Annals of Botany **65**, 513–524, 1990

Growth and Variability in Crowded and Uncrowded Populations of Dwarf Marigolds (*Tagetes patula*)

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Accepted: 15 October 1989

ABSTRACT

To study the effects of competition on growth and variability, dwarf marigolds (*Tagetes patula*) were grown in a greenhouse for 11 weeks, (1) individually in pots, and (2) at a density of 1500 individuals m^{-2} in flats. Both sequential harvests and non-destructive measurements were performed weekly. Relative growth rate decreased over time for both crowded and uncrowded populations. The growth in d. wt of crowded populations was close to linear, and the growth of uncrowded plants was intermediate between linear and exponential. The leaf area of crowded individuals reached a maximum after 6 weeks, but the leaf area of uncrowded plants continued to increase throughout the course of the experiment. Size variability increased greatly and then decreased somewhat in the crowded populations, whereas the size variability of uncrowded populations remained low over the entire period of growth. From the 3rd to the 11th week, growth increment was correlated with initial size within crowded populations, but there was no evidence of a relationship between initial size and growth increment for uncrowded individuals. Similarly, size rank at 3 weeks was highly correlated with rank at 11 weeks in crowded, but not uncrowded, populations. Our results point to the limits of relative growth rate as a descriptor of plant performance, and emphasize the need to develop models of plant competition and stand structure which are: (1) based on the behaviour of uncrowded plants, and (2) consistent with observed plant growth curves.

Key words: Competition, growth, monoculture, relative growth rate, size distributions, size variability, *Tagetes patula*.

INTRODUCTION

Plant biologists have begun to appreciate the ubiquity and implications of size variation in plant populations (Benjamin and Hardwick, 1986; Weiner, 1988), and there has been much interest in the role of competition in generating and exacerbating size differences. Researchers are just beginning to understand the relationship between competition and size variation, and there is much controversy about the role of competition in determining the size structure of plant populations (Hutchings, 1986). For example, competition may alter the form of the population's size structure, or may only alter the speed at which the population develops (Morris and Myerscough, 1984). Generally, plants grown at higher densities show greater size variation than populations grown at lower densities for a given period of growth (Weiner and Thomas, 1986). This supports the hypothesis that competition between plants is 'asymmetric' or 'one-sided', i.e. larger plants are able to usurp resources and suppress the growth of smaller individuals. Experimental evidence suggests that this asymmetry is primarily due to competition for light and that competition for soil resources may be more symmetric (Weiner, 1986).

A reductionist, mechanistic theory of competition between plants should be based on the growth of plants without competition. When plants are competing, this growth is altered through mechanisms of interference. Current mathematical models of density/yield relationships (Watkinson, 1980; Vandermeer, 1984) are a first step in this direction in that one of their parameters is the yield of uncrowded plants. This general approach can be expanded to address the next lower level of analysis: variation in the growth of individuals within the population (e.g. Benjamin, 1988). In contrast with the more common density series experiments, experiments designed to pursue the approach described above should, to the extent possible, obtain data on the growth of non-competing plants, each of which has the same resource base as whole competing populations. Even if uncrowded plants do not occur in nature

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(which may be the case for many species), the behaviour of uncrowded plants provides a genotypic and environmental base-line for the understanding of competition. The eventual goal is to predict the behaviour of competing plants from that of non-competing plants via mechanistic theories of competition.

Researchers have chosen one of two methodologies for looking at the growth of individual plants over time. Sequential harvests of similar plots, which is commonly used in growth analysis (e.g. Hunt, 1982) allow accurate measurement of plant biomass, but the growth of individual plants within a population cannot be followed over time. Demographically-oriented studies, on the other hand, employ repeated non-destructive measurements on the same population (e.g. Mohler, Marks and Sprugel, 1978; Cannell, Rothery and Ford, 1984; Schmitt, Eccleston and Ehrhardt, 1987), thus enabling researchers to follow individuals over time. However, such studies can use only limited measures of size, such as height or stem diameter, since the direct measurement of biomass is not possible. To gain a more complete picture of plant growth and stand development, we performed a series of experiments incorporating both methodologies. Harvest data were then used to develop an accurate prediction equation for plant weight from height and stem diameter measurements, thus improving the usefulness of the non-destructive measurements.

MATERIALS AND METHODS

Seeds of dwarf French marigolds [*Tagetes patula* L. var. 'yellow boy' (Asteraceae)], purchased from Geo. W. Park Seed Company, were planted in three 91 cm × 82 cm × 13·5 cm wooden flats at a density of 1500 seeds m^{-2} in the Luzerne Livingston Greenhouse at Swarthmore College on 16–20 Sep. 1986. The area in each flat was divided into four 32·8 cm × 28·4 cm sample plots. To reduce edge effects, an 8·4 cm buffer zone separated each sample plot both from its neighbouring plots and from the edge of the flat. We planted the seeds for each of the 12 plots and its buffer zone through the holes of a 50 cm × 45 cm masonite template. The coordinates of the holes in this template were randomly generated at the appropriate density, using graph paper and a random number table. The method ensured an identical random pattern of seeds for each of the plots. The sample sizes were approximately 130 plants per plot. To insure a high degree of competition for light, we used high nutrient PRO MIX RX potting soil. Uncrowded plants were grown by planting three or four seeds in each of 120 15·2-cm diameter pots. These were thinned to one plant per pot after germination, always leaving the centre-most individual.

One plot of crowded plants and ten uncrowded plants were numbered by placing a small stake with a tag in the soil to the right of each seedling. Late germinators were tagged as they appeared. These plants were the subjects of our non-destructive measurements.

