Allocation, plasticity and allometry in plants

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Abstract

Allocation is one of the central concepts in modern ecology, providing the basis for different strategies. Allocation in plants has been conceptualized as a proportional or ratio-driven process ('partitioning'). In this view, a plant has a given amount of resources at any point in time and it allocates these resources to different structures. But many plant ecological processes are better understood in terms of growth and size than in terms of time. In an allometric perspective, allocation is seen as a size-dependent process: allometry is the quantitative relationship between growth and allocation. Therefore most questions of allocation should be posed allometrically, not as ratios or proportions. Plants evolve allometric patterns in response to numerous selection pressures and constraints, and these patterns explain many behaviours of plant populations.

In the allometric view, plasticity in allocation can be understood as a change in a plant's allometric trajectory in response to the environment. Some allocation patterns show relatively fixed allometric trajectories, varying in different environments primarily in the speed at which the trajectory is travelled, whereas other allocation patterns show great flexibility in their behaviour at a given size. Because plant growth is often indeterminate and its rate highly influenced by environmental conditions, 'plasticity in size' is not a meaningful concept. We need a new way to classify, describe and analyze plant allocation and plasticity because the concepts 'trait' and 'plasticity' are too broad. Three degrees of plasticity can be distinguished: (1) allometric growth ('apparent plasticity'), (2) modular proliferation and local physiological adaptation, and (3) integrated plastic responses. Plasticity, which has evolved because it increases individual fitness, can be a disadvantage in plant production systems, where we want to optimize population, not individual, performance.

Key words: allometric growth, biomass allocation, partitioning, size-dependence

Introduction

Allocation is the central concept in life history theory, one of the most successful theories in modern ecology (Stearns 1992). Because resources allocated to one function or organ are therefore not available to other functions or organs, allocation implies tradeoffs. This leads directly to the idea of strategies, in which natural selection prioritizes some capabilities at the expense of others. Differences in allocation to structures and therefore functions appear to be more important for many ecological questions than differences in physiological mechanisms at the cellular or molecular levels (Schwinning & Weiner 1998).

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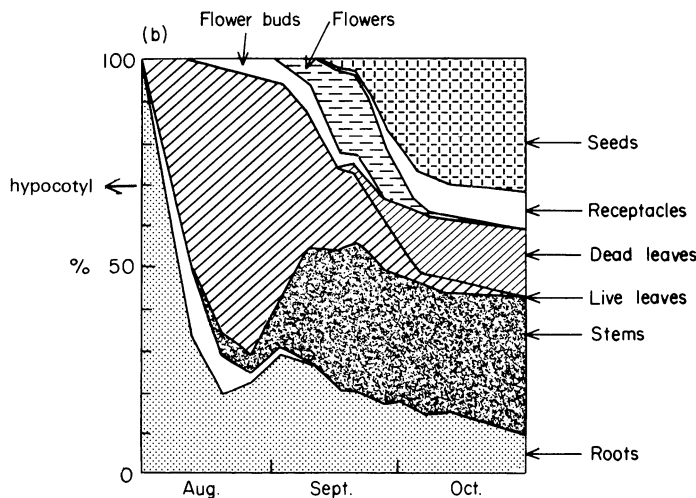
Fig. 1. Percentage allocation of biomass to different structures during the life cycle of *Senecio vulgaris* (from Harper & Ogden 1970; Harper 1977).

The relationship between structure and function is not always straightforward because organs can have several functions – roots function as nutrient uptake, storage and anchoring organs. Also, the unit of allocation (e.g. biomass) may not be the unit of function (e.g. surface area). But despite these problems, the analysis of allocation patterns is the best available tool for investigating plants' priorities. Most studies have looked at allocation of biomass, and this appears to reflect allocation of many other resources (Reekie & Bazzaz 1987), but there will certainly be cases in which the most important limiting resource being allocated is not highly correlated with biomass allocation. Plants also allocate some structures to alternative functions, e.g. meristems can remain inactive, or they can be used for branching or flowering (Bonser & Aarssen 2001), and this can be easily observed.

