ALLOMETRY AND DEVELOPMENT IN HERBACEOUS PLANTS: FUNCTIONAL RESPONSES OF MERISTEM ALLOCATION TO LIGHT AND NUTRIENT AVAILABILITY

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We examined the relationship between meristem allocation and plant size for four annual plant species: Arabidopsis thaliana, Arenaria serphyllifolia, Brassica rapa, and Chaenorrhinum minus. Gradients of light and nutrient availability were used to obtain a range of plant sizes for each of these species. Relative allocation to reproductive, inactive, and growth meristems were used to measure reproductive effort, apical dominance, and branching intensity, respectively. We measured allocation to each of these three meristem fates at weekly intervals throughout development and at final developmental stage. At all developmental stages reproductive effort and branching intensity tended to increase with increasing plant size (i.e., due to increasing resource availability) and apical dominance tended to decrease with increasing plant size. We interpret these responses as a strategy for plants to maximize fitness across a range of environments. In addition, significant differences in meristem response among species may be important in defining the range of habitats in which a species can exist and may help explain patterns of species competition and coexistence in habitats with variable resource availability.

Key words: allometry; development; functional response; light gradient; meristem allocation; nutrient gradient.

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Size is an important indicator of plant fitness. Large plants tend to have higher absolute fecundity than small plants (Aarsen and Taylor, 1992), and because competitive interactions tend to be asymmetric (Ellison and Rabinowitz, 1989; Geber, 1989; Thomas and Weiner, 1990; Weiner, 1990), large plants tend to be better competitors than small plants. Plant size is a product of factors including age (old plants tend to be larger than young plants) and resource availability (plants in resource-rich habitats tend to be larger than plants in resource-poor habitats). Thus, traits that are differentially expressed through development or across resource gradients should be related to size.

Some plant traits show consistent patterns of size dependence (i.e., allometry). For example, allometry in reproductive effort (the relative allocation to reproductive vs. vegetative structures) has been noted in many plant populations (Waite and Hutchings, 1982; Samson and Werk, 1986; Klinkhammer and De Jong, 1987; Olshon, 1988; Hartnett, 1990; Thompson et al., 1995; Mendez and Obeso, 1993; Reekie, 1998; Sugiyama and Bazzaz, 1998; Cheplick, 2001). While allometry in reproductive effort across environments does not demonstrate adaptive responses to environmental variability (e.g., Weiner, 1988; Shipley and Dion, 1992), examining patterns of allometry can be an effective method for assessing the change in relative allocation traits across environments (Müller et al., 2000; Bonser and Aarsen, 2001). Considering allometric relationships for both reproductive and vegetative traits could reveal functional responses to resource availability. Plants displaying allometric relationships between certain traits across environments should have higher relative fitness than plants lacking these allometric relationships. For example, vegetative traits such as branching intensity may also show size-correlated responses to resource availability. Differences in branching allocation through development across environments can produce a range of plant sizes as high allocation to branching increases the potential production of new plant modules (Watson and Casper, 1988; Geber, 1990; Fagerström, 1992; Bonser and Aarssen, 1996; Watson et al., 1997; Huber and During, 2001), and allocation to branching tends to be greater in more favorable resource environments (e.g., Donohue et al., 2000; Bonser and Aarssen, 2001; Huhta et al., 2001). In this study, we interpret size-correlated patterns of response to variation in resource availability in terms of meristem allocation.