Both harvest and non-destructive measurements were collected weekly, beginning 1 week after sowing. For harvest measurements we cut down, at soil level, all of the plants within a crowded plot and a set of ten individually-grown plants. Height to the apex of each plant was measured with a ruler, stem diameter above the base was measured with digital calipers, and leaf area was determined with a LI-COR Area Meter. Plants were then dried at 70 °C in a drying oven for 1 week and weighed. Data for the non-destructive measurements consisted of: (1) height (to apex), measured with a ruler, and (2) stem diameter, measured for the first 3 weeks with digital calipers, and with a ruler for the remainder of the experiment. During the first half of the study, the plants were small and uncrowded enough so that damage from measuring was minimal. However, after week 6 it became impossible to make the measurements without disturbing the plants. To keep this damage to a minimum, non-destructive data were not collected for weeks 8 and 10.

The leaf area index (LAI) for the crowded plots was calculated by dividing the total leaf area of all the harvested plants by the area of each plot (934·36 cm^2). Although some of the leaves of the harvested plants undoubtedly extended over the boundaries of the plot, we assumed that this was compensated for by an equal leaf area from plants in the buffer zone extending into the plots. Since the individually-grown plants were not contained within an area but covered more ground area as they grew, only leaf area per plant, not LAI, could be accurately determined for the uncrowded plants.

We measured the variability of the sequentially-harvested populations with the Gini coefficient (Weiner and Solbrig, 1984). The Gini coefficient is highly correlated with the coefficient of variation (Weiner, 1988); the correlation between the Gini coefficient and the coefficient of variation for the weight distributions presented below was 0·998. Mean relative growth rates of the sequentially-harvested populations were calculated according to Hunt (1982).

To observe the size-dependency of growth we looked at the relationship between size increment (absolute growth rate, AGR) and size in the repeatedly-measured populations. Changes in the distribution over time can be explained, therefore, by the differences in absolute growth of different sized plants within the population. Equations fit to AGR-size relationships have been called 'distribution-modifying functions' by Westoby (1982), and $G(t, x)$ functions by Hara (1984*a*, *b*).

Dry weight for the repeatedly-measured populations was estimated from an allometric regression equation fit to all the harvested individuals from crowded plots over the course of the study. Log weight was regressed on log height and log diameter. The least-squares fit of this equation accounted for 80·5 % of the variance in log weight. Weight (w) for sequentially measured plants was estimated from height (h) and diameter (d) using an exponential version of this regression equation ($w = 0{\cdot}00198h^{0{\cdot}8103}d^{2{\cdot}87}$) with a bias-correction factor ($CF = 1{\cdot}137$; see Sprugel, 1983). Since allometric relations are different for crowded and uncrowded plants (Weiner and Thomas, unpubl. res.), a separate regression equation fit to all the harvested uncrowded data ($w = 0{\cdot}00185h^{2{\cdot}12}d^{1{\cdot}35}$; $CF = 1{\cdot}078$) was used to estimate the weight of repeatedly-measured uncrowded plants. The regression of log weight on log height and log diameter accounted for 97·5 % of the variance in log weight of uncrowded plants.

RESULTS

Mean plant growth

Mean weight of both crowded and individually-grown plants increased over time. Mean weight of crowded and uncrowded plants was not significantly different for the first 2 weeks, but differed significantly starting in week 3 (t-test; $P < 0{\cdot}02$), and highly significantly thereafter ($P < 0{\cdot}001$). At the end of the experiment, the mean weight of uncrowded plants was 5·826 g, whereas the mean weight of crowded plants was 0·253 g: a 23-fold difference in mean size. The relative growth rate of both crowded and uncrowded populations decreased over time, but it decreased more rapidly in crowded populations (Fig. 1). Both the relationship between time and mean d. wt and the relationship between time and log mean d. wt were significantly curvilinear for uncrowded plants (Fig. 2; $P < 0{\cdot}001$ for second-order polynomial term in multiple regression). Thus, the growth in weight of uncrowded plants can be described as being intermediate between linear and exponential, but closer to exponential (Fig. 2). The mean weight of crowded individuals, on the other hand, increased in an almost linear fashion (r^2 of 98·4 % for a linear regression of mean weight on time, second order polynomial term n.s.; Fig. 3). The low growth on certain weeks was associated with

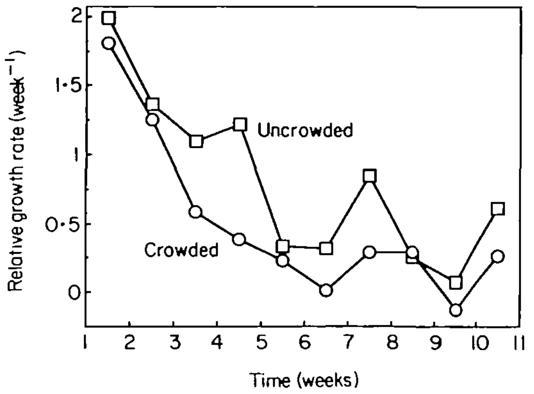

FIG. 1. Change in mean relative growth rate over time for sequential harvests of crowded and uncrowded populations of *Tagetes patula*.

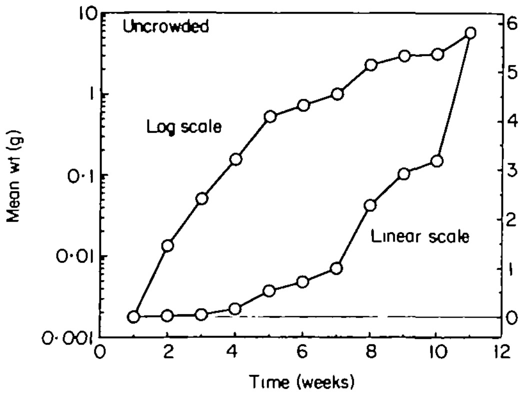

FIG. 2. Change in mean d. wt over time for sequential harvests of individually-grown *Tagetes patula*. The same data are shown on a log and a linear scale.

