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11

The Influence of Competition on Plant Reproduction

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Competition or interference is ubiquitous in its influence on plants. It is rare to find a plant which has not been affected negatively by neighboring plants. For the plant population ecologist, competition or interference is best defined as any negative effect due to the proximity of neighbors.[16] Thus, interference is something that occurs between individuals, reducing their growth and/or increasing their probability of death. In this chapter, I use the terms competition and interference interchangeably, although the latter term may be a better one to encompass all negative neighbor effects. I do not discuss competition for the services of pollinators, as this is a separate topic that has recently been reviewed elsewhere.[49]

For the purpose of this chapter, I will interpret the concept of reproduction broadly to include both sexual and asexual means of propagation. Several authors (e.g., Harper[17] and Abrahamson[3]) have pointed out the similarity between the growth of plants and what has been called "vegetative reproduction." Plant growth is usually modular, and if some of the modules are capable of independent existence (such as bramble shoots that have layered or strawberry ramets that have become separate) the result has been referred to as vegetative reproduction. Because of this similairty, Harper[18] has suggested that we consider such forms of propagation as clonal growth, while the term reproduction should be reserved for processes that produce offspring sexually. In fact, since asexually produced offspring are genetically identical to the parent, while sexually produced offspring are genetically different from both parents, it would perhaps be more logical to refer to asexual propagation as "reproduction" (*re*—Latin: again) while sexual forms of propagation be called "neoproduction" (*neo*—Latin: new). Since such a change in terminology appears unlikely, the traditional terminology is used here and both sexual reproduction and clonal growth are considered as different modes of reproduction.

In discussing the influence of a factor such as interference there can be confusion between ecological and evolutionary effects. There is no reason to assume that an individual plant's plastic response to a factor is similar to the effect of natural selection in response to that factor. Some debates on the influence of competition on reproduction (e.g., the exchange between Abrahamson[2] and Law et al.[33]) appear to be based on the confusion that occurs when some of the same terminology is used to refer to ecological (e.g., plastic) and evolutionary (genetic) responses. In this chapter, I address first the ecological question: How does competition affect the reproductive behavior of individuals and, therefore, populations? I do not attempt to review the literature on life history strategies in plants, as this has been done elsewhere (Willson[75]; other chapters in this volume, e.g., 2, 9, 13–15), although I refer to this literature when it bears directly on individual plants' responses to interference. Herein I briefly review the literature on the effects of competition on the reproductive behavior of plants, and compare alternative evolutionary hypotheses to explain these observations.

There are several possible effects of competition on the reproductive behavior of plants. Interference may

1. Reduce the probability that an individual will reproduce or reduce the amount of reproduction (number or size of seeds or ramets produced)[32];
2. Change the plant's reproductive allocation (proportion of resources in reproductive tissues)[11];
3. Change the timing of reproduction (onset and duration of reproductive activities);
4. Change the mode of reproduction (e.g., the proportion of ramet versus genet production, or sexual versus apomictic seed production);
5. Change mating behavior (e.g., gender allocation, proportion of cleistogamous versus chasmogamous flowers) (see Zimmerman,[78] this volume);

Also, competition may change the frequency and spatial distribution of these behaviors within a population (e.g., the amount of individual variation).

Each of these effects is discussed below.

DENSITY-YIELD RELATIONSHIPS AND REPRODUCTIVE ALLOCATION

When plants are grown at a range of densities for a given period of time, yield per unit area increases with increases in density. At higher densities, progressively smaller increases in total yield are observed. Above a certain density, yield no longer increases with density. This "asymptotic" relationship between density and yield ("law of constant final yield") has been documented for many plant species[17,56] (Fig. 11.1a,b). This effect is due to density-dependent mortality and the plastic reduction in size of individual plants. The asymptote reflects the limit on total biomass that is determined by the total amount of available resources. Numerous field and experimental studies have demonstrated that density can reduce almost every aspect of individual yield. Several mathematical relationships between yield and density have been described.[17,29,64,73]

