

## Competition and Allometry in *Kochia scoparia*

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Comparisons between crowded and uncrowded *Kochia scoparia* individuals demonstrate pronounced effects of competition on plant allometry as well as on the distributions of different aspects of size. Non-destructive measurements of height and stem diameter and, for a subset of the populations, the number and length of leaves and branches, were taken at three times, and the plants were harvested after the third measurement. The sequential measurements afforded the opportunity to obtain information of the effects of competition on allometric growth trajectories of individuals, as well as on static inter-individual allometric relationships.

The distributions of most size measures appeared to be normal for the uncrowded population. Crowded populations developed a negatively-skewed height distribution and a high-inequality mass distribution, whereas the diameter distributions remained normal. Plants grown without neighbours showed simple allometric relationships between height, diameter and weight. For isolated plants, the 'static' allometric relationship between plants of different sizes and the allometric growth trajectory of individuals were similar. Crowded populations showed complex allometry; the static inter-individual relationships between height, diameter and weight were curvilinear (on log-log scale). There were large differences in the allometric growth slopes of uncrowded *vs.* crowded plants. Allometric relationships between stem diameter and plant mass, and between total length of leaves and total length of branches, did not seem to be altered by competition.

The data suggest that height was the most important aspect of size influencing future growth of individuals in the crowded population. Only plants above a certain height were able to continue to grow from the second to third measurement in the crowded population. This supports the hypothesis that asymmetric competition for light is the cause of the allometric changes and of the increase in size variability due to competition.

**Key words:** Allometric growth, allometry, competition, growth, *Kochia*.

### INTRODUCTION

Interactions with neighbouring individuals alter the form, as well as the growth, survival and reproductive output of plants (Harper, 1977; Weiner, Berntson and Thomas, 1990). Though the effects of competition on growth (density-yield relationships), survivorship and, more recently, size variability have received the most study, there has been a recent emphasis on the importance of the effects of competition on growth form and *vice versa* (Ellison, 1987; Ellison and Rabinowitz, 1989; Geber, 1989; Weiner and Thomas, 1992). Plant form changes in response to competition, while simultaneously mediating competitive interactions. For example, since the above-ground growth pattern of the plant (e.g. height/biomass relationship, leaf area deployment) determines light interception, and since competition for light is 'asymmetric' [larger plants obtain a disproportionate amount of light relative to their smaller neighbours (Weiner, 1990)], height may become a primary determinant of individual success in dense plant stands. Thus, a given plant's growth potential depends upon its own size and form in relation to that of its neighbours. Since the form of plants changes with size, an allometric approach to plant growth form is necessary.

Some clarification of terminology is required because the word 'allometry' has several different meanings in the literature (Gould, 1966; Weiner and Thomas, 1992). We use the term in the general sense of Gould to mean the study of the effects of size. This usage makes no assumptions about the mathematical form of the relationship between parts or measures of organisms, except that such relationships are not simple, unchanging proportions (e.g. isometric growth). To distinguish our general usage from the 'allometric equation' [ $y = ax^b$ , where  $x$  and  $y$  are organs or size metrics and  $a$  and  $b$  are constants (Huxley, 1932)], we refer to relationships which fit the allometric equation as 'simple allometry' (Gould, 1966; Jolicoeur, 1989). For a discussion of the difference between the allometric equation and the more general concept of allometry, see Smith (1980).

For three species of annual plants, Weiner and Thomas (1992) showed that the relationships between stem diameter, height and mass of plants grown in isolation generally show simple allometry. The relationships between (1) plants of different sizes at one point in time and (2) the growth of individuals over time were indistinguishable. When plants were crowded, however, these relationships became curvilinear, and the two classes of allometric relationships [(1) and (2) above] were very different. Thus, Weiner and Thomas questioned the implicit assumption of most research on plant allometry (e.g. McMahon, 1975; White, 1981; Weller, 1987) that one can make direct inferences about

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allometric growth from static data on individuals of different sizes. Because of this, they concluded that dynamic data on the growth of individual plants over time are needed to further our understanding of the relationship between plant allometry and competition. Such data are in short supply, and the present study is an attempt to obtain some.

We address the following questions: (1) What is the effect of crowding on the distributions of plant height, stem diameter, and mass? (2) Do the general patterns of allometric change due to competition observed in the three species studied by Weiner and Thomas (1992) also occur in a species with a tree-like architecture? (3) What is the relationship between static inter-individual allometry and allometric growth for both isolated and crowded plants? (4) Are the differences between large and small plants within a crowded population simply a function of the size of the individual when the allometric shift due to competition occurs, or does competition cause large and small plants to have different allometric growth curves? (5) Which aspect of plant size is most important in determining future growth in a crowded population?