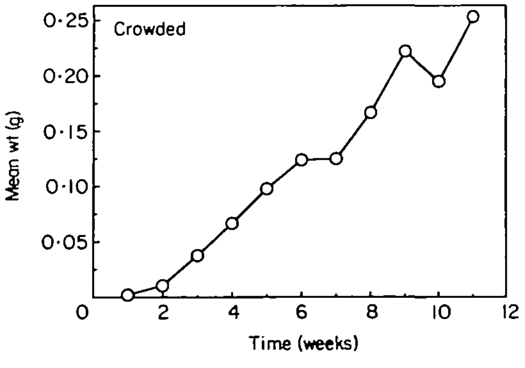

FIG. 3. Change in mean d. wt over time for sequential harvests of crowded populations of *Tagetes patula*.

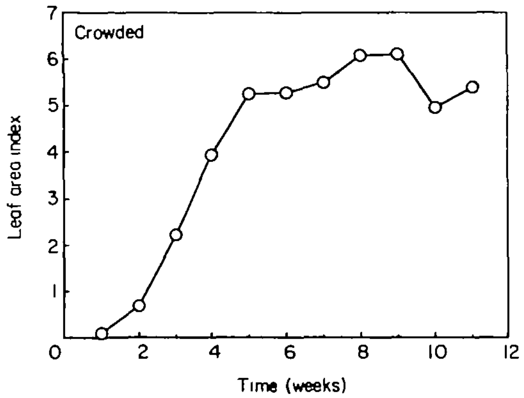

FIG. 4. Change in leaf area index over time for sequential harvests of crowded populations of *Tagetes patula*.

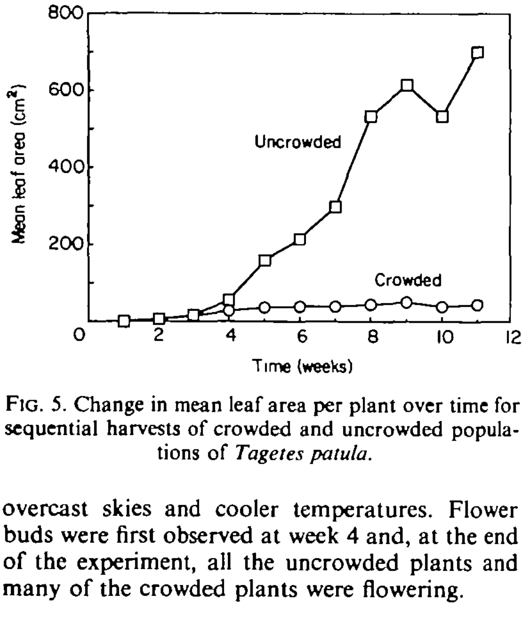

FIG. 5. Change in mean leaf area per plant over time for sequential harvests of crowded and uncrowded populations of *Tagetes patula*.

overcast skies and cooler temperatures. Flower buds were first observed at week 4 and, at the end of the experiment, all the uncrowded plants and many of the crowded plants were flowering.

Leaf area

The leaf area index (LAI) for crowded stands increased steadily over time until week 5 at which point it leveled off at approximately 5·5 (Fig. 4). Mean leaf area of crowded plants leveled off at approximately 45 cm² per plant, while the mean leaf area of uncrowded plants continued to rise (Fig. 5).

Size distributions and variability

Dry weight distributions for crowded populations (Fig. 6) appeared normal at the beginning of the experiment, and then became more positively skewed and variable until week 6, after which both variability and skewness decreased somewhat. Dry weight distributions for uncrowded populations (Fig. 7) showed low variability throughout the course of the experiment and showed no tendency to change over time (Fig. 8). Height distributions for crowded populations (Fig. 9) also appeared normal at the beginning, and became somewhat more variable and negatively skewed. Height distributions for uncrowded populations showed very low variability which decreased significantly over time ($P = 0{\cdot}01$), with no tendency towards negative skewness (Fig. 10).

Non-destructive measurements

Growth and size distributions for estimated d. wt of the repeatedly-measured populations were generally similar to the growth in actual weight and size distributions of sequentially harvested populations. There were some differences between crowded harvested populations and the repeatedly-measured population (e.g. repeatedly-measured plants were slightly smaller than harvested plants at the end of the experiment). These differences were apparently due to damage which occurred during the non-destructive measurements of crowded plants.

The relationship between growth increment from week 3 to week 11 and size at week 3 shows that growth was size-dependent for the crowded population (Fig. 11). Small plants grew little while larger plants had larger absolute growth rates. Mortality was limited to the small and average-sized individuals. Mean size of plants that died was significantly smaller than those that survived (t-test, $P < 0{\cdot}01$). There was no evidence of size-dependent growth rate for uncrowded plants over the same period ($r = 0{\cdot}03$ for correlation between size at week 3 and growth increment from week 3 to week 11).

Size rank in the third week was highly correlated with rank at the end of the experiment for crowded populations ($P < 0.001$), but there was a small non-significant negative correlation between size rank over the same period for individually-grown plants. Growth curves for the ten smallest, ten largest and ten median sized plants (Fig. 12) in the crowded population show that growth during the later portion of the experiment was concentrated among the larger plants.