Although the response of total yield to density is usually asymptotic, different components of yield can respond quite differently. Reproductive yield, as measured by fruit or seed production, may follow a pattern similar to that of total yield,[41,66] but fruit and seed production usually increases and then decreases as plant density is increased (Fig. 11.1c,d). This "parabolic (sic) relationship" between density and reproductive components of yield has been observed in many crop[73] and weed[58] species. Thus, as density is increased a greater proportion of the population's biomass is in vegetative structures as opposed to reproductive tissues. I know of only one case in which increased density resulted in increased sexual reproductive allocation: Assemat and

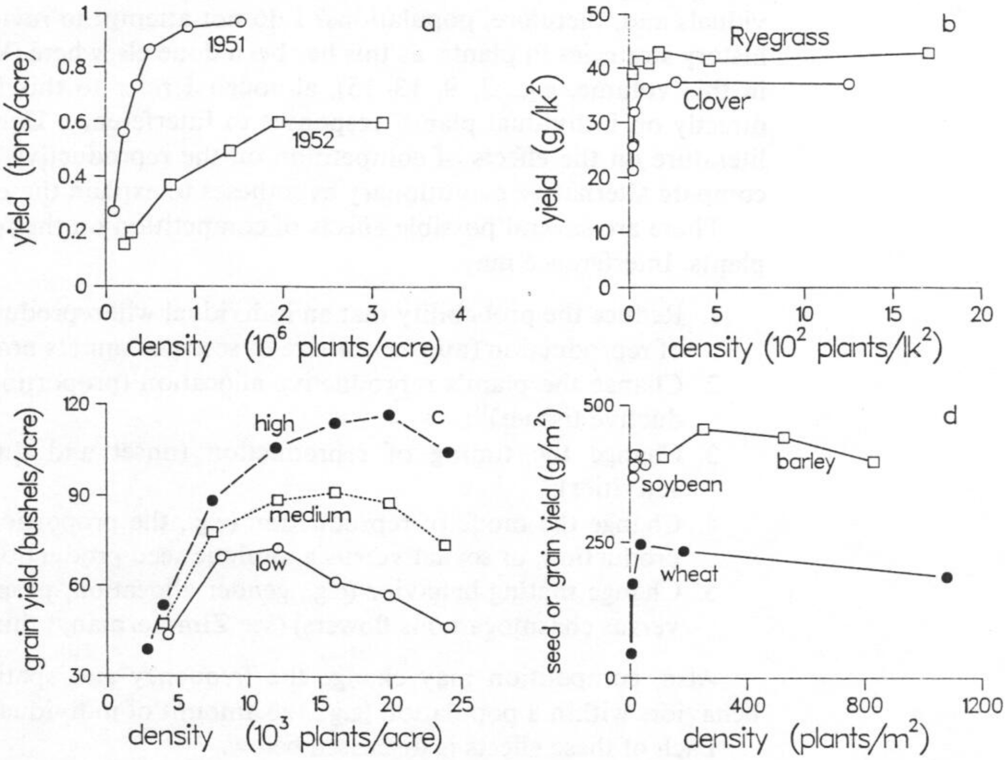

Fig. 11.1. Total yield (a,b) and reproductive yield (c,d) as a function of planting density for selected crops. (a) Total dry matter of Essex Giant rape; (b) total dry matter of Wimmera ryegrass and subterranean clover, units are plants/link^2; (c) mean grain yield of maize grown at low, medium, and high levels of nitrogen; (d) reproductive yield for soybean, barley, and wheat. (a–c after Willey and Heath;[73] d after Willey,[72] from various sources.)

Oka[5] report higher reproductive allocation in the weed *Echinochloa crus-galli* at high density than at low density.