Strategies of meristem allocation—Different patterns of plant form and function are fundamentally a product of patterns of meristem allocation (Harper, 1987). Meristem allocation to vegetative and reproductive meristems determines the schedule of growth and reproduction, respectively. All of the above-ground meristems on a plant are derived from apical meristem activity. New meristems are added in the axils of leaves and it is generally the case for flowering plants that each leaf axil subtends one meristem (or the product of its development) (Bell, 1991). These axillary meristems have one of three fates: a reproductive (R) meristem forms a flower or inflorescence; an inactive (I) meristem is quiescent or undeveloped because of meristem suppression (by apical dominance), senescence, or death; and a growth (G) meristem becomes an apical meristem forming a vegetative branch. A growth meristem, however, produces vegetative biomass and new meristems and then becomes either inactive or reproductive. A G meristem, therefore, has two fates separated in time: G then I or G then R. Hence, there are two populations of both J and R meristems: those which that are apical (ap), at the terminal ends of shoots, and those that are axillary (ax), in the axils of leaves. At any one stage in development, the number of reproductive meristem fates is equal to the number of apical ($R_{ap}$) plus axillary ($R_{ax}$) flowers or inflorescences. The number of inactive meristem fates is equivalent to the number of axillary meristems.
(I_{ax}) not committed to growth or reproduction plus the number of apical meristems (I_{ap}) that fail to become reproductive and become inactive at final development. The number of growth meristem fates is equivalent to the number of times between seedling emergence and the current developmental stage that axillary meristems were committed to branching or growth (G_{ax}). The total number of meristem fates is equal to the sum of each of the meristem fates on both the apical and axillary positions. In this study, we examine meristem allocation as an alternative to biomass allocation (see Bonser and Aarsen, 1996). Plant responses to resource availability through continuous adjustments in vegetative and reproductive allocation can be followed by examining patterns of meristem allocation through development.

The aboveground meristems on a plant form a population of functional units with a particular distribution among the different fates at any one point in the life of a plant. Three life history traits can be defined by the relative allocation to each meristem fate. Reproductive effort (RE) is a measure of the proportion of the total number of reproductive meristem fates vs. those that could have but did not or have not yet become reproductive, i.e.,

\[
RE = \frac{(R_{ap} + R_{ax})(I_{ap} + I_{ax} + G_{ax})}{I_{ax} + G_{ax}}
\]  

Apical dominance (AD) is a measure of the suppression of axillary meristem development and is defined as the proportion of axillary meristems that remain inactive vs. those that are committed to growth or reproduction, i.e.,

\[
AD = \frac{I_{ax}}{R_{ax} + G_{ax}}
\]  

Branching intensity (BI) is defined as the number of axillary meristems producing a new shoot vs. those that could have produced a new shoot but did not, i.e.,

\[
BI = \frac{G_{ax}}{R_{ax} + I_{ax}}
\]  

Correlation or regression analysis between reproductive and vegetative allocation has been an effective method of examining size-dependent reproductive effort (e.g., Samson and Werk, 1986). Similarly, relative allocation to reproductive effort, apical dominance, and branching intensity can be examined using the relationship between the numerator and the denominator for each of the above equations.

Light and nutrient availability should be important selective forces in plant populations (Tilman, 1988; Bonser and Aarsen, 1996). We grew four species of annual plant on gradients of nutrient and light availability to examine the relationship between meristem fates across a range of plant sizes. We conducted this study on two resource gradients to extend our understanding of the generality of meristem responses to variable resource availability. We addressed the following questions:

1. Are there significant allometric relationships between meristem allocation and size within a species where age is held constant and size differences are due to variable resource availability, i.e., do plants respond to resource availability by altering meristem allocation? In annual plants, branching will maximize the number of reproductive meristems at the end of the growing season (Duffy et al., 1999). Allocation to growth meristems (branching intensity) should be relatively high in favorable resource environments. Conversely, allocation to inactive meristems (apical dominance) should be relatively high in unfavorable resource environments. This response in apical dominance should be particularly important in light-limiting environments as plants shaded by neighbors may undergo a shade avoidance response to maximize their ability to compete for light (e.g., Schmitt and Wulff, 1993). Differences in the response between light and nutrient gradients within each species should demonstrate that the type and/or strength of response are resource dependent.

2. How are patterns of response expressed throughout development? The examination of patterns of responses throughout development can lead to the identification of developmental stages in which plants have a greater capacity to respond to resource availability or stages where response in meristem allocation is important for attaining an optimal growth form. In annual plants, available resources and meristems should be committed to reproduction at the end of the growing season. Thus, fitness increases gained through strong apical dominance or branching intensity should diminish towards final development (Bonser and Aarsen, 2001). We predict that responses in meristem allocation should occur at a relatively early age.

3. Are there significant differences in the patterns or strength of response across species? Differences in species ability to respond to resource availability have important implications in determining the range of habitats different species can occupy.