## MATERIALS AND METHODS

### Experimental

*Kochia scoparia* (L.) Schrad (Chenopodiaceae), known in commerce as *Kochia trichophylla* (Schmeiss) Schinz and Thell or 'burning-bush', is an upright annual herb which may produce up to five orders of branches, resulting in a dense, tree-like growth form when grown in isolation (Franco, 1985; Franco and Harper, 1988). Seeds of *K. scoparia* were purchased from Thompson and Morgan Co. and sown in the Luzern Livingston Greenhouse at Swarthmore College on 22 Feb. 1991. For the crowded treatment, *K. scoparia* was grown at a density of 600 plants  $m^{-2}$  in an  $85 \times 85 \times 25$  cm box filled with "Pro-Mix" potting soil. Seeds were sown in a hexagonal pattern on the soil surface through holes in a template to assure uniform inter-plant distance; two seeds were planted in each location. Uncrowded plants were grown singly in 40 7-6-1 containers. Three days after planting, approximately half of the seeds had germinated. Over the next 10 d, duplicate plants per location and stunted individuals were carefully removed. Reserve seedlings of the same age were transplanted into missing locations in the boxes and pots. Monitoring of transplanted and non-transplanted seedlings showed no difference in initial vigour or measured growth parameters. Both uncrowded and crowded treatments were fertilized with Peter's 10-10-10 (N-P-K) fertilizer after the first and second measurement periods.

In the crowded plot, 196 individuals in a central block comprising half of the planted area, and the 40 uncrowded plants, were tagged with numbers. Height ( $H$ ) from the soil surface to the plant's apex was measured with a ruler to 1 mm, and diameter ( $D$ ) at cotyledon-level was measured to 0.01 mm with digital calipers at 32 d after planting (time 1), at which point the canopy was beginning to close. These measurements were repeated on days 42 and 52 (times 2 and 3). Additionally, for a subset of the plants in each treatment, all branches and leaves on each plant were counted and

measured. To speed the process of measuring, branches were placed into 2 cm size classes and leaves measured to the nearest cm. At the first two measurement periods, leaf and shoot counts were recorded for an interior block of 49 crowded individuals. The number of plants was decreased to 30 at time 3. The leaves and shoots on 20, ten and three uncrowded plants were counted and measured at times 1, 2 and 3, respectively; the time required to count and measure the huge number of leaves and branches on uncrowded individuals made large samples impossible. By the third measurement period, many plants were beginning to flower, and all tagged individuals were harvested at cotyledon level on 24 Apr., oven-dried for 50 h at 80 °C, and weighed.

### Statistical

The  $F$  test for linearity (Neter and Wassermann, 1974) was used to test the log-transformed static inter-individual allometric relationships. In this test, the  $x$  variable is grouped into intervals, and the error sum of squares for a linear regression model is decomposed into a 'pure error' (unbiased estimate of error within intervals) and a 'lack of fit' sum of squares (deviations from the linear model), which are compared with an  $F$  test. We used 12 intervals from the minimum to the maximum log mass. When the log-transformed data were not significantly different from linear, they were fitted with linear regression. There is no general agreement about the best regression model to use in allometric analyses (Seim and Sæther, 1983), and standard linear regression is still the most widely-used method. When the correlation is high, differences between the models will be very small. When linearity was rejected, the height-diameter data were fitted with Ogawa's "generalized allometric equation" (Ogawa and Kira, 1977; Kohyama and Hara, 1990):

$$\frac{1}{H} = \frac{1}{aD^b} + \frac{1}{c},$$

where  $a$ ,  $b$  and  $c$  are parameters, using an iterative non-linear fitting program (SAS, 1989).

Differences in coefficient of variation (CV) were tested for significance with the "bootstrapping" method, using 1000 paired artificial "bootstrapped" samples in each case (Dixon *et al.*, 1987).

We analysed the allometric growth relationships by linear regression of sequential log height-log diameter data for each individual. Slopes were arc-tangent transformed because angular transformation is usually appropriate for ratios such as slopes (Sokal and Rohlf, 1981) and because arc-tangent transformed allometric slopes were normally distributed.

To look at the relationship between different aspects of size and growth in the crowded population from the second to the third measurement, we estimated the biomass of plants using a prediction equation obtained by multiple regression of log final mass on log diameter and log height for the crowded population. This equation accounted for 89% of the variation in log final mass. The use of a prediction equation for biomass obtained from plants at time 3 may introduce some bias into the estimates of the

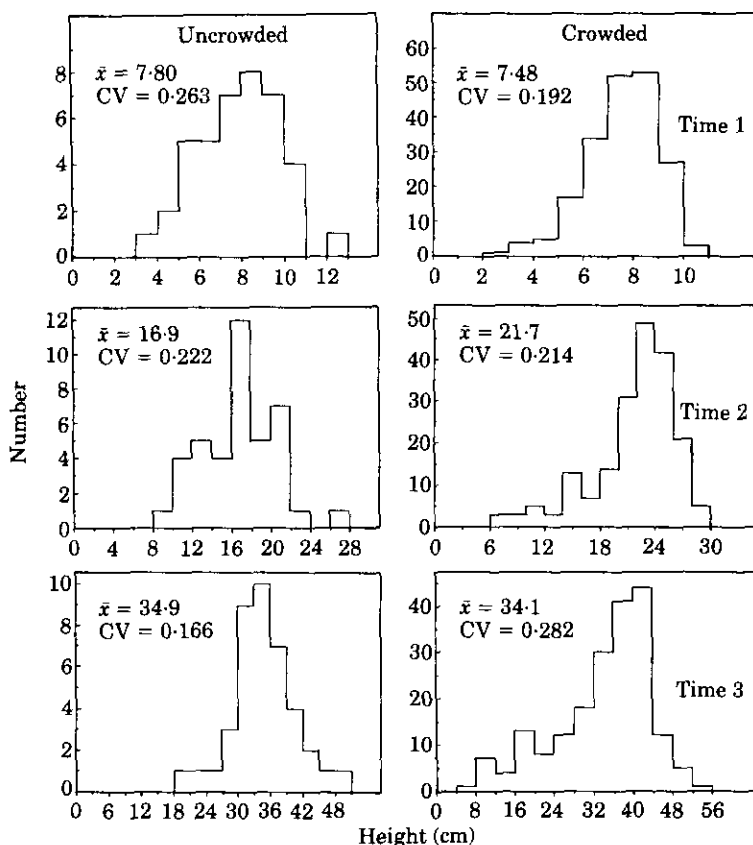


FIG. 1. Height distributions for uncrowded and crowded plants at the three measurement times.  $\bar{x}$  is the mean, CV is the coefficient of variation.