Since most of the data on yield versus density are obtained at the population level (i.e., total yield versus density),[17,64,72] it is not clear in most cases whether the reduction in reproductive yield at high density is due to a change in reproductive allocation (harvest index) of most individuals or a change in the reproductive allocation of the smaller plants only. Decreasing reproductive allocation in individuals grown at higher densities has been observed in *Plantago major,*[24] *Plantago coronopus,*[62] *Chamaesyce hirta,*[58] *Coix mayuen,*[31] *Bellis perennis,* and *Prunella vulgaris.*[53]

Recently there have been attempts to quantify the effect of competition on individuals. In this approach, the growth, size, or reproductive output of a plant is considered to be a function of its neighborhood conditions, such as the number, distance, size, and angular dispersion of neighbors.[12,36,55,63,67,68] In two of these studies,[55,67] neighborhood formulations have been shown to account for a large fraction of the variation in individual reproductive output.

We conclude that competition reduced reproductive output and, in most cases, reproductive allocation as well. The relationship between density and reproductive yield is related to the effects of density on plant size and timing of reproduction (see below, Competition and the Timing of Reproduction, and Competition and Reproductive Allocation: A Question of Size and Allometry?)

While the reproductive yield of individuals decreases at higher densities, one component of reproductive yield, mean weight of seeds produced by an individual, appears to be affected much less than other yield components.[17] While data have been accumulating that show the mean seed size is plastic (e.g., Marshall et al.,[37] Pitelka et al.,[46] Cavers and Steel[10]), the observation that mean seed weight is one of the least plastic characters of plant growth[20,27,48] still stands as a valid generalization. Although mean seed weight may differ among populations of the same species or even among co-occurring individuals within the same population[75] it appears to be relatively nonplastic for a given genotype. Plants reduce their seed output primarily by producing fewer, and, secondarily, by producing smaller, seeds.

COMPETITION AND THE TIMING OF REPRODUCTION

Often, interference delays the onset of reproductive activity. High density has been shown to delay heading in cereal crops.[9] Removal of neighbors advanced the flowering date in *Senecio viscosus* but had no effect on flower initiation in *Serecio sylvaticus.*[41] In some cases, annuals reproduce later in the season when grown at higher densities. There are several examples of monocarpic plants that normally behave as biennials reproducing in their third, or even later years at higher densities.[15,61,71] Some "biennials" may even flower in their first year of growth under very favorable conditions, including low density. A wide range of reproductive timing in response to density has been shown for *Plantago coronopus.*[30] Individuals with few and distant neighbors reproduced sooner and sometimes showed repeated reproduction, whereas plants with many and near neighbors showed delayed reproduction and, in some cases, died without producing.

The influence of competition on the timing of reproduction and on reproductive allocation is often confounded. If interference delays reproduction, individuals grown at low density will show higher allocation to reproductive structures than individuals grown at higher densities after a given period of growth. It is possible that plants suffering from competition may achieve the same reproductive allocation as plants grown at lower density if the former were given a longer period to develop, even if they do not achieve the same size as low-density individuals. Very few studies have taken this possibility into account. A notable exception is the study by Waite and Hutchings,[62] in which energy allocation patterns were studied in *Plantago coronopus.* They found that plants at high density in the field and greenhouse still show lower reproductive allocation when allowed to complete their life cycle.

Interference seems either to delay the time of reproduction or have no effect on it. In mineral nutrition experiments, nitrogen deficiency can produce precocious flowering, so one might expect competition for nitrogen to have a similar effect. I have found only one report of such a response in the published literature: Palmblad[42] reported that flowers appeared earlier in stands of increasing density in *Silene anglica* and *Bromus tectorum,* although he presents no data. Although it might seem adaptive for some plants to respond to a deteriorating environment (perhaps caused by increasing interference from neighbors) by reproducing sooner, I know of no data which show earlier reproduction due to competition. This suggests that there are qualitative constraints on strategies that can evolve in response to competition.

