A leaf-height-seed (LHS) plant ecology strategy scheme

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Abstract

A leaf-height-seed (LHS) plant ecology strategy scheme is proposed. The axes would be specific leaf area SLA (light-capturing area deployed per dry mass allocated), height of the plant's canopy at maturity, and seed mass. All axes would be log-scaled. The strategy of a species would be described by its position in the volume formed by the three axes.

The advantages of the LHS scheme can be understood by comparing it to Grime's CSR scheme, which has Competitors, Stress-tolerators and Ruderals at the corners of a triangle. The CSR triangle is widely cited as expressing important strategic variation between species. The C–S axis reflects variation in responsiveness to opportunities for rapid growth; in the LHS scheme, SLA reflects the same type of variation. The R axis reflects coping with disturbance; in the LHS scheme, height and seed mass reflect separate aspects of coping with disturbance.

A plant ecology strategy scheme that permitted any species worldwide to be readily positioned within the scheme could bring substantial benefits for improved meta-analysis of experimental results, for placing detailed ecophysiology in context, and for coping with questions posed by global change. In the CSR triangle the axes are defined by reference to concepts, there is no simple protocol for positioning species beyond the reference datasets within the scheme, and consequently benefits of worldwide comparison have not materialized. LHS does permit any vascular land plant species to be positioned within the scheme, without time-consuming measurement of metabolic rates or of field performance relative to other species. The merits of the LHS scheme reside (it is argued) in this potential for worldwide comparison, more than in superior explanatory power within any particular vegetation region.

The LHS scheme avoids also two other difficulties with the CSR scheme: (a) It does not prejudge that there are no viable strategies under high stress and high disturbance (the missing quadrant in the CSR triangle compared to a two-axis rectangle); (b) It separates out two distinct aspects of the response to disturbance, height at maturity expressing the amount of growth attempted between disturbances, and seed mass (inverse of seed output per unit reproductive effort) expressing the capacity to colonize growth opportunities at a distance.

The advantage of LHS axes defined through a single readily-measured variable needs to be weighed against the disadvantage that single plant traits may not capture as much strategy variation as CSR's multi-trait axes. It is argued that the benefits of potential worldwide comparison do actually outweigh any decrease in the proportion of meaningful variation between species that is captured. Further, the LHS scheme opens the path to quantifying what proportion of variation in any other ecologically-relevant trait is correlated with the LHS axes. This quantification could help us to move forward from unprofitable debates of the past 30 years, where CSR opponents have emphasized patterns that were not accommodated within the scheme, while CSR proponents have emphasized patterns that the scheme did account for.

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Introduction

Plant ecology strategy schemes (PESSs for short) arrange species in categories or along spectra according to their ecological attributes. 'Strategy' is used here to mean how a species sustains a population. The concept compares between species rather than between individuals or between activities at different times by one individual. A species strategy needs to be thought of over a series of generations, and as operating in the presence of competing species, in varied landscapes, and under regimes of disturbance.

One aim of a PESS is to express an understanding of important opportunities and selective forces that shape the ecologies of plants. Another aim is to describe the plant componentry of ecosystems in terms of a limited number of ecological component-types. Then when vegetation descriptions were condensed into PESS categories rather than listing each species individually, ecologically important information would be retained and instructive comparisons between ecosystems would emerge. In many ways the quest for a PESS encapsulates the whole research agenda of plant ecology (Grime, 1979; Keddy, 1989, 1992; Myerscough 1990).

There is a continuing tension between the two aims, however. If someone's expectation from a strategy scheme is that it will express whatever they see as most important in strategic variation between species, they will often be dissatisfied with schemes proposed by others, because they disagree about what is most important and because the vegetation type they are most concerned with may have different predominant influences compared to the vegetation type where the scheme was devised. In consequence, the potential benefits that a consensus scheme could bring have not materialized. Although a number of schemes have been proposed at different times, only the Raunkiaer life-form scheme has gained wide acceptance in the sense that publications report life-form categories for their study species as a matter of routine.

In fact, over the last couple of decades the research objective of actually agreeing on a consensus PESS, that could provide a common language for comparing species and vegetation types worldwide, seems to have dropped below the horizon, with the notable exception of a sustained campaign from the Unit for Comparative Plant Ecology at Sheffield (e.g. Grime, 1974, 1977, 1979; Grime et al., 1988, 1997), of which more later. Rather, the attention of most researchers has been directed at the more abstract problem of un-derstanding trade-offs that might underpin ecological strategies. Very large literatures have developed that report studies comparing sets of a few related or co-existing species, or that develop theory for trade-offs among life-history elements.

This paper proposes a PESS designed to express variation similar to that expressed by Grime's CSR triangle, while at the same time enabling any species worldwide to be readily categorized, in order that the potential benefits of a consensus scheme might be realized. The benefits of the proposed LHS (leaf-height-seed) scheme lie in the potential for worldwide comparison, more than in having superior explanatory power compared to particular existing schemes in particular situations.

The sequence of argument is as follows. First some major purposes for a consensus PESS are outlined. Second, existing schemata are briefly discussed, especially Grime's CSR triangle, which in my view exemplifies both the strengths and the limitations of our present situation. This leads on (third) to a list of attributes a PESS would need for the benefits of worldwide comparison to materialize. Fourth, the proposed LHS scheme is described, with the argument that this scheme, or one with similar properties, could achieve sufficient worldwide consensus. Finally some comments are made about application and quantification.