biomass at time 2, since the results here and in other studies (e.g. Weiner and Thomas, 1992; Kohyama and Hara, 1990) demonstrate that such allometric relationships change over time. This is unlikely to have a major influence on the general question these estimates are being used to address here.

## RESULTS

### Frequency distributions

The size distributions of the uncrowded and crowded populations of *K. scoparia* were statistically indistinguishable at time 1, but developed in different ways as the plants grew. At time 1, the mean heights for the uncrowded and crowded treatments (7.8 and 7.5 cm) were not significantly different (Fig. 1). The distribution of heights for the crowded population became negatively skewed at times 2 and 3, while the heights of the non-competing plants remained symmetrically distributed. The mean height for the uncrowded population was significantly less than that of the crowded individuals at time 2. Although the final mean height for the two treatments was not significantly different (34.9 and 34.1 cm), the CV of height had decreased to 0.166 for the uncrowded plants but had increased to 0.283 for the crowded plants, such that the difference was highly significant ( $P < 0.001$ ).

The frequency distributions of diameters (Fig. 2) were similar in shape for both the uncrowded and crowded plants and showed no signs of marked skewness. The mean

diameters for the crowded and uncrowded populations at time 1 were not significantly different. By time 2 there was a significant difference in mean diameter. By time 3, the mean diameter for uncrowded plants (4.7 mm) was more than twice that of the crowded plants (2.16 mm). The uncrowded plants were generally much stouter, with the smallest diameter for the uncrowded plants equaling the maximum diameter of the crowded population. Variability in diameter over time increased for the crowded plants and decreased for the uncrowded plants (Fig. 2), such that the uncrowded plants had a higher diameter CV at time 1 ( $P < 0.05$ ), there was no significant difference at time 2, and the crowded population had the higher diameter CV at time 3 ( $P < 0.01$ ).

The distribution of final mass (Fig. 3) demonstrates the great differences in individual plant size and population size structure between the uncrowded and crowded treatments. The uncrowded plants displayed a fairly symmetric distribution of masses with a mean of 4.5 g and a CV of 0.403. The masses of crowded plants yielded a highly spread (CV = 0.680) and skewed distribution with a mean of 0.3 g. The mass distribution of crowded plants was not log-normal (the log mass distribution was negatively skewed), but it was closer to log-normal than to normal.

### Static inter-individual allometry

The population of uncrowded plants demonstrates simple allometric relationships between height and diameter at

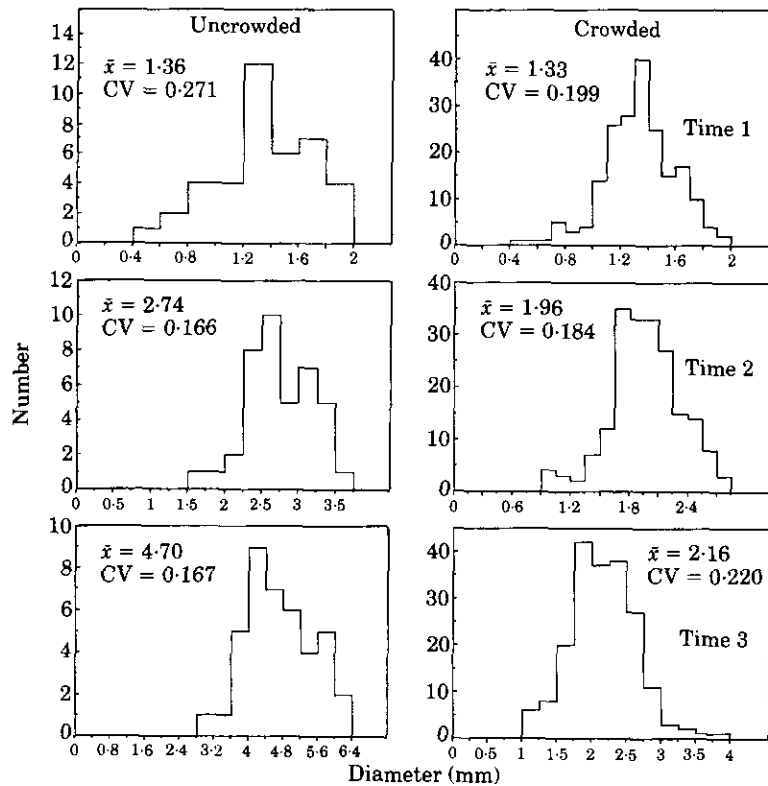


FIG. 2. Diameter distributions for uncrowded and crowded plants at the three measurement times.  $\bar{x}$  is the mean, CV is the coefficient of variation.

