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MODELING THE GROWTH OF INDIVIDUALS IN PLANT POPULATIONS: LOCAL DENSITY VARIATION IN A STRAND POPULATION OF *XANTHIUM STRUMARIUM* (ASTERACEAE)[1]

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We studied the growth of individual *Xanthium strumarium* plants growing at four naturally occurring local densities on a beach in Maine: (1) isolated plants, (2) pairs of plants ≤1 cm apart, (3) four plants within 4 cm of each other, and (4) discrete dense clumps of 10–39 plants. A combination of nondestructive measurements every 2 wk and parallel calibration harvests provided very good estimates of the growth in aboveground biomass of over 400 individual plants over 8 wk and afforded the opportunity to fit explicit growth models to 293 of them. There was large individual variation in growth and resultant size within the population and within all densities. Local crowding played a role in determining plant size within the population: there were significant differences in final size between all densities except pairs and quadruples, which were almost identical. Overall, plants growing at higher densities were more variable in growth and final size than plants growing at lower densities, but this was due to increased variation among groups (greater variation in local density and/or greater environmental heterogeneity), not to increased variation within groups. Thus, there was no evidence of size asymmetric competition in this population. The growth of most plants was close to exponential over the study period, but half the plants were slightly better fit by a sigmoidal (logistic) model. The proportion of plants better fit by the logistic model increased with density and with initial plant size. The use of explicit growth models over several growth intervals to describe stand development can provide more biological content and more statistical power than ‘‘growth-size’’ methods that analyze growth intervals separately.

Key words: annual plants; Asteraceae; beach community; growth curves; plant competition; size inequality; *Xanthium strumarium.*

In plants and other sessile organisms with indeterminate growth, the basic demographic processes, birth and death, are very closely linked with the process of growth. For example, the mortality rate is often highest during periods of rapid growth through the process of self-thinning (Harper, 1977) in which it is the smallest plants that tend to die (Watkinson, Lonsdale, and Firbank, 1983). When plants reproduce, size is highly correlated with reproductive output (Samson and Werk, 1986; Hartnett, 1990; Aarssen and Taylor, 1992). The struggle for existence among plants is, to a large extent, the struggle to grow in the face of competition from neighbors. Thus, the question of how competition alters the growth of plants is central to understanding the role of competition among plants in nature. Field removal studies (reviewed by Goldberg and Barton, 1992) usually detect competition, but that is only the first step towards understanding its role. While numerous studies have attempted to measure the influence of competition on plant size or growth over one or several independent intervals, few have attempted to evaluate the influence of competition on individual plant growth curves (Stoll, Weiner, and Schmid, 1994; Nagashima, Terashima, and Katoh, 1995; Weiner, 1995).

This is, in part, because there is a trade-off in practice between following growing individuals over time and making good measures of their size. Demographically oriented studies (e.g., Sarukhán and Harper, 1973; Mack, 1976; Symonides, 1983a) have followed the fate of individuals, but, because measurements need to be nondestructive and nondisruptive, size has usually been measured in a very crude way, e.g., number of leaves, size of the largest leaf, or stem diameter. Such measures allow us to show whether growth is occurring, and perhaps whether one plant is growing faster than another, but the relationships between these crude size measures and more biologically fundamental aspects of size such as biomass or reproductive output can be weak and nonlinear. ‘‘Demographic growth analysis’’ (McGraw and Garbutt, 1990) can be a valuable tool in studying the growth of individuals without harvesting them, but strong inferences can be made about biomass or reproductive output only when these quantities are very highly correlated with the numbers of the module used in the analysis.

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Harvesting is traditionally the best way to obtain accurate measures of plant biomass (and therefore energy content), but the ability to follow individuals over time is lost: a plant can be harvested only once. Some researchers have used data from sequential harvests to study the overall change in size distributions over time (e.g., Ford, 1975), but only at great cost in statistical power and/or unwarranted assumptions (e.g., size ranks do not change over time). The ubiquitous high variation among replicates is especially problematical with sequential harvests. Plant ecology suffers from the lack of an efficient technology for measuring plant size nondestructively and nonintrusively.

