The Evolution of Allometry in Modular Organisms

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The variation in organismal form that arises from size-dependent relationships among parts is a fundamental aspect of development and evolutionary change. Allometric analysis was one of the earliest morphometric tools developed to reveal ontogenetic or evolutionary changes in shape as a consequence of changes in organ or body size (Gayon, 2000). As allometric analysis has become more sophisticated, it has continued to provide insights into patterns and mechanisms of multivariate evolution (e.g., Niklas 1994; West et al. 1999). Although studies of allometry have been particularly prevalent in the animal literature, recent work has demonstrated the power of allometric analysis for interpreting morphological variation in plants as well (e.g., Armbruster 1991; Weiner and Thomas 1992; Jones 1993; Mazer and Wheelwright 1993; Niklas 1994; Ackerly and Donoghue 1998; Niklas and Enquist 2002).

A striking feature of plant populations is that individuals range widely in size, often as a result of asymmetric competition for light (Weiner et al. 2001) or patchy distribution of other resources. The ultimate basis for this dramatic variability lies in the way plants are constructed. Plants, and some animals, grow through the repeated addition of similar morphological subunits, that is, metamers and modules. This mode of development contributes to size variation by creating the potential for both indeterminate and exponential growth. Size variation, in turn, affects the expression of many other traits (reproductive allocation, resource capture, biomechanical stability, etc.), and plant functional morphologists have used allometry to examine these evolutionary and ecological consequences (Armbruster 1991; Jones 1993; Weiner and Thomas 1992; Mazer and Wheelwright 1993; Niklas 1994; Ackerly and Donoghue 1998; Niklas and Enquist 2002).
Modularity presents special challenges and opportunities for allometric analysis. In addition to generating size variation, modular construction also complicates the interpretation of allometry by blurring the meaning of apparently straightforward concepts such as size, age, and developmental stage. In this chapter we discuss the expression of allometry in modular organisms, its biological interpretation, and its consequences for multivariate trait evolution. We also ask what can be learned from modular organisms about the evolution of allometrically related traits in general.

Character Variation and Covariation at Several Levels of Biological Organization

Much of the complexity in biological systems arises from their tendency to be organized into levels. Individuals come from genetic families and exist in populations that belong to communities. Populations constitute species, and species ultimately are grouped into nested series of increasingly inclusive clades. Modular organisms have additional levels of organization because of their clear within-individual substructure. In this section we connect the levels of interindividual variation (the usual subject of allometry) with several kinds of intraindividual variation resulting from modularity. After a brief introduction to the traditional categories of allometry, we explore the sources of within-individual variation and the complex part-whole relationships of modular systems.

Levels of Allometric Analysis

Organismal traits covary at several levels of biological organization, and at each level it is possible to characterize the form of the relationship allometrically. Interspecific allometry (sensu Gould 2002), or “evolutionary allometry” (sensu Cheverud 1982; Klingenberg 1998), is based on species means and is thought to reflect adaptive relationships between traits, or fundamental developmental or functional constraints (e.g., Niklas 1994; West et al. 1999). Intraspecific allometry is based on individuals measured either at a common developmental stage (“static,” sensu Cheverud 1982; Klingenberg 1996) or at different points in development (“ontogenetic”). Several thoughtful reviews have addressed the relationships among evolutionary, static, and ontogenetic allometry (Cheverud 1982; Armbruster, 1991; Klingenberg and Zimmermann 1992; Klingenberg 1998). Here we focus primarily on different ways of measuring allometry within a species.

The raw material for any allometric analysis is variation among individuals, or among modules, in traits of interest. Interpretation of allometry requires careful consideration of the factors contributing to this variation. Four important sources are usually recognized: (1) ontogenetic variation due to differences in age and/or developmental rates; (2) environmental variation due to differences in conditions influencing growth; (3) genetic variation in heritable factors that influence the traits under consideration; and (4) developmental noise or experimental error unexplained by other sources. In experimental settings it may be possible to
distinguish and control the relative contributions of each of these factors, but in field populations they are both difficult to measure and intertwined in a complex fashion. For example, ontogenetic variation may arise from the chronological age of an individual or module or its developmental stage (see below). However, age and stage are decoupled (and thus separable) only in individuals growing at different rates, which may in turn be traced to environmental or genetic differences. Moreover, in a temporally varying environment, two individuals of different age will have experienced different environments at corresponding stages in their growth. It is also well known that genetic and environmental variation may be confounded in the field when genotypes occupy different environmental conditions (Falconer 1989). The biological significance of static allometric relationships among individuals or modules depends on these many underlying sources of variation, which we shall revisit below in the context of various experimental studies.

While interspecific allometry reflects the outcome of evolutionary divergence, intraspecific allometry reflects adaptive evolution and developmental constraints operating within populations; as such it has provided insight into patterns of phenotypic integration and multivariate evolution (Olson and Miller 1958; Klingenberg and Zimmermann 1992; Jones 1993, 1995; Huber and Stuefer 1997; Ackerly and Donoghue 1998; Wright et al. 2001). For example, intraspecific allometry itself may be treated as an evolving character, and the slopes and intercepts of intraspecific relationships compared among species to test for evolutionary shifts in functional relationships between traits (Whitehead et al. 1984; Ackerly and Donoghue 1998; Klingenberg 1998; Wright et al. 2001; Preston and Ackerly 2003). More importantly, ontogenetic allometry describes the joint developmental trajectory of correlated traits, and static intraspecific allometry reflects their phenotypic architecture (analogous to genetic architecture). To the extent that these relationships reflect pleiotropic effects of genes acting during development, intraspecific allometry may also be paralleled by genetic correlations between the traits at the population level. Therefore, both types of intraspecific allometric analysis may help predict the way selection will act on correlated traits (Olson and Miller 1958; Schluter 1996; Klingenberg 1998).