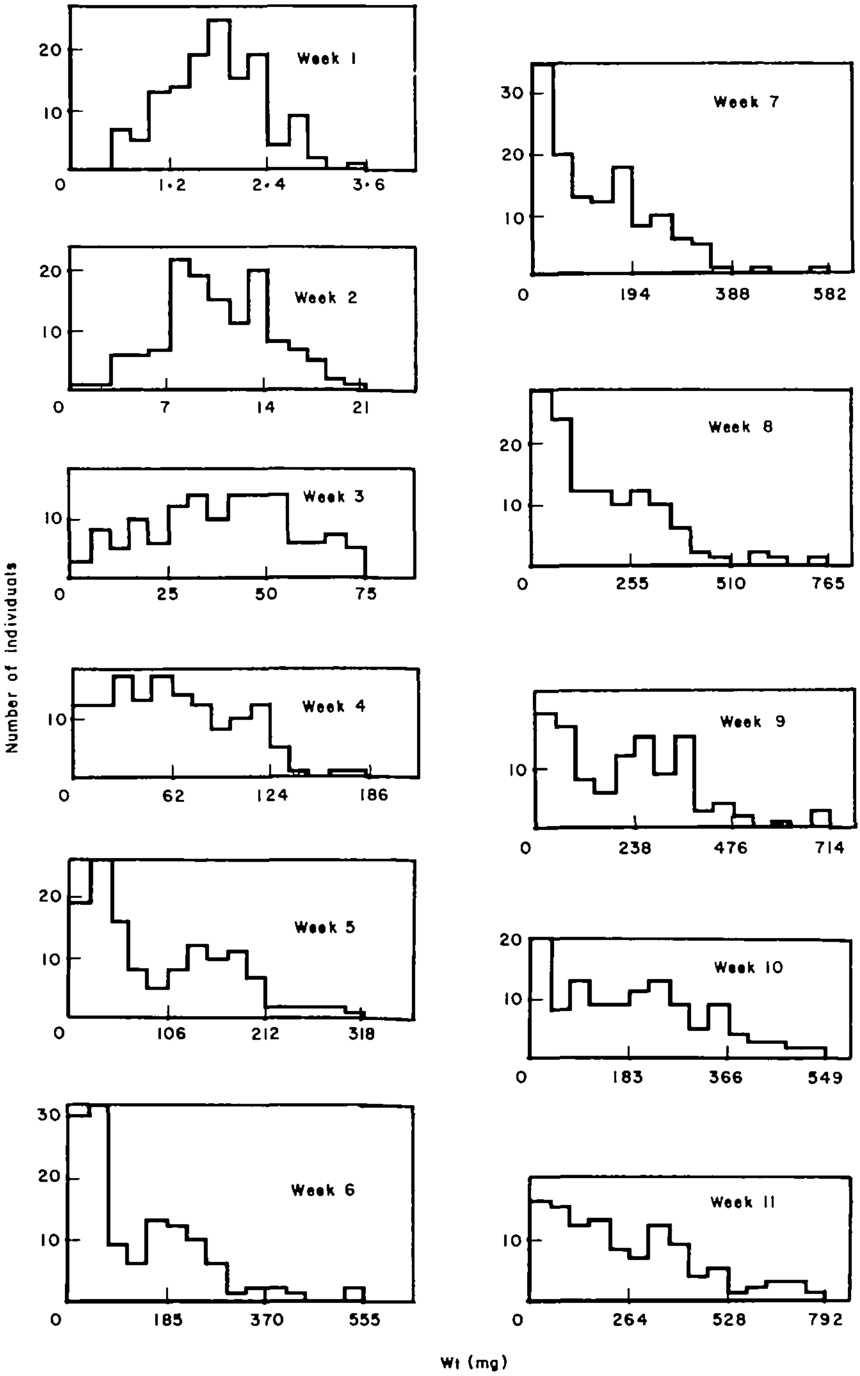

FIG. 6. Dry weight distributions for sequential harvests of crowded populations of *Tagetes patula*.