In lieu of such a technology, there is a well-established, albeit time- and labor-intensive, method for obtaining good measurements of size for individuals over time. Sequential nondestructive measurements on individuals can be used in parallel with sequential harvests to produce accurate estimates of individual size over time. By making numerous nondestructive, minimally intrusive measurements on individuals in a population, and also fitting prediction equations to harvests of similar plots, one can obtain accurate estimates of plant size for individuals in the repeatedly measured population. Since the relationship between the different aspects of size may change over ontogeny (Coleman, McConnaughay, and Ackerly, 1994) and may be altered by competition (Weiner and Thomas, 1992; Nagashima and Terashima, 1995), it is often necessary to use separate calibration harvests for different stages of development and/or for different densities.

Using this method, we investigated the influence of competition on the growth of individual *Xanthium strumarium* plants growing at four different densities under natural conditions, to address the following questions: (1) Is the variation in local density observed in the field an important influence on variation in the growth of *X. strumarium* individuals? (2) If so, what is the influence of natural variation in density on the growth curves of plants in the field: (A) Does competition alter the general form of plants' growth curves? (B) How does competition alter the parameters of specific growth models? (3) If competition is not a major cause of size variation in *X. strumarium* populations, what other factors may account for the variation observed in the field?

MATERIALS AND METHODS

Study site—The study site is a 1.5-km undeveloped barrier beach at the Bates Morse Mountain Coastal Research Area in Sagadahoc County in southern Maine (69° 49' W, 43° 43' N), USA. The beach supports a native plant community dominated by five species: the rhizomatous perennial grass *Ammophila breviligulata*, and four nonclonal summer annuals: *Xanthium strumarium*, *Atriplex patula*, *Salsola kali*, and *Cakile edentula*. During the growing season, plants on the beach are subject to partial and sometimes complete burial by sand. Occasionally more severe disturbances to the beach profile and associated dunes are caused by wind and winter storms that shift sand. The presence of endangered species of nesting birds has led to protection of the beach, so disturbance by humans is minor.

Study species—*Xanthium strumarium* L. (Asteraceae) typically occurs on predominantly bare sand above the high tide mark, but solitary individuals are occasionally found below this level, and solitary plants and clusters can occur near and within dense stands of *Ammophila breviligulata* on the frontal dune. *Xanthium strumarium* occurs over a wide range of densities in this community. Solitary individuals and ''pairs'' (two plants emerging from one double-seeded propagule) are common, as are discrete clumps of up to 100 individuals surrounded by bare sand.

Seedlings of *X. strumarium* typically emerge from mid-May through mid-June; most seedlings appear during a 2-wk period in late May and early June. During most years, growth is nearly complete by early or mid-August when flowers appear. Fruits mature through October.

Field methods—We made measurements on 415 individual plants over 8 wk of growth in 1990, including repeated nondestructive measurements on some plants and sequential harvests of others. The detailed repeated measurements were possible with minimal damage because *X. strumarium* is robust, with simple, large, xeromorphic leaves (Weaver and Lechowicz, 1982). The largest leaves were 16 cm long, and no plant bore >180 leaves. The five measurement dates spanned the period of plant growth from the seedling stage (early June) to ~ 2 wk prior to flowering (which occurred in mid-August).

In late May and early June over 500 *X. strumarium* seedlings growing on open sand at the site were labeled individually with numbered plastic tags that were attached loosely around the base of the stem with thin, plastic-coated wire. We used four naturally occurring densities representative of the range of densities observed in this population: (1) solitary plants separated at least 1 m from other plants (of any species) by bare sand; (2) pairs of plants with stem bases <1 cm apart, and separated from other plants by at least 1 m; (3) small clusters of four plants (some of which were created by thinning clusters of five to eight individuals to four); (4) clusters of 11–39 plants. Interplant distances were quite small within densities (2)–(4); distance to nearest neighbor was always <2 cm, and aboveground parts were almost always in physical contact. In the larger clusters (4), a few seedlings emerged after the study began. These were tagged and included in the study for those analyses not restricted to plants that were measured five times (see below). There was no evidence of density-dependent mortality in these populations.