**MATERIALS AND METHODS**

**Study species**—We examined the capacity for meristem allocation to respond to resource availability in four species: Arabidopsis thaliana Heynh. (Brassicaceae), Arenaria serpenthifolia L. (Caryophyllaceae), Brassica rapa L. (Brassicaceae), and Chaenorrhinum minus Reichb. (Scrophulariaceae). Henceforth, each species will be referred to only by its generic name. These species were chosen for a variety of reasons. Seed sources for each species were readily available, and they are all semelparous annuals with very short life cycles, thus allowing data collection for final developmental stage (i.e., when meristem production and allocation is complete). In addition, the four species represent a variety of different developmental programs and body plans. Arabidopsis develops as a rosette of basal leaves, each capable of subtending an erect shoot or branch that develops from an axillary meristem. On each shoot, cauline leaves subtend meristems capable of initiating new shoots or inflorescences or of remaining inactive. Flowers are borne in terminal, elongating, bractless racemes. Arabidopsis is predominantly self-fertilizing. Arenaria is a trailing or partly erect plant capable of self-fertilization. Basal branches are produced early in life resulting in a number of primary shoots. Branches are also produced at distal ends of shoots prior to flowering. Flowers are borne singly in the axils of leaves on the distal ends of shoots. Brassica is an erect outcrossing plant. Cauline leaves each subtend a meristem that is capable of producing a new branch, an inflorescence, or remaining inactive. Flowers are borne in terminal bractless elongating racemes. Chaenorrhinum is an erect plant capable of self-fertilization. Flowers are borne singly in leaf axils. Cauline leaves each subtend two meristems each capable of producing a new branch, a flower, or remaining inactive.

**Seeds of Arabidopsis** (Kil genotype) were obtained from the Arabidopsis information service (Frankfurt, Germany) and were originally collected from natural populations. Brassica (wild genotype) was obtained as seed from the Crucifer Genetics Cooperative (Madison, Wisconsin, USA). Seeds of Arenaria and Chaenorrhinum were collected from natural populations in the vicinity of Kingston, Ontario, Canada (44°20'N, 76°30'W). For these species, seeds were collected from a small number of plants (less than 25) growing in large populations. Seeds of each species were germinated on moist filter paper in sterilized petri dishes. Chaenorrhinum seeds required scarification prior to germination. Individual plants were transplanted individually into pots (10 cm diameter, 400 cm³ volume) containing sterilized potting mix (Fison’s Sunshine Basic Mix #2, Bellevue, Washington, USA) at the emergence of both cotyledons. Individuals of each species were grown separately on nutrient and light gradients in order to produce a range of plant sizes.

**Nutrient gradient**—Pots were placed in a growth chamber under 16-h light (250 μmol·m⁻²·s⁻¹, 23.0°C, 75% relative humidity) and 8-h dark (21°C, 75%
Spectral shade
noted in the last few weeks of each experiment, as many plants were only
development. Meristem allocation was difficult to assess late in life due to the large
during development and the measure of meristem allocation at final devel-
position within the growth chamber. Plants were watered evenly with RO
®ltered appropriately from above, all treatments were surrounded by a thick
quality and quantity of each treatment are summarized in Table 1.
®ltered light through a solid sheet of plastic. Light
treatment was included to control for any unintended effects (e.g., changes in
plastic ®lm (Lee Filters; Number 130 Clear), which reduced light transmit-
quality of light caused by the green ®lters approximates the change resulting
8-h dark (21°C, 75% relative humidity). Morphological responses to shading
have been demonstrated to be due to changes in the spectral quality of light (e.g., Schmitt and Wulff, 1993). We simulated the effect of light being filtered
through a canopy of competing plants by adding a layer of green plastic film
(Lee Filters, Andover, UK; number 121 Lee green) for each of the shading
treatments. The ®lter reduced the photosynthetic photon ®ux density (PPFD)
by 35% and produced a red : far-red ratio of 0.20. The change in the spectral
light caused by the green ®lters approximates the change resulting from
light ®ltered through leaves of competing plants. Further shading was achieved through the addition of 1–4 layers of a single sheet of neutral density
shade cloth (Plant Products, Brampton, Ontario, Canada), which reduced
PPFD by 33% with each successive layer without further changing the spectral
quality of the light. The control treatment consisted of a single layer of clear
plastic film (Lee Filters; Number 130 Clear), which reduced light transmitt-
tance by 5%, but had no effect on the spectral quality of the light. This
treatment was included to control for any unintended effects (e.g., changes in
humidity, air ®ow, etc.) of ®ltering light through a solid sheet of plastic. Light
guality and quantity of each treatment are summarized in Table 1.
Each of the six light ®lter treatments was suspended 48 cm above the pots.
To ensure that the light received in each of the treatments was predominantly
®ltered appropriately from above, all treatments were surrounded by a thick
(95% shade) neutral density shade cloth (Plant Products). Each week, plants
received 25 mL of a 2.00 g/L 20 : 20 : 20/N : P : K fertilizer and were re-
positioned within the growth chamber. Plants were watered evenly with RO
water as required.
Plants were grown to final developmental stage (i.e., when seed set was
completed and when there was no further change in the number or allocation
of meristems). Meristem allocation was recorded for all individuals of each
cpecies and resource treatment at regular intervals throughout development
and at final developmental stage. Recording meristem allocation throughout
development did not have any apparent unintended effects on the plants. There
were often several weeks between the last measure of meristem allocation
during development and the measure of meristem allocation at final develop-
ment. Meristem allocation was dif®cult to assess late in life due to the large
size of many plants. In addition, few changes in meristem allocation were
noted in the last few weeks of each experiment, as many plants were only
setting seeds at this time.

