COMPETITION AND ALLOMETRY IN THREE SPECIES OF ANNUAL PLANTS[1]

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Abstract. Comparisons between competing and noncompeting populations of three annual plant species demonstrate that plant allometry is altered by competition. When plants are grown in isolation, relationships between stem diameter, height, and plant mass generally show simple allometry (i.e., the relationships are linear on log-log scale). When plants are competing, however, these relationships are curvilinear or discontinuous.

We attempt to clarify the relationship between interindividual allometry (the usual source of allometric data) and allometric growth. When plants are not competing, the allometric relationships among individuals of different sizes at one point in time and the allometry of individual plants as they grow appear to be similar, but these two classes of allometric relationships are very different for competing plants. We present a simple model that explains both static and dynamic patterns of plant allometry in terms of (a) the allometric responses of individual plants to competition, and (b) the size dependence of growth after the onset of competition.

Our results illustrate the importance of reciprocal interactions between competition and allometry, and emphasize the difficulty in making inferences from one size measure to another. We conclude that the commonly held assumption that plant size is a single entity, which can be reflected by any of several measures, may not be justified.

Key words: allometric growth; allometry; competition; plants; size.

Introduction

Competition alters the form, as well as the growth, survival, and reproductive output of plants (Harper 1977, Weiner et al. 1990*a*). While the effects of interference on growth (e.g., density-yield relationships and neighborhood interference) and survivorship (density-dependent mortality) have been studied extensively, less is known about the influence of competition on growth form. Understanding the relationship between competition and plant growth form is important if we are to explain stand structure in terms of the behavior of individual plants and the evolution of plant morphology in response to competition. An allometric approach is necessary in this effort, since the form of most organisms changes during growth.

Allometry plays an important role in determining competitive interactions between plants. A plant's aboveground allometric growth pattern (e.g., the relationships between biomass, leaf area, and canopy projection area) determines its pattern of light interception. Because competition for light is "asymmetric" (Weiner and Thomas 1986) or "one-sided" (Gates 1978, Cannell et al. 1984), height becomes an extremely important determinant of success when plants are shading one another. The relationships between these components of size for an individual and its neighbors determine how much of the available light a given plant will obtain. Several researchers have argued that the self-thinning trajectory for a population of plants is strongly influenced by plant allometry (Miyanishi et al. 1979, White 1981, Weller 1987), although we do not yet understand the nature of this relationship. Plant allometry also has a strong effect on the dynamics of population size structure and the nature of plant–plant interactions within populations (e.g., Thomas and Weiner 1989*a*).

Allometric relationships among measures of plant size have usually been treated as genetically fixed characteristics of a species (e.g., species-specific allometric exponents have been reported for forest trees [White 1981, Weller 1987]). Often, allometric relationships for a particular species are hypothesized to be the product of biomechanical or other physical constraints (McMahon 1975, Givnish 1986). However, the plasticity of plant growth form in response to competition (Franco 1986, Jones and Harper 1987, Geber 1989, Holbrook and Putz 1989, Weiner et al. 1990*a*) suggests that allometric relationships may be, in part, a result of competitive interactions between plants. In forest trees, growth in diameter but not height is often sensitive to density (Sjolte-Jorgensen 1967, Lanner 1985), with the result that trees in crowded plantations often have more slender stems than they do if thinned (e.g.,

Petty and Worrell 1981). However, with one exception (Holbrook and Putz 1989), the effects of competition on plant form have not been studied allometrically. To test the hypothesis that competition alters the allometric patterns of plants, we performed experiments on three species of annual plants: *Impatiens pallida, Tagetes patula,* and *Polygonum pensylvanicum.*

In the interests of clarifying terminology and concepts, it is important to note that there are several different meanings of allometry in the literature (Gould 1966). There are two definitions that are relevant here:

1) One definition of allometry is based on the "allometric equation," $Y = aX^b$, where X and Y are organs or size metrics and a and b are constants (Huxley 1932). Here, allometry is defined by a type of mathematical relationship that has been applied to many different types of data.