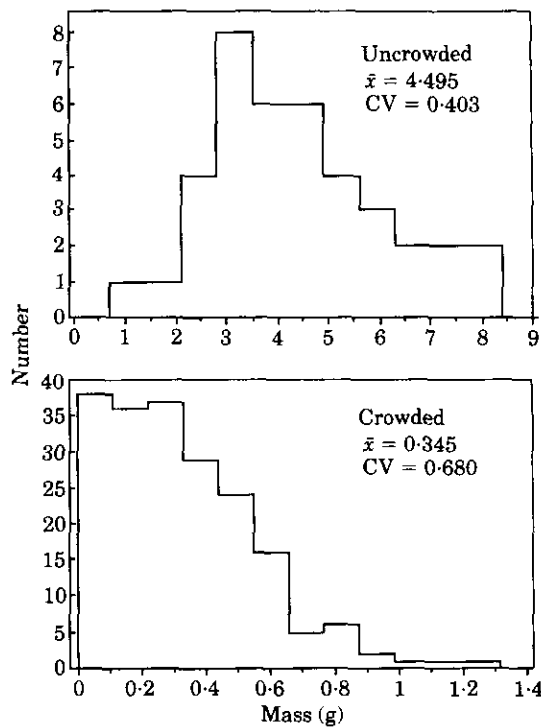


FIG. 3. Mass distributions at harvest (52 d) for the uncrowded and crowded plants.

each of the three measurement times. The log  $H$ -log  $D$  data appear linear for all three times with  $r^2$  values of 0.712, 0.655, 0.599 for times 1, 2 and 3, respectively. Ninety-five

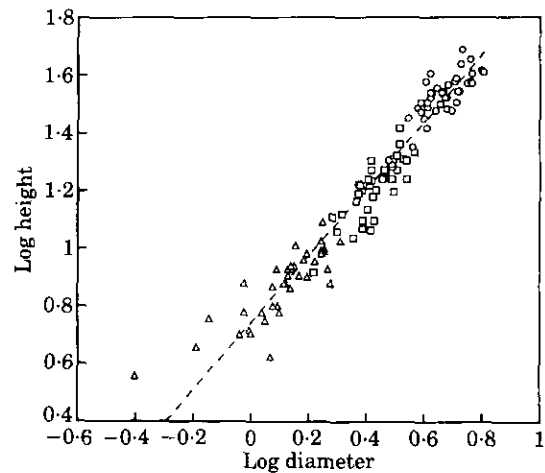


FIG. 4. Static allometric relationship between height and diameter for uncrowded plants at 32 ( $\Delta$ ), 42 ( $\square$ ), and 52 ( $\circ$ ) d after sowing. There were no significant differences in the log  $H$ -log  $D$  relationship for the three measurements, so one line is drawn through all the points;  $y = 1.13x + 0.752$ ;  $r^2 = 0.94$ .

percent confidence intervals for the three regression slopes overlap. Indeed, if all of the points are treated as a single data set, the  $r^2$  value for the resultant regression line (slope = 1.1) is 0.940 (Fig. 4).

The height-diameter relationship for the crowded population appears to change over time, becoming increasingly convex (Fig. 5). At time 1, the log  $H$ -log  $D$  relationship for the dense population does not deviate significantly from linearity. The slope of the linear regression is 0.837,

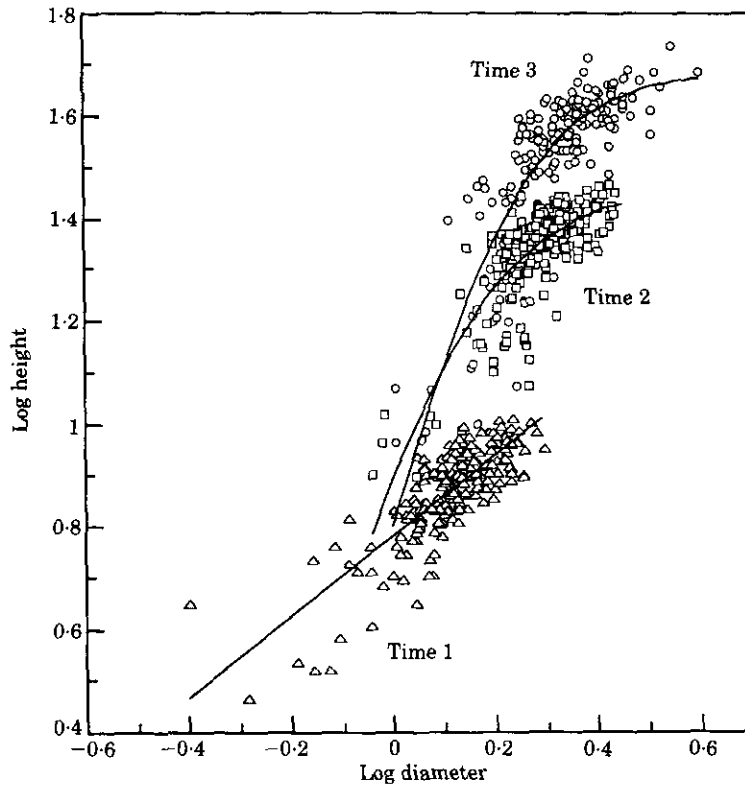


FIG. 5. Static allometric relationship between height and diameter for crowded plants at 32 ( $\Delta$ ), 42 ( $\square$ ), and 52 ( $\circ$ ) d after sowing. The relationships for the three measurement times are different, so separate lines are fitted to each measurement. When there is no significant deviation from linearity (time 1), the simple linear regression is used;  $y = 0.798x + 0.775$ ;  $r^2 = 0.67$ . When the relationship is significantly different from linear (times 2 and 3), the curve shown is that from Ogawa's equation (see text). Parameter estimates for Ogawa's equation at time 2,  $a = 10.5$ ,  $b = 3.28$ ,  $c = 29.3$ , adjusted  $r^2 = 0.74$ ; at time 3,  $a = 7.28$ ,  $b = 3.86$ ,  $c = 48.5$ , adjusted  $r^2 = 0.81$ .