What purposes would a consensus PESS serve?

If a PESS could be agreed to the point that it was widely adopted, several benefits could result:

1. Meta-analysis of field experiments. Hundreds of experiments have now accumulated on competition between plants, on herbivory and on other interactions involving plants (e.g. Connell, 1983; Crawley, 1983; Goldberg, 1996; Goldberg and Barton, 1992; Gurevitch et al., 1992; Hairston, 1989; Price et al., 1986; Schoener, 1983; Sih et al., 1985; Wilson and Agnew, 1992). Generalizing across these experiments is now an outstanding question for ecology. Up till the present, species in experiments have usually been categorized for meta-analysis into growth form or life form or annual vs perennial. It seems reasonable to hope that if species could be categorized according to a PESS that captured a better proportion of ecologically-significant variation between species, then improved meta-analysis might result.

2. Placing ecophysiological studies in comparative context. Field measurements of gas exchange or other metabolic fluxes can only be made on a few species in any one study (e.g. reviews in Lambers et al., 1989; Lange et al., 1984; Mulkey et al., 1996; Roy and Garnier, 1994; Schulze and Caldwell, 1994). Often these studies aim to compare between ecological categories of species, for example gap-requiring with shade-tolerant. But synthesis across separate studies will remain difficult until there is a consensus basis for categorizing species.

3. Vegetation dynamics under global change. Future temperature zones are expected to migrate polewards, atmospheric CO_2 to continue increasing, and land use to continue intensifying. Projecting future vegetation dynamics on a worldwide basis has become an important test for ecology's grasp on substantial applied questions (Körner, 1993; Steffen et al., 1992). Global vegetation dynamics models must work with 'functional types' of plants, they can not be parameterized for all 300,000 vascular plant species individually (recent workshops on this problem edited by Woodward and Cramer, 1996; Smith et al., 1997)

In summary of the current situation: more field experiments and ecophysiological studies have been accumulated than have been satisfactorily digested and interpreted; global change research urgently needs plant functional type classifications; and the gradual accumulation of comparative information in electronic databases is reaching critical mass, allowing patterns to have their generality quantified much more widely and quickly than a decade ago. Together, these trends should bring the prospect of a worldwide consensus PESS back near the top of plant ecology's research agenda.

Outline of literature on plant ecological strategies

The literature on plant ecological strategy schemes can be summarized into three main strands of thinking (with more than one strand present in some publications). One strand defines schemes by reference to distribution (realised niche) on one or more environmental gradients. Dyksterhuis (1949) distinguished increasers vs decreasers in response to livestock grazing pressure. The 'vital attributes' of Noble and Slatyer (1980) categorize species according to which of their life-history phases are present at different numbers of

years after a fire or other repeating disturbance. Ellenberg (1988), masterfully drawing together a great volume of experience in central Europe, attributed ratings for nitrogen, soil moisture and other environmental preferences to large numbers of species.

A second physiognomic strand has been active especially within plant geography, with a tradition going back to de Candolle and Warming. Raunkiaer's life-form scheme (1907, English translation 1934) is based on the location of the buds where regrowth arises after the unfavourable season of the year. Because schemes in this strand use physiognomic, phenological or other attributes that can be assessed by looking at the plants, without need to map them onto an environmental space or measure physiological responses in the lab, they can readily be applied for worldwide comparison. It remains very common for publications to report life-form categories for the species they have studied, and indeed the life-form system is the only scheme that has been really widely adopted in this sense. Subsequent structural schemes include Dansereau (1951), Mueller-Dombois and Ellenberg (1974), Box (1981), Sarmiento and Monasterio (1983), Barkman (1988), Orshan (1989) and Prentice et al. (1992), but none of these have superceded the Raunkiaer scheme in general practice.

The third strand has built schemes that distinguish categories according to the types of ecological opportunity exploited within a landscape. These schemes are overtly conceptual: that is, while the first two strands assuredly had conceptual reasons for choosing the criteria or axes in their scheme, in this third strand axes or categories are actually named along conceptual lines. For example the r-K spectrum (Cody, 1966; MacArthur and Wilson, 1967) and a scheme used in the textbook by Begon et al. (1996, p 541) distinguish opportunities according to the strength and functioning of density-dependence. A number of schemes have developed this spectrum into a three-cornered arrangement, adding a category of opportunities where the physical environment permits only slow acquisition of resources (Greenslade, 1972, 1983; Grime, 1974; Southwood, 1977; Whittaker, 1975). Many schemes focus on the successional cycle, with species exploiting the early years after disturbance called 'pioneers' or 'early-successional'. 'Tolerance' (meaning capacity to establish under shade) has long been a key element of silvicultural information about tree species in the northern hemisphere (e.g. Shugart and Urban, 1989; Spurr and Barnes, 1980). Rainforest species similarly are categorized along a spectrum from species requir-