At weekly intervals, every plant was located, and information on mortality, inundation, and degree of burial by sand was recorded. To prevent factors other than conspecific density from affecting growth, we excavated plants and plant parts covered by accreting sand, and cut at ground level any stems of *Ammophila breviligulata* that emerged near study plants. Plants that were not repeatedly measured but were to be used in sequential harvests were monitored and treated in the same way. At 2-wk intervals, within a 2–3 d period (5–6 June, 18–19 June, 2–3 July, 16–17 July, and 30 July–1 August), the following measurements were made on each plant: (1) stem diameter of the first internode (between cotyledons and first pair of true leaves) of the central stem using digital calipers; (2) largest diameter of central stem above the cotyledons; (3) height from base of cotyledon to the highest apical meristem recorded to nearest 0.5 cm; (4) length of each cotyledon, recorded to nearest 0.5 cm; (5) length (to nearest 0.5 cm) and width at the widest point (to nearest 0.5 cm) of each leaf >1 cm long; and (6) number, order (primary, secondary, tertiary),and length of each branch >1 cm long.

Some plants were not measured at every 2-wk interval because the management plan for endangered bird populations nesting on the beach did not always permit access to all individuals. These plants were measured and monitored again at the next measurement date. Thus, some plants were not measured on every measurement date. For the analysis of size distributions on individual dates we used all plants for which we had four or five measurements (sample sizes in Table 1). For the fitting of growth curves we used only plants that had been measured all five times (sample sizes in Table 2).

Sequential harvests—For the first four measurement dates the nondestructive measures of the repeatedly measured plants were accom-

TABLE 1. Analysis of variance of estimated log mass on density level for each measurement date for plants that were measured at least four of the five times. $N = 414$ (week 1), 416 (week 3), 419 (week 5), 313 (week 7), 411 (week 9).

Week	Source	df	MS	*P*
1	density	3	0.014	n.s.
	residual	410	0.108	
3	density	3	0.455	<0.0001
	residual	412	0.056	
5	density	3	0.545	0.0002
	residual	415	0.082	
7	density	3	1.941	<0.0001
	residual	309	0.127	
9	density	3	6.70	<0.0001
	residual	407	0.273	

panied by harvests of nearby *X. strumarium* plants. The objective of the sequential measurements was to obtain good prediction equations for biomass of the repeatedly measured plants. Thus, the harvested plants were chosen to represent a range of sizes and densities. We measured these plants in the field, with the same procedures and protocols used for the repeatedly measured plants. We then harvested the aboveground parts, which were then washed, dried, and weighed. For the final measurement, the plants that were harvested for biomass were a subsample of the repeatedly measured plants. Over the summer, we harvested a total of 377 plants over a wide range of sizes and densities.

Estimation of biomass of growing plants—For each of the five measurement dates, we examined the relationship between the nondestructive field measures and dry mass of the harvested plants. To develop prediction equations, we used stepwise multiple regression of dry mass on the various nondestructive measurements with appropriate transformations of the variables for homoscedasticity and normality of the residuals. Only terms that represented a significant ($P < 0.05$) improvement in the stepwise regression were included in the prediction equation. We fit and used a different prediction equation for each harvest/measurement date, except the third and fourth measurements, which were combined. This was done because available samples sizes were limited and the data we could obtain showed no evidence of any differences in allometric relationships between those two dates. In all cases, the relationship of several measures to dry mass is quite good (Fig. 1), and the residuals fit the assumptions of regression very well. We found no evidence of different relationships for the different densities at each date. The prediction equations used were

Harvest 1: mass = $-55.05 + 9.23$ (total cotyledon length) + 10.05 (total leaf length) + 10.69 (total leaf width); $r^2 = 0.94$; $N = 84$

Harvest 2: log mass = 2.582 + 1.134 log stem diameter + 0.131 log (total cotyledon length) + 0.334 log (total leaf length) +0.431 (total leaf width); $r^2 = 0.93$; $N = 87$

Harvest 3 and 4 (combined): log mass = $-0.633 + 0.744$ log stem diameter + 0.864 log (total leaf width); $r^2 = 0.984$; $N = 53$

Harvest 5: log mass = 1.822 + 0.921 log stem diameter − 0.151 log (total branch length + 1) + 1.198 log (total leaf length); $r^2 = 0.99$; $N = 153$ (Fig. 1).