This use of intraspecific allometry is complicated, however, because the trait relationships it captures are frequently not fixed for species or genotypes. The nature of covariation between characters may vary during development (Olson and Miller 1958; Coleman et al. 1994; Mazer and Delesalle 1996; Pigliucci et al. 1996; Acosta et al. 1997; Bonser and Aarssen 2001; López et al. 2001), and it can be phenotypically plastic (e.g., Lechowicz and Blais 1988; Weiner and Thomas 1992; Weiner and Fishman 1994; Müller et al. 2000; Bonser and Aarssen 2001). In many such cases, developmental stage and environment alter not merely the strength of the correlation between traits, but even their functional relationship, as measured by shifts in allometric slope or intercept. Thus the joint response to selection by a pair of related traits cannot be predicted reliably from their phenotypic covariation measured at any one time under one set of circumstances (Pigliucci et al. 1996).

The conceptual relationship between ontogenetic and static allometry is also complicated. Armbruster (1991) and Klingenberg and Zimmermann (1992) have
argued that a similarity between them indicates that developmental processes contribute to trait covariation at the population level. To the extent that this is true, the developmental component itself may also be plastic. For example, in several different annual plant species, Weiner and Thomas (1992) and Weiner and Fishman (1994) found that ontogenetic and static allometry did coincide for uncrowded populations, but that they diverged under crowded conditions.

Nearly all organisms potentially exhibit ontogenetic and environmental variation in allometry, but some of the mechanisms behind this variation are unique to modular organisms. For example, modular growth permits serial adjustments to the phenotype through the addition of new parts during development. In the following sections we consider in detail the role that modularity plays in generating variation in allometrically related traits. Although we draw exclusively on examples from the plant literature, many of the issues we raise will be relevant to a variety of modular organisms, from bryozoans to eusocial insects.

Modularity and Trait Expression In Plants

Types of Modularity

Two related but distinct conceptions of modularity are prominent in morphology and evolutionary biology. The concept we use in this chapter is not the one applied in most work on multivariate trait evolution (cf. other chapters in this volume), so it is important to clarify their differences and draw comparisons between them. In developmental genetics, modules refer to largely autonomous, developmentally and functionally integrated units (Raff 1996; Wagner 1996; Carroll 2001; Chapters 2, 3, and 10 in this volume). In this context, modules usually correspond to developmentally independent nonhomologous parts (e.g., heads and limbs; Magwene 2001) or homologous metameric units that have become highly differentiated (e.g., arthropod limb types; Carroll 2001). There is little overlap between the sets of interacting genes that control each module, thus modularity may be selectively advantageous because it preserves functional coherence of interdependent parts while allowing evolutionary flexibility of the entire organism (Wagner 1996; Wagner and Altenberg 1996; Magwene 2001).

Here we apply another concept of modularity, which originated in comparative morphology and gained prominence within the field of plant population ecology (for historical overview see Harper and White 1974; White 1979). Under this usage, modular growth occurs through the reiteration of the same few types of structure, such as branches and flowers in plants and zooids in bryozoans. In contrast to developmental genetic modules, the modular subunits comprising an organism are similar to each other (serially homologous; Stevens 1984) and loosely analogous to individuals in a population. The concept of the plant as “metapopulation” (sensu White 1979) appeared as early as Theophrastus and continued through Goethe and Darwin (Harper and White 1974; White 1979). More recently, the analogy has proved especially fruitful for studies of plant population ecology (White 1979, 1984; Watson and Casper 1984; Sarukhán et
Under both concepts, an evolutionary advantage of modularity is the flexibility it affords to complex organisms. Developmental genetic modularity allows separate parts, organs, or structures to respond more or less independently to selection (Wagner 1996; Magwene 2001), and this decoupling may explain some major evolutionary trends within multicellular lineages (Carroll 2001). Presumably, developmentally autonomous parts could also express separate adaptive plastic responses, providing some morphological adaptability to individuals (Berg 1959; Armbruster 1991). The second kind of modularity also provides flexibility since modular growth allows individual plasticity in size, shape, and resource allocation. Examples of adaptive modular plasticity include the shade avoidance response (Schmitt et al. 1995; Dudley and Schmitt 1996), regrowth following herbivory (Haukioja 1991; Rosenthal and Welter 1995), foraging for resources in a heterogeneous environment (Slade and Hutchings 1987; de Kroon and Hutchings 1995; Huber 1996), shifting root-to-shoot ratio (see Müller et al. 2000), and partitioning fixed resources among structures in different combinations of size and number (Williams 1986). In eusocial animal colonies, modular plasticity can be seen in caste-specific nest defense behaviors in response to intruders (e.g., Duffy et al. 2002).