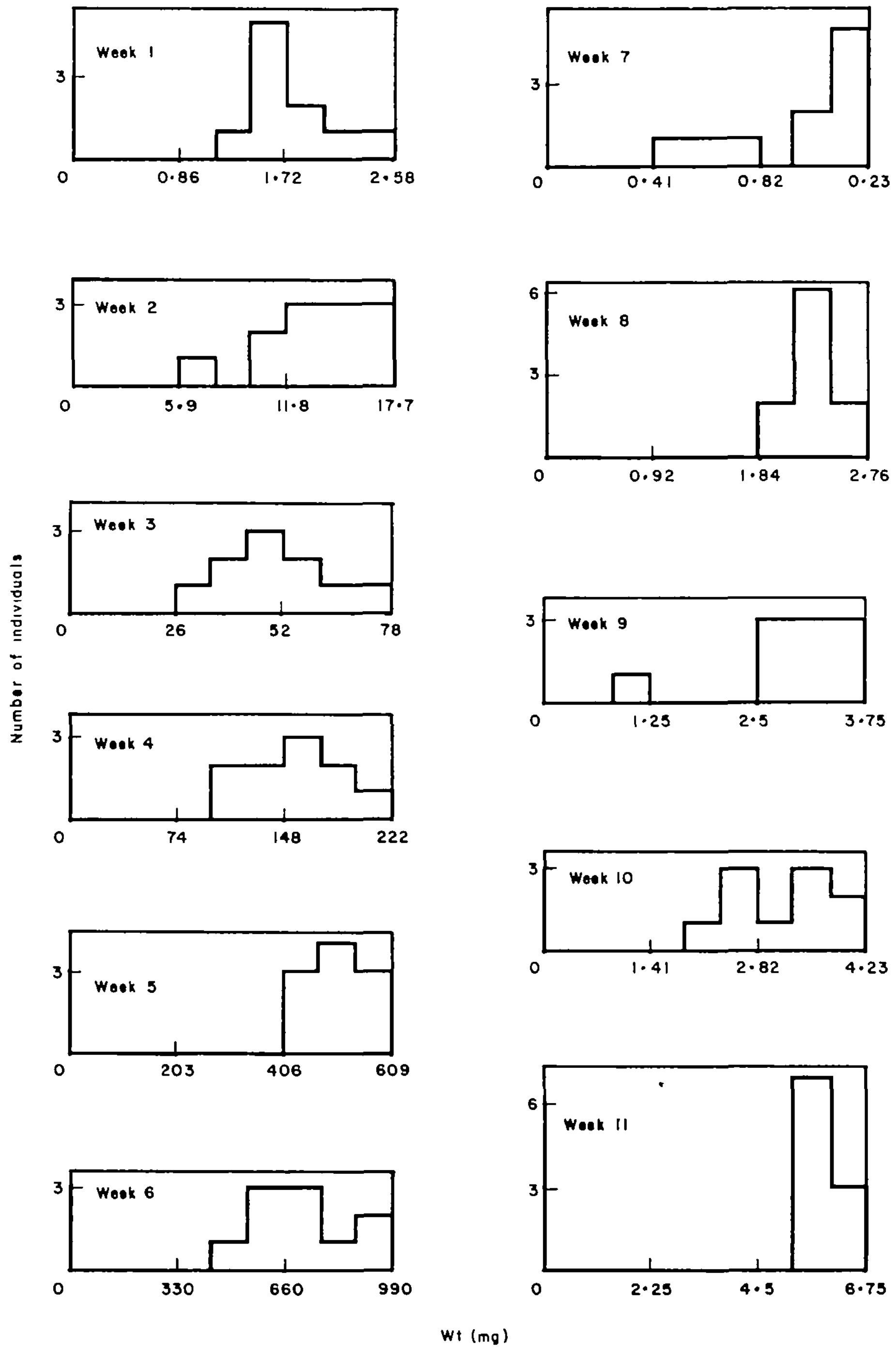

FIG. 7. Dry weight distributions for sequential harvests of uncrowded populations of *Tagetes patula*.

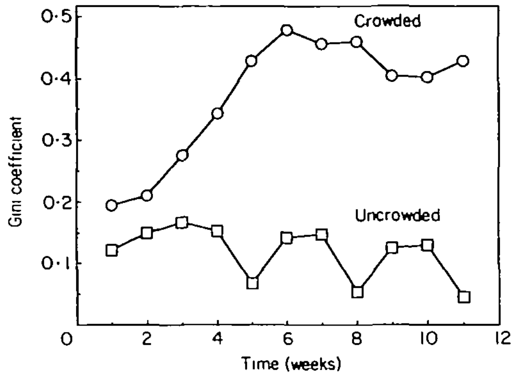

FIG. 8. Change in the Gini coefficient of d wt. over time for sequential harvests of crowded and uncrowded populations of *Tagetes patula*.

DISCUSSION

Plant growth curves

Growth of *T. patula* was not exponential; relative growth rate decreased for individually-grown, as well as crowded plants. While the slope of the weight growth curve of individually-grown plants increases over time, the slope for log-weight decreases over time, and relatively constant RGR is maintained for only short intervals (Fig. 2). Even though this 11-week-experiment did not span the full growth curve for these plants, the continual decrease in RGR for both crowded and uncrowded plants is evidence that growth in these plants is sigmoidal, as is generally the case in growth-analysis studies (Hunt, 1982). This raises questions about the usefulness of the numerous models of competition and stand structure (e.g. Koyama and Kira, 1956, Turner and Rabinowitz, 1983; Huston, 1986; Huston and DeAngelis, 1987) which are based on the assumption that the growth of plants (even when they are competing) is exponential. While the literature of plant growth analysis (Evans, 1972; Causton and Venus, 1981; Hunt, 1982) has established the generality of asymptotic growth curves for plants, plant population biologists have been slow to incorporate this generality into their models of stand structure (notable exceptions include Aikman and Watkinson, 1980; Bonan, 1988; Benjamin, 1988). While differences in RGR can be very useful in comparing the growth of individuals of the same size or over the same period of time (e.g. Cannell *et al.*, 1984), models of population size structure based on the assumption of constant RGR over the time are incompatible with the fundamentals of plant growth and competition, e.g. density-yield relationships. This conclusion brings into question the biological basis for the widespread emphasis plant biologists have put on RGR as a generally-applicable measure of plant growth. RGR loses much of its biological meaning if growth is not exponential. For example, the custom of estimating mean instantaneous relative growth rates in growth analysis studies may not be justified if the growth during the interval is not exponential. The tendency to assume that plants maintain a constant RGR is a result of confusion over the two different meanings of RGR: (1) a descriptor of growth, and (2) a parameter in an exponential growth model (Weiner and Thomas, 1986). These two meanings correspond to considering the equation for RGR to be two very different things: (1) a mathematical 'identity' and (2) a 'conditional' hypothesis (Warren Wilson, Hunt and Hand, 1986).

There are several reasons why the growth of isolated plants will show decreasing RGR over time. (1) As plants grow, there is a reduction in resources available per unit of plant tissue. If resources become available at a constant rate, the amount of resources available per unit of plant tissue will decrease as plants grow. Just as there is a carrying capacity for a population of animals in a given environment, there is a carrying capacity for an individual plant, which can be viewed as a population of modules (Harper, 1981). While plants are able to intercept more resources as their leaves and roots grow, their ability to expand the resource base is limited (except in cases of unrestrained clonal spread). A plant is unable to expand its resource base in proportion to the increasing amount of plant tissue because some costs increase disproportionately as it gets larger. For example, biomechanical constraints may limit the size that upright plants can achieve without investing increasing amounts of energy in structural tissue. In addition to biomechanical costs, the biomass of respiring tissue and the cost of transporting photosynthate eventually increase more than the amount of photosynthesizing tissue. (2) As plants mature they begin to allocate resources to reproduction, producing flowers and fruits at the expense of leaves, stems and roots. Reproductive organs represent investments in future generations, rather than in continued growth of the individual. Thus, the relative growth rate of a plant would be expected to decrease when reproduction begins. Finally, (3) seasonal changes in temperature and solar radiation (such as shortening day length during these experiments) may contribute to the reduction in relative growth rate.