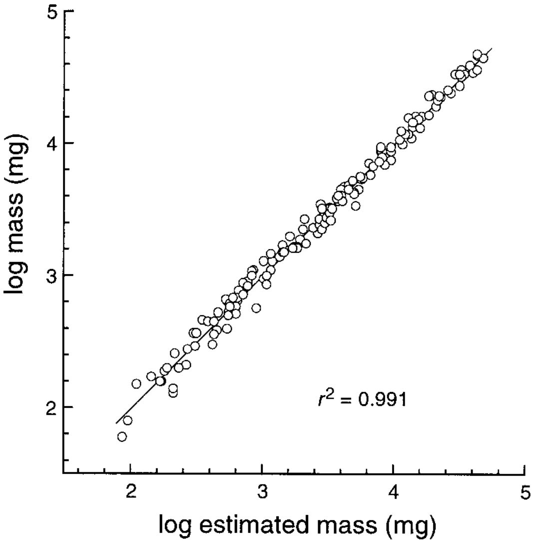

Fig. 1. Relationship between log estimated and log measured plant mass for *X. strumarium* at the final measurement ($N = 153$).

All analyses presented below are on the masses or log masses estimated for the sequentially measured plants.

Statistical methods—Using the method described in Stoll, Weiner, and Schmid (1994), we fit two growth models,

$$\text{exponential model} \qquad W_t = W_0 e^{gt}, \tag{1}$$

where W_t is the mass of a plant at time t, t is time, and W_0 is the initial mass and g is the instantaneous relative growth rate (RGR), and

$$\text{logistic model} \qquad W_t = \frac{K}{1 + ([K/W_0] - 1)\, e^{-gt}} \tag{2}$$

with g in this case representing the initial RGR and the additional parameter K representing the asymptotic mass.

The exponential model was fit using linear regression on the estimated log mass, and the logistic model (also log transformed) was fit using an iterative, nonlinear model fitting procedure (JMP Statistical Program, SAS Institute). While the fitting of a model of growth with two or three parameters to five points would and should arouse suspicion in a single case, this is not a problem but, rather, an advantage when such fitting is done for many individuals and the parameter estimates analyzed as variables (Meredith and Stehman, 1991; Stoll, Weiner, and Schmid, 1994; Weiner, 1995).

The logistic model could not be fit to all plants. When it could, the goodness of fit of these two models was compared on the basis of Akaike's information measure (Sakamoto, Ishiguro, and Kitagawa, 1986), which allows comparison of models with different numbers of parameters. For models with normally distributed errors, Akaike's measure is equivalent to using the adjusted r^2. We analyzed the binary variable: which of the models fit better (i.e., higher adjusted r^2), as well as the distribution of parameter estimates for both models.

TABLE 2. Percentage of *X. strumarium* plants better fit (i.e., higher adjusted r^2) by a logistic than by an exponential model for different densities. The first row is for all plants that were measured five times, the second row includes only those for which the difference in adjusted r^2 between the two models is >1%. Sample sizes are in parentheses.

Group	Isolated	Pairs	Quadruples	Clumps	χ^2	*P*
All plants	36.7 (60)	43.8 (89)	40.8 (71)	69.9 (73)	18.8	0.0003
>1% difference in adjusted r^2	59.3 (27)	44.9 (49)	58.9 (39)	76.4 (55)	10.85	0.0126

