

Form defining function: interpreting leaf functional variability in integrated plant phenotypes

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The universal importance of leaf structure and function to plant physiology, evolution, and ecology has generated great interest in developing a general understanding of leaf trait strategies (Reich et al. 1997, Westoby et al. 2002, Wright et al. 2004). Across vascular plants, variability in leaf function is restricted to a continuum of phenotypes from leaves with high rates of carbon return but short lifespan to leaves with low rates of carbon return but long lifespan (Reich et al. 1997). While leaf function varies tremendously across vascular plants, much of the total variation in leaf function occurs within coexisting species, and climate (environmental) variability explains little of the total variability in leaf function (Wright et al. 2004). Explaining how such a diverse range of leaf strategies can evolve and coexist under common environmental selection pressures is presents a major challenge to ecologists. Here, I suggest that interpreting leaf functional variability can be advanced by considering how leaf biomass is allocated in integrated plant body plans. Since the adaptive value of a phenotype must be measured in terms of individual fitness, any examination of leaf trait strategies must take into account that leaves function within the broader biological context of the individual plant.

The evolution of leaf strategies is based on a series of functional tradeoffs. Leaf traits associated with light

interception such as specific leaf area (SLA, leaf area per unit mass), and traits associated with carbon fixation such as photosynthesis, respiration, and nitrogen concentration tend to be positively correlated with one another but negatively correlated with leaf life span. Leaf trait correlations promote the evolution of syndromes ranging from highly productive short lived leaves to minimally productive long lived leaves (Reich et al. 1997, 1999). Other combinations are not observed as they are either not viable or not practical. Leaves with low rates of carbon fixation (productivity) can only return the plant's investment in the production of the leaves over a long period of time. By contrast, leaves with high rates of carbon fixation are damaged easily and are susceptible to herbivory (nutritious leaves, high in nitrogen and low in structure) and should have a relatively short functional lifespan (Reich et al. 1997). This continuum of leaf trait strategies is observed across vascular plants and is related to plant growth rate (i.e. the rate of biomass accumulation) and life history. For example, fast growing short-lived plants tend to have leaves with higher SLA than slow growing long-lived plants (Reich et al. 1997, Wright and Westoby 2000). The link between leaf form (SLA) and leaf function is fundamental in understanding how plants partition total leaf biomass to potentially competing functions.

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Allometry and the rules of plant growth

Many aspects of plant form and function are governed by scaling relations between traits. These scaling relations are controlled by physiological and architectural constraints. Energy production and carbon gain is a product of photosynthesis and scales isometrically (linearly) with leaf biomass allocation. Thus, plant growth rate (i.e. the rate of biomass production) also scales isometrically with leaf biomass (growth rate \propto leaf mass) (Niklas and Enquist 2002a, 2002b). However, as plants increase in size, they tend to allocate relatively more biomass to the stem and relative allocation to leaves decreases with increasing size (leaf mass \propto stem mass^{3/4}) (Enquist and Niklas 2002). The scaling relationship between leaf and plant biomass is due to the relationship between stem geometry and plant size. Stem diameter increases as plants become larger to increase mechanical stability of the stem and decrease vascular hydrodynamic resistance within the stems (Brouat and McKey 2001, Preston and Ackerly 2003a). Assuming density of stem tissue remains relatively constant, any increase in stem diameter will result in an exponential increase in stem mass and total mass (plant mass \propto stem diameter^{8/3}) (West et al. 1999, Enquist 2003). Leaf mass also scales exponentially with stem diameter (leaf mass \propto stem diameter²) due to an increase in both mechanical stability and vascular supply, and a decrease in hydrodynamic resistance (Niklas 1994, West et al. 1999) but the scaling exponent for leaf mass is less than that for stem mass. Under these scaling relationships, leaf mass allocation and growth rate should decrease with increasing plant size.

The rules of plant growth result in a high degree of integration between many plant traits describing overall plant size, patterns of allocation, and growth rates. Integrated relationships forming the rules of plant growth should constrain the range of possible growth forms. However, the evolution of allometric relationships in modular organisms is hierarchical (Preston and Ackerly 2003b), and constraints at the level of the whole plant need not constrain trait expression within modules (e.g. leaf traits). Thus, while total leaf allocation will be limited by stem size, leaf traits are not necessarily constrained by the same rules that govern the construction of the whole plant.