comparable to the initial value for the population of isolated plants. In addition to shifting upward and increasing in initial slope (crowded plants were relatively thinner for their height) the  $\log H$ - $\log D$  relationship is significantly curvilinear ( $P < 0.001$ ) at times 2 and 3.

There is no evidence of non-linearity in relationship between  $\log$  height and  $\log$  mass for the uncrowded plants, but this relationship is convex for the crowded plants (Fig. 6;  $P < 0.01$ ). For a given height, uncrowded plants are much more massive than crowded plants. The  $\log D$ - $\log W$  allometric relationships do not appear to be different for the crowded and uncrowded plants (Fig. 6). Rather, uncrowded and crowded plants seem to occur along different regions of the same line.

There was a simple linear relationship between the total length of all branches on a plant and the total length of all leaves (Fig. 7). Competition seemed to determine where along this line plants were found, but it did not seem to alter the relationship. The relationship between total leaf length and plant diameter, however, was very much altered by crowding, although it appears to be linear in both cases (Fig. 8).

#### Dynamic individual allometry

The mean allometric growth trajectories (determined from the mean  $\log H$  and mean  $\log D$  values for each

measurement) for uncrowded and crowded plants are very different, diverging from the same initial point (Fig. 9). Allometric growth trajectories of crowded plants (estimated by linear regression of  $\log H$  on  $\log D$  for each plant) are much steeper than those of the uncrowded plants, and the difference is highly significant ( $P < 0.001$ ;  $t$ -test; Fig. 10). The mean allometric growth slope for the  $\log H$ - $\log D$  relationship for all uncrowded plants ( $n = 40$ ) is 0.82, and is not significantly different from the slope of the static inter-plant allometric relationship for the uncrowded population or for the crowded population at time 1.

There was no clear relationship between the individual  $\log H$ - $\log D$  allometric growth slope and final plant mass for the uncrowded plants (Fig. 11). Except for the very smallest plants, there is a suggestion of a decreasing  $\log H$ - $\log D$  slope with increasing final size for crowded plants (Fig. 11). The very smallest individuals showed the greatest variation in slope, and the lowest slopes were found among this group. Because of the large variation in slope among the smallest plants, we could find no statistical support for a simple relationship between size and allometric growth slope within the crowded population.

#### Growth-size relationships

Investigation of growth in estimated mass from time 2 to time 3 as a function of the different measures of size

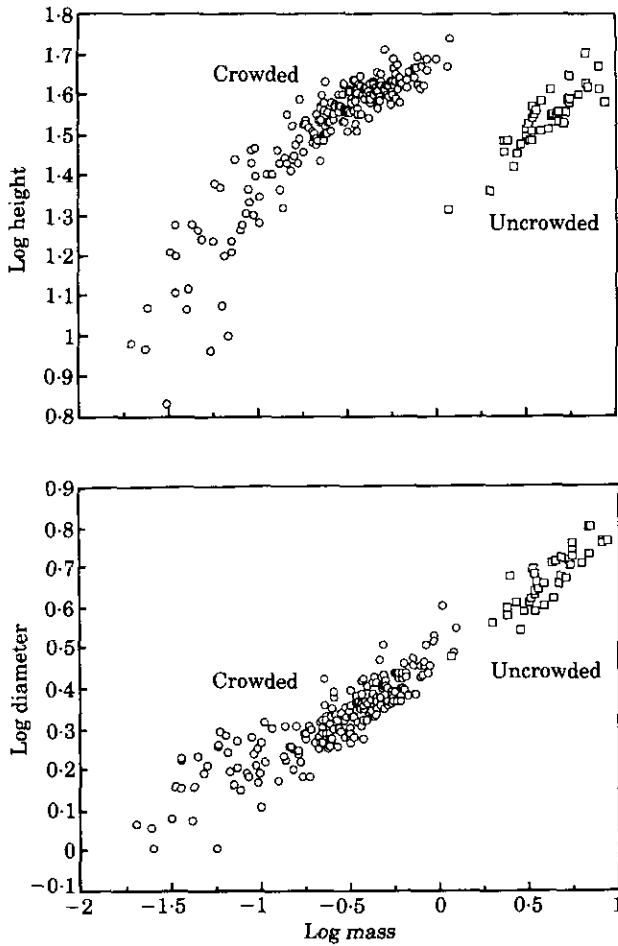


FIG. 6. Static allometric relationships between height and mass (above), and between diameter and mass (below), for the crowded and uncrowded population at harvest (time 3). Linear regression for the uncrowded plants,  $\log \text{ height} = 0.363 (\log \text{ mass}) + 1.313$ ,  $r^2 = 0.777$ ; linear regression not appropriate for the crowded plants. Linear regression of log diameter on log mass not significantly different for crowded and uncrowded plants; for both together  $\log \text{ diameter} = 0.268 (\log \text{ mass}) + 0.485$ ,  $r^2 = 0.91$ .