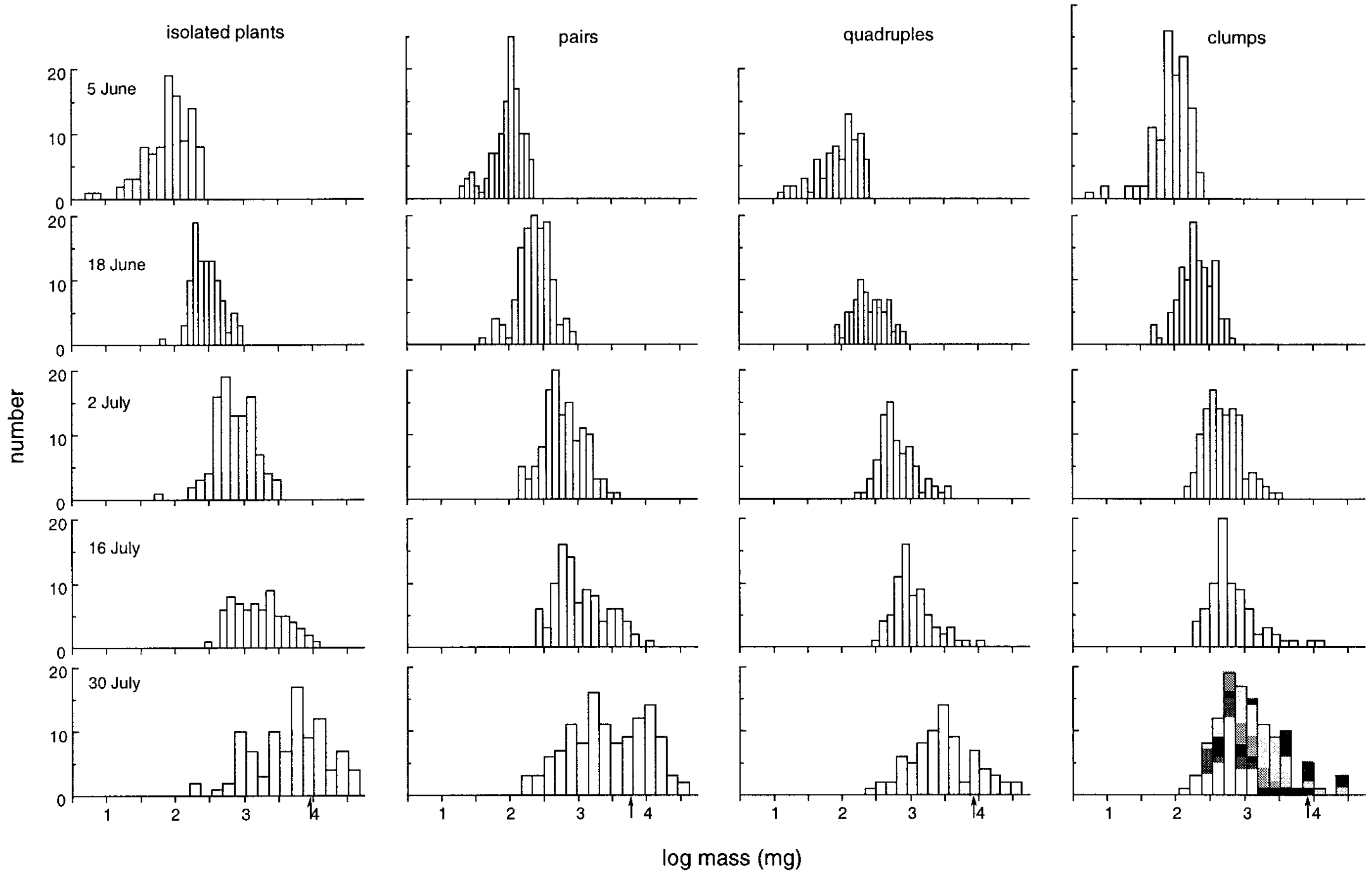

Fig. 2. Frequency distributions of log estimated plant mass of *X. strumarium* plants for all densities and measurements. Histograms are based on 15 intervals from the minimum to the maximum. Arrows along the axes represent the log (mean estimated plant mass) for the last measurement date. Different shadings represent different clumps for the last measurement date. Results for analysis of variance are in Table 1.

RESULTS

Mean performance—Density accounted for a highly significant proportion of the variance observed in log estimated mean plant mass at the final measurement (Table 1; Fig. 2). Post hoc tests showed significant differences in log estimated mean plant mass at the final measurement between all densities except pairs and quadruples, which were very similar in mean and distribution (Fig. 2). Plants growing in clumps were, on average, one-quarter the size of isolated plants. There was no significant difference in estimated mean plant mass among the densities at the first measurement, so differences can be attributed to different growth rates occurring at different densities over the course of the study.

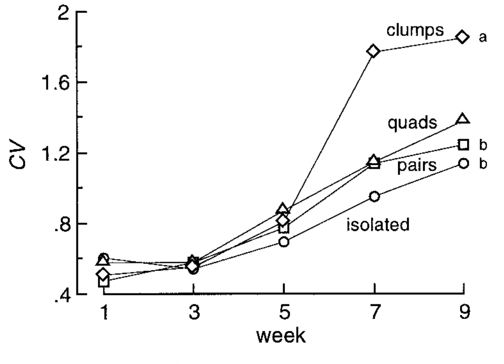

Fig. 3. Change in coefficient of variation of estimated mass over time for the four densities. Different letters represent significant differences in CV at the final measurement ($P < 0.05$; paired bootstrap method).

Size variability—Size variability (as measured by the coefficient of variation in estimated plant mass) increased over time at all densities and was higher at higher densities at the last two measurements (Fig. 3). The paired bootstrap method (Dixon et al., 1987), based on 1000 bootstrapped estimates, showed significant differences in the CV between individually growing plants and plant growing clumps, and between pairs and clumps ($P < 0.05$ in both cases).