ing large canopy gaps to those capable of establishing in small gaps or under closed canopy (e.g. Denslow, 1980; Richards, 1952; Whitmore, 1975). In arid zones growth opportunities of varying quality and duration occur following rain: Westoby (1980) distinguished three 'types of time' according to the opportunities presented to different life-histories. Plant defences have been related to apparency (Feeny, 1976; Rhoades and Cates, 1976), to tissue longevity (Loehle, 1988), and to slow growth rates (Coley et al., 1985). Tilman (1982) focussed on the ratio between different consumable resources (archetypally mineral nutrients) as decisive for which species will be successful. Tilman (1988, 1990) concentrated on the ratio between soil nitrogen and light, and argued that change in this ratio through the course of succession favours species with different root-shoot allocation. Smith and Huston (1989) built a theory for distribution of plant functional types across spatial zones and through temporal succession, with an associated paper by Austin and Smith (1989) specifying in more detail how species having different fundamental niches should be distributed along an environmental continuum. Smith and Huston's (1989) functional types were differentiated in terms of trade-offs for use of water and light, and accordingly were laid out in a two-dimensional table.

An extensive literature relates sclerophylly and evergreenness to low soil nutrients (Beadle 1954; Loveless, 1961). Some have argued for a single spectrum from sites that sometimes permit rapid growth to sites that always enforce slow growth. This view has been closely connected to research on factors determining potential growth rates of species (Aerts and Van der Peijl, 1993; Chapin, 1980, 1991; Chapin et al., 1993; Grime, 1979; Poorter, 1989; Van der Werf et al., 1993). Others (e.g. Grubb, 1985, 1992) have emphasized that there are different specific adaptations to different causes of unfavourability. Keddy and McLellan (1992) proposed a centrifugal scheme in which different axes of unfavourability led away from a single strategy for exploiting the most favourable sites.

Grime's Triangle

Grime's CSR triangle (1974, 1979; Grime et al., 1988), also called by Grime 'plant strategy theory', commands more extended comment when discussing plant ecological strategy schemes. Grime has campaigned energetically over more than 20 years both

for the general proposition that a PESS is important and achievable, and for his particular scheme. The CSR triangle has two dimensions, the C–S axis reflecting adaptation to opportunities for rapid growth versus continuing enforcement of slow growth (Competitors to Stress-tolerators), the R-axis reflecting adaptation to disturbance (Ruderals). Thus the thinking behind the CSR scheme has been focussed mainly on differences between coexisting species in how they make use of a site, and between species occupying sites of different favourability and different disturbance regime within a landscape. Certainly the CSR-mixture might be expected to shift along geographical-scale gradients of rainfall and temperature also, but the justifications for the CSR scheme's axes are not oriented towards geographical-scale variation.

In my view it is widely agreed that exploiting opportunities for fast versus slow growth, and coping with disturbance, are among the most important forces shaping the ecologies of plants within landscapes. Grime (1988) does not claim the main axes of the CSR scheme as original with himself, but cites them back to Ramenskii (1938). Greenslade (1972, 1983), Whittaker (1975) and Southwood (1977) have similarly argued for habitat templates with axes reflecting adversity and disturbance. The CSR scheme is widely cited in textbooks (e.g. Begon et al., 1996, Cockburn, 1991, Colinvaux, 1993, Crawley, 1996, Ingrouille, 1992). Accordingly the present paper takes it as given that axes of adaptation for rapid growth and for coping with disturbance express at least some significant strategic variation between plant species. It does not reargue that question, rather it addresses the question why the CSR scheme has not been widely *implemented* (as opposed to cited).

Grime's triangle exemplifies problems we need to overcome before the benefits of consensus and worldwide comparison can materialize. Impediments to wider implementation of the CSR scheme arise from its defining axes by reference to concepts. First, in using the terms 'Competition' and 'Stress' the scheme enmeshes itself in controversies and semantic issues with a considerable history. People have felt they could not accept the scheme without also accepting particular useages for these terms. Second, although much has been published about the correlations between plant attributes and CSR positioning, an explicit quantitative protocol is lacking for positioning a species in the strategy scheme, and in consequence definite CSR positions have been attributed to few species beyond the datasets for Sheffield and the UK

(Grime et al., 1988). Third is the question how patterns that can not be condensed into the CSR triangle should be handled. The triangle has been criticized as failing to account satisfactorily for a number of specific phenomena, and also on the more general grounds that the plant world is too complicated to be summarized by any simple scheme – an outlook encapsulated in phrases in Grubb's (1985, 1992) titles, 'Problems of generalization' and 'A positive distrust in simplicity'. To me it would seem obvious that any scheme will express some differences between species but not all of them. But regrettably, this difference in outlook has persisted as an unresolved dispute over the general merit of the CSR scheme, rather than being resolved through quantifying what is versus what is not explained by the scheme. The difficulty in quantifying arises from the second point above, that a simple agreed protocol to position a species in the CSR space is lacking.

What attributes would a PESS need in order to realize the potential benefits from consensus?

1. First and most obviously, it would need to be agreed that the PESS expressed meaningful differences in ecological behaviour between plant species. The present paper does not seek to innovate in this regard. The three traits proposed as axes all reflect well-established trade-offs that have substantial consequences for the manner in which a species copes with the physical environment or the presence of competitors and other biota (discussed below). The three axes chosen reflect mainly the differentiation of species strategies within a site or within a landscape, and one way to think of the LHS scheme is as a recasting of the CSR scheme. It is *not* essential that the attributes adopted as PESS-axes be universally agreed to be the most ecologically-significant traits that could possibly be chosen. If agreement about the exact ranking of importance among ecologically-significant traits is set as a target, then consensus will be very difficult to achieve.