Traditionally, allocation has been considered as a proportional process: 'partitioning', as in a pie chart. In this view, a plant has a given amount of resources at any point in time, which it divides among different structures or activities. Different allocation patterns reflect different strategies resulting from different selection pressures. Similarly, changes in allocation during ontogeny reflect the changing priorities of an organism during the course of its development, as documented in the milestone work of Harper & Ogden (1970; Fig. 1). Such allocation strategies are often considered to be genetically determined, i.e. species- or genotype-specific.

Plasticity, a widely appreciated, but still poorly understood characteristic of plants, can be thought of as a flexible strategy, which allows a genotype to give rise to different phenotypes depending on the biotic as well as abiotic environment in which the plant grows and develops (Bradshaw 1965; West-Eberhard 2003). It is clear that many allocation patterns are plastic. The same genotype can show different allocation patterns in different environments, and much of the renewed interest in plasticity in plants has focused on allocation patterns. Consistent with the 'partitioning' perspective, changes in allocation patterns have been conceptualized and analyzed as ratios, e.g. shoot:root ratio or reproductive effort (reproductive mass/total mass; Poorter & Nagel 2000). Optimal allocation theory, borrowed from economics (Bloom et al. 1985), is firmly within the 'partitioning-ratio' perspective. According to this theory, plants should allocate resources to increase their uptake of the resource that is most limiting growth. The optimal behaviour results when all resources are equally limiting.

Allometry and apparent plasticity

The 'partitioning' perspective is difficult to reconcile with the observation that plant growth is allometric in the broad sense: it changes with size. Many allocation patterns follow allometric trajectories and are therefore a function of plant size. The partitioning-ratio view is size independent, but almost all plant allocation patterns are size-dependent. Let us imagine a factor that affects only the rate of growth of the plant (Fig. 2), simply stretching or compressing the time axis on the plant's growth curve, but not affecting allocation to different structures at a given size. If allocation is allometric, then any factor that affects size will also affect the percent allocation to different structures and functions. Some of the plasticity in allocation reported in the literature turns out to be simply the result of size. This phenomenon has been called 'passive plasticity' (Wright & McConnaughay 2002), but 'apparent plasticity' (McConnaughay & Coleman 1999) is a better term, because this is not really plasticity. Below I describe to two examples of apparent plasticity.
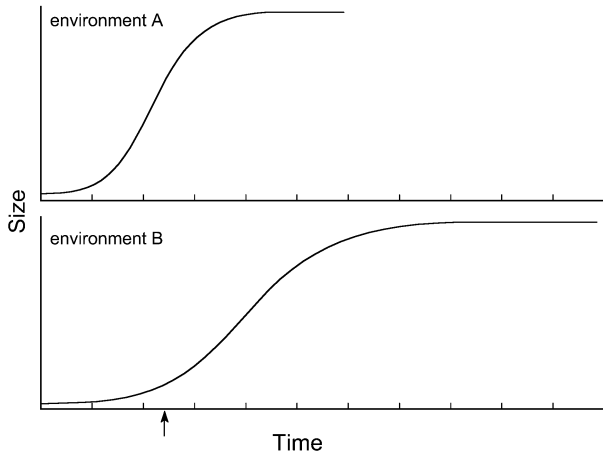
Fig 2. Apparent plasticity. If the rate of growth and development is different in two environments and allocation is allometric in the broadest sense, then allocation ratios will be different for plants compared at the same point in time (arrow), as in most experiments, even if allocation at a given size is the same in both environments.

Fig. 3. If the relationship between total and reproductive biomass is linear and there is no minimum size for reproduction (Case a), then reproductive effort (reproductive biomass / total biomass) would be a constant proportion of the plant's biomass. But there is a minimum size for reproduction (Case b), so reproductive effort increases with size (Crawley 1983; Samson & Werk 1986; Weiner 1988).