Data analyses—Meristems from each individual across the six light and
nutrient treatments for each species at each age were used to test for signif-
icanct allometry in meristem allocation. For a given genotype at a given age,
the total number of reproductive (R) and vegetative (I + G) meristems in
each plant was used to test for an allometric relationship between reproductive
effort and plant size across individuals that differ in size due to primarily
resource treatment (Eq. 1). Total number of vegetative meristems (I + G) was
used as a measure of plant size rather than total number of meristems (R + I
+ G) since the latter can result in spurious correlations that may obscure
the relationship between reproductive and vegetative components (e.g., Sam-
son and Werk, 1986; Klinkhammer et al., 1990). Similarly, the relationship
between axillary I and R + G meristems (Eq. 2) can be used to test for
allometry of apical dominance, and the relationship between axillary G and
R + I meristems (Eq. 3) can be used to test for allometry of branching
intensity. We tested for allometric relationships between meristem fates and
size for all individuals for each species at a given time (static allometry). We
do not test for allometric relationships due to changes in relative meristem
allocation within individuals throughout development (dynamic allometry).

Reduced major axis (model II) regression was used to test for an allometric
relationship between meristem fates across a range of plant sizes. Model II
regression is appropriate where there is error in both the x and y variables of the
regression model (Sokal and Rolf, 1995). A signi®cant allometric relation-
ship is indicated where the slope (scaling exponent) of the relationship
between log y and log x is different from 1 (McArdle, 1988; Henry and Aarssen,
1999).

Allometry in meristem allocation is indicated where the slope of the above
relationship between a given meristem fate and plant size differs from iso-
metry. A signi®cant difference of a reduced major axis slope (b) from a known
slope (b) can be performed on the test statistic (Clarke, 1980; McArdle, 1988):

$$ T = \frac{\log b - \log \beta}{\left(1 - r^2\right)\left(n - 2\right)^{1/2}} $$

where $r^2$ is the square of the correlation coef®cient of the relationship be-
 tween x and y, and n is the number of observations. A signi®cant difference of a
reduced major axis slope (b) from a known slope (b) can be performed on the test statistic (Clarke, 1980; McArdle, 1988):

$$ T = \frac{\log b_1 - \log b_2}{\left(1 - r_1^2\right)\left(n_1 - 2\right)^{1/2}} $$

where $r_1^2$ is the square of the correlation coef®cient of the relationship be-
 tween x and y, and n is the number of observations. A signi®cant difference of a
reduced major axis slope (b) from a known slope (b) can be performed on the test statistic (Clarke, 1980; McArdle, 1988):

where $r_2^2$ is the square of the correlation coef®cient of the relationship be-
 tween x and y, and n is the number of observations. A signi®cant difference of a
reduced major axis slope (b) from a known slope (b) can be performed on the test statistic (Clarke, 1980; McArdle, 1988):

RESULTS

Allometry and meristem responses to resource treat-
ments—For each species, the nutrient and light gradients pro-
duced a range of plant sizes at all ages throughout develop-
ment. The total number of meristems increased with increasing
light and nutrient availability. For each relation tested, the