2) Another definition of allometry is the "differential growth of parts or metrics of an organism." This definition makes no assumptions about the mathematical form of the relationship between parts, other than that it is not a simple, unchanging proportion (i.e., isometric growth). Thus, a linear relationship between two size variables that intercepts the origin would not be considered "allometric," but a linear relationship that does not intercept the origin (e.g., size-fecundity relationships described in Samson and Werk [1986] and Weiner [1988]) would be (Gould 1966). It should be emphasized that although allometry, according to this definition, refers to changes in individuals over time, the data used to determine allometric relationships are usually from individuals of different sizes measured at one point in time. This is done for convenience (or necessity in the case of long-lived organisms), and because some of the most valuable size metrics (e.g., dry mass) can only be evaluated destructively. If allometric relationships between different individuals at one point in time are different from those of one individual over the course of its growth, then many of the inferences about allometric growth in the literature may not be valid.

To distinguish allometric relationships as described in (2) from the "allometric equation," we refer to relationships that fit the allometric equation as "simple allometry" (Gould 1966, Jolicoeur 1989). Smith (1980) clarifies the difference between the allometric equation and the more general concept of allometry.

METHODS

Data from three series of experiments were used. Field experiments were performed on *Impatiens pallida,* and greenhouse experiments were performed with *Tagetes patula* and *Polygonum pensylvanicum.*

Impatiens pallida Nutt. (Balsaminaceae) is a large, erect, summer annual of mesic woodlands of eastern North America, which often forms monospecific stands in partially shaded areas (Thomas and Weiner 1989*b*). Field studies were conducted in the Crum Woods of Swarthmore College (39°54' N, 75°21' W) in Delaware County, Pennsylvania, at the edge of a disturbed forest, on the 50-yr floodplain of the Crum Creek. A more complete description of the study area is given in Thomas and Weiner (1989*b*). Five naturally occurring crowded populations were harvested between 11 June and 11 July in 1985, and five more were harvested between 8 June and 26 June in 1987. In each case, the height of each plant was measured to the nearest centimetre, and the stem diameter at the middle of the first internode was measured to the nearest 0.1 mm with digital calipers. Plants were harvested at ground level, dried in a drying oven (70°C) for 2 d and weighed. In addition we harvested 30 naturally occurring uncrowded plants (no neighbors >8 cm tall within 1 m) nearby on 1 July 1985, and we experimentally thinned (no neighbors within 1 m) two populations early in the growing season in 1987. All neighbors within 1 m that appeared during the course of the study were removed periodically, and these populations were harvested on 1 July and 6 August.

Marigolds (*Tagetes* spp.) have served as a model organism in studies of plant population structure (Ford 1975, Ford and Diggle 1981). Seeds of *Tagetes patula* L. var. 'Yellow Boy' (Asteraceae), were planted in 12 replicate plots at a density of 1500 seeds/m² in wooden flats in a greenhouse at Swarthmore College on 16–20 September 1986. Uncrowded plants were grown individually in each of 120 15.2 cm diameter pots. Replicate plots and groups of 10 individually grown plants were harvested weekly for 11 wk. Size metrics were measured as in the *Impatiens* populations. In addition, one plot of crowded plants and 10 pots of uncrowded plants were individually numbered and the height (to apex) and stem diameter were measured weekly (except for weeks 8 and 10). A more complete description of the experiments is given in Weiner et al. (1990*b*).

Polygonum pensylvanicum L. is an old-field successional dominant that forms transient monocultures in disturbed areas of northeastern North America. Here we analyze part of the data from an experiment conducted from 1 July to 25 September 1988, in a greenhouse at Harvard University. Plants were of 25 genotypes, cloned via meristem culture from individuals collected from an old field at the University of Illinois Biological Research Area, 6 km east of Urbana. Individually grown plants ($N = 200$) were grown in 5-L pots spaced on greenhouse benches at a density of 11.8 individuals/m². Crowded plants ($N = 300$) were grown in 38 × 34 cm tubs clustered in two blocks of six tubs each, to give a density of 263 individuals/m². A complete description of the experiments is given in S. C. Thomas and F. A. Bazzaz (*unpublished manuscript*).

Second-order polynomial regression on log-transformed data was used to test for deviations from linearity in the allometric relationships examined. A significant second-order polynomial term was considered evidence that a relationship was curvilinear or discon-

TABLE 1. Tests for nonlinearity of allometric relationships in crowded and uncrowded field populations of *Impatiens pallida*.*