COMPETITION AND THE MODE OF REPRODUCTION

Interference not only reduces reproductive output, it can also influence the mode of reproduction. Many plants are able to propagate themselves vegetatively via stolons, rhizomes, roots, tubers, bulbs, etc., as well as performing sexual reproduction resulting in seed production. (In some species seeds may be produced asexually.) There appear to be trade-offs between these two modes of reproduction. Plants that utilize both methods usually do so at different times during the growing season,[75] although there are cases in which plants practice both forms of reproduction at the same time.[8]

Abrahamson[3] has studied vegetative and seed reproduction in *Rubus* and *Fragaria* and has developed a model that predicts changes in the mode of reproduction in response to density. His model is based upon life history strategies and the costs and benefits of sexual versus asexual reproduction (clonal growth), and predicts that a strategy with flexible allocation to the two different modes of reproduction should be found in plants that grow in "stable" habitats. When density is low in such habitats, he argues that vegetative spread should be favored as an efficient way to colonize available area and propagate a genotype that is successful in that habitat. At high density, it may be advantageous to emphasize sexual reproduction through seeds as a way to produce highly dispersible novel genotypes that have the best chance of reaching and colonizing new sites. Thus, his model predicts that at low density more resources should be allocated to vegetative propagation, whereas at high density there should be a shift to sexual seed reproduction. He found data consistent with such a switch in field populations of *Rubus hispidus* and *Rubus trivialis* growing in different successional stages.[1] He hypothesized that plants were changing their reproductive behavior in response to nutrient conditions, but his data do not exclude the alternative hypothesis that genotypes in field and forest were different.[33] Holler and Abrahamson[28] tested the model with *Fragaria virginiana.* They found a decrease in percent allocation to clonal growth at high density but no change in allocation to seed production with density. Similar results were reported in density experiments on *Hieracium floribundom.*[3] In density experiments on *Tussilago farfara,* Ogden[38] observed a decrease in percent allocation to vegetative reproduction but no change in allocation to seeds at high density. These results are similar to those for *Fragaria.* Other studies have not supported Abrahamson's model. The herbaceous forest perennial *Aster acuminatus* showed no change in allocation to sexual reproduction or clonal growth over several densities.[45] Removal of weeds did not affect the ratio of sexual reproduction to clonal growth in *Fragaria virginiana.*[57] Percent allocation to tubers as opposed to inflorescences increased considerably at high density in the weed *Cyperus rotundus,*[74] a result opposite to the model's prediction. This is the only case of which I am aware in which increases in density resulted in increases in vegetative reproductive allocation. The limited data available suggest that interference usually decreases allocation to clonal growth more than allocation to seed reproduction, but perhaps such a generalization is premature.

Interference can also serve to change the proportion of propagule types in species that produce polymorphic seeds or fruits. The annual *Hypochoeris glabra* produces two distinctly different achene types, beaked and unbeaked. Due to changes in receptacle size with density, a greater proportion of the beaked achene type is produced at low density than at high density.[6]

COMPETITION AND GENDER

Interference can influence the gender allocation of a plant or the sex ratio in a population of plants. In dioecious plants, male and female plants may show niche differention that can result in differential responses to interference. Male spinach *(Spinacia oleracea)* plants show significantly higher survivorship at high density than do females, resulting in a population that is predominantly male.[39] At low density there was no difference in survivorship between males and females. Populations of *Silene alba* are typically female biased, and this bias increased with increasing density in field and glasshouse populations.[35]

Interference may affect gender distribution through mechanisms other than survivorship. Competition seems to reduce sexual expression in females more than in males in the cycad *Macrozamia riedlei.*[40] Gender has been shown to be associated with size in *Arisaema triphyllum,* an herbaceous forest perennial that can change sex.[7,34,47] Larger individuals tend to be female, smaller individuals are more likely to be male. While the effect of interference has not been studied directly, we might expect it to increase the proportion of male plants in the population by decreasing mean plant size. *Acer saccharinum* trees can be male, female, or bisexual, and individuals may switch from female to bisexual.[51] Bisexual trees tend to be larger than male or female trees. Since mean size is smaller at higher densities, higher density populations might have a higher proportion of unisexual trees.