We compared CVs via randomization for given sample sizes. The mean CV of actual pairs of plants at the final measurement was 0.404, but the mean CV of randomized pairs was 0.784, which is very similar to the mean CV of isolated plants randomly assigned to pairs (0.773). Thus, inequality among the plants growing in pairs was due primarily to differences among pairs rather than differences within pairs. Similarly, the mean CV of quad-

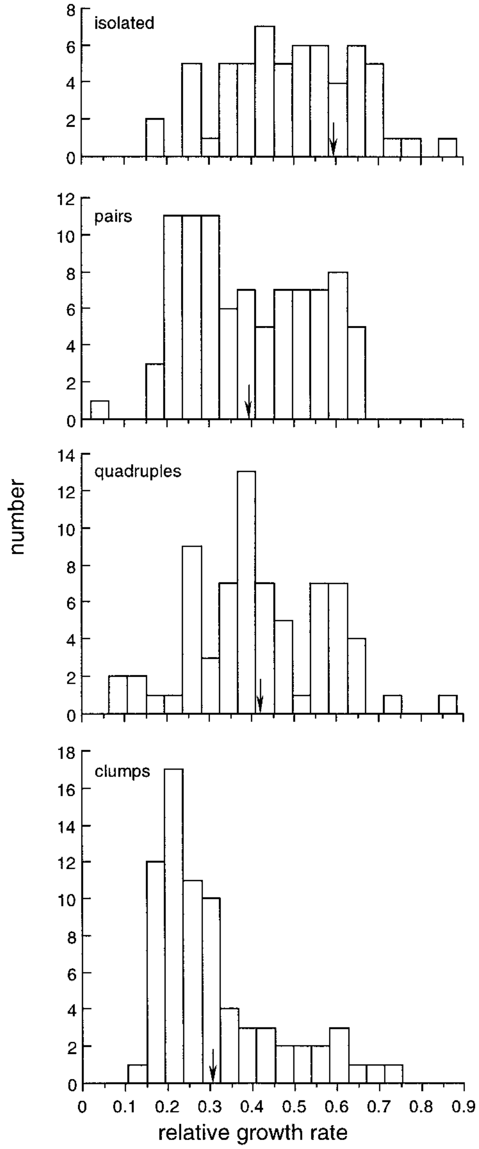

Fig. 4. Distribution of relative growth rates (slope of the linear regression of log estimated mass on time) over the entire period of growth at the four different densities for all plants that were measured five times. Arrows represent means.

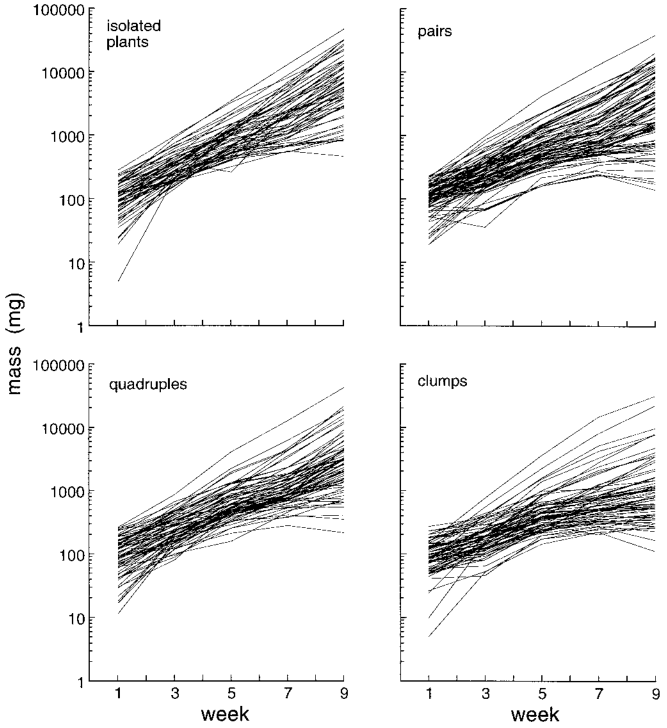

Fig. 5. Growth curves for all plants that were measured five times. Plants at higher densities and plants that were larger at the first measurement were more likely to show evidence of declining relative growth rate during growth.

ruples was 0.473, but the mean CV randomized quadruples was 0.900, which is very close to the mean CV of isolated plants randomly assigned to groups of four (0.913). The mean CV of the six clumps at the final measurement was 0.861, but the CV was 1.36 when these plants were randomly assigned to groups of the same size as the real clumps. The CV of the mean plant mass per clump (1.160) was higher than the mean CV within clumps (Fig. 2, final histogram).