The growth in mean size of crowded plants in these experiments was close to linear. Near-linear

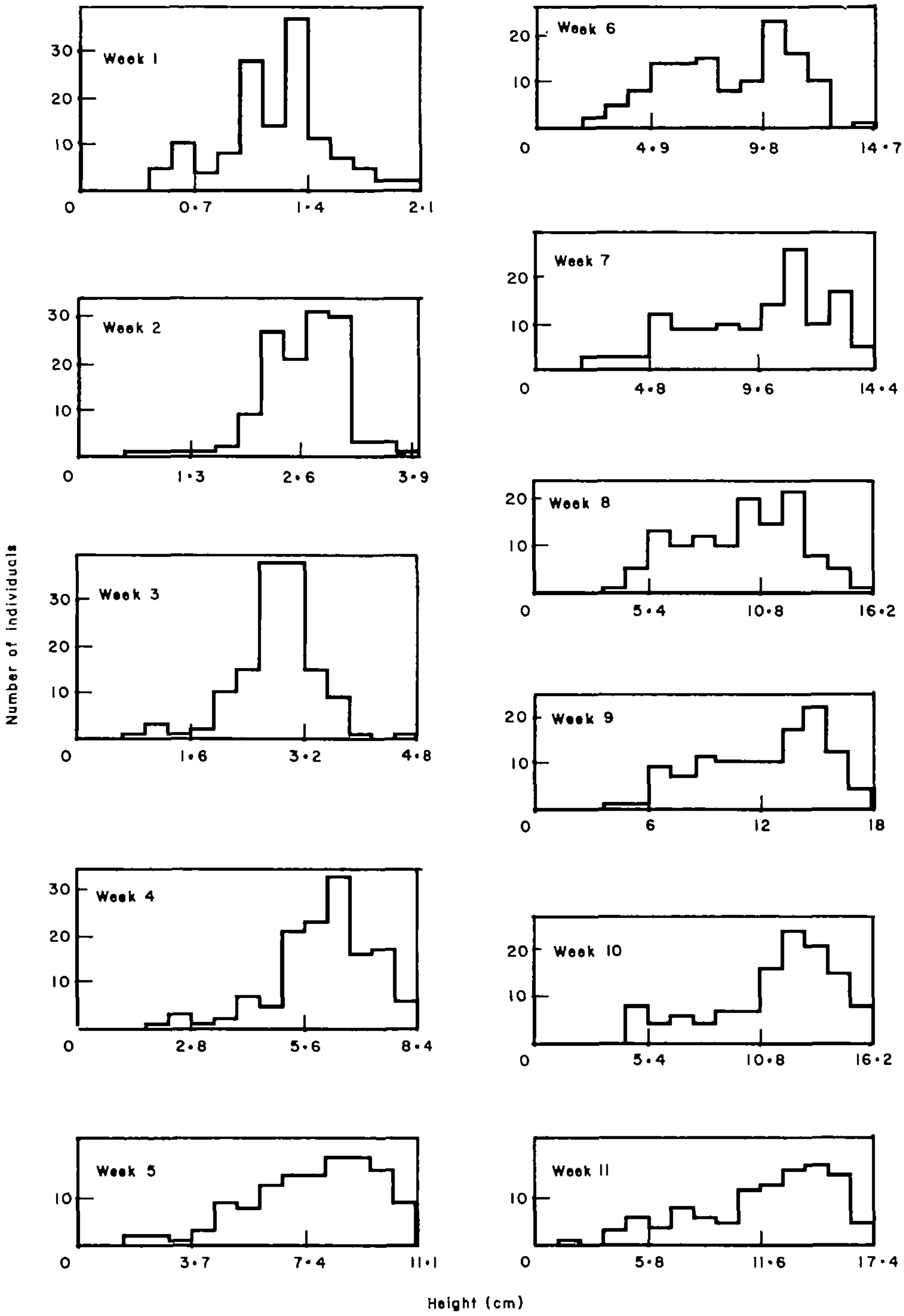

FIG. 9. Height distributions for sequential harvests of crowded populations of *Tagetes patula*.