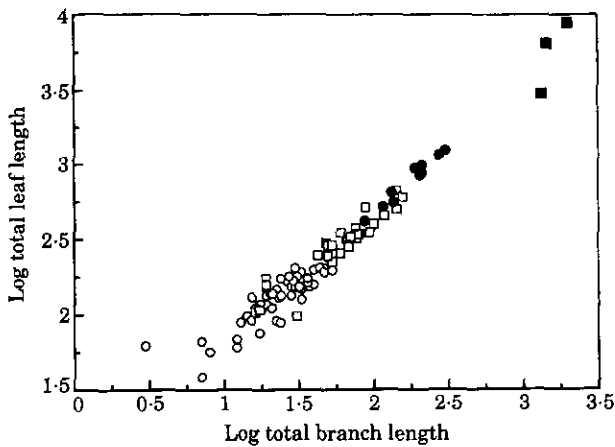


FIG. 7. Relationship between the total leaf length and total branch length for the crowded and uncrowded populations at times 2 (○, ●) and 3 (□, ■). Open symbols, crowded population; closed symbols, uncrowded population.

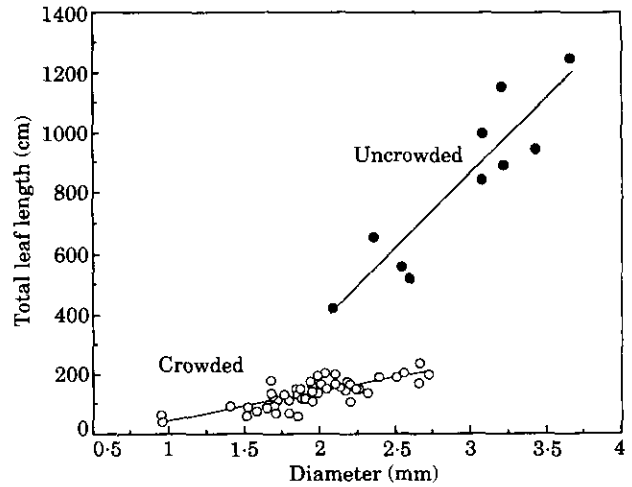


FIG. 8. Relationship between the total leaf length and diameter for the crowded and uncrowded populations at time 2.

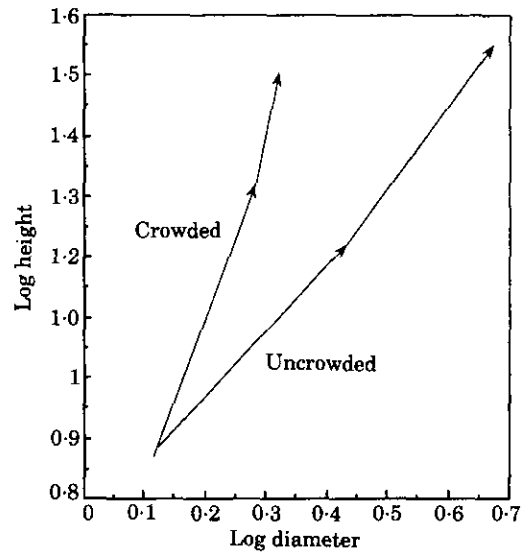


FIG. 9. Mean height-diameter allometric growth trajectories for the crowded and uncrowded populations.

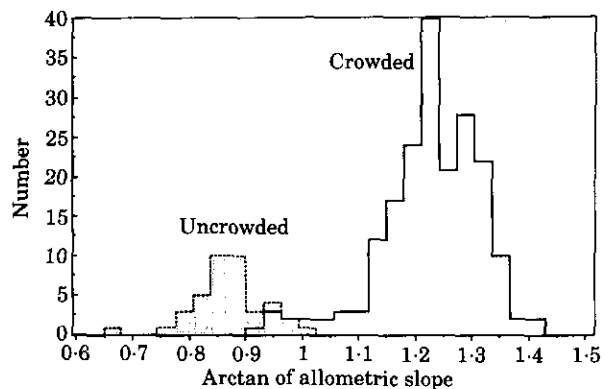


FIG. 10. Distribution of slopes for the allometric growth trajectories (expressed as the arc tangent of the regression line for the three measurements for each individual) for the crowded and uncrowded populations.