A fundamental aspect of plant construction is that photosynthesis is a function of leaf surface area (Niklas 1995). Leaf area per unit leaf mass (SLA) is variable both within (Shipley 2000) and between species (Reich et al 1997), but it is unclear if variability in leaf functional traits are related to whole plant leaf allocation. Variability in SLA is an important starting point for examining the evolution of plant functional traits and strategies.

Plant form defining leaf function

Varying leaf form (SLA) permits plants to differentially allocate limited leaf biomass to competing functions of productivity and longevity. Furthermore leaf form should be free from the constraints of whole plant allometry. For example, plants can achieve a given growth rate through either low leaf biomass but high specific leaf area or high leaf biomass but low specific leaf area (Fig. 1). Selection or constraints resulting in reduced stem diameter also limit leaf biomass allocation, but losses in potential growth rate can be limited through increasing SLA (and leaf productivity). Thus, at the level of individual leaves, variability in leaf form should be a product of selection on leaf physiology. In contrast, at the level of the whole plant, leaf form variability could be the product of constraints on total leaf allocation.

The importance of examining leaf traits in the context of the entire plant is highlighted where plant responses to environmental adversity requires coordinated responses of both whole plant traits and leaf traits. For example, plants grown in light competitive environments often maximize their ability to compete for light by increasing height relative to stem diameter (Rich et al. 1986, Weiner and Thomas 1992). SLA often increases in these plants under light competition (Shipley 2000), presumably to maximize light interception, and to offset the loss in photosynthesis due to reduced stem diameter and total leaf biomass. Similarly, plants grown in water limited environments limit relative stem diameter in order to resist cavitation and xylem damage (Preston and Ackerly 2003a). However, in these water limited environments, SLA often decreases in order to limit water loss through leaf surfaces relative to their ability for water uptake and transport (Preston and Ackerly 2003a). In these environments, variability in leaf form and function could arise due to conflicting selection pressures at the level of individual leaves (i.e. minimizing surface area and water

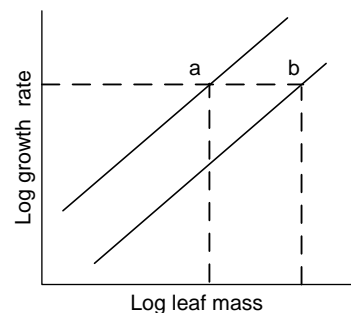


Fig. 1. Hypothetical invariant isometric (slope=1) scaling relations between plant growth rate and leaf biomass. The two lines represent the scaling relations for two plant taxa. The taxon describe by the upper line has greater SLA than the taxon described by the lower line. A given growth rate can be achieved with less leaf biomass in plants with high SLA (line a) than with plants with low SLA (line b).

loss) and at the whole plant (i.e. maximizing leaf surface area and growth rate in the face of restricted total leaf allocation). Shifting correlations within and between suites of traits could promote diversity of functional traits within a given environment.

Size dependence of plant growth rate

Plant relative growth rate (RGR – plant growth rate per unit plant biomass) has been fundamental in defining plant adaptive strategies and life history (Grime and Hunt 1975, Tilman 1988, Grime 2001). RGR is the product of net carbon assimilation rate for an area of leaf tissue (NAR, $\text{g cm}^{-2} \text{ day}^{-1}$), specific leaf area (SLA, $\text{cm}^2 \text{ g}^{-1}$), and total leaf mass relative to plant mass (leaf weight ratio, LWR, g g^{-1}) and can be described by the following equation (Porter and Remkes 1990, Shipley 2000):

$$\text{RGR} = \text{NAR} \times \text{SLA} \times \text{LWR} \quad (1)$$

Scaling relationships between leaf and stem biomass will result in decreasing LWR with increasing plant size. Where NAR and SLA are fixed throughout development, RGR will also decrease with increasing plant size. While this relationship is not in itself surprising as growth rates tend to decrease with increasing body size across species (Damuth 2001), the nature of the relationship between RGR and size should depend on leaf construction. Plants producing leaves with relatively high SLA will also have relatively high RGR across plant sizes, but the growth rate advantage accrued by highly

productive leaves diminishes as plant size increases (Fig. 2). High SLA will be favored only where the advantages of higher growth rate outweigh the costs of decreased leaf lifespan, and increased susceptibility to herbivory and physical damage. Decreasing benefits relative to costs should favor decreasing SLA through development (i.e. as plant size increases), and relatively low SLA in large species or genotypes.