Date	Density (ind/ m²)	N	Mean mass (g)	Height–mass allometry			Mass–diameter allometry			Height–diameter allometry		
				P	Sign	r²	P	Sign	r²	P	Sign	r²
Crowded populations												
15 Jun 1987	91	80	0.448	<.001	−	.912	<.001	−	.948	<.001	−	.873
17 Jun 1987	131	80	0.390	<.001	−	.880	=.006†	−	.954	<.001	−	.824
11 Jun 1985	248	49	0.251	=.022†	−	.919	<.001	−	.930	<.001	−	.877
9 Jun 1987	76	80	0.830	<.001	−	.954	NS	0	.930	<.001	−	.917
18 Jun 1985	97	50	0.670	NS	0	.911	=.030†	−	.950	<.001	−	.882
8 Jun 1987	84	80	0.805	<.001	−	.977	=.006†	+	.945	=.060†	(−)	.855
25 Jun 1987	177	81	0.470	<.001	−	.927	NS	0	.816	=.003	−	.767
26 Jun 1985	212	31	0.419	<.001	−	.946	<.001	−	.967	<.001	−	.762
19 Jun 1985	126	26	1.010	=.033†	−	.971	=.034†	−	.983	=.004†	−	.958
11 Jul 1985	215	29	0.629	NS	0	.893	=.039†	−	.886	=.005†	−	.859
Uncrowded populations												
1 Jul 1987		51	2.08	=.016†	+	.803	NS	0	.837	=.028†	+	.523
1 Jul 1985		30	2.66	NS	0	.586	NS	0	.832	NS	0	.268
6 Aug 1987		23	5.38	NS	0	.896	NS	0	.905	NS	0	.878

* P: significance of second-order term (b) in regression: $y = ax + bx^2 + c$ (on log-transformed data). Sign: sign of significant second-order term. Significance is evidence for curvilinearity; nonsignificance is consistent with linear allometric relationship. r^2 is for polynomial regression model (including only significant terms).

† Significant second-order term was not significant "table wide" ($P > .05$) with sequential Bonferroni correction.

tinuous (rejecting the null hypothesis of linearity). Least squares second-order polynomials were fit to these relationships. In cases where linearity could not be rejected, we used standard (Model I) linear regression. It has been argued (Harvey 1982) that some form of Model II regression is more appropriate for fitting allometric functions. Others (Seim and Sæther 1983) disagree. In any case, since basic problems of nonlinear Model II regression have not been solved, we used Model I regression in both cases. In cases where a large number of statistical tests (e.g., for deviations from linearity) were conducted, both standard and sequential Bonferroni-corrected (Rice 1989) confidence levels were determined.

RESULTS

Impatiens pallida populations tended to show simple allometric relationships between height (H), diameter (D), and aboveground biomass (M) when plants were uncrowded (Table 1); height–mass allometric plots for the three uncrowded populations are displayed in Fig. 1a. In two out of the nine cases, the allometric relationships for noncompeting plants deviate from linearity at $P < .05$, but these deviations are not significant ($P > .05$) if sequential Bonferroni-corrected confidence levels are used. Three typical height–mass allometric plots for crowded populations are shown in Fig. 1b. In the crowded populations 24 out of 30 of the allometric relationships between height, diameter, and mass were significantly curvilinear (17 out of 30 using sequential Bonferroni-corrected levels). Crowding changes the position of the log H-log M relationships and makes the relationship convex (i.e., of decreasing slope; Fig. 2). In the two cases of (noncorrected)

significant curvilinearity in uncrowded populations, the sign of the second-order term was opposite that of the crowded populations (Table 1). The implications of these patterns for plant shape can be seen in the effect of crowding on a simple measure of plant shape, H/D, and M (e.g., Fig. 3). In the crowded population, H/D increases and then decreases with increasing M. For plants <0.2 g, larger individuals tend to be "thinner," whereas for plants >0.2 g, larger individuals tend to be "fatter." No such relationship exists for uncrowded plants.

Tagetes patula populations also show simple allometric relationships between H, M, and D when plants are not competing (Table 2). When log H is plotted against log M for all 110 individually grown plants harvested over all 11 wk (Fig. 4), there is a very tight linear relationship ($r^2 = 0.965$). The result is similar for the log H-log D and log M-log D relationships for these plants ($r^2 = 0.922$ and 0.951, respectively). Crowded populations consistently show curvilinear H-W and H-D allometric relationships after 4 wk of growth (Table 2). M-D allometric plots for crowded populations did not show significant curvilinearity. Crowded plants are taller than uncrowded plants of the same mass (Fig. 4). As in *Impatiens*, crowded *Tagetes* plants are taller than uncrowded plants of the same diameter (or mass), and the log H-log D curves are consistently convex (Fig. 5).