Several studies have reported that plants changed their reproductive allocation patterns in response to competition (e.g. Waite & Hutchings 1982). When plants were not crowded, they behaved more like 'r-selected' species, allocating a large proportion of their biomass to reproductive structures (high reproductive effort). When plants were crowded, on the other hand, they behaved more 'K' like, allocating less of their biomass to reproductive structures and a greater proportion to competitive structures such as stems and leaves. But a much simpler explanation for these observations is the allometric relationship between reproductive and non-reproductive biomass, and the fact that mean plant size decreases with increasing density. All plants have a minimum size for reproducing. If we assume that plants allocate a constant proportion of their biomass above this minimum to reproductive structures, then reproductive effort, defined as the proportion of biomass in reproductive structures, will increase with size asymptotically (Fig. 3). Several studies have provided support for this simple model of size-dependent reproductive output (Fig. 4; Thompson et al. 1991; Aarssen & Taylor 1992; Schmid & Weiner 1993). This very simple model of size-dependent reproductive allocation accounts for one of the basic patterns in agronomy: the 'parabolic' [sic] relationship between harvestable yield and density (Silvertown & Charlesworth 2001). While total crop biomass increases with density and then levels off ('Law of Constant Final Yield'), harvestable yield, which is usually reproductive output, decreases at higher densities.
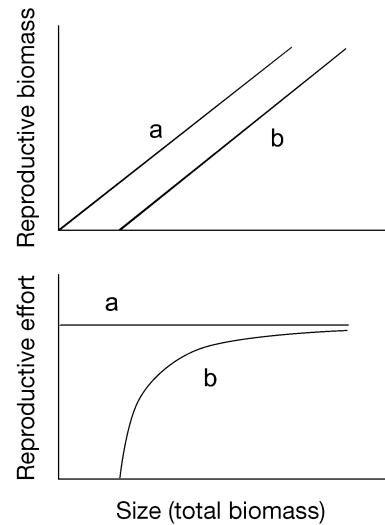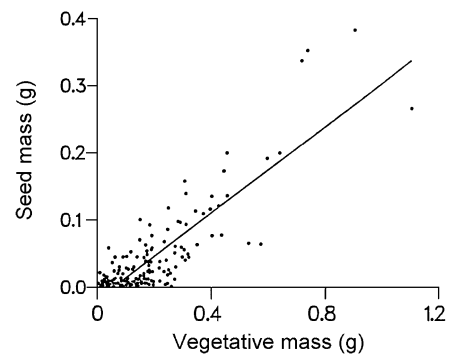

Fig. 4. Relationship between seed mass and vegetative dry mass for *Plantago major* individuals grown at three sowing densities (from Weiner 1988, data from W. Hawthorne). Vegetative mass accounted for 72% of variation in seed mass produced by individuals, and density accounted for an additional 3.7% of the variation. The X-intercept, an estimate of the minimum size for reproduction, is significantly greater than zero ($P < 0.01$).

This reflects the allometry of reproductive allocation. When plants are crowded, they are smaller, and more of them are close to, or even under, the minimum size for reproduction. Therefore, while the total biomass produced does not decrease at higher densities, production of reproductive biomass, e.g. fruits and seeds, does.

Another example of apparent plasticity comes from the application of optimal allocation theory to the study of plant growth under resource limitation, mentioned above. According to optimal allocation theory,
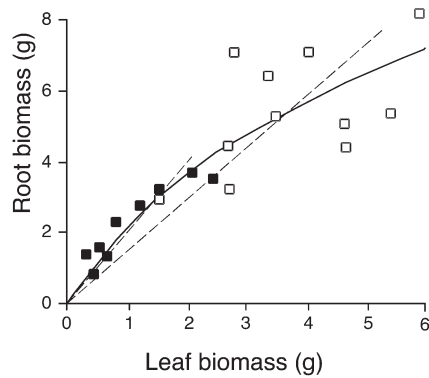
Fig. 5. Differences in biomass allocation to roots vs. leaves in *Trisetum flavescens* in response to nutrient level (black symbols: low-nutrient level; open symbols: high-nutrient level). Analysis of biomass ratios (represented by the dashed lines) indicates a significant (P < 0.001) difference in allocation between nutrient treatments. In contrast, allometric analysis of the same data indicates no significant difference between nutrient treatments. The solid line is the joint allometric regression line for both treatments (from Müller et al. 2000).