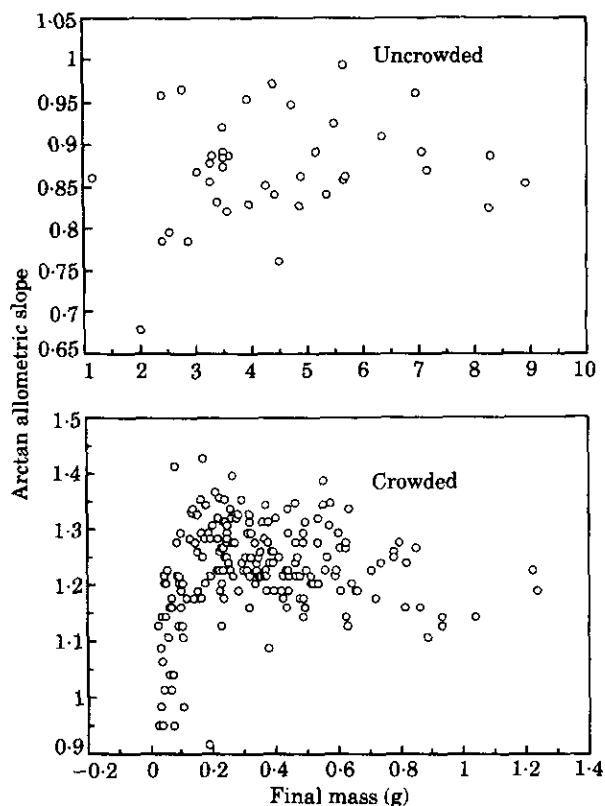


FIG. 11. Relationship between the slope for the allometric growth trajectories, (expressed as the arc tangent of the regression line for the three measurements for each individual) and final plant mass, for the crowded and uncrowded populations.

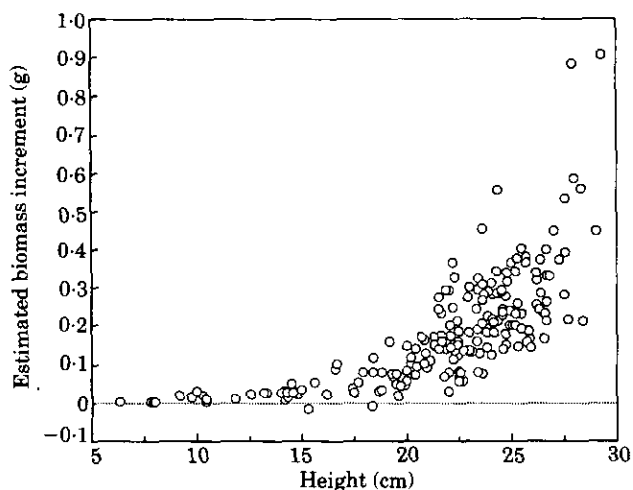


FIG. 12. Estimated biomass increment from time 2 to time 3 vs. height at time 2 for the crowded population.

(diameter, height, estimated mass) at time 2 demonstrated significant relationships between growth and all three size measures. The strongest relationship by far, however, was with height, with evidence of either a threshold height for growth over this interval or a concave relationship between the two (Fig. 12).

## DISCUSSION

The distributions for height, diameter and mass in uncrowded and crowded plants of *K. scoparia* were similar to those observed in other experimental populations. Uncrowded plants had a normal distribution of height, whereas the crowded population developed a negatively skewed distribution with a mode near the top reflecting the stand's canopy (Fig. 1). This is typical for crowded plant populations (e.g. Hara, 1984; Berntson and Weiner, 1991).

As observed in numerous studies on forest trees, (e.g. Lanner, 1985), crowded plants grew, on average, as much in height as uncrowded plants but their girth increase is sharply curtailed by competition. Mean diameter for crowded plants increased by only 10% from time 2 to time 3, whereas the increase for uncrowded plants over the same period was 74%. Crowded plants were much thinner than uncrowded plants of the same height. Diameter distributions appeared to be normal in both populations, with the crowded population having a much smaller mean. Diameter variability decreased over time in the uncrowded plants and increased over time in the crowded population, so that by the end of the experiment diameter inequality was markedly higher in the crowded population (Fig. 2), supporting the hypothesis of asymmetric competition (Weiner, 1990). The mass distribution of uncrowded plants appeared to be normal, whereas that of the crowded plants showed high skewness and inequality. The latter is characteristic of the 'size hierarchies' usually observed in crowded populations before extensive self-thinning (Harper, 1977; Weiner and Thomas, 1986).

Competition altered the allometric relationships between different measures of plant size, as well as the distributions of these measures. Uncrowded plants show 'simple allometry', i.e. linear relationships between log height, log diameter and log mass. For the uncrowded plants there was no evidence of a difference between (1) inter-individual static allometric relationships and (2) intra-individual dynamic growth. In other words, the allometric growth of isolated individuals is the same as the relationships among different-sized isolated individuals at one point in time. A small, slower-growing plant will have the same shape as a large, faster growing plant if and when it reaches the larger size. When plants are grown in isolation, the growth rules give rise to simple, allometric changes in form as plants grow. We believe that this observation provides insight into the biology of plant form, and provides a base-line for understanding changes in plant form induced by biotic and abiotic environmental factors.

Competition is such a factor, causing distinct and predictable changes in this pattern. Individuals interfering with neighbours are thinner than non-competing plants of the same height. In the crowded plot, inter-individual relationships between height and diameter are increasingly convex as plants grow and the intensity of competition increases (Fig. 5). For competing plants, inter-individual allometric relationships are very different from the trajectories of individual growth. The interactions with neighbours experienced by a relatively small plant in a crowded population puts it on a different allometric trajectory from

that of its larger neighbours, and prevents it from achieving the shape of an initially larger plant, even if it attains the same mass. Static allometric relationships between height and diameter (Fig. 5), and height and mass (Fig. 6) of crowded plants are convex, whereas the allometric growth relationship between these variables is concave (Fig. 9).