To explore the relationship between static interindividual allometry and the allometric trajectories of individuals during growth, we have plotted H-D trajectories for the repeatedly measured *Tagetes* populations (Fig. 6). Allometric trajectories for all nine surviving uncrowded plants are shown. For clarity, the
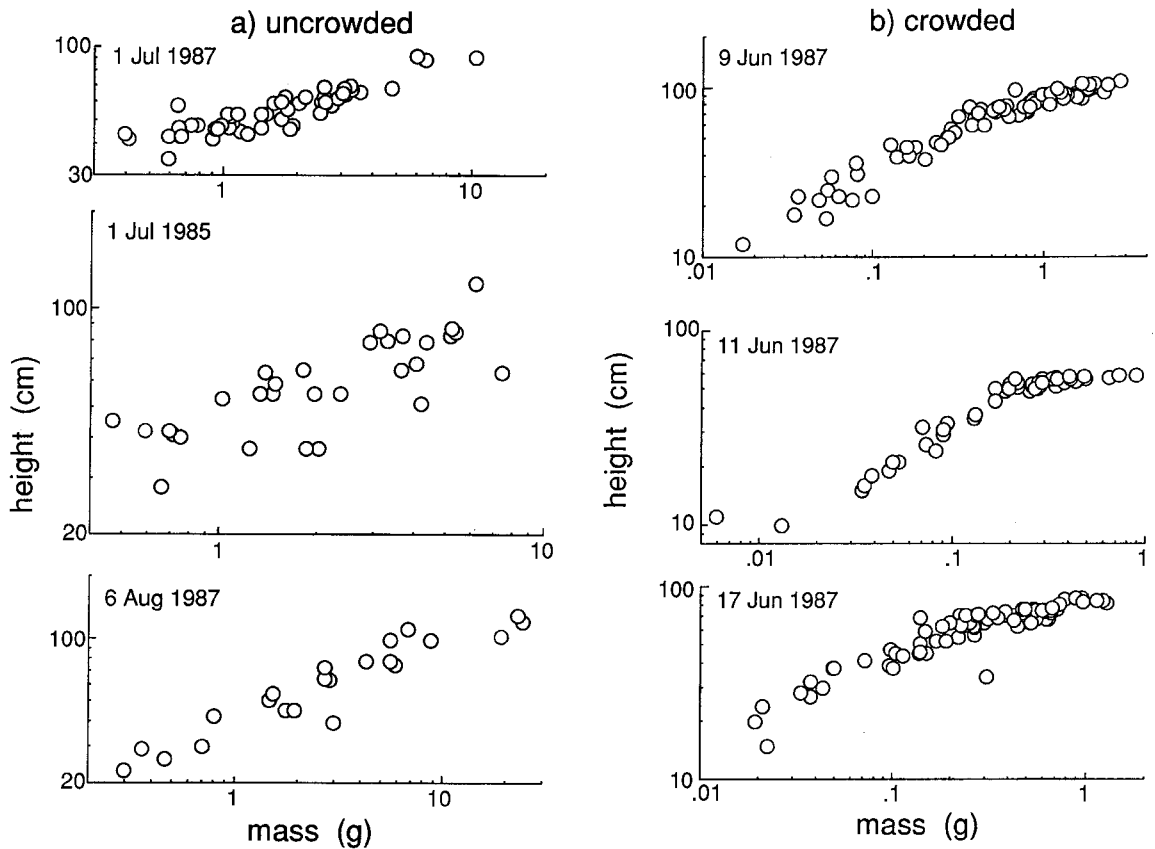
FIG. 1. Allometric relationship between height and aboveground biomass for (a) three uncrowded and (b) three of the crowded *Impatiens pallida* populations.

allometric trajectories for the crowded plants are based on the means of 10 groups of 13 individuals, ranked by height at the first measurement. Trajectories for crowded plants were steeper than those of the uncrowded groups ($P < .001$; t test). Tests for nonlinearity of trajectories were not possible because of nonindependence of repeated measures and the limited number of time intervals measured. The data do not appear to indicate nonlinear trajectories for the uncrowded or crowded plants.