plants should allocate more resources to organs that capture the most limiting resource and less to organs that are involved in obtaining non-limiting resources (Bloom et al. 1985). For example, under low nutrient conditions, plants should allocate relatively more of their biomass to roots, and under higher nutrients conditions, where light is more limiting, plant should allocate more to shoots. While some studies provide support for the optimal allocation model (Shipley & Meziane 2002), others suggest that the differences in allocation patterns under varying nutrient conditions are largely due to allometric growth (Fig. 5; Müller et al. 2000; Cahill 2003). Plants are generally more 'rooty' early in development when they are young and small and become more 'shooty' as they get larger (cf. Fig. 1). Since the radicle emerges first from the seed, plants have more root than shoot soon after germination. After this, shoots generally grow faster than roots (allometry literally means unequal growth)[1]. There are many possible explanations for the trend towards increasing relative allocation to aboveground structures during growth. One hypothesis is that it leads to a generally optimal allocation pattern over the course of

growth and development (Müller et al. 2000). Such a hypothesis puts the concept of optimal allocation into an allometric context: plants evolve towards the optimal allometric trajectory. When sufficient, we would expect this to be a simpler solution, and therefore in some sense cheaper, than a flexible allocation strategy.

The allometric relationships of biomass allocation are fundamental aspects of the genotype's strategy, which is the result of natural selection. Such relationships may reflect biomechanical or other constraints, in which case we might expect relatively little genetic variation for these relationships within a population, or they may be subject to numerous selection pressures. There was significant genetic variation for both the minimum size for reproduction and the slope of the relationship between reproductive and vegetative biomass within an invading population of *Solidago altissima* (Schmid & Weiner 1993). Thus, the allometric relationship between size and reproductive output can evolve in this population.

Plastic allometry

This is not to say that all changes in reproductive effort or shoot:root ratio due to the environment are simply allometric. Rather, I propose that allometric growth be considered the null hypothesis in studies of allocation. Allometric relationships can themselves be plastic. We can define plasticity in allocation as a change in the allometric trajectory, not just a change in the rate of growth, in different environments. Even some of the data that generally support the simple allometric model contain some evidence for plastic allometry. While vegetative mass accounted for 72% of variation in seed mass produced by *Plantago major* individuals grown at three different densities (Fig. 4), density accounted for an additional 3.7% of the variation. This means that plants of the same size but growing at different densities were significantly different in their seed production. While 3.7% is not very much in comparison to the 72% of the variation due to size, it could still be important in nature. Variation in biomass allocation pattern and geometry in natural populations of *Laportea canadensis* growing in different environments were mostly due to allometric growth, but some variation among environments at the same plant size was detectable (Menges 1987).

There are numerous examples of true (as opposed to apparent) plasticity in allocation patterns. *Betula pendula* seedlings can alter their allocation to roots versus shoots in response to varying levels of some nutrients (Ericsson 1995). *Glycine max* individuals competing belowground allocated more biomass to roots at a given size than plants growing in the absence of