The most significant difference between the two concepts concerns their assumptions about the relations among modules. In the first, modules are genetically independent, but they interact in the proper functioning of a physiologically integrated organism. They are generally not autonomous with regard to resource uptake and use, and they do not have the potential for truly independent survival. By contrast, the second version of modularity often confers physiological substructure (Watson and Casper 1984) and in some cases the capacity for full physical independence, especially in clonal plants (e.g., Cook 1983; Petelka and Ashmun 1985); but there is little if any genetic autonomy between modules. Although gene expression patterns may vary, the same set of genes controls development in each iteration of similar structures: there is not a separate set of genes for each successive leaf or branch produced. Of course, dissimilar modules, such as roots, flowers, and vegetative branches, may be genetically decoupled from each other. In that case, different types of morphological module also qualify as distinct modules in the developmental genetics sense (see Armbruster et al. Chapter 2, this volume). Even so, phenotypic correlations between the size of an inflorescence and the stems and leaves that support it have been found both within and among species (Corner 1949; Bond and Midgley 1988; Le Maître and Midgley 1991; Ackerly and Donoghue 1998), which suggests that development in vegetative and reproductive modules is not entirely independent.
Modularity in Plants

In the specific case of plant shoots, we consider modules to be the products of apical meristems, for example, branches, cones, or flowers (following Prévost 1978; White 1979, 1984). Vegetative modules produce new meristems that may give rise to additional vegetative or reproductive modules, creating a nested modular hierarchy (Fig. 4.1). Usually, modules are themselves composed of repeated units, or metamers. For example, a typical vegetative metamer consists of a node and an internode, a leaf (or leaf homolog), and an axillary meristem (White 1979, 1984).

Each level of morphological organization potentially has its own demographic properties, and the interplay between modular and whole-plant demography has important consequences for trait expression at different levels. Some of these morphological, physiological, or life-history traits are expressed by subunits,

![Diagram](image)

**Figure 4.1** Modular construction in plants. We define a module as the product of an apical meristem (following Prévost 1978). New modules arise from existing ones through the differentiation of axillary meristems. Modules are indicated here by curly braces. Metamers are serially homologous repeated units along an axis and are usually subunits of modules. A vegetative metamer (shown in inset) consists of a leaf, the segment of stem subtending it, and its axillary meristem.
and some apply only to the entire organism. For example, modules and metomers originate, mature, senesce, and die, often independently of the whole plant. In addition, individual parts each have their own size (mass and extension), shape, and developmental potential, which may change over ontogeny. Likewise, whole plants age, become reproductively mature, senesce, and die, and they also have size, shape, and architecture arising from growth rules that regulate metamer development in space and time. Although both subunits and whole individuals partition resources between vegetative growth and reproduction, the concept of reproductive effort typically applies to whole organisms. Fitness also is generally assessed at the level of the whole plant because it is a property of the genetic individual. The state of the individual plant provides a developmental context for the parts (age, access to resources), and the properties of the parts influence whole-plant characters (e.g., architecture, reproduction) (Diggle 1994; Colasanti and Hunt 1997; Preston 1999; Jones 2001; Jones and Watson 2001). These whole-part relationships are the source of some key conceptual issues addressed in the next section.

**Allometry in Modular Organisms**

Two aspects of modular construction have important implications for both the measurement and interpretation of allometry. First, modular organisms consist of multiple subunits, and traits expressed independently by each subunit can be measured repeatedly on a single individual. Examples include branch length, stem diameter, leaf number and size, flower number, etc. Metameric structures, such as leaves, provide yet another level of replication. As a result, allometric relationships among these traits emerge at the level of a single individual (Fig. 4.2). We refer to this intraindividual trait relationship as "modular allometry."

Second, modules develop sequentially as new growth arises from older growth. Modular construction thereby imposes both temporal and spatial structure on the population of subunits that comprise an individual, and also onto the traits expressed within each module (or metamer). Consequently, modular allometry measured in a single genetic individual may be based on a population of units just as phenotypically and demographically heterogeneous as the population of individuals underlying an intraspecific static or ontogenetic allometry. The modular allometric relationship will reflect several interacting sources of size variation, including age and developmental stage, resource status, and environment.

**Ontogenetic Variation**

One of the main sources of size variation in modular allometry is age. We distinguish three main units of developmental age and ontogeny in plants, which may or may not be distinct depending on the life history and phenology of the organism (Table 4.1). The most inclusive unit is *whole-plant ontogeny*, which covers
Figure 4.2 Modular allometry. A. Relationship between stem diameter at the base of a branch and total mass of that branch, where size variation is due to branch age. B. Diameter-mass allometry where size variation is due to both architectural position and age. Shoots 1, 2, and 3 are all the same age, as measured by plastochron index (sensu Erickson and Michelini 1957), but shoot 4 is older than the others.

germination to plant death. Whole-plant ontogeny may then be divided into a series of distinct reproductive or developmental cycles each with its own rhythmic ontogeny (following Hallé et al. 1978). "Rhythmic" ontogeny encompasses any regular sequence of developmental events, so it is not necessarily defined by a particular season or time period, although rhythmic cycles may be adapted to a predictable season length or cued by the environment. Examples include an interval of growth between periods of dormancy, a flowering phase in tropical plants (which may occur several times a year, or once every several years), or the maturation of a cohort of pine cones or acorns (often lasting more than a year). Finally, modular ontogeny applies to the development of each module and metamer, beginning with its differentiation and extending over its lifetime. In most woody perennials, these three categories are distinct; however, in annuals, whole-plant lifetime ontogeny, rhythmic ontogeny, and in some cases modular ontogeny,
Table 4.1 Levels at which developmental age may be measured in plants, and their manifestation according to life history, and phenology and architecture, expressed as both time periods and structural units.