TABLE 2. Tests for nonlinearity of allometric relationships for sequential harvests of crowded (1500 individuals/m²) and uncrowded (individually grown in pots) populations of *Tagetes patula*.*

	N	Mean mass (g)	Height–mass allometry			Mass–diameter allometry			Height–diameter allometry		
			P	Sign	r^2	P	Sign	r^2	P	Sign	r^2
					Crowded populations						
Week 4	132	0.064	<.01†	−	.736	NS	0	.837	<.001	−	.674
Week 5	131	0.098	<.01†	−	.826	NS	0	.930	<.02†	−	.734
Week 6	126	0.125	<.05†	−	.765	NS	0	.806	NS	0	.810
Week 7	127	0.130	<.001	−	.905	<.05†	+	.868	<.01†	−	.770
Week 8	122	0.174	<.001	−	.766	=.05†	−	.882	<.001	−	.597
Week 9	114	0.223	<.001	−	.822	NS	0	.765	<.005	−	.533
Week 10	120	0.195	<.05†	−	.730	<.05†	−	.831	<.002	−	.513
Week 11	111	0.254	<.001	−	.813	NS	0	.719	<.001	−	.506
					Uncrowded populations						
All weeks	110	1.32	NS	0	.965	NS	0	.951	NS	0	.930

* P: significance of second-order term (b) in regression: $y = ax + bx^2 + c$ (on log-transformed data). Sign: sign of significant second-order term. Significance is evidence for curvilinearity; nonsignificance is consistent with linear allometric relationship. r^2 is for polynomial regression model (including only significant terms).

† Significant second-order term was not significant "table wide" ($P > .05$) with sequential Bonferroni correction.
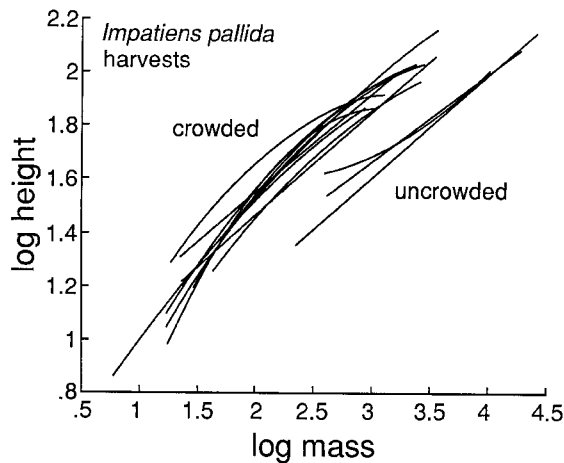
FIG. 2. Curves fit with second-order polynomial regression to log height–log biomass data for the nine crowded and three uncrowded populations of *Impatiens pallida*. Where coefficient of second-order (squared) term was not significant, simple linear regression was used. Lines also reflect the ranges of biomass for each population.

FIG. 3. Height/diameter vs. biomass for (a) one uncrowded and (b) one crowded *Impatiens pallida* population.

Polygonum pensylvanicum shows patterns similar to those of the other two species. The composite log H–log D relationship for all the crowded plants was highly curvilinear ($P < .001$), whereas the relationship for uncrowded plants does not deviate significantly from linearity (Fig. 7). H-M and D-M allometric relationships for the competing populations (not shown) also deviate significantly from a linear model. As in the other two species, the log H-log M plot is concave and, as in *Impatiens*, the log D-log M plot is convex.