TABLE 1. Light quantity (percentage of maximum radiation) and light
quality (red : far-red ratio) for each of the six light treatments.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Radiation (%)</th>
<th>Red : Far-red ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>100</td>
<td>1.0</td>
</tr>
<tr>
<td>Spectral shade</td>
<td>65</td>
<td>0.2</td>
</tr>
<tr>
<td>Spectral shade + neutral shade</td>
<td>46</td>
<td>0.2</td>
</tr>
<tr>
<td>Spectral shade + neutral shade × 2</td>
<td>36</td>
<td>0.2</td>
</tr>
<tr>
<td>Spectral shade + neutral shade × 3</td>
<td>20</td>
<td>0.2</td>
</tr>
<tr>
<td>Spectral shade + neutral shade × 4</td>
<td>15</td>
<td>0.2</td>
</tr>
</tbody>
</table>
Fig. 1. Model II regressions of the allometric relationship for reproductive effort (a, d), apical dominance (b, e), and branching intensity (c, f) for *Arabidopsis* (○), *Arenaria* (□), *Brassica* (▽), and *Chaenorrhinum* (▽) at final developmental stage growing on a light gradient (a, b, c) and a nutrient gradient (d, e, f). Closed symbols represent the mean meristem allocation for the six resource treatments for each species. Each line represents the regression line plotted through the individuals (not the means) for each species. The leading diagonal line represents the slope (equal to one) of an isometric relationship. Solid lines represent slopes that are significantly different (*P* < 0.05) from isometry; dashed lines represent slopes that are not different from isometry. Regression lines coded with different letters are significantly different.
slope of the relationship between the number of meristems committed to one fate and the number of those committed to others was linear and highly significant. There were significant responses of patterns of meristem allocation defining each life history trait. In general, relative allocation to reproductive effort and branching intensity was greater for larger plants (slopes of the allometric relationships for these traits tended to be greater than one), and relative allocation to apical dominance was greater for smaller plants (slopes of the allometric relationship tended to be less than one) (Figs. 1 and 2). Where patterns of meristem allocation responded to resource availability, the response tended to be initiated early in development and was significant at every age (Fig. 2). Meristem response for Arabidopsis was significant throughout development for each of the three life history traits on both environmental gradients (Fig. 2). Meristem response was also significant for each life history trait on both gradients for Arenaria, with the exception of meristem response for young plants grown on the nutrient gradient. Brassica showed similar patterns; however, reproductive effort showed no significant response on the nutrient gradient at any age. The response in reproductive effort was significant at all ages in Chaenorrhinum on both nutrient and light gradients. However, there was no consistent pattern of significance for either apical dominance or branching intensity (Fig. 2).

Few of the pairwise comparisons between allometric relationships throughout development were significantly different (results not shown). This is in part due to the low power associated with the high number of pairwise comparisons for each species and treatment combination. However, there are cases where the strength of allometric relationships change through development. For example, the strength of response in patterns of meristem allocation to light availability for Arabidopsis and Arenaria tends to decrease towards final development (converging on isometry) for each life history trait (Fig. 2a, b). While the magnitude of these responses is diminished, they remain significantly different from isometry.

Intraspecific differences in meristem response—Within species, the degree of response in meristem allocation to environmental conditions (i.e., the slope of the allometric relationship) tended not to differ significantly between plants grown on light gradients with those grown on nutrient gradients (Fig. 3). The response in reproductive effort and apical dominance were significantly different between light and nutrient gradients for both Arenaria and Chaenorrhinum.

Interspecific variation in meristem response—Species differ in their total accumulation of each meristem fate at final developmental stage. Brassica tended to have the fewest meristems of each meristem fate, while Arenaria and Chaenorrhinum tended to accumulate the most meristems of each fate by final developmental stage (Fig. 1). The capacity for plants to respond to variable resource availability by changing patterns of meristem allocation differs among species. At final development, there were significant differences in allometric relationships between
Fig. 2. Continued.

Nutrient gradient

![Graphs showing meristem allocation and allometry patterns across different species.](image)

Species for reproductive effort and apical dominance on the light gradient (Fig. 1a, b) and for apical dominance and branching intensity on the nutrient gradient (Fig. 1e, f).