<table>
<thead>
<tr>
<th>Time period:</th>
<th>Whole plant lifetime</th>
<th>Rhythmic varies, and is defined by development</th>
<th>Modular seasonal or subseasonal</th>
<th>Metameric seasonal or subseasonal</th>
</tr>
</thead>
<tbody>
<tr>
<td>Structural unit:</td>
<td>The product of a seed or propagule: also some long-lived ramets (e.g., <em>Populus</em>)</td>
<td>Nested set of modules from a meristem activated to start a developmental cycle</td>
<td>Morphological subset of the shoot produced from an apical meristem</td>
<td>Leaf or leaf homolog (e.g., bracts, spines, petals); axillary meristem</td>
</tr>
<tr>
<td>Woody perennials</td>
<td>*</td>
<td>*</td>
<td></td>
<td>*</td>
</tr>
<tr>
<td>Herbaceous perennials with indeterminate aerial shoots</td>
<td>*</td>
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<tr>
<td>Herbaceous perennials with determinate aerial structures (e.g., <em>Podophyllum</em>, <em>Dentaria</em>, <em>Arisaema</em>, <em>Sanguinaria</em>)</td>
<td>*</td>
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<td>Annuals</td>
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Asterisks indicate distinct levels; double lines join levels that coincide for a given group of plants.
coincide; and in many perennial woodland herbs, a season’s rhythmic growth is reduced to the differentiation of one module or even a single metamer (e.g., *Podophyllum peltatum*; Jones and Watson 2001).

Over each of these developmental time periods, allometric relationships among traits may change. For example, size-dependent reproductive allocation (reproductive effort) generally increases with whole-plant age in annuals (King and Roughgarden 1982) and some long-lived perennials (e.g., Piñero et al. 1982; López et al. 2001). Within a season, the total leaf area on a shoot declines relative to the size of the stem supporting it (K. Preston, unpublished data). At the module level, several studies have shown increased allocation to pollen relative to ovules within an inflorescence over development (Diggle 1994, 1995; Ashman and Hitchens 2000).

**Modular Demography**

Significantly, ontogenetic changes in allometry at relatively higher morphological levels emerge from demographic processes operating at lower levels (e.g., Colasanti and Hunt 1997). For instance, reproductive allocation at the level of the whole plant depends on the number, type, and characteristics of its modules (Bonser and Aarssen 2001; López et al. 2001). The composition of the subunit population at any one time depends in turn on modular demography (birth rate and life span), identity (vegetative or reproductive), and development (e.g., size, gender expression). Similar lower-level processes affect allometry at the module level; for example, total shoot leaf area depends on the number and size of individual leaves, and gender expression within an inflorescence is a consequence of metamer (stamen and carpel) development (Lloyd 1980). In a simulation of modular plant growth, Colasanti and Hunt (1997) found that whole-plant characteristics as diverse as root-to-shoot ratio, foraging behavior, and even self-thinning under crowded conditions could be generated from purely module-based dynamics, independent of the status of the whole plant.

Nevertheless, some empirical studies suggest that whole-plant allometry is not simply “bottom-up,” with module demography and modular traits generating allometric relationships; there are also “top-down” effects, where module development responds to the condition of the whole plant. Bonser and Aarssen (2003) showed that in four different annual herbs, greater overall plant size and resource status influenced module demography, thereby increasing the proportion of meristems devoted to reproduction and branching. In a Mediterranean shrub, reproductive effort rose with plant age through a change in module demography (i.e., the proportion of reproductive modules), with no effect on within-module characteristics (López et al. 2001). Whole-plant ontogeny also has an effect on stem-leaf allometry in several myrmecophytic tropical tree species that develop stem cavities housing ants (caulinary domatia). Brouat and McKey (2001) found that stem-leaf allometry in young plants is consistent with the high biomechanical demands that cavities impose on smaller stems. As stem and leaf size increase with plant age, hydraulic demands exceed structural requirements, and the slope of the stem-leaf allometry shifts to reflect shoot water relations.
Allometry in Plants

The morphological hierarchy described above grows out of a series of developmental events that unfold over time. At any given moment, the phenotype of a single plant part is influenced by its temporal location within several developmental phases at different hierarchical levels. In addition to expressing its own developmental stage, the part is located within the ontogenetic progression of a larger module. The final size and shape of a leaf, for example, often varies with node position along an axis (Jones 1999; Kaplan 2001). Its phenotype will also depend on when it was initiated during a seasonal or rhythmic cycle. Preformed leaves overwintering in bud have been found to differ morphologically, anatomically, and physiologically from leaves initiated and matured later in the season (Roy et al. 1986). In a Mediterranean grassland shrub (*Baccharis pilularis*), life span is shortest for those leaves produced early in summer, just before the onset of the driest period (K. Preston, unpublished data; see also Abul-Fatih and Bazzaz 1980). Leaf shape in *Viola septemloba* depends on the interaction of a seasonal cue (photoperiod) with an inherent developmental shift (Winn 1996). Finally, the age of the parent plant may influence not only the identity of an individual part (e.g., vegetative versus reproductive; López et al. 2001), but also its shape (as in juvenile versus adult leaves), and the way resources are partitioned within it (e.g., size-number allocation in fruits; Acosta et al. 1997). Thus each plant part develops within a complex ontogenetic context (Diggle 1995; Watson et al. 1995); moreover, at any one time a plant is likely to be composed of many such individual parts, initiated at different points during modular, seasonal, and whole-plant development.

