with a fixed number of dimensions. The present situation is that a degree of consensus is emerging about LMA-LL, seed mass-seed output, and height. These three dimensions of variation capture important generalities about how plant species make a living. They can be measured relatively easily, which is important if they are to serve for coordinating information worldwide.

What are the likeliest directions for future progress? First, these dimensions have not been tried out much as potential explanatory variables during literature synthesis. Plainly they do have some explanatory power in relation to some kinds of phenomena, for example LMA-LL in relation to ecophysiological traits such as leaf nitrogen and potential photosynthetic rates. At this stage we cannot be sure the dimensions will be much help in pulling together the large literature on a few species at a time in ecophysiology, succession, or experimental ecology, but it is worth trying. Otherwise we default to the discouraging conclusion that each species is idiosyncratic and a separate problem.

A second direction for further progress is through adding dimensions to a list of those that are most informative. An obvious deficiency is the lack of something indicating temperature preferences, whether as optima for growth or as lower or upper tolerances. This is crucial for the position of a species on global climate maps and for its future under climate change. Unfortunately, there is no obvious candidate for a simple measurement that would capture temperature preference.

A third direction for research progress would be to clarify and separate the different elements of height: the pace of height growth, the asymptotic height, and the capacity to persist at a height. A fourth direction would be to clarify costs and

benefits along the leaf-size-twig-size dimension, which is conspicuous but poorly understood. A fifth direction would be to develop convincing models that predict both the spread of species traits observed and shifts in the upper and lower bounds of the spread from one environment to another. It is understood what is needed in principle to support a broad mixture of coexisting strategies, but this has yet to be modeled in detail and with convincing experimental evidence for any particular strategy dimension.

There is much to be done. There is also a real hope that we may be getting somewhere.

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