DISCUSSION

The results demonstrate that competition between plants can cause major alterations in the allometric relationships between plant height, stem diameter, and aboveground plant biomass. These changes were similar for the three species studied. Uncrowded plants usually show simple allometric relationships between these variables. In the one species for which we have extensive data on allometric growth (*Tagetes*), there appears to be no difference between the allometric growth of uncrowded individuals and the allometric relationship between uncrowded individuals of different sizes at the same time. In other words, smaller plants will have the same shape as larger plants when they reach the larger size. However, competition fundamentally changes these relationships. In dense stands allometric relationships among individuals are nonlinear over the course of stand development, and the location of these relationships is shifted. Competing plants are taller and thinner than noncompeting plants of the same mass. The changes that competition induces in the form of allometric relationships seem to
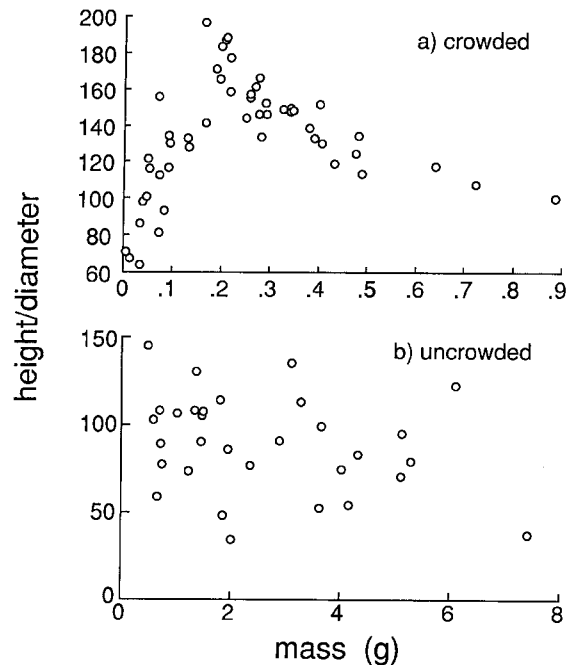
be similar for the three species studied. When plants are competing, static allometric relationships between individuals are not the same as the allometric growth trajectories of individuals. A small plant in a crowded stand will not have the same shape as the large plant in that stand if it achieves the size (i.e., vegetative mass) of the larger plant. This is clearly illustrated in terms of plant shape in Fig. 3a, which shows the relationship between a simple measure of plant shape (height/diameter) and dry mass for a typical crowded *Impatiens*
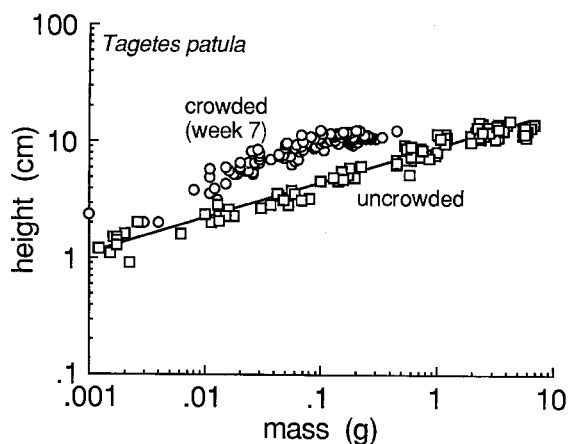

FIG. 4. Height–biomass allometric plot for one of the crowded harvests (week 7) and all of the uncrowded *Tagetes patula* individuals.
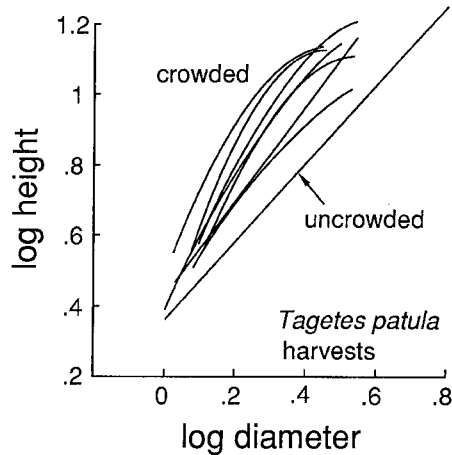
FIG. 5. Curves fit with second-order polynomial regression to height–diameter relationships for the seven sequential harvests of crowded *Tagetes patula* populations and all the sequentially harvested uncrowded plants. Where coefficient of second-order (squared) term was not significant, simple linear regression was used. Lines also reflect the ranges of diameters for each population.

plot. Plants of intermediate size had the greatest ratio of height : diameter, and it is worth noting that these are the individuals that tended to lodge (Thomas and Weiner 1989*b*).

A graphical model of the relationship between dynamic allometric trajectories and static among-individual allometric relationships in competing and noncompeting populations is illustrated in Fig. 8 (model 1). Plants follow a simple allometric trajectory in the absence of competition. Crowded individuals follow this trajectory until they start to compete. When competition commences, allometric trajectories change and become steeper on the log *H*-log *M* graph (and the log *H*-log *D* graph). Because plants are different sizes when competition commences, the change in slope of their trajectories occurs at different points along the original noncompeting trajectory. An alternative model (Fig. 8, model 2) includes differences in the slopes of allometric trajectories for plants of different sizes at the onset of competition. Analysis of the dynamic *Tagetes* data (Fig. 6) and data from large numbers of crowded *Impatiens* individuals, which were measured at only two or three points in time (J. Weiner and S. C. Thomas, *unpublished data*) are more consistent with the simpler model (model 1). There was no relationship between plant size and slope of the log *H*-log *D* trajectory. Rather, the data support the hypothesis that individuals of different sizes show different amounts of growth along parallel trajectories, as in model 1 (Fig. 8).