To see how this kind of interplay among morphological and developmental levels affects allometry, it is useful to return to the analogy of the plant as a population of subunits. Modular allometry, which describes covariation between traits expressed by multiple parts of a single plant, can then be likened to static or ontogenetic allometry of multiple individuals in a population. Static allometry for a population of unitary organisms is based on individuals measured at the same developmental stage, typically at reproductive maturity (Cheverud 1982; Klingenberg and Zimmermann 1992). The challenge presented by modularity is that there are several ways to define developmental stage, and one must decide which of these should be constant among the parts measured. For example, if all branches on a shrub are flowering, they are at the same seasonal reproductive stage; however, branches are likely to have been initiated at different times and so will vary in the length of their vegetative phase before the onset of flowering. Therefore, a sample of flowering branches will include branches of different chronological age but at the same stage in seasonal ontogeny. The length of the vegetative period can also be measured on two different scales. If shoots initiate growth at different times and also grow at different rates, they may have the same number of nodes (plastochron index; Erickson and Michelini 1957) but differ in chronological age (Ritterbusch 1990). For similar reasons, modular systems do not lend themselves to the method commonly used to estimate ontogenetic allometry in unitary organisms, in which individuals ranging in age are measured at a single sampling time to construct a composite ontogeny (but see Klingenberg 1996). In modular organisms, a collection of variously aged shoots measured
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Figure 4.3 Trait relationships characterized allometrically and as ratios. When the slope of the allometric relationship between log-transformed variables is isometric ($=1$), then the ratio between the untransformed variables is constant. When the slope is greater than 1 (positive allometry), the ratio increases with size; when the slope is less than 1 (negative allometry), the ratio declines with size. Müller et al. (2000) found a positive allometric relationship between stem and leaf biomass, and consequently an increasing stem-to-leaf ratio with overall plant size. Conversely, they found that root-to-stem and root-to-leaf ratios declined with overall plant size due to their negative allometric relationship.

These results are intriguing because they suggest two very different interpretations. One holds that the treatment differences in biomass ratio were an allometric consequence of differences in plant size, and therefore not a result of adaptive plasticity in biomass allocation (Coleman and McConnaughay 1995; McConnaughay and Coleman 1999). An alternative interpretation focuses on the adaptiveness of allometry itself, emphasizing that optimal biomass allocation varies with plant size in a predictable way, so that the best allometric relationship is one that yields the optimal ratio across a range of plant sizes. From this standpoint, allometry is itself an evolved strategy to maintain the functionally appropriate biomass partitioning as plant size varies over development or in response to environmental variation (cf. Chapter 7 by Pigliucci in this volume). Müller and colleagues see their results as evidence for such an allometric strategy in most of the species they examined. We return to the evolutionary potential of allometric strategies below.
Interestingly, each study’s conclusions can be justified. As with any complex character, the question of whether a fixed ontogenetic allometry acts as a constraint on phenotypic expression (as in Huber and Stuefer) or the means to an adaptive response (as in Müller et al.) must be decided in context and on the basis of other evidence. For example, adaptive plasticity must ceteris paribus involve the expression of an appropriate phenotype for a given environment (Sultan and Bazzaz 1993). In the first study, root-to-leaf and root-to-stem ratios generally declined with overall plant size, as predicted by “economic” models of allocation for optimal resource acquisition (e.g., Bloom et al. 1985). Moreover, the observation that numerous distantly related species have similar root-shoot allometry suggests either a widespread fundamental constraint on biomass allocation, or convergence on an adaptive strategy. In the second example, plants appeared to adopt a linear clonal morphology consistent with optimal foraging, yet Huber and Stuefer’s developmental analysis showed this response to be only temporary. Eventually, the shaded plants would literally grow out of their supposedly adapted phase, while the resource environment remained unchanged.

A second kind of evidence for the adaptive nature of allometry depends on its role in the overall phenotype. Because the root-shoot allometry of a species is a direct manifestation of individual root-to-shoot ratios, it is plausible that an allometric relationship could evolve entirely under selection acting on biomass allocation in individual plants as a function of their size. By contrast, allometry in a branching shoot is likely to be a purely geometric consequence of a complex developmental program, whose evolution has been shaped by numerous biomechanical, physiological, and ecological forces. Such a developmental program is integral to whole-plant functioning, and its features carry constraints as a consequence of this integration. Therefore, the potential for optimal allocation in a particular environment will be limited by the larger phenotypic context. The contrast between these two studies demonstrates that judgments about the role of allometry in adaptive plasticity depend on the relative weights of at least these explanatory considerations: the apparent “fit” between phenotype and environment (including changes in fit over time), and the potential for an allometric strategy to evolve, given the role of allometry in phenotypic integration.

**Allometry of Meristem Allocation**

A third example of whole-plant allometry combines features of the two studies described above by including both ontogenetic and static allometry measured across a resource gradient. Bonser and Aarssen (2001) used nutrient treatments to generate size variation among individuals from five genotypes of *Arabidopsis thaliana* and examined patterns of meristem allocation as a function of plant size weekly throughout development. At each census, they characterized allometric relationships among three meristem fates (inactivity, I; vegetative growth, G; and reproduction, R) in individuals of the same chronological age. Each of these relationships could in turn be followed across censuses to generate an ontogeny of allometries (Fig. 4.4). In other words, their data show the effect of size on allocation at each time point, as well as the allometric effect of achieving a given size at different times. For example, reproductive effort (R versus G + I) increases
Figure 4.4 Allometry throughout development for one genotype (Kil) of Arabidopsis thaliana. Lines represent Model II regression of log $R$ (number of reproductive meristems) versus log $(I + G)$ (number of inactive and vegetative growth meristems). Regressions labeled with different letters differ significantly in slope. Reproduced with permission from Bonser and Aarssen (2001).

more sharply with plant size early in development than late; and for a given size, reproductive effort increases with plant age (cf. Pigliucci et al. 1996). This multidimensional data set allowed the authors to use an ontogenetic series of static allometries to demonstrate the ways in which meristem identity depends on the combination of plant size and plant age.