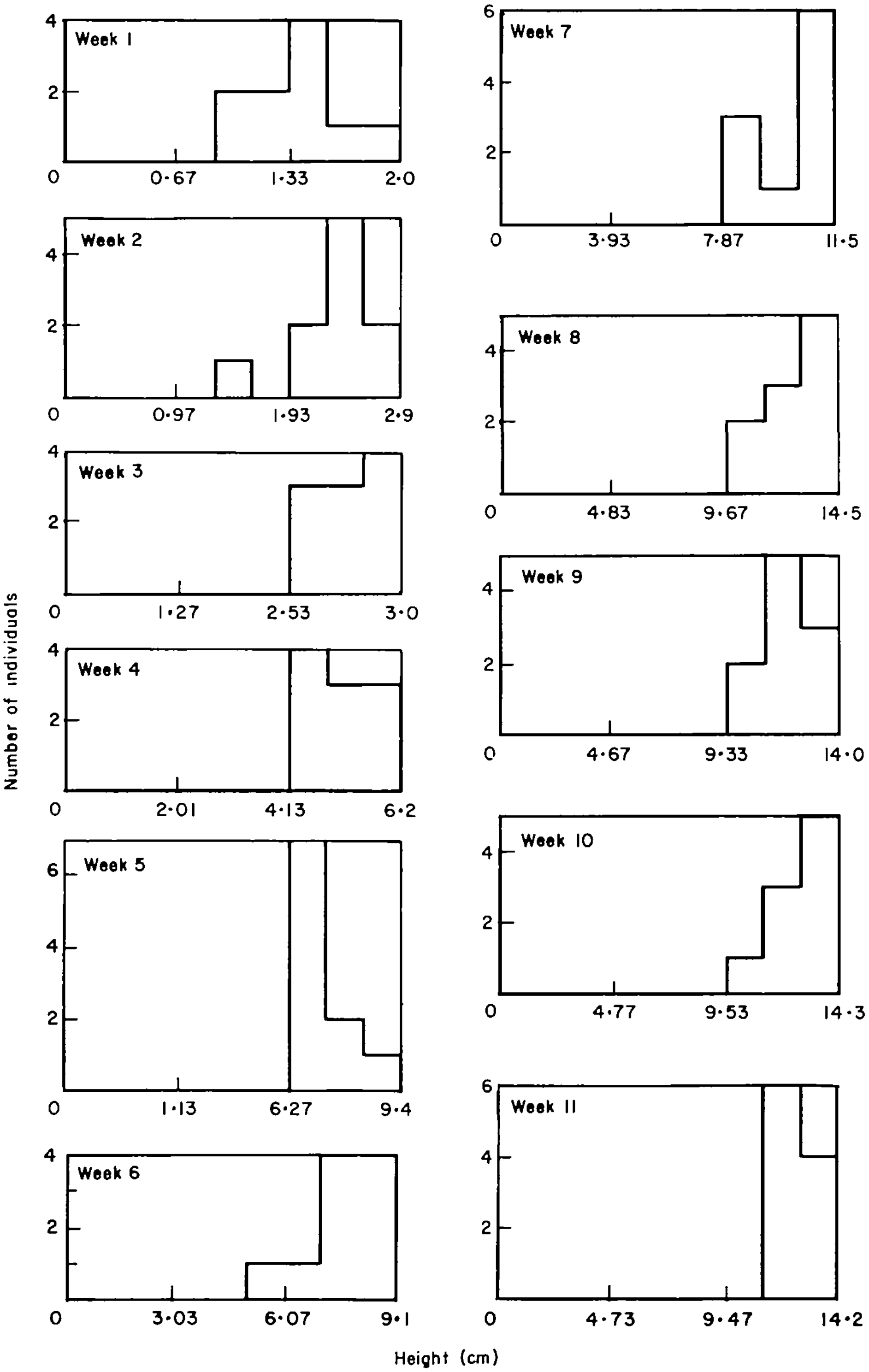

FIG. 10. Height distributions for sequential harvests of uncrowded populations of *Tagetes patula*.

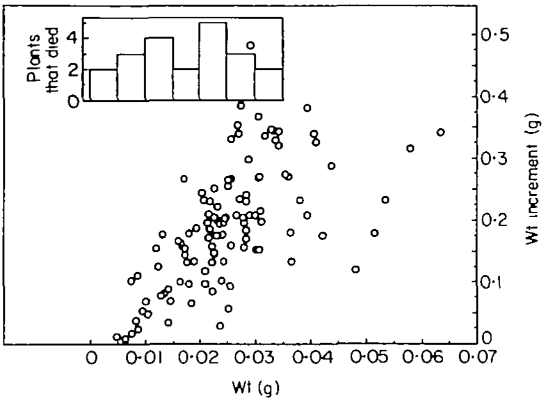

FIG. 11. Relationship between estimated d. wt at week 3 and estimated d. wt increment from week 3 to week 11 for repeatedly-measured crowded individuals of *Tagetes patula*, and the distribution of estimated d. wt. at week 3 of plants which died before week 11.

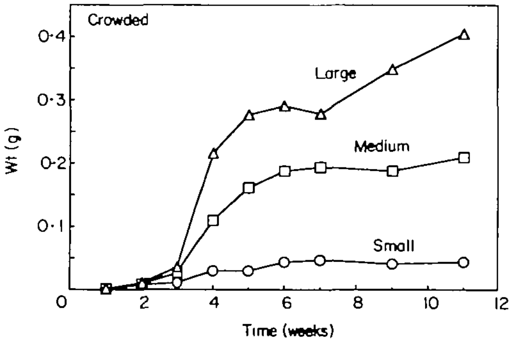

FIG 12. Growth in mean estimated d. wt of the ten largest, the ten median-sized, and the ten smallest individuals in repeatedly-measured crowded population of *Tagetes patula*.

growth of a stand of plants has been observed in other studies (e.g. Ellison, 1987; Thomas and Weiner, 1989), and can be understood in terms of resource availability and utilization. For example, solar energy falls within a plot at a relatively constant rate. Once the leaf area of the plant population is such that essentially all the light is being intercepted, the gross primary production of the population cannot increase further. A constant rate of energy input would be expected to produce a constant rate of biomass increase (i.e. linear growth in the population's biomass) until some cost (e.g. biomechanical support or respiration) increases disproportionately. Put another way, a sigmoidal curve consists of a period of increasing AGR over time, a period of relatively constant AGR (linear growth), and a period of declining AGR. For a crowded population the linear phase may be relatively long.

As in other studies (Mohler *et al.*, 1978; Hutchings and Budd, 1981) LAI for crowded populations levels off (Fig. 4), although biomass continues to increase (Fig. 3). Presumably, heavily shaded lower leaves which are below the compensation point are dying. Unlike a crowded stand, individually-grown plants are able to continually increase their energy resource base and, therefore, continually increase the leaf area that can be maintained, as long as they are increasing in size (Fig. 5), although they are not able to increase their resource base in proportion to their size.