2. It should be possible to position a plant species from anywhere in the world within the PESS by reference to attributes measurable on the plant itself. Existing protocols for attributing a CSR triangle location to a species on the basis of plant traits are qualitative and partly subjective (see keys in Grime, 1984; Grime et al., 1988). Alternatively

a CSR location can be assessed from the environmental distribution of species relative to each other. This relates species within a given landscape or flora, but cross-relating to a different flora demands a whole separate project. In order to achieve the purposes of meta-analysis across species from all over the world, and global vegetation modelling, it is essential that there be an explicit protocol for determining a species' position in the PESS, and that this protocol not rely on local-context information. The simplest way to achieve this is for a scheme to have axes defined by single plant traits, each chosen to express as best as possible spectra of variation that are agreed to be important.

3. It is also important that the PESS-attributes chosen require little enough effort to estimate that experimentalists may be willing to report them for their species with a view to subsequent meta-analysis by others, even though they have no immediate use for the data themselves. The three axes of the scheme proposed here are defined by single plant traits and require relatively little effort to estimate, as illustrated by draft protocols provided in Appendix 1.

4. It should be possible to quantify the extent to which the PESS captures variation in other plant attributes, besides those that are actually used as dimensions of the PESS. For the three-axis scheme proposed here, this can be achieved simply through estimating the correlation of other attributes with the three used in the scheme, that is, assessing how reliably any other attribute can be predicted, knowing the position of a species in the PESS. The point of this is to have a sensible understanding of what is and what is not achieved through a given PESS, since it is not reasonable to expect any PESS to capture 100% of ecologically interesting differences between species. Of course, if a given attribute were largely independent of the existing axes of a PESS, and were thought to be important, then the research community might eventually agree to add it as a further consensus axis.

A proposed LHS (leaf-height-seed) scheme

The particular scheme suggested consists of three axes:

- specific leaf area SLA, area per unit dry mass (of mature leaves, developed in full light, or the fullest light the species naturally grows in)
- height of the canopy of the species at maturity ('design height')
- seed mass

Each of these traits is correlated with a number of others (as outlined below), but they have not been chosen only as conveniently-measured indicators. Rather it is believed that they themselves are fundamental trade-offs controlling plant strategies. They are fundamental because it is ineluctable that a species can not both deploy a large light-capturing area per gram and also build strongly reinforced leaves that may have long lives; can not support leaves high above the ground without incurring the expense of a tall stem; can not produce large, heavily-provisioned seeds without producing fewer of them per gram of reproductive effort.

All three axes would be log-scaled. The strategy of any one species would be characterized in the scheme by a position in a 3-D volume. The PESS as a whole can be visualized as the 3-D volume that encloses all competent plant strategies.

Each dimension is known to vary widely between species at any given level of the other two. For example in several temperate floras, 70–83% of the variation in log seed mass runs independently of variation in log height (Leishman et al., 1995); similarly SLA varies widely between species and is only weakly correlated with the other two axes (unpublished data). As might be expected for traits of such ecological importance, there is some capacity for them to be modulated in response to the environment faced by an individual plant, and also some genetic variation between individuals and populations. The LHS scheme does not assume that these traits are species-constants, but does operate on the premise that differences in the traits between species are ecologically meaningful.

Specific leaf area SLA

Specific leaf area is the light-catching area deployed per unit of previously-photosynthesized dry mass allocated to the purpose. SLA is like an expected rate of return on investment; high SLA permits (given favourable growth conditions) a shorter payback time on a gram of dry matter invested in a leaf (Poorter, 1994). At first glance it might appear that a low rate of return on investment would not be evolutionarily competitive, but low SLA species achieve greater leaf

life-span (Reich et al., 1992, 1997), through extra structural strength and sometimes through allocation to tannins, phenols or other defensive compounds. Therefore light capture across the whole life of the investment can be at least as great per dry mass invested in a low-SLA species. Reich et al. (1997) have shown across six biomes that SLA is closely correlated with mass-based net photosynthetic capacity and mass-based leaf N and negatively with leaf life-span. Higher leaf water content and reduced lamina depth can both contribute to higher SLA (Cornelissen et al., 1996; Cunningham et al., in review; Garnier and Laurent, 1994; Witkowski and Lamont, 1991). Grime et al. (1997) found SLA to be among the major contributors to the 'primary axis of specialization' they identified by ordination of 67 traits among 43 species, corresponding to the C–S axis of the CSR scheme.