COMPETITION AND VARIATION IN REPRODUCTIVE BEHAVIOR

Considerable data are accumulating in support of the generalization that competition among plants increases variability in many aspects of plant performance, including individual size and reproductive output.[69,70] At higher densities a larger proportion of the population has no offspring at all. In experimental populations of the annuals *Trifolium incarnatum* and *Lolium multiflorum,* I found that variability in size always increased at higher densities, and that variability in reproductive output was always greater than variability in size (e.g., Fig. 11.2). Increased variability in reproductive behavior due to competition may provide phenotypic differences within populations that may not be expressed at low density. Thus, competition may increase the range of material on which natural selection can act.

The effect of competition on variability in size and reproductive output seems to be a function of the mechanism of competition: competition for light appears to increase variability, but competition for nutrients may tend to decrease such variability.[64] On a sandy beach where the competition was for water and nutrients and the canopy was not closed, higher-density patches of *Xanthium strumarium* showed lower variability in fruit production.[77] This situation may be the exception. A review of density experiments shows increased variability in size at higher densities in 14 out of 16 cases.[70]

Interference seems to increase variability in phenology, as well as size and reproductive output. Density was correlated with increased variability in the duration of flowering and therefore reduced flowering synchrony in *Linathus androsaceus.*[54]

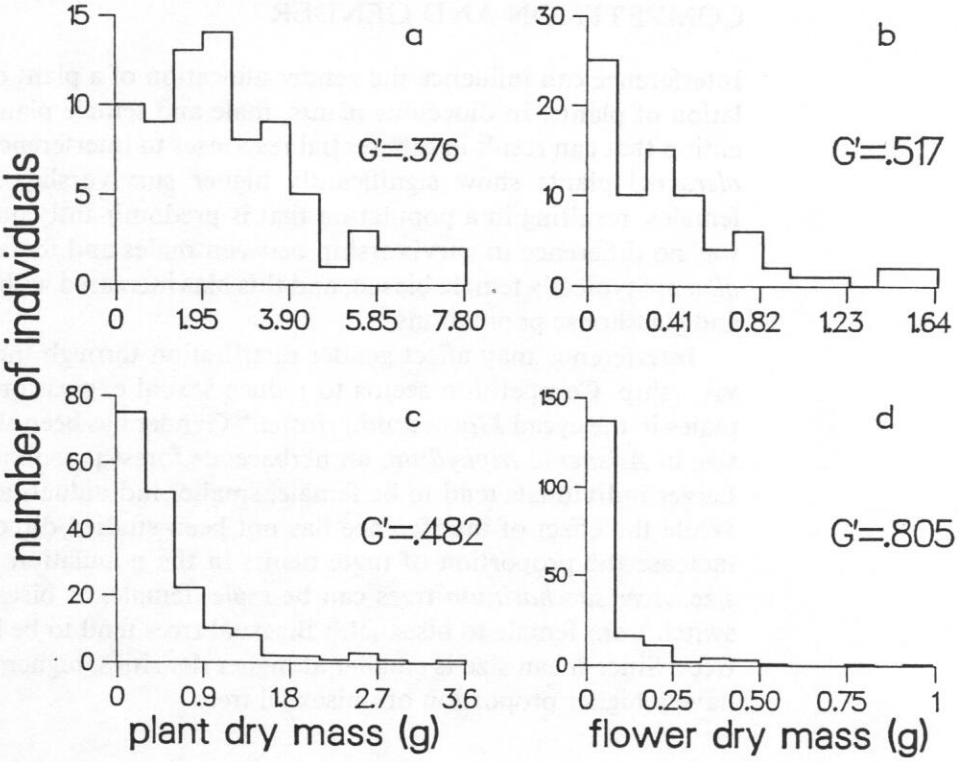

Fig. 11.2. Distribution of above-ground dry weight (a,c) and flower head dry weight (b,d) for experimental populations of *Trifolium incarnatum* grown at low (a,b) and high (c,d) densities with fertilizer. (Corrected from Weiner,[69] Figs. 4 and 7.) G′, unbiased Gini coefficient, a measure of variability or inequality.

ARE PLANTS' REPRODUCTIVE RESPONSES TO COMPETITION PART OF A "REPRODUCTIVE STRATEGY"?