Size variability

One surprising result is that there was no increase in size variability over time for uncrowded plants. Variability in height actually showed a significant decrease over time. Exponential models (e.g. Koyama and Kira, 1956; Turner and Rabinowitz, 1983; Huston, 1986; Huston and DeAngelis, 1986) predict ever-increasing size variation for uncrowded plants if there is any variation in growth rates. Sigmoidal models of plant growth in which there is variation in growth rates predict increasing size variability for an even-aged population during the early phase of plant growth when absolute growth rates are increasing over time, and decreasing variability in size during the later stages when absolute growth rates are decreasing. Thus, our results are consistent with current models only if the models have zero variation in growth parameters. This emphasizes that it is not the particular form of the growth curve, but differences in the growth curves of plants, which generate size differences in even-aged populations. If growth curves of different individuals are very similar, then size variation will be low. Our results suggest that variation in growth curves of individual plants is lowest when plants are not interacting. The fact that size variability never increased for individually-grown populations in these experiments is probably due, in part, to the high degree of genetic uniformity in this commercial variety and the relatively homogeneous environmental conditions in this greenhouse study.

Size variability increased and then decreased somewhat in crowded populations (Fig. 7). The increase is the result of 'asymmetric' or 'one-sided' competition (Cannell *et al.*, 1984; Weiner and Thomas, 1986), in which larger individuals are able to obtain resources disproportionate to their size and suppress the growth of smaller plants. This can be seen in the AGR-size relationship for crowded plants (Fig. 11), and the growth curves for groups of similar-sized plants (Fig. 12), which show that smaller plants grow much less than larger plants. Because of asymmetric competition, size rank tends to be conserved when plants are crowded. Evidence is accumulating (Weiner, 1986, 1988) that shading is the primary mechanism for the asymmetry of competition, and our data are consistent with this hypothesis. On the other hand, if competition were totally one-sided (e.g. Ford and Diggle, 1981), the largest plants in a crowded stand would be the same size as uncrowded plants. But at the end of these experiments the largest individual in the crowded population was only 13·4% of the size of the average uncrowded plant. The relationships between the size of the largest individuals in a crowded stand and the size of uncrowded plants may be a useful index of competitive asymmetry. It has been suggested (Weiner, 1986; Wilson, 1988) that competition for below-ground resources may be more symmetric than competition for light. There was clear evidence of nutrient competition in the crowded populations: by the end of the experiment crowded populations showed symptoms of nitrogen and phosphorus deficiencies.

While size variation increased in crowded populations over the first 6 weeks of the experiment, there was a notable decrease in size variation in the crowded populations during the latter half of the experiment. It has been shown (Weiner and Thomas, 1986; Weiner and Whigham, 1988) that, in crowded monocultures, size variability increases until the onset of self-thinning (density-dependent mortality) and decreases as mortality, which is concentrated among the smaller individuals, continues. Although mortality was very limited in these populations (0–16%), the decrease in variability in the crowded population does coincide with the onset of mortality.

While the size distributions for crowded populations in this study appear to be similar to those from Ford's (1975) experiments on *T. patula*, we do not find convincing evidence for bimodality in either Ford's or our data. There is some suggestion of bimodality in the weight distributions for weeks 5 and 6 (Fig. 6), and in some of the height distributions after week 5 (Fig. 9). It was not possible to reject the null hypothesis of unimodality for any of the distributions using the 'dip' test (Hartigan and Hartigan, 1985), but it should be noted that this test, the only relevant test available, is weak (high probability of type II error) and, therefore, very large sample sizes are needed. The evidence for the hypothesis that competition results in size bimodality in plant populations (Ford, 1975; Gates, 1978) is disputable at this point. More data and improved statistical methods are needed if its existence and generality are to be established.

Height distributions (Figs 9 and 10) showed very different trends than weight distributions. While competition did increase variability in height as well as weight, height distributions for crowded populations were always less variable than weight distributions. Height distributions for crowded populations were negatively skewed, and this seems to be a general feature of crowded, even-aged monocultures (Cannell *et al.*, 1984; Hara, 1984*b*). The differences between height and weight distributions in crowded populations are complicated by the fact that competition between plants induces complex allometric relationships between plant parts (Weiner and Thomas, unpubl. res.). Researchers should be very cautious in making inferences from one size metric to another.

Size-dependent growth

Because of competition, growth of crowded populations was size-dependent, with larger individuals having higher absolute growth rates (Fig. 11). For uncrowded plants, there appears to be no correlation between size at time t and the amount of growth from time $t \rightarrow t+x$ (Geber, 1989). Plants that were larger than others at 3 weeks did not tend to be larger 8 weeks later. The data suggest that there is no inherent relationship between size and future growth when plants are not competing. Since plant growth is sigmoidal, there is a period of increasing growth rate, a linear growth phase, and a period of declining growth rate. Not only do the relative lengths of these three phases vary with species and environmental conditions but, within a population, different aspects of the growth curve, e.g. initial RGR, maximum size, position of the inflection point [which can be estimated by parameters of growth curve equations such as the Richards equation (Causton and Venus, 1981)] may vary between individuals. There is no *a priori* reason why we should expect these parameters to be positively correlated. (They may even be negatively correlated if there are tradeoffs, e.g. between high initial RGR and maximum size which can be achieved.) Individuals which initially grow most quickly may not have the greatest maximum size when growth levels off. Thus, size rankings are not retained over long periods of growth when plants are not competing.

ACKNOWLEDGEMENTS

We thank K. McBroom for assistance with the data analyses, J. Boccio for providing computer equipment, and S. C. Thomas, H. deKroon, G. M. Berntson, J. Wormser and an anonymous reviewer for helpful comments on the manuscript. This research was supported by National Science Foundation grant BSR-8604710 and Swarthmore College Faculty Research Funds.

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