Potential relative growth rate potRGR, measured on exponentially-growing seedlings given plentiful water and nutrients, has been seen as an indicator of responsiveness to favourable conditions (e.g. Aerts and Van der Peijl, 1993; Chapin et al., 1993; Grime, 1977; Grime and Hunt, 1975; Leps et al., 1982; Loehle, 1988; Poorter, 1989; Reich et al., 1992; Turner, 1994; Van der Werf et al., 1993). Because potRGR is made up of net assimilation rate × leaf mass fraction × SLA, variation in SLA necessarily influences potRGR. Indeed, in most comparative studies SLA has been the largest of the three sources of variation in potRGR (Cornelissen et al., 1996; Garnier and Freijsen, 1994; Grime et al., 1997; Lambers and Poorter, 1992; Poorter, 1989; Poorter and Lambers, 1991; Poorter and Remkes, 1990; Poorter, in press; Reich et al., 1992; Saverimuttu and Westoby, 1996; Swanborough and Westoby, 1996). High SLA species can have strategies associated with rapid production of new leaf during early life; faster turnover of plant parts permits also a more flexible response to the spatial patchiness of light and soil resources (Grime, 1994b). On the other hand, species with low SLA and therefore long-lived leaves can accumulate a greater mass of leaf and capture a great deal of light in that way; and the long mean residence time of nutrients made possible by leaf longevity permits a progressively larger share of nitrogen pools to be sequestered (Aerts and Van der Peijl, 1993).

Canopy height at maturity

Height obviously conditions how plants make a living, in different ways depending on vegetation dynamics.

In some vegetation types a characteristic vertical profile of leaf area and light attenuation persists over time, through the turnover of individual plants. Species with canopies at different depths in this profile are operating at different light incomes, heat loads, wind speeds, humidities, and with different capital costs for supporting leaves and lifting water to the leaves (Givnish, 1995; King, 1991). In other vegetation types disturbances, or the death of large individual trees, destroy canopy cover and daylight becomes available near the ground. The successional process that ensues can be understood as a race upwards for the light. Because light descends from above, the leading species at a given time have a considerable advantage. In this race, unlike a standard athletic contest, there is not a single winner determined after a fixed distance. Rather any species that is among the leaders at some stage during the race is a winner, in the sense that being among the leaders for a reasonable period permits sufficient carbon profit to be accumulated for the species to ensure it runs also in subsequent races. The 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 vegetative growth. Races are restarted when a new disturbance destroys the accumulated stem height. (In a few very tall vegetation types races may end in attrition when leaves have been lifted to a height where water can barely be drawn up to them, and stomates are closed much of the day.) The duration of an individual race can be measured in years, or ideally in units of biomass accumulation, calibrating intervals between disturbances to the productivity of a site. But within a race-series having some typical race duration, one finds successful growth 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. Species that achieve most of their lifetime photosynthesis with leaves deployed at 10–50 cm have different stem tissue properties from those designed for 1–5 m, and those in turn are different from species that achieve 30–40 m. The canopy height that species have been designed by natural selection to achieve is the simplest measure of this spectrum of strategies.

Seed mass

Seed mass variation expresses a species' chance of successfully dispersing a seed into an establishment opportunity, from a given area of ground already occupied by a species. Seed mass is also quite a good indicator of a cotyledon-stage seedling's ability to survive various hazards.

Species having smaller seed mass can produce more seeds from within a given reproductive effort, and seed mass therefore is the best easy predictor of seed output per square meter of canopy cover. It might be thought that distance of dispersal would be the major influence on a species' chance of dispersing a seed to a forest gap or another establishment opportunity. However, dispersal distances have not proved tidily related to dispersal morphology, to seed mass, or to any other plant attribute (reviewed in Hughes et al., 1994). Among unassisted species, larger seeds do not travel as far from a given height of release, but on the other hand larger seeds tend to have wings, arils etc or to be released from a greater height. Similarly among wind assisted species, larger seeds tend to have larger wings or longer pappuses. Because reduced dispersal associated with larger seed mass tends to be counteracted by investment in more expensive dispersal-assisting structures, or sometimes by being released from a taller plant, the net effect is that dispersal distance is not tidily related to any of these attributes. Seed mass (as a surrogate for seed output per ground area occupied) is the best predictor, for the present, of the chance that an occupied site will disperse a propagule to an establishment opportunity.

Species having larger seed mass have been shown experimentally to survive better under a variety of different seedling hazards (tabulated in Westoby et al., 1996), including drought, removal of cotyledons, and dense shade below the photosynthetic compensation point. The tendency to survive longer applies only during cotyledon phase while seed reserves are being deployed into the fabric of the seedling (Saverimuttu and Westoby, 1996). Capacity to continue growth into later seedling life under a low light level is determined more by canopy architecture and leaf properties (Kitajima, 1994). It seems likely that tolerance of seedling hazards is endowed not by seed mass as such, but by a tendency for larger seeds to retain more metabolic reserves uncommitted to the fabric of the seedling over a longer period, and therefore available to support respiration while in carbon deficit (Westoby et al., 1996).

Attribution of SLA, canopy height and seed mass to species

Because each trait varies within species to some extent, judgments about sampling and estimation are required when trait values are to be attributed to species. In order to sketch out how such judgments might be made, and to support this paper's assertion that an LHS position could be quite rapidly and conveniently estimated for species from anywhere in the world, Appendix 1 puts forward draft protocols for attributing trait values to species. These protocols are put forward with diffidence and the concept of the LHS scheme should not stand or fall by their perfection or otherwise. Rather it is hoped that plant ecologists who find useful the concept of the LHS scheme will then bring their common wisdom to bear on improving the attribution protocols.

LHS scheme compared to CSR scheme

Where each axis of the CSR scheme implies a complex of plant traits (e.g. Grime et al., 1997), the LHS scheme has axes defined by single quantitative traits. The benefit is the simple protocol for positioning a species in the LHS scheme compared to the CSR scheme. There may be a cost, in that a compound axis might be able to convey more total information about a species strategy. For reasons discussed earlier, I suggest the benefit outweighs the cost.