While some allometric relationships were altered by competition, others were not, and the latter may reflect constraints on plant growth form and its response to competition. For example, the relationship between height and mass was very different for uncrowded and crowded populations, suggesting great developmental plasticity with respect to the relationship between these two aspects of size. This suggests that either there has been no evolutionary pressure for *Kochia* to maintain specific height–mass relationships as it grows, or that crowding in our experimental population did not put *Kochia* individuals, even the relatively thin ones, near the limits of biomechanical stability. Unlike naturally-occurring crowded *Impatiens pallida* populations (Thomas and Weiner, 1989), there was no evidence of lodging resulting from biomechanically unsound growth form in response to crowding.

On the other hand, there was no indication that crowding caused a change in the diameter–mass relationship at harvest; crowded plants just seemed to be smaller (Fig. 6). This suggests that either a different type of biomechanical constraint (e.g. compression at the base of the plant rather than lodging due to bending) is operating, or that the growth rules for *Kochia* give rise to a specific, unalterable diameter–mass relationship, which may have little to do with biomechanical constraints.

There also appears to be a very simple linear relationship between total leaf length and total branch length on a plant (Fig. 7), and the data suggest that this relationship is not altered by competition. As a *Kochia* individual grows among neighbours, it develops fewer and shorter branches than it would without interference. But *Kochia* appears to commit a constant amount of leaf to each unit of branch it produces with or without neighbours, again suggesting that relatively simple rules govern the growth form of this plant. The relationship between total leaf length and diameter, on the other hand, was very much changed by competition, although the relationship appears to be very simple in both cases (Fig. 8). We conclude that leaf length is a simple function of the number and length of branches produced, and diameter is constrained by the plant's biomass, not its leaf area or height. This is evidence against both the operation of biomechanical constraints on the growth form plasticity in *Kochia* (Givnish, 1986), and the diameter leaf-area constraints we would expect from the 'pipe-model' of Shinozaki *et al.* (Shinozaki *et al.*, 1964; Mäkelä, 1988), which predicts a direct relationship between cross-sectional xylem area and leaf area.

These results conform to the basic model presented by Weiner and Thomas (1992). Their model predicts an increase in the slope of the  $\log H$ – $\log D$  trajectory after the onset of competition (Fig. 8 in Weiner and Thomas, 1992). However, it was not possible to distinguish between the alternative versions of the model which they proposed as possible explanations for the curvilinear static allometric relations in

crowded stands. In one version of their model, competition causes a similar shift away from the uncrowded allometric growth trajectory in all competing plants. Larger and smaller plants in a crowded population differ primarily in the size they have achieved when the allometric shift begins. In the second version of their model, there is not only a difference between allometric growth of crowded and uncrowded plants, but there is size-dependent variation in allometric slope within a crowded population. There is some evidence that the slope of allometric growth trajectory varies with size within the crowded population from time 2 to 3 (Fig. 11), but it was not possible to obtain clear statistical support for such an hypothesis. The analysis is problematic because the smallest plants in the crowded populations show highly variable behaviour (Fig. 11), perhaps because they are near the limits of their tolerance of the low resource levels created by competition, i.e. the small plants are close to the point where plasticity gives way to mortality. There was no evidence of any relationship between the allometric growth slope and final mass for the uncrowded plants (Fig. 11).

Two types of evidence support the hypothesis that the allometric shifts induced by competition are driven by asymmetric competition for light. First, the inequality in biomass was much higher when plants were competing (Fig. 3). This is evidence for asymmetric competition (Weiner and Thomas, 1986). Second, there is evidence of a size threshold for further growth in the crowded population or a concave relationship between growth and size (Fig. 12). Weiner (1990) argues that this is evidence of asymmetric competition, and this conclusion was supported by Hara (1992). When we ask which size measure shows the clearest evidence for such a threshold, we find that it is plant height. Thus, it may be more appropriate in many cases to talk about a height threshold, rather than a 'size' threshold, for further growth in this case. This suggests that the asymmetry of competition is due to shading.

The results illuminate the differences between static (inter-individual) and dynamic (individual growth) allometry. Inter-individual  $\log H$ – $\log D$  relationships among crowded plants are convex, while the individual allometric growth trajectories are linear or concave. Previous data on allometry will need to be re-examined in light of this distinction, since the two concepts have often been conflated in practice: almost all published allometric data are static, but they are used to make inferences about allometric growth. Future experimentation and modelling should focus on the patterns of individual growth which give rise to both types of relationships. Once these relationships are understood, however, it may be possible to infer trajectories of individual growth from static data on uncrowded plants and crowded stands. Further clarification of the nature of the dynamic allometry of competing plants is required, but a basic pattern may be emerging. Interference from neighbours alters the growth of crowded plants from the base-line model of uncrowded plant behaviour in ways that appear to be predictable.

Allometry, as a multidimensional way of looking at plant growth and form, can serve as an indicator of the mechanism of competition, and as a measure of the plant's response to



competition. However, plant form also determines, in part, the degree and direction of interactions with neighbouring individuals. Thus, allometric analyses may provide a much-needed link between individual plant behaviour and population-level processes. Study of the allometric growth of plants in dense stands and in non-competing individuals will increase our understanding of the effect of competition on plant growth and the influence of plant growth form on competitive interactions. Plant allometry responds with predictable plasticity to the biotic environment. The goal is now to explain these patterns in terms of the growth rules for individual plants as modified by specific mechanisms of competition.

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