Growth curves—When all plants were fit with the exponential model, the mean estimated relative growth rate was lower for higher local densities ($P < 0.001$ for ANOVA of RGR by density), and post hoc tests showed significant differences in mean RGR between all densities except pairs and quadruples. Local density also changed the distribution of RGRs (Fig. 4). The distribution of RGRs within clumps was skewed, with most plants having low RGRs, but with a tail of individuals that had RGRs almost as high as those at lower densities. The results are similar if the analysis of RGR is restricted to those plants that were better fit by the exponential than by the logistic model.

The growth of most plants fit both the exponential and the logistic model quite well, and differences in the adjusted r^2s were very small. Some plants showed no evidence of a decline in RGR over time (Fig. 5), and it was impossible to fit the logistic model to such individuals or the fit yielded estimates of asymptotic size that were unrealistically large. Plants that yielded such large estimates of asymptotic size in the logistic model always showed a better fit to the exponential model.

The percentage of plants better fit by the logistic model was significantly higher for the highest density (Table 2). The probability of a plant being better fit by a logistic model also increased with initial size (first measurement). In a logistic regression analysis, size at first measure and density both had significant effects on the probability of a plant being better fit by a logistic vs. an exponential model ($P = 0.02$ and $P = 0.0002$, respectively), i.e., plants that were larger at the first measurement and plants that were more crowded were more likely to show evidence of a size asymptote (Fig. 5). Among plants better fit by the logistic model, those growing at higher densities showed significantly lower asymptotes (density df = 3, MS = 9.516, $P = 0.003$; residual df = 137, MS = 1.96), but there was no significant influence of density on the initial RGRs in the logistic model.

DISCUSSION

Competition and individual growth—Competition among sand beach and dune annuals has been observed in several studies (Pemadasa and Lovell, 1974; Mack and Harper, 1977; Watkinson and Harper, 1978; Symonides, 1983a, b; Watkinson, 1990; Rees, Grubb, and Kelly, 1996), although competition in dune communities is thought to be weak compared to competition in more nutrient-rich or later successional environments. In these field populations of *X. strumarium*, we can reject the null hypothesis of no competition (Ellison, Dixon, Ngai, 1994) and conclude that naturally occurring variation in local crowding by conspecifics (siblings in many cases) has a significant influence on individual growth and resultant size (Table 1). Individuals that have fewer neighbors grow exponentially for longer and are therefore significantly larger than individuals with one or more neighbors.

Significant differences in final size were observed between all densities except plants growing in pairs and those growing as quadruples. Thus, while mean final size decreased with increasing local density from none, to one or three, to more neighbors, there was no evidence that plants with three near neighbors experienced more competition than those with only one neighbor. This could be because plants suffer competition primarily from neighbors that are extremely close. Pairs usually arose from seeds from the same fruit and therefore very close together. Quadruples were usually from two or three fruits. Competition between seeds from the same fruit may be much stronger than usually occurs between seeds from nearby fruits.

When treated as populations, plants growing at higher densities were more variable in growth and final size than plants growing at lower densities (Fig. 3). The increase in overall inequality at higher densities was primarily due to differences among groups rather than variation generated within groups. The fact that the *CV* of the mean plant mass per clump (1.160; Fig. 2, final histogram) was higher than the mean *CV* within clumps (0.861) is strong evidence that size inequality at the highest density was primarily due to inequality among clumps rather than inequality within clumps. Thus, we conclude that there is no evidence of asymmetric competition (Weiner, 1990a) within this population. Since competitive asymmetry appears to be driven primarily by shading, we would not expect competition to be asymmetric in such a high-light, low-cover, strand community. Rather, the increase in inequality observed at higher densities is probably caused by environmental heterogeneity (Mitchell-Olds, 1987) and/or variation in local density (Bonan, 1988; Miller and Weiner, 1989) in this population that contains many discrete clumps. The highest density category includes a wide range of densities, thus resulting in wide variation in mean plant size among clumps. Even pairs represent a range of densities compared to isolated plants, in that the distance between individuals within a pair varies to some degree. If the effect of competition decreases steeply with the distance between plants, small differences in distance within pairs could result in large differences in mean plant size among pairs.