The CSR scheme has been made triangular rather than rectangular because the most stressful and most frequently disturbed corner is said not to be occupied (Grime et al., 1988), or because ineluctable trade-offs are said to prevent a species from being highly adapted to more than one of the three 'primary strategies' C, S or R (Grime, 1994a). The idea that a whole quadrant is missing due to the combination of high stress and high disturbance has been criticized (Grubb, 1985) and experiments with crossed gradients of fertility and disturbance (Burke and Grime, 1996; Campbell and Grime, 1992) have not produced wholly unoccupied space at the low-fertility high-disturbance corner. The LHS scheme avoids prejudging the question whether any particular corner of the LHS volume is not viable.

Another difficulty in the CSR scheme is the ruderality axis. Adaptation to disturbance might in principle include adaptations for surviving individual disturbances, together with adaptations for completing life history within a short interval between disturbances,

together with adaptations for dispersing through space or time to freshly disturbed locations. Grubb (1985) criticized the CSR scheme for not distinguishing continuing from episodic disturbance. According to Grime (Grime et al., 1988; Grime and Hillier, 1992) the scheme is for adults not juveniles: a given adult strategy can occur in combination with several different juvenile strategies, which has the effect of separating out dispersal and seed bank strategies from the main CSR categorization of a species. The LHS scheme disentangles these disparate elements to some extent. The canopy height at maturity axis reflects adaptation to the interval between disturbances (calibrated in units of height growth rather than time). The seed mass axis (more exactly its inverse, seed number per mass allocated to seed production) reflects the potential for dispersal to freshly-disturbed locations. Adaptations for continuing the lineage through particular types of disturbance (e.g. lignotubers for resprouting after fire, soil seed banks with a light requirement for germination following soil turnover, basal tillering in graminoids for grazing tolerance) have deliberately been left outside the LHS scheme, since they do not lend themselves to any simple generalization.

In summary, the LHS scheme captures a substantial part of the same spectra of strategy variation as the CSR scheme, while resolving some difficulties with it. SLA variation is crucial to the CS axis (Grime et al., 1988, 1997), that is to leaf longevity, mean residence time of nutrients, soil nutrient adaptation and potential RGR. Canopy height at maturity is arguably the most central single trait that needs to be adjusted to the duration of the growth opportunity between disturbances (R-axis); it is also treated by Grime et al (1988) as a significant predictor of C versus S strategy. The LHS scheme avoids assuming that high-S high-R strategies are not viable. By separating out seed mass as a distinct axis, it expresses something about dispersal to new growth opportunities, independently of what is expressed by canopy height about the duration of the growth opportunity between disturbances. Seed mass also expresses some significant differences between species about seedling establishment. Most importantly, because species can be positioned within the LHS scheme according to a clear protocol, with modest effort, and without reliance on observed species distributions relative to each other, the scheme opens up the path to worldwide comparisons and meta-analyses.

Applications and quantification

The purpose of this paper will have been achieved if a sufficient proportion of future publications reporting field experimentation, demography or ecophysiology can be persuaded to report characteristic species values for SLA, seed mass and canopy height at maturity, for the species they have studied. This would permit their species to be positioned within a consistent worldwide PESS. There is reason to hope the benefits in allowing improved synthesis of results by literature reviews or other meta-analyses would be sufficient to justify the extra effort needed to estimate these quantities, a modest effort for the 2–10 species that typically might be included in studies of this kind.

The research path towards quantifying what is and what is not captured by the LHS scheme is straightforward. For any ecological attribute or outcome, the cross-species relationship between it and each PESS axis can be graphed. A correlation coefficient summarizes in one number how well or how poorly the PESS expresses that aspect of ecological variation between species. Nonlinear or threshold relationships, where a correlation coefficient might be misleading, would be apparent from the graph.

The only complication that arises is, across what set of species should the correlation be estimated or the relationship be graphed? The simple answer to this question is that for purposes of a worldwide consensus PESS, such correlations should ideally be estimated across a substantial random sample of the world's species. But how much difference might it actually make, if such a correlation were estimated from different sets of species? This question actually exposes an issue that has been hidden implicitly within many debates about plant strategies, and moreover points to a practicable way of addressing that issue empirically.

By way of illustrating the issue, consider environmental gradients at two scales: from fertile to infertile soils within a landscape, and also across a macroclimate gradient from higher to lower rainfall. Along both gradients, conditions are becoming less favourable for plant growth. Accordingly we might expect SLA to shift downwards along both. Similarly we might expect changes in many other attributes, for example lignin concentration in leaves, epidermis thickness, proportion of the leaf that is spongy mesophyll. But would these change in the same *relationship* to SLA along the two scale-gradients? A continuing issue in thinking about plant strategies is whether different sources of unfavourability for plants

have sufficient in common that they can usefully be grouped together as 'stress'. Clearly low rainfall and low soil nutrients are not literally the same problem for a plant. Equally clearly, some elements of typical plant adaptive responses are in common between the two scale-gradients, and various arguments as to why this should be so can be mounted, for example one effect of low soil moisture must be to reduce access to soil nutrients (Grime, 1994a). This issue can now be addressed quantitatively by building cross-species graphs relating SLA to (say) leaf epidermis thickness. If one such graph is built from a species-set spanning a within-landscape soil fertility gradient, and another from a species-set spanning rainfall zones, then comparing those two graphs gives a quantification of the extent to which the two scale-gradients should be regarded as equivalent or different, from the point of view of attribute-combinations found in plants. Such an approach holds the promise of resolving quantitatively the extent to which different environmental stressors should be regarded as equivalent. It could also lay the necessary basis for articulating within-landscape treatments of vegetation with zonal plant geography treatments.