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[1] Allometric growth is not to be confused with interspecific allometric relationships among adult plants (e.g. Enquist & Niklas 2002). There is no basis for the assumption that the allometric growth trajectories of individuals are similar to these broad static interspecific relationships. For example, larger species have a lower shoot:root ratio than smaller species (Enquist & Niklas 2002; Zens & Web 2002), but we know that shoot:root ratio increases as a plant grows. Conflation of static interspecific allometric relationships with allometric growth has been the source of great confusion within the literature on plant allometry (Weller 1989).
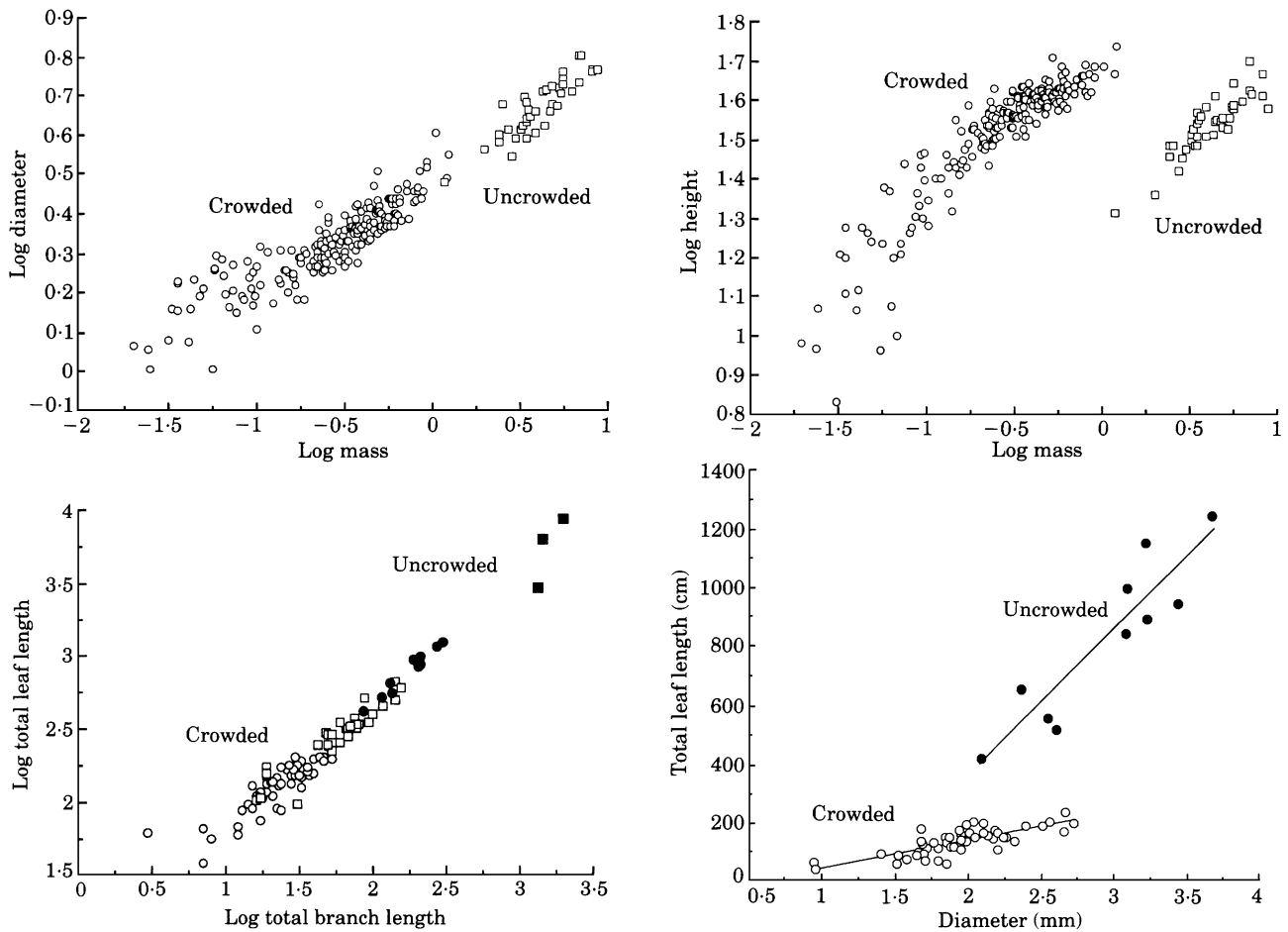
Fig. 6. Some allometric relationships in *Kochia scoparia* do not change in response to crowding (two figures on the left), whereas other relationships are radically altered (figures on the right; after Weiner & Fishman 1994).