Two observations are consistent with the prediction that the advantages of producing highly productive leaves diminish with increasing size. First, SLA generally decreases across functional groups of increasing size (relatively high in herbaceous plants, intermediate in pioneer woody species, and low in late successional trees) (Reich et al. 1997, Poorter et al. 2004). Second, SLA often decreases within individuals through development (Shipley and Almeida-Cortez 2004). However, constraints in developmental plasticity in leaf form should prevent the expression of optimal leaf form throughout development. For example, tree seedlings tend to have higher SLA than herbaceous plants of the same age and in common environments (Loveys et al. 2002, Shipley 2002). These constraints could arise through genetic correlations between leaf form in adult plants and young plants, and selection on relatively low SLA late in development prevents the expression of high SLA early in development. Several plant taxa (e.g. the Australian *Acacias*) undergo a developmental shift in leaf form, expressing productive ‘true’ leaves early in development. Shifting selection pressures on leaf form as trees increase in size appear to have promoted the expression of modified petioles (relatively low SLA) as the functional leaf tissue later in development. Homologous leaf structures in different developmental stages may be a mechanism of expressing adaptive leaf forms throughout development despite constraints on leaf form variability.

Several predictions can be made under the framework for the expression of leaf form and function outlined above. First, where plant fitness and growth rate are functionally related, environmental adversity constraining leaf allocation should favor responses to maximize leaf productivity. Second, the allometric relationship between leaf mass and stem mass will favor decreasing leaf productivity with increasing plant size. Since the slope of the leaf mass versus stem mass relationship defines how quickly the benefit of producing productive leaves diminishes with increasing size, differences (if any) in this slope between species (or genotypes) will be a key factor contributing to variability in leaf trait strategies across plant taxa of similar size or within the same functional group. Third, conflicting selection pressures on leaf function (leaf traits) and leaf allocation (whole plant traits) should increase the number of viable leaf trait strategies within a given habitat. Future studies addressing these predictions will demonstrate the potential for plastic or evolutionary shifts in plant form to

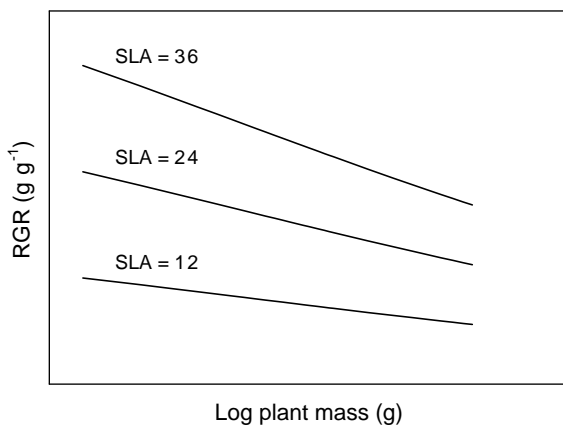


Fig. 2. Relationships between RGR and plant mass for three hypothetical plant taxa with differences in SLA (following Eq. 1). Each relationship is modeled so that each unit of leaf area returns one unit of plant mass. NAR is assumed to be constant and leaf mass \propto stem mass^{3/4}. Relative growth rate is expressed as the unit return of leaf mass per unit of plant mass. Total plant mass modeled ranges from 0.1 to 30 g of biomass. The relationships presented represent the approximate mean (middle line) \pm SD (top and bottom lines) SLA values recorded for juvenile plants for over 200 vascular plant species (including herbaceous plants, shrubs, and trees) (S.P. Bonser, unpubl.).

precipitate correlated changes in leaf physiology and function. Our understanding of leaf function will greatly improve if we interpret functional variability within plants rather than simply within individual organs.

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