If growth is size dependent and trajectories are parallel (Fig. 8, model 1), then the process producing the resulting pattern of within-stand allometry can be modelled using empirical relationships between absolute

growth rate (AGR) and size in multidimensional space, in which each axis is a size metric. (Equations fit to AGR–size relationships have been called Distribution-Modifying Functions [Westoby 1982] or *G* (*t,x*) functions [Hara 1984]). Consider the *H*-*D* relationships in Fig. 8, model 1. If the diameter increment vs. diameter and the height increment vs. height relationships are exponential in form and the initial diameter and height are those at the onset of competition, then the resulting static allometric curve following competition will be linear. For a concave allometric relationship between *H* and *D* to result (as found in all three species studied) the AGR–size relationships for *D* and *H* must be concave on a log-log scale. A number of empirical studies have described AGR–size relationships in which only plants above some minimal size show positive growth rates and the AGR–size relationship above this size is linear (Mohler et al. 1978, West 1980, West and Borough 1983, Westoby 1984, Thomas and Weiner 1989*b*). For plants above the minimal size for growth, such relationships will be concave on a log-log plot. Such AGR–size relationships may be general for plants grown at high densities as a consequence of (a) a positive relationship between certain aspects of a plant's size and its ability to acquire resources and (b) the existence of some minimal resource requirement for growth. The most obvious example of such a relationship would be that resulting from the extinction of light through a canopy and the existence of a whole-plant light compensation point.

To summarize our model, competition induces allometric shifts in the growth of individuals in plant
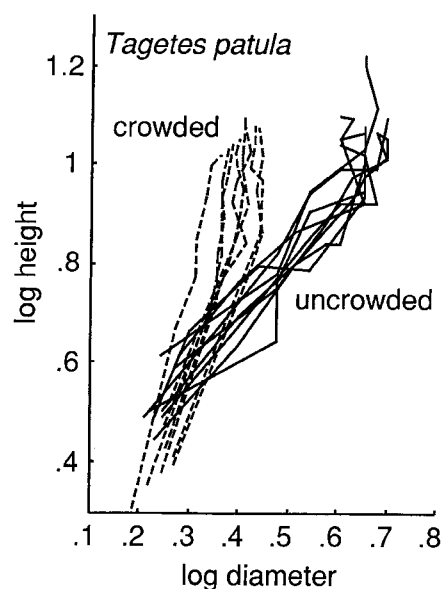

FIG. 6. Height–diameter allometric trajectories for the repeatedly measured *Tagetes patula* populations. Trajectories for all nine uncrowded plants, and means of 10 groups of 13 crowded plants, ranked by initial height, are shown.

populations. The resulting population-level allometric relationships are therefore the result of both the allometry and the size dependence of individual growth. Because there is often some minimum size required for growth in a competing population of plants, AGR–size relationships for growing plants will generally be concave on a log-log scale. This results in static patterns of allometry, which are concave if the allometric slope for individuals becomes steeper after the onset of competition. One possible criticism of our model is that plants may begin to experience competition at different points in time as well as at different sizes.

Our results have potentially important implications for the study of plant competition and for the study of plant allometry. While our results are consistent with the idea that allometry is important in determining competitive relationships between plants, these relationships between competition and allometry are not simple and straightforward. Plant allometry certainly has important effects on plant–plant interactions and consequent population-level phenomena, but allometric trajectories are themselves strongly affected by competitive interactions. Thus, difficulties in elucidating the relationships between plant allometry and self-thinning trajectories (White 1981, Weller 1987) may be due, in part, to treating the problem as one of simple cause and effect, rather than as one of reciprocal interaction. Allometric changes due to competition are an essential part of the hierarchical relationship between stand-level phenomena (e.g., density-yield relationship and self-thinning trajectories) and individual behavior (the survival, growth, and form of individual plants).