another plant's roots, even when the total amount of soil resources per individual was the same with and without neighbouring roots (Gersani et al. 2001). Allocation to roots and shoots in *Abutilon theophrasti* and *Chenopodium album* showed some plasticity in response to changes in nutrient levels, but this plasticity was highly constrained allometrically (Gedroc et al. 1996). Allocation to roots by *A. theophrasti*, on the other hand, was not affected by aboveground competition (Casper et al. 1998). Some aboveground allometric relationships in *Kochia scoparia* were unaltered by competition, whereas other relationships were changed dramatically (Fig. 6). The question becomes when do plants show fixed allometric growth trajectories and when do they show plastic allometry? This may be a function of organs or functions involved (Weiner & Fishman 1994), the specific resources limiting growth (Ericsson 1995), the source of the resource limitation (Gersani et al. 2001), or the plant's developmental stage (Gedroc et al. 1996).

A fixed allometric trajectory tells us something important about a plant's strategy and the constraints under which it operates. Crowding does not change the relationship between branch length and leaf area in *Kochia scoparia* (Fig. 6). The plant seems to follow simple, non-plastic rules of allocation with respect to these two structures, placing the same leaf area along every centimetre of branch formed. But crowded plants have much less leaf area at given stem diameter than uncrowded plants, so there is a large degree of plasticity in this relationship.

Is it useful to talk about plasticity in plant size?

Plant growth is indeterminate and modular. Plants grow by producing more modules (Harper 1977). Unlike unitary organisms such as most animals, which achieve an adult size and cease growth, plants have the potential to continue to grow throughout their life-

times. Although plants must reach a minimum size before they can reproduce, this size is usually quite small compared to the maximum size the plant can achieve. A very small adult human may weigh 40 kg; a very large one 200 kg. But this is nothing compared to the range of reproducing adult sizes in a population of *Chenopodium album*, which would span more than two orders of magnitude. The indeterminate, modular growth form of plants makes the idea of plasticity in size problematic or even meaningless.

Let us consider again the case of a factor that only affects the growth rate of a plant, stretching the time axis (Fig. 2) but changing nothing else. If a plant's behaviour, such as allocation, is primarily a function of size, then it is misleading to talk about plasticity in size. In this sense plasticity in size could be considered analogous to plasticity in age, which is absurd. It might be more meaningful to talk about plasticity in the growth rate, which allows the plant to have different sizes after a given period of growth. Plants that grow in resource poor conditions have less plasticity in their growth rates than plants from more nutrient-rich environments: the former can not grow very fast, even under ideal conditions (Chapin 1980). Much apparent plasticity in plant allocation can be better understood as allometric growth and plasticity in growth rate.

Towards a classification of plastic responses

Many problems with the concept of plasticity arise because it is defined too broadly. The classical definition of plasticity is the ability of a genotype to produce different phenotypes, depending upon the environment in which it grows (Fig. 7). The Y-axis on such a graph is usually labelled as something like 'phenotypic trait'. I am arguing here that the definition of plasticity is too broad, because the definition of trait is too broad. This
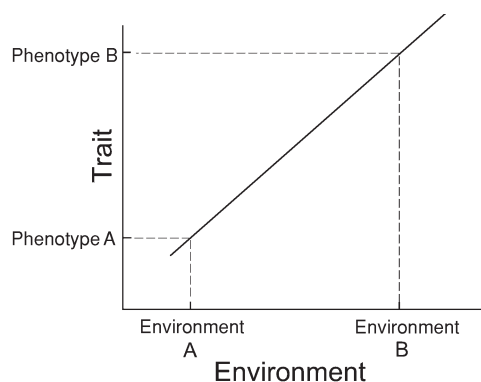

Box 1. A classification of plastic responses.