**DISCUSSION**

Meristem allocation and allometry—Patterns of meristem allocation should represent plant strategies to maximize fitness across a range of environments as relative allocation to each potential fate directly controls allocation to fitness-related traits such as growth and reproduction (Bonser and Aarssen, 1996). Increases in plant size increase the absolute number of meristems available to commit to each fate. The relationship between meristem fates across a range of plant sizes (in which size differences were due to differences in resource availability) was highly significant at all ages on both light and nutrient gradients. Larger plants tended to have a higher absolute number of reproductive (R), inactive (I), and growth (G) meristems. However, differences in the relative accumulation of a meristem fate in relation to the accumulation of other meristem fates across sizes result in allometric relationships between meristem fates. Thus, plants change their relative allocation to different meristem fates in response to resource availability.

The allometric relationships between meristem fates were strikingly constant across the four species studied (Fig. 1). This indicates that there may be a common response in meristem allocation that may maximize fitness in a given environment in plants of very different body plans. The relatively high allocation to both growth (and reproductive) meristems in large plants (under low resource availability) may be products of natural selection acting on plants with a common annual life history. Plants with allometric relationships in branching intensity (BI) and apical dominance (AD) across these resource gradients should be relatively more fit than plants with isometric relationships in these traits.

Coefficients of allometry were significantly different between light and nutrient gradients for only two of a possible 12 contrasts (Fig. 3). This suggests that the type and magnitude of response is consistent across different resource environments. It is reasonable to assume that the response in apical dominance would be greater across the light gradient than the nutrient gradient, as light with low red : far red can promote a shade-avoidance response in plants (see Schmitt and Wulff, 1993; Dudley and Schmitt, 1996) and decrease the probability of axillary meristem development (e.g., Robin et al., 1994a, b). However, the response in apical dominance for *Arenaria* was significantly greater for plants grown on the nutrient gradient than for plants grown on the light gradient. There was no significant difference in the apical dominance response for the other three species. Short-lived annuals generally grow in open and disturbed habitats where competition for light should not be intense. Thus, the ability to respond to variable nutrient availability may be as important as the ability to respond to variable light availability. The consistency of the type and magnitude of response of meristem allocation on different resource gradients suggests that allometric relationships may be general responses in plants of different body plans to resource gradients.

While the patterns of response (slope greater than or less than isometry) were constant across species, we found signif-
Fig. 3. Model II regressions of the allometric relationship for reproductive effort, apical dominance, and branching intensity for *Arabidopsis*, *Arenaria*, *Brassica*, and *Chaenorrhinum* grown on light (●) and nutrient (○) gradients. The leading diagonal line represents the slope (equal to one) of an isometric relationship. *T* and *P* values for the significance of the difference between each pair of slopes appear on each plot. Bold *P* values indicate significant differences after sequential Bonferroni correction.

A significant difference in the magnitude of response across species on both light and nutrient gradients. Variability in the magnitude of response across species in branching intensity and apical dominance demonstrates that plants differ in their ability to respond to environmental conditions. This suggests that either selection continuously modifies the magnitude of response to environmental variability or that the magnitude of response is constrained in some species by architectural or body plan traits. Differences between species in these traits were not consistent between resource gradients. For plants growing on the light gradient, *Arabidopsis* had the strongest response in apical dominance and *Chaenorrhinum* had the weakest response. On the nutrient gradient, *Chaenorrhinum* had the strongest response in apical dominance and *Brassica* had the strongest response in branching intensity; *Arenaria* had the weakest response in both of these traits. The shift in relative strengths of response across species between gradients indicates that the magnitude of response is not entirely due to body-plan constraints. Further studies are required to explore how plants of contrasting body plans respond to selection for strong allometric responses to resource availability.

Interspecific differences in allometry of reproductive effort must be interpreted differently than interspecific differences in allometry of apical dominance or branching intensity. Significant differences in allometric coefficients between two species in reproductive meristem allocation demonstrate instances in which one species has relatively higher allocation to reproduction in low resource environments while the other species
has relatively higher allocation to reproduction in high resource environments. These differences become especially important when the regression lines cross at intermediate sizes, as differences in allometry represent absolute differences in allocation to reproduction. For example, the regression lines cross for *Anenaria* and *Chaenorrhinum* for plants growing on the light gradient (Fig. 1a). Allocation to reproduction was greater for *Arenaria* in low resource environments and greater for *Chaenorrhinum* in high resource environments. Because reproductive meristems in both of these species form single fruits rather than inflorescences, differences in the number of reproductive meristems likely reflect differences in fitness between these species (*Arenaria* being more fit in the low light environments and *Chaenorrhinum* being more fit in high light environments). These changes in relative fitness across plant sizes could be an important mechanism for species coexistence across heterogeneous resource gradients.