Modeling individual plant growth—The choice of growth model has major effects on the results and subsequent interpretation of the data. When we fit the exponential model to all plants, we observe that crowding reduces RGR and changes the distribution of RGRs within the population. A description of this population's development based on exponential growth is reasonably ''accurate'' in the sense that plants fit the exponential model quite well. However, half the plants were slightly better fit by the logistic model, and analysis based on the logistic model leads to a very different picture of population development. When we analyzed the logistic model in those cases in which it fit better than the exponential model, we see that crowding reduced the asymptotic size but not the initial RGR (Shinozaki and Kira, 1956). The conclusion that competition reduced plants' initial RGRs is as much a function of the statistical model employed as of the data themselves. Because many plants were still growing exponentially by the end of the study (Fig. 5), it was not possible to fit the logistic model to all plants. Thus, it was not possible to compare an analysis in which all plants are modeled exponentially with one in which all plants are modeled sigmoidally, but such an analysis offers promise for future studies.

The growth of individual plants is exponential at the beginning but eventually becomes asymptotic if we look over the whole life of the plant. There are several reasons why the RGR of plants decreases over time, including reduction in resources per unit plant tissue with increasing size, and increased allocation to structural and reproductive rather than photosynthetic tissues (Weiner, 1990b). Many of the plants in this study were still in an exponential growth phase and showed no evidence of a reduction in RGR over time (Fig. 5). Local crowding increased the probability that a plant would show evidence of beginning to level off in size. The main effect of competition for certain resources may be to decrease the maximum size that a plant will achieve, rather than reducing the initial relative growth rate. Indeed, since the intensity of competition in a growing cohort of plants increases over time as plants at a given density get larger, we would not necessarily expect competition to affect plants' initial growth. As Stoll, Weiner, and Schmid (1994) observed in a population of *Pinus sylvestris*, individuals that are larger at the beginning are also more likely to show evidence of leveling off by the end, and our results are consistent with this observation.

Explicit growth curves vs. ''growth-size'' models—The basic modeling tool for the description and analysis of population size development in recent years has been based on the relationship between the sizes of plants within a population at some point in time (t) and their growth over a subsequent interval ($t \rightarrow t + x$). We refer to such models as ''growth-size'' models. Westoby (1982) called the relationship between size and subsequent growth increment (absolute growth rate) the ''distribution-modifying function'' (DMF), because the relationship describes how the size distribution changes over the interval. Hara (1984) expanded the DMF approach into a full diffusion model based on the Kolmogorov forward equation, adding a diffusion equation [''$D(t,x)$''] to the DMF or ''drift'' equation [''$G(t,x)$'']. The practical value of the diffusion term has yet to be established: very large sample sizes are required to obtain reasonable estimates of $D(t,x)$ functions, and the biological interpretation of the $D(t,x)$ function is still unclear (Hara, 1988).

Growth-size models have proven to be very useful as analytical tools. For example, Weiner (1990a) argued that certain types of growth-size relationships are incompatible with the hypothesis of symmetric (''two-sided'') competition. Thus, predicted types of growth-size relationships can serve as testable hypotheses. In the growth-size approach each time interval is treated separately: no assumptions are made about the time course of plant growth beyond the single growth interval analyzed. We can increase both the biological content and the statistical power of models of stand development by basing them on explicit growth equations. First, this would provide a biologically meaningful connection between the different growth intervals, rather than looking at each interval independently. Second, by making reasonable assumptions about the growth of individual plants over several intervals, we can increase our statistical power enormously. It follows from basic principles that statistical power increases with the number of assumptions made. Thus, while inappropriate assumptions are to be avoided, it is equally true that not making reasonable assumptions is not taking advantage of all the available information. Since we know that the growth of plants can be fit to several general equations (Hunt, 1982), these can provide powerful tools for the modeling of stand development, enabling us to apply the knowledge about individual plant growth we do have in our analyses. Of course, any tool must be evaluated in the context of the purpose of the particular study and the type of data available, and there may be situations in which ''growth-size'' models will be more appropriate than growth curve models, e.g., when sample sizes are large but size measurements are very limited (such as stem diameter only) or infrequent. In many situations, however, the analysis and interpretation of population development in terms of explicit models of growth offer major statistical and biological advantages over other approaches.

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