1. Allometric growth ('apparent plasticity')

2. Modular plastic responses
   A. Local proliferation
   B. Local physiological adaptation (e.g. sun vs. shade leaves)

3. Integrated plastic responses
   A. Plastic allometry (changes in allometric trajectory)
   B. Integrated physiological differentiation (e.g. induced defences)

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general representation of plasticity can be applied to any attribute, whether it is leaf number, shoot:root ratio, or slope of the log shoot vs. log root relationship. The fact that such a comparison can be made does not *ipso facto* mean that this is a useful way to describe the phenomenon. While the current wave of interest in phenotypic plasticity is clearly justified, some researchers may be focusing on inappropriate 'traits'. We need to refine the concept to plasticity so that we can analyse and interpret the relationships between genotype, phenotype and environment in more meaningful ways.

I propose that we rethink the concept of plasticity in terms of a hierarchy of plastic responses (Box 1). If a trait does not change at all with the environment, it is completely non-plastic. These are the traits taxonomists like to use to delimit taxa, but these are usually not the most important traits ecologically (Harper 1982). Since allometric growth is almost universal in plants, I propose that allometric growth be considered the null hypothesis for studies of plasticity in allocation. If the shoot:root ratio or reproductive effort is solely a function of size, this should not be considered true plasticity, or, if it is, it is surely a very low degree of plasticity. The basic structure of such a null hypothesis is genotype + environment → plant size → trait. Local proliferation and local physiological adaptation represent a higher degree of plasticity. Many clonal plants growing in heterogeneous environments respond to high-resource patches by proliferating modules locally, whereas they branch less when resource levels are low (Huber & Stuefer 1997). While this is clearly plasticity, it can be close to a local version of simple allometric growth. Plants sometimes show physiological adaptation, such as the development of sun versus shade leaves on an individual tree. As with local proliferation, this type of plasticity occurs at the level of an individual organ or ramet. The highest degree of plasticity occurs when the whole plant responds in an integrated way. Examples of this include induced defences (Karban & Baldwin 1997), or changes in the growth of modules or organs in response to signals coming from distant parts of the

Fig. 7. Classical representation of the norm of reaction. This representation is too general, because the term 'trait' is too broad, making this misleading for many size-dependent traits.

plant (Novoplansky et al. 1989). This type of plasticity requires a degree of communication among the parts of a plant. Distinguishing these different levels of plasticity may help us make better comparisons and develop testable hypotheses. Understanding the genetic and physiological bases, as well as the ecological and evolutionary consequences for these different levels of plasticity, are important goals for plant evolutionary ecology in the coming years (Sultan 2004).

Is plant behaviour a function of time or size?

An allometric perspective helps, clarify the distinction between two different but interdependent perspectives on ecological processes. We often think of ecological processes as being a function of time. A classic example of this conceptual framework is the life table: the birth and death schedule of a cohort. But many plant ecological processes are better understood in terms of size, rather than in terms of time (Coleman et al. 1994). Sometimes a life table based on size categories is a better way to describe a plant population than a life table based on age categories (Caswell 2001). For example, it was just 25 years ago that plant demographers showed that many biennial plants are actually 'facultative' biennials (Werner 1977; Gross 1981). They flower and reproduce when they achieve a certain size, and while this usually requires two years of growth, it can take longer. Another example is the effect of increased soil fertility on the process of self-thinning (density-dependent mortality) in crowded plant populations. The primary effect of increased nutrients is to increase the rate at which the trajectory is followed. While measurable effects of soil nutrient level on the self-thinning trajectory have been documented (Morris 2003), they are relatively small compared to the effects on the speed of stand development.