As discussed by Bonser and Aarssen, allometry is neither a mechanism for adaptive plasticity nor a constraint on it. Rather, allometry measured at a common age is a manifestation of plasticity, where steeper slopes indicate a greater response to nutrient availability in allocation patterns (assuming that most size variation was due to nutrient treatment). Like Müller et al. (2000), Bonser and Aarssen see allometry in allocation as an evolved strategy, but the two versions differ somewhat. Whereas the earlier study found that a fixed allometric relationship generated plasticity in ratios, Bonser and Aarssen found that within-genotype allometry varied with plant age, and this temporal dimension was an essential axis of plant allocation strategy. Interestingly, they found very little variation in allocation patterns among the five genotypes measured. Results from a similar study that included three additional, architecturally diverse, species suggest that these patterns can be generalized beyond Arabidopsis thaliana at least to other annuals (Bonser and Aarssen 2003).

**Modular Allometry**

As discussed above, modular organisms are composed of reiterated morphological subunits, and traits expressed in each module can be used to construct an intraindividual modular allometry. Here we describe two studies that use modular allometry to examine evolution in functionally related traits.
Foraging in Clonal Plants

Another classic example of apparently optimal allocation is foraging in clonal plants. Because of their spreading habit and adventitious roots, clonal plants can explore horizontal space more efficiently than upright plants can, and they are able to concentrate growth in high-resource patches to the benefit of the entire plant (e.g. Cook 1983; Slade and Hutchings 1987; de Kroon and Hutchings 1995, and references therein). However, the patterns of ramet placement often interpreted as foraging could also arise from nonadaptive growth responses to resource availability by individual modules (ramets), rather than from a whole-plant growth strategy. To distinguish these possibilities, Huber and Stuefer (1997) compared growth rate and branch production by individual stolons of *Potentilla reptans* under three different light treatments: full light (control), neutral shade, and canopy shade (reduced red:far-red). Compared to the controls, both of the shade treatments reduced final biomass, growth rate of the primary axis, and the rate of new branch initiation. Slower branch production resulted in a much less branched architecture at final harvest for the shaded plants relative to the controls. Thus, when plants were compared at the same chronological age, those grown under higher light had allocated resources to new branches, allowing more intensive use of the habitat, whereas shaded plants had adopted a more linear growth form, allowing plants to escape poor local conditions. Nevertheless, Huber and Stuefer’s results tell a very different story when plants are compared at the same developmental stage (plastochron index). Under shaded conditions, primary ramets (arising from nodes along the main axis) were chronologically much older than unshaded ramets, but they did not differ in developmental stage at the time they produced their first branch. The authors speculate that if shaded plants had been allowed to reach the same whole-plant developmental age as the unshaded plants at the time they were harvested, there would have been no treatment effect on branching intensity. They conclude that the response of clonal morphology to shading should not be interpreted as an adaptive plastic change in growth form, but rather as a simple artifact of comparing plants at different points along their ontogenetic trajectory.

Adaptive Interpretations of Plasticity and Allometry

Both the Müller et al. study (2000) and the Huber and Stuefer study (1997) question common assumptions about adaptive plasticity in biomass allocation and use allometric analysis to reveal the developmental mechanisms producing an apparently appropriate phenotype. In both studies, plants adopted the phenotype predicted for their treatment environment under an optimal allocation model, but treatment differences disappeared when plants were compared at the same size or developmental age rather than the same chronological age. Despite these similarities, the authors of the two studies draw contrasting conclusions: Müller and colleagues argue that for most species root-shoot allometry represents an evolved strategy for plasticity, whereas Huber and Stuefer see allocation patterns as simply conforming to a “null” model and reflecting the effects of resource limitation on the expression of a fixed developmental program.
Stem-Leaf Allometry and a Novel Stem Function

Leaf performance depends crucially on the hydraulic and biomechanical support provided by stems, and this relationship is reflected in the widely observed positive correlation between leaf area and stem size, both within and among species (Corner 1949; White 1983, Bond and Midgley 1988; Ackerly and Donoghue 1998; Brouat et al. 1998). Brouat and McKey (2001) examined the evolutionary changes in stem-leaf allometry that accompany the integration of a new function into the usual suite of stem functions. In three lineages of tropical trees, they characterized stem-leaf allometry for myrmecophytic species that develop enlarged hollow stems specialized for housing ants, and compared them with stem-leaf allometries found in the species’ close nonmyrmecophytic relatives. In the myrmecophytic species, leaf and stem size both increase with whole-plant age, while cavity size remains relatively constant; thus the role of hollowed stems in overall stem function was predicted to change as plants age. The authors therefore based their functional interpretation on whole-plant ontogenetic allometry. Although each sample was taken from a different tree, they minimized the potentially confounding effects of module age and developmental stage (discussed above) by measuring only the terminal leaf on a stem and the internode subtending it.