Considering how traits are interpreted within plants increases our understanding of how plants respond to environmental variables (e.g., Schlichting and Pigliucci, 1998). A change in reproductive effort (RE), apical dominance (AD), or branching intensity (BI) can be correlated with the allocation to one or both other traits (Duffy et al., 1999). For example, apical meristems are committed to reproduction by final development in three of the species examined here (*Anenaria*, *Arabidopsis*, *Brassica*). In favorable resource environments, increased allocation to new branches (growth meristems) will be positively correlated with reproductive meristems and negatively correlated with inactive meristems. Increasing reproductive effort with increasing plant size is a common relationship in plant populations. Reproductive allometry is potentially caused by a number of factors (Sugiyama and Bazzaz, 1998), including a minimum size threshold required for reproduction (Weiner, 1988). Our results are consistent with the hypothesis that adaptive responses in traits such as apical dominance and branching intensity can lead to allometry in reproductive effort. Results of a recent study demonstrate that allocation to reproductive meristems is not correlated with growth meristems in perennial species (Huber and During, 2001). Future studies on species of different life histories on a number of other environmental gradients are needed to establish the degree to which these meristem allocation patterns are general strategies.

**Allometry and development**—In general, where significant responses of meristem allocation were detected, these responses were initiated relatively early in development. Capacity to alter patterns of meristem allocation early in development should be very important for both branching intensity and apical dominance. The potential increases in size and fitness (through a larger absolute number of meristems available to be allocated to reproduction) gained from greater commitment to growth meristems should be maximized earlier in development, as this maximizes the number of growing stems accumulating size and meristems early in development. Similarly, in resource-impoverished environments, suppressing axillary meristem activity relatively early in development through strong apical dominance could conserve limited resources in order to maximize lifetime reproductive success. In a previous study (Bonser and Aarssen, 2001), we found the strength of meristem response tended to decrease toward final development in genotypes of *Arabidopsis*, demonstrating the decreasing value of later life responses in these meristem fates. While there were several cases where the strength of meristem response seemed to decline through development (e.g., Fig. 2a, b), these late-life allometric coefficients were not significantly different than earlier-life allometric coefficients.

Factors controlling plant growth and development (the pattern of meristem allocation) can be altered by the environment in a fairly consistent manner across species. While allocation to meristem fates may be guided by a set of rules in which the placement and timing of meristem activation (or inhibition) gives rise to species growth form, total meristem allocation is not a fixed property within a species. These results mirror the results found in plasticity through development in genotypes of *Arabidopsis* (Bonser and Aarssen, 2001) and are consistent with the notion that the nature of the relationship between traits can change through development (Pigliucci et al., 1996; Schlichting and Pigliucci, 1998).

The differences in the range of meristem allocation found here may be due in part to differences in body plan (architecture) between each of the four species studied here. Floral meristem fates have been found to be contingent on architectural effects within individuals (Diggle, 1994, 1997). Similarly, differences in morphology between species significantly affect competitive interactions (Geber, 1989). Further tests are required to examine the role of body plan on functional allocation to meristem fates in competitive interactions and the constraints that body plan sets on the evolution of adaptive strategies (Gould and Lewontin, 1979). Studies on a range of species and a number of environmental gradients are required to further test the evolution of meristem allocation strategies and the evolution of the capacity to respond to environmental selection pressures.

**Conclusions**—We found significant allometry in meristem allocation for each of the four species examined in this study. Allocation to reproduction and growth meristems (reproductive effort and branching intensity, respectively) increases with increasing plant size (where differences in plant size are due to differences in light and nutrient availability). Allocation to inactive meristems (apical dominance) tends to decrease with increasing plant size. Since size variability was due to differences in light and nutrient availability, we suggest that allometry in meristem allocation demonstrates important functional responses of meristem allocation to resource availability. Species showed significant differences in the strength of meristem response to variable resource availability. These differences may be important in defining the range of habitats in which a species can exist and help to explain patterns of species competition and coexistence in habitats with variable resource availability.

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