But in some cases time can be as important, or more important, than size. An annual plant has to complete its life cycle within one growing season – time is a real constraint. Therefore, many annual plants have a very small minimum size for flowering and setting fruit. There exist obligate, as well as facultative, biennial plant species (Byers & Quinn 1998), and these represent different strategies. Certain processes are scheduled using environmental cues such as day length.

Recent discussions about the causes of changes in productivity over the course of forest development clearly demonstrate the difference between a time- and a size-based perspective on stand development. The net primary production of forests increases and then decreases during forest growth. Tree ecophysiologists have considered this to be function of the forest's age, even referring to the phenomenon as the "age-related

decline in forest productivity" (Gower et al. 1996; Ryan et al. 1997). We have argued that the so-called 'age-related' decline is actually a 'size-related' decline, because the growth rate of trees in large part a function of their size (Weiner & Thomas 2001). The relative growth rate of organisms decreases with size: growth itself is size-dependent, i.e. allometric. Tree physiologists have noted that the 'age-related' decline in forest productivity occurs sooner on better soils (Ryan et al. 1997). This is consistent with the hypothesis that the decline in productivity is primarily 'size-related', not 'age-related'. Plants will approach their maximum size sooner on better sites (cf. Fig. 2).

Of course, plant size and time are correlated, so it is therefore not obvious whether a particular process is driven by time, size, or a combination of the two. Within a population, a small individual can be old if it has been suppressed, growing in an unfavourable environment, or has suffered from extensive herbivory or disease. But a very large individual cannot be young, because it takes time to achieve a large size under even the best conditions. Similarly, whether or not a tobacco plant flowers is partly a function of its size – there is a minimum size for flowering. Above that size, flowering is determined by day length. But when a plant does reproduce, its reproductive output is largely determined by plant size (Weiner 1988). The plant's developmental stage determines whether or not it will flower, and in some cases this cannot be predicted very well by either size or age (Clauss & Aarssen 1994). Teasing apart the interactions among time, size and environmental cues in determining plant developmental stage and behaviour is an important objective for developmental ecology.

Potential applications: plasticity and plant production systems

The study of the plasticity and allometry of allocation has important implications for plant production systems such as agriculture and forestry. For example, the 'Harvest Index' (harvestable biomass / total biomass), a commonly used parameter in agronomic research, exemplifies the 'partitioning-ratio' perspective. Agronomic research would probably benefit by replacing this measure with an allometric analysis of yield components, in which the effects of different agricultural practices on biomass production and on harvestable yield are not confounded.

Plasticity is selected at the individual level, but some forms of plasticity can be disadvantageous at the population level. Consider again the case of competition among individual plants. The plastic responses of individuals to competition from neighbours, such as etio-

lation, reduced tillering in grasses, or increased root proliferation in response to neighbouring roots, have evolved because they increased individual fitness. But such responses can be disadvantageous at the population level, especially in monocultures such as most plant production systems. Yield should be higher if all individuals allocate less to competitive structures and functions than if all individuals respond to competition by allocating more resources to competitive structures (Weiner 2003). High-yielding modern cereal varieties have lower stature and lower competitive ability than older lower-yielding varieties. Put in the language of evolutionary theory, agronomist C.M. Donald's concept of the crop 'ideotype' (Donald 1968) was that crop breeders should practice group- not individual selection, since not all attributes that increase individual yield are advantageous for population yield. Some plastic responses to competition from neighbours may be such attributes. While plasticity may be essential for plants' survival in nature, the environment in production systems is highly influenced by human interventions, such as ploughing, sowing, fertilization and irrigation. My hypothesis is that under these conditions, higher yields can be obtained in many production systems if we remove or reduce some forms of plasticity in allocation within our target species, so that allocation to harvestable yield can be maximized. If *Glycine max* plants 'overproduce' roots when they compete with neighbouring individuals, then reducing this plasticity should result in higher yields in a soybean field (Gersani et al. 2001). Plasticity is such an integral aspect of plant behaviour, however, that reducing it through plant breeding may not be easy.

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