Whereas nonmyrmecophytic species showed a nearly constant proportionality between leaf area and stem cross-sectional area, the stems of myrmecophytic species were relatively large early in development and did not increase in proportion to leaf size. The resulting shallow allometry can be explained by the age-dependent effect of stem cavities on the relative importance of biomechanical and hydraulic support. The structural integrity of a hollow stem depends on the ratio between the thickness of the ring of wood and the radius of the whole twig (ring and cavity), and on the mechanical properties of the wood. The authors propose that when plants are young, the amount of wood required to supply water to a small leaf is biomechanically adequate for solid stems but not for hollow ones, which must allocate relatively more to stem tissue. As leaf size increases with plant age, the stem tissue required to meet hydraulic demands also meets structural requirements. As predicted under this scenario, the species with hollowed stems showed age-dependent stem-leaf size relationships but a nearly constant ratio of wood thickness to stem size.

Brouat and McKey conclude that in these species, stem-leaf allometry should be interpreted as a line of functional equivalence across a range of plant sizes. Their study also shows that the form of stem-leaf allometry has evolved repeatedly in three independent clades, leading to convergence in slope when a new role is integrated into the usual suite of stem functions. Thus, they argue, the phenotypic correlation between stem and leaf size in solid stems does not represent a constraint on the evolution of this relationship in hollow stems; rather, in both solid and hollow stems, allometry can be seen as the by-product of selection on stem function.
Within-Module Trait Correlations

A second example of modular allometry explores the tension between mechanisms that may underlie correlations between modular traits. Mazer and Delesalle (1996) examined phenotypic and genetic correlations among floral parts in a highly selfing annual species (*Spergularia marina*) in order to disentangle the various forces that generate trait covariation within flowers. Strictly speaking, sepals, petals, stamens, and carpels are metamers composing a floral module; consequently, these floral parts may show interdependent developmental responses to shared external and internal environmental conditions. Moreover, floral traits have sometimes been found to be more highly integrated than vegetative traits of the same species (Berg 1959; Armbruster et al. 1999). Although strong within-flower trait correlations should be less common in self-pollinating than in animal-pollinated species (Berg 1959), Mazer and Delesalle argue that stabilizing selection should favor equal numbers of male and female gametes within self-pollinating flowers (a special case of isometry). These conditions lead to conflicting predictions. For example, strong stabilizing selection to maintain optimal gender allocation (pollen: ovule = 1) should generate positive genetic correlations between anther number and ovule number. Alternatively, resource limitation within a flower could lead to a tradeoff in allocation to male and female gametes. Mazer and Delesalle found no correlation between family means in the number of male and the number of female floral parts (controlling for flower size), which suggests that stamen and ovule number per flower have evolved independently among these genotypes. They speculate that the evolutionary decoupling of these traits has resulted from the tension between selection favoring isometry in gender allocation and a negative genetic correlation due to tradeoffs in resource allocation.

Selection on Allometry in Modular Organisms

The studies described above provide evidence that allometry should not always be viewed simply as evidence for a constraint on evolution, but that allometry itself evolves, and that the form of the relationships among traits may be shaped by selection (see Chapters 2, 7, and 18 in this volume). Evolutionary changes in allometry reflect shifts in two or more traits with respect to each other, so they represent a form of multivariate phenotypic evolution. Understanding the evolution of allometry thus requires consideration of the full scope of evolutionary processes involved in multivariate evolution: genetic and phenotypic variation and covariation, plasticity, and selection (Lande and Arnold 1983; Wagner and Altenberg 1996; Schlichting and Pigliucci 1998). Evolution of modular allometry presents yet another factor for consideration, namely the role of selection at different hierarchical levels.

Allometric relationships in unitary organisms are observed among individuals (static) or within individuals over time (ontogenetic). In both cases, the traits involved exhibit a single value in each individual at a particular moment in time (Fig. 4.5A,B). In evolutionary terms, selection acts on variation in the traits
and the trait combinations exhibited by individuals, and allometric relationships emerge at the population level. If there is plasticity in the traits or their relationship to one another, then the dynamics of selection depend on patterns of environmental heterogeneity, and the genetics of the underlying reaction norms (Schlichting and Pigliucci 1998). The resulting allometric relationships within populations will depend on the effects of genetic and environmental variation (and their interaction) among individuals.

At a higher level of organization, interpopulational or interspecific allometry may arise as populations and species, respectively, evolve to different trait means (Fig. 4.5A). The important point about variation at this level is that the allometry itself is not under selection. If the optimal relationship of two traits \((X, Y)\) is \(Y = bX^a\), then within each population selection will lead to shifts in \(X\) and/or \(Y\), moving toward the joint optimum described by this equation. This would appear as an allometric relationship at a higher level of analysis considering multiple populations or species. Quantitative analysis of the \((X,Y)\) relationship might reveal the underlying values of coefficients \(a\) and \(b\), describing the optimum value that was favored by selection in each population; yet these values are not properties of the evolving genotypes or populations that are directly under selection. The evolutionary allometry is thus a consequence of selection within populations and species, not a property directly targeted by selection.