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Section editor: H Lambers

Appendix: Suggested protocols for attributing SLA, height and seed mass to a species

Status

The protocols outlined here are intended as a first draft, and as an illustration that simple protocols are possible. The author would not presume to dictate unilaterally what procedures should be adopted. If a variety of people interested in using the LHS scheme were to contribute, the procedures could be refined and improved by this common wisdom and experience of the plant ecology community, and consensus would be more achievable.

Coverage

The LHS scheme is about green vascular plants growing on land. Aquatics and non-green plants are not included. Some species may be able to be positioned in some dimensions but not others, for example epiphytes do not have a characteristic canopy height, and ferns do not have a seed mass.

Some general principles

The premise of the LHS scheme is that differences between species in traits such as SLA, height and seed mass are meaningful, even though the traits are certainly not constant within species. The trait values attributed to species are to be seen as characterizing species relative to each other, not as species-constants.

Because the LHS dimensions are ecologically important for a species, it need be no surprise that mechanisms exist for modulating each of them in response to environmental circumstances during development of an individual plant. In addition some genetic variation can be expected for the traits within species. A principle for dealing with these sources of variation is that we should seek to characterize the 'design' height or SLA, that is, the height or SLA at which leaves operate while making most of the carbon profit which is the first essential for sustaining a population. This height or SLA is the one that should be under selection to make a carbon profit most effectively under the circumstances of the plant's life history and environment, and should be designed by natural selection in this sense.

In the LHS scheme all three of SLA, height and seed mass are to be log-scaled. This is for a combination of reasons. First, the traits are known empirically to be approximately lognormally distributed between species, that is, when they are represented on log scale, the median or most common value is roughly similar to the mean and roughly halfway between the extremes. Second, the relationship between any two species is best characterized by the difference in logs, that is by the ratio of SLA, heights or seed masses, rather than by the absolute difference.

A strategy is conceived as a property of a lineage of genes through a series of generations. It would not be consistent with this concept to attribute separate strategies to individual genotypes within an interbreeding population, or to different developmental phases in the life of an individual. If there were important ecotypic variation between sites, it would be possible to attribute strategies separately to different ecotypes within a species. As a general proposition, though, the LHS scheme is designed more for broad comparisons

across many species than for detailed comparisons between closely related lineages.

Variation and replication

Naturally variation will exist between sites within the range of the species, between individuals within sites, and for SLA and seed mass between leaves or seeds within individuals. In an ideal detailed study each of these levels of variation might be formally quantified through randomization and replication, leading to an estimate of the SD of log(trait) arising at each level. (For SLA and seed mass it is already known that variation within individuals resulting from developmental processes is typically the largest of the three levels of variation.) But because the purpose of the LHS scheme is to encourage comparisons across large numbers of species, the protocols suggested below are towards the simple rather than the demanding end of the spectrum of possibilities, their aim being merely to obtain a reasonable average for each species not to obtain formal estimates of within-species variation.

Further it has been assumed that the set of species to be characterized is the set occurring at a single site, hence between-site variation can not conveniently be included without a major expansion and restructuring of the study. Naturally more replication, within and between sites, would always be desirable if there were no trade-off. For most real-world researchers, however, setting higher standards for replication has the direct consequence that fewer species can be studied, so it would be a matter of judgment whether the ultimate aim of generalizing across species would benefit more from increased replication within species or more from increased coverage of different species.

Because of variation within species, a species-characterizing value for an LHS dimension needs to be understood as including a range of variation as well as the stated central value. Many authors have chosen to divide continuous traits such as height, leaf area and seed mass into classes, reflecting an appreciation of this degree of imprecision. However this solution is unsatisfactory for species near the arbitrary boundaries between classes. The LHS scheme attributes a species to a single value on each continuous dimension, and relies on users not to interpret that location with undue precision.

Specific leaf area SLA: suggested protocol

SLA is the photosynthesizing area deployed per dry mass devoted to the photosynthesizing structures. The term 'leaf' is to be interpreted as referring also to phyllodes, cladodes or even green stems if these carry out the majority of photosynthesis in the species.

Young mature leaves are to be sampled, i.e. from among the younger of those leaves that are fully expanded and hardened. Leaves are to be taken from full light positions, or for shade plants, from the fullest light to which a substantial proportion of the plant's canopy is exposed. Leaves with serious herbivore or pathogen damage or epiphyll loads are to be rejected. At least 5 leaves should be taken at a site, distributed across 5 different individuals if available. Petioles should be included, or for leaves without petioles, they should be separated from stems at the location where abscission would normally occur, if this is known.

Area is to be measured on a one-sided basis, i.e. the photosynthetic structure is laid on the scanner or squared paper without forcing it flat in such a way as to damage the tissue, but oriented such as to project the largest possible area onto the scanner surface. Mass is weighed after drying to constant mass at 80 °C.