These observations bring into question much of what is known about plant allometry, because most of the data on which allometric relationships have been determined are static data from crowded populations (e.g.,
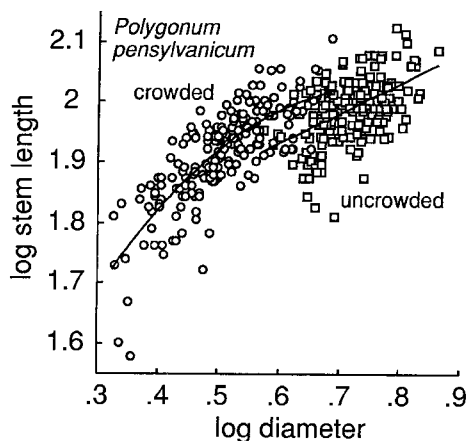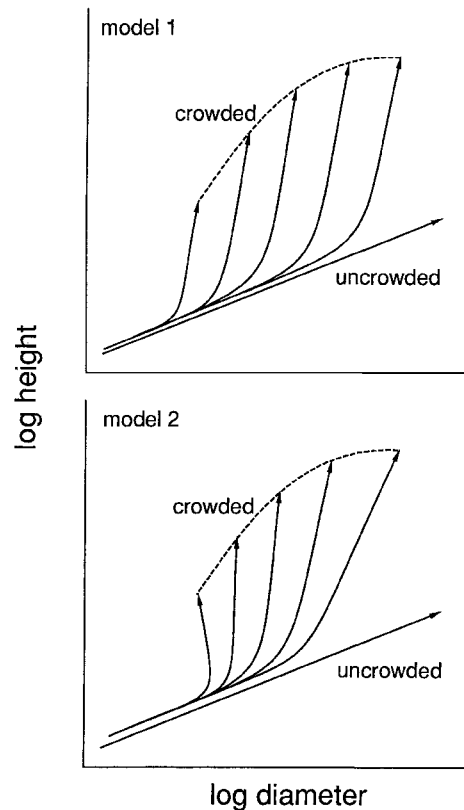

FIG. 8. Alternative models for the relationship between intrapopulation static allometric relationships and allometric growth of individuals in crowded and uncrowded plant populations. In both models the allometric growth of individuals over time and allometric relationships among individuals at one point in time are the same when plants are not competing. For crowded populations, dashed lines represent static, intrapopulation allometric relationships and solid lines represent individual allometric trajectories. Competing plants diverge from the noncompeting trajectory when competition commences. In model 1, the slopes of the allometric trajectories for competing plants of different sizes are the same. In model 2, the slopes of the allometric trajectories for competing plants of different sizes are different.

forestry data on height-dbh [diameter at breast height] relationships), and it is assumed that these static relationships reflect the dynamic trajectories of individuals. The differences shown here between static inter-individual allometry and dynamic individual allometry suggest that dynamic and/or experimental data will be necessary to determine the allometric growth curves of crowded plants. On the other hand, if the size-dependent growth model presented above (Fig. 8, model 1) is valid, it may be possible to infer allometric growth curves from static data on uncrowded individuals and crowded stands. Thus, as we have argued elsewhere (Weiner and Thomas 1986, Weiner et al. 1990a, b), the basis for a mechanistic model of stand development is the behavior of uncrowded plants, which is altered in predictable ways by interference from neighbors.

FIG. 7. Height–diameter relationships for crowded and uncrowded populations of Polygonum pensylvanicum.

Our results also have implications for the study of size distributions in plant populations. Many inconsistencies in the results of different studies on plant size distributions may be due to the fact that the term "size" has been used to refer to height, diameter, and mass in different studies, without sufficient reference to the allometric relationships between these different measures. For example, forest ecologists often refer to tree diameter distributions as size distributions (e.g., Knowles and Grant 1983), some plant ecologists have referred to height distributions as size distributions (e.g., Cannell et al. 1984), whereas many researchers assume that size refers to dry mass or volume. Inferences from one size metric to another may not be valid, nor can they be deduced by simple allometric transformations if the underlying allometric relationships change over time and become nonlinear. This problem is especially serious when ecologists use height as a measure of size (e.g., Cannell et al. 1984, Pitelka et al. 1985). Data from this study and others (King 1981, Menges 1987, Weiner et al. 1990a) show that, after equal periods of growth, crowded plants are often taller, but thinner and less massive, than uncrowded plants. We conclude that "size" should not be considered a unified concept in organisms like plants, which show great plasticity in growth form. We suggest that the term "size" be restricted to measures of biomass, and that other metrics be referred to only by name (e.g., diameter, height, leaf area, etc.).

We conclude that allometric growth in plants is not a fixed characteristic of a genotype, nor are allometric patterns simply a reflection of biological constraints (although constraints will certainly set limits on the range of allometries observed in nature). Rather, observed allometric patterns in plants are the results of dynamic interactions between organisms. While allometry can affect competitive relationships, allometry is also a product of competitive interactions. Models incorporating such reciprocal interactions are necessary to further our understanding of both plant allometry and plant competition.

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