The evolution of modular allometry differs from this standard scenario in a way that has significant consequences for the efficacy of selection in shaping allometric relationships. In indeterminate modular organisms, many phenotypic traits contributing to organismal function are expressed at the modular level (e.g., stem diameter, leaf area, etc.). These traits are expressed simultaneously in multiple modules, and as a consequence the allometric relationship itself becomes a feature of the organismal phenotype, in a way not generally possible in unitary organisms (Fig. 4.5C). As a simple example, consider the allometry of basal stem diameter and total stem mass in the branches of a woody plant. Biomechanical theory predicts an allometric relationship between these traits to maintain a safety factor against failure, where the coefficient of the safety factor depends on the role of static versus dynamic loading of the stem (Holbrook and Putz 1989; Niklas 2000). The diameter-mass relationship across a broad size range can be evaluated on a single tree, based on the size and diameter of each branch (e.g., Niklas 1999). Ontogenetic relationships also would emerge during the growth of each branch and of the central trunk itself. The allometric relationship is thus a phenotypic property of the individual, and selection can operate directly on allometry at the level of individuals within populations. Assuming there is an optimal relationship favored by selection, there would be costs to diverging from the optimum at any point in the allometry. Conversely, the success of a genotype with the optimal relationship would result in selection on the entire allometry within one generation.

To understand how modular allometries may evolve as traits of the individual, it is important to consider the multiple interacting sources of modular variability that generate allometric relationships. When the allometry is a property of an individual organism, the integration of the individual phenotype demands that all of these underlying sources of variation be considered together. As noted above, in the course of indeterminate growth modules may be initiated at different times,
Figure 4.5 Schematic diagram of the role of selection shaping allometric relationships at the interspecific, intraspecific, and intraindividual (modular) levels. Individuals with relatively high fitness are indicated with black symbols, and less fit individuals are depicted in lighter grey. A. Across species, stabilizing selection favoring species means that fall along a bivariate axis leads to interspecific allometry. Within each species, the joint mean for the two traits is favored, but the allometric relationship per se is not under selection. B. Similarly, within populations of unitary organisms, selection favoring genotypes that lie close to the optimal bivariate trait values leads to intraspecific allometry. C. For modular organisms, allometric relationships may be expressed by the individual, based on trait variation among modules (e.g., leaves, zooids). The allometric relationship is thus an individual trait subject to direct selection within populations. See additional discussion in text.
resulting in a range of sizes within the individual that correspond to an ontogenetic sequence (Fig. 4.2a). We have also noted, however, that trait relationships are shaped by both internal and external environmental conditions throughout development. Returning to our biomechanical example, wood production is stimulated by biomechanical demands, a response seen in localized wood growth in areas of compression stress ("reaction wood"; Gartner 1991), and in the greater inherent stability of plants exposed to wind (e.g., Holbrook and Putz 1989). Presumably, then, the typical ontogenetic trajectory of a growing branch is influenced by both external and internal biomechanical forces normally generated during growth (see Niklas 1999). Module development is also sensitive to ambient light levels and the supply of water, nutrients, and plant growth substances at each growing point. These factors depend on the dynamic interaction between plant architecture and the internal and external environment (which are essentially equivalent from the point of view of a module). For example, self-shading produces a vertical gradient of light from upper to lower canopy, affecting leaf physiology and subsequent shoot growth.

In these situations, traits covary across modules as a function of their joint plastic response to fine-grained environmental heterogeneity (Lloyd 1984). We therefore argue that allometric relationships are a special case of the more general potential for selection on reaction norms as individual traits (Winn 1996, 1999). The expression of variable phenotypes within the individual is itself an adaptive strategy (Lloyd 1984; Diggle 1994; Winn 1996). Allometry in modular organisms not only reflects functional and developmental relations among traits, as it does in unitary organisms, but it is also one of the direct targets of selection. As a result, allometric strategies of the sort suggested by Müller and colleagues (2000) are of special interest for empirical study.

Conclusions

The significance of modular allometry for phenotypic evolution rests on two related questions: whether a given allometric relationship is adaptive, and if so, how it responds to selection. In this chapter, we have drawn on several recent studies presenting examples of apparently adaptive allometric relationships that maintain organismal function across a range of environments (Müller et al. 2000; Bonser and Aarssen 2001) and throughout development (Bonser and Aarssen 2001; Brouat and McKey 2001). We contrasted these studies with one in which a nonadaptive allometric relationship appears to be the consequence of a fixed developmental program (Huber and Stuefer 1997). Together, these results demonstrate that the adaptive value of allometry should be judged not only on its particular "fit" to the environment, but also on its larger phenotypic context. We have also argued that modular allometry itself can become a target of selection, thereby gaining standing as a biologically significant property of the integrated phenotype, in addition to serving as a measure of integration.

The potential for allometry to respond to selection depends on the sources of character variation and covariation, and the extent to which the allometrically
related traits are integrated with the rest of the organism. For whole-organism intraspecific allometry, the most common sources of trait variation (genotype, microhabitat) are not fundamentally related to phenotypic integration. By contrast, many of the sources of variation contributing to within-individual modular allometry arise directly from the relationship between the allometric traits and the rest of the organism. As we have discussed in detail, modular traits are expressed within a spatial and temporal context that grows out of the dynamic interplay between body plan (architecture) and phenology. In addition, trait expression in each module is more or less contingent on prior developmental decisions (Diggle 1994, 1995; Watson et al. 1995). The integration of modular allometry with other whole-plant traits and processes (architecture, phenology) should limit the range of allometric relationships among individuals available for selection (see Badyaev, Chapter 3, this volume, for discussion of allometry and integration in a unitary organism). However, selection may act very efficiently on modular allometry, because the allometric relationship is an individual trait and a wide range of allometries may be exposed to selection within populations.

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Literature Cited