Specific leaf area SLA: issues

When assessing what constitutes the 'photosynthetic structure', the formulation provided is that it should be the structure that carries out the 'majority of photosynthesis'. It is appreciated that this formulation will not always lead to an easy decision, for example for species with perennial green stems and very ephemeral true leaves, or for twiners with small leaves spaced widely on green stems. In the absence of time and resources for a detailed study of where the 'majority of photosynthesis' is carried out, a judgment must necessarily be made.

The specification that SLA should be measured on young mature leaves, not suffering from significant herbivory, and developed in full light or as full as the species grows in, arises also from the criterion that SLA should correspond to leaves that carry out the majority of photosynthesis.

It has been common in ecophysiological work to measure SLA from leaf discs punched from the lamina. The lamina will generally have higher SLA than the whole leaf including midrib and major veins, but for many species the difference will not be great, and

leaf-disc measurements might be used, provided they were appropriately noted and taken into account in drawing conclusions.

The 'leaf' should be taken as ending at the natural point of abscission from the remainder of the plant, if such an abscission point exists. Thus petioles should be included as part of the leaf, and compound leaves that abscised as wholes would be taken as wholes. The idea behind this criterion is that it is best if the 'leaf' for which SLA is measured corresponds to the tissue that has a characteristic longevity or turnover rate. For 'leaves' such as cladodes or the green twigs of leafless species it may be difficult to decide where to draw the line. Guidance for such judgments should come from the same criterion, that the 'leaf' should if possible be an entity with a distinct turnover rate.

In relation to the one-sided measurement convention, it is appreciated that actual light interception is also very much affected by leaf orientation, e.g. erect needles or grass leaves, but the LHS scheme does not take this into account because there is no easy way to do so.

The 5 leaves recommended should certainly be regarded as a minimum. Depending how leaf areas are being measured, it may be equally convenient to scan and weigh much larger numbers of leaves as a single measurement, thus obtaining a physical average across them. If an estimate is sought of the SD of SLA, it needs to be appreciated that there are many different SD's depending on what sources of variation are included, so the sources of variation to be included need to be specified explicitly and the sampling protocol designed accordingly.

Design height of the plant's canopy: suggested protocol

The height to be recorded is the height of foliage of the species, not the height of inflorescences in those cases where the inflorescence projects above the foliage. Height should be assessed in the field not in botanical gardens, and at sites where the population is no longer gaining height rapidly (for species that grow up after fire or other vegetation-clearing disturbances). The height recorded should correspond to the top of the general canopy of the species, discounting any exceptional individuals or branches projecting above the others. As a rule of thumb the height recorded should correspond to the upper 20% of the leaf display of the

species (which would correspond to more than 20% of the total carbon acquisition by the species).

Heights should not be attributed to species that do not support their own height, that is to epiphytes, mistletoes, twiners and vines. The reason for this is not (mainly) that heights would be difficult to attribute to such species, but that their heights would not reflect an underlying trade-off between access to light and expenditure on tall and long-lived stems for supporting foliage at height.

Design height of the plant's canopy: issues

Canopy height is perhaps harder to define than seed mass or SLA, because it changes during the growth of an individual plant and because leaves are deployed at a range of heights, as well as because variation between sites and between individual plants is greater than for seed mass or SLA. These can not be regarded as insuperable difficulties, however, since many authors have felt able to record maximum heights in comparative work (e.g. Bugmann, 1996; Chapin et al., 1996; Grime et al., 1988; Hubbell and Foster, 1986; Keddy, 1989). Log-scaling the height expresses the fact that the difference between 30 and 31 m is not nearly so important as the difference between 30 cm and 130 cm.

Seed mass: suggested protocol

The seeds weighed should be mature and alive, which can be demonstrated by germination or tetrazolium testing on seeds of similar appearance or after weighing. Seeds should be dried to constant mass at 80 °C. Dispersal structures such as wings, elaiosomes, flesh for vertebrates or pappuses should be removed, but the testa should be left on.

A minimum of 5 seeds should be weighed, preferably more, distributed across 5 individual plants unless this is impossible. Sets of 10, 100 etc. seeds can be weighed as aggregates to avoid the need for a microbalance or to gain the benefit of averaging out some variation between seeds, but non-viable seeds should not be included, and the aggregation approach has the disadvantage of not generating a standard deviation between seeds.

A 'seed mass' should not be attributed to fern spores, not only for the semantic reason that they are not seeds, but for the substantive reason that a

single seed can colonize an establishment opportunity whereas two or more fern spores are required to establish a sporophyte.

Seed mass: issues

Excluding dispersal structures but including the testa is a compromise. From the point of view of resources available to the seedling the testa would be excluded and only seed reserve mass, embryo plus endosperm, would be included. From the point of view of estimating how many seeds are expected from a gram of reproductive effort, dispersal structures and indeed other structures associated with the infructescence but not attached to the seed would be included. The compromise of including testa but not dispersal structures has the merit of corresponding to the way most existing seed mass datasets have been collected.

For species with an impermeable testa, drying seeds intact will not actually remove all the water from the seed contents. However, such seeds have only a few percent water content, so the difference between drying seeds intact and drying them after breaking open the testa will be small compared to variation between individual seeds.