A plant's response to competition may be the result of physiological or developmental constraints and may not represent a genetically based "strategy." While many would agree, in principle, that we should not assume every attribute or behavior of an organism is adaptive,[13,19] the goal of many a research program is to find the adaptive significance of specific traits or behaviors. Lack of empirical support for a hypothesized adaptive significance often leads to a search for alternative adaptive hypotheses, rather than a questioning of the assumption of adaptation. This very prevalent attitude is usually implicit but it is sometimes stated explicitly, as in an important recent paper[62]: "Since a weight-related plastic reproductive allocation has been demonstrated under both laboratory and field conditions it can be considered an evolved adaptive trait which may be explained in terms of individual plant fitness." While the conclusion may be correct, it does not follow from the premise. If we substitute "response to a new herbicide" for "plastic reproductive allocation" in the sentence, the assumptions are illuminated. Although plants may show a size-related response to a new herbicide, we would not consider this response to be an adaptation. That a behavior is adaptive should be an hypothesis, not an assumption, and alternative hypotheses should be sought if the adaptive hypothesis is to obtain strong support.

The assumption that behaviors are adaptive becomes even more problematic when one is referring to specific instances of individual variation within a population. An organism may have a fixed behavior pattern or a flexible behavior. In either case we can attempt to test the hypothesis that the observed pattern of behavior is adaptive (i.e., confers an increase in fitness). However, the hypothesis that any particular manifestation of plastic behavior is adaptive is much more risky, and requires more assumptions than the hypothesis that the behavioral plasticity itself is adaptive. Even if a plastic behavior pattern is adaptive, it does not follow that every manifestation of this plasticity confers fitness. Thus, the life history of a species is the product of natural selection, but changes in this life history pattern due to stresses such as competition may not be adaptive. Students of plant physiology do not assume that the behaviors of plants under experimental conditions of specific nutrient deficiencies are part of an evolved strategy to maximize fitness under such conditions, yet this may be exactly what ecologists are doing when they assume that responses of organisms to some of the difficult conditions nature often presents are strategic. Even if ultimate biological constraints do not limit the possibilities for adaptive responses, the behavior of organisms under extreme conditions (sugh as high density) may be the result of selection to optimize fitness under conditions that are more typical, conditions that usually have a greater effect on fitness, or conditions for which possible changes in the genome will have a greater effect on fitness.

The advantage of the adaptationist or "strategy" approach is that it readily leads to testable hypotheses, whereas alternative nonadaptationist perspectives may not generate hypotheses as readily. The ability to produce testable hypotheses is a necessary attribute of a scientific theory, and there is great need to develop alternative hypotheses that are not based on adaptation.

I propose three alternative interpretations of a plant's response to interference from neighbors. (1) It is possible that the plant's response is not adaptive in any sense. The plant may not have the ability to deal with the degree of interference it is experiencing. Even if an organism is adapted to tolerate a particular stress, or even maximize its fitness in the face of this stress, there will be levels of the stress above which the adaptive response breaks down. Such situations are beyond the range of adaptive tolerance, even if the organism is able to continue to live. Many of the behaviors observed in organisms at high density may fall into this category. In many cases a high degree of stress may result in increased variation in individual behavior within a population. For example, *Senecio vulgaris* individuals growing in very small pots showed much more variation in reproductive behavior than individuals growing in larger pots.[21] Since organisms cannot do everything, what may be selected in such a case may not be a plastic strategy that maximizes fitness under conditions of either small or large root volumes, but an ability to tolerate the extreme conditions. There may be trade-offs between the ability to survive and grow under extreme conditions and the ability to grow well under better conditions.[14] Such trade-offs may provide the basis for alternative hypotheses relating plant behavior to natural selection.

(2) Plants may have evolved fixed responses to the environment that are independent of competition per se. For example, plants may grow as best they can until they reach a threshold size for reproduction. If and when they attain this size, a certain proportion of resources above this level is then allocated to reproduction (Fig. 11.3). In this model competition is no different from any other resource limitation, and responses are fixed. This can be expected to be true for some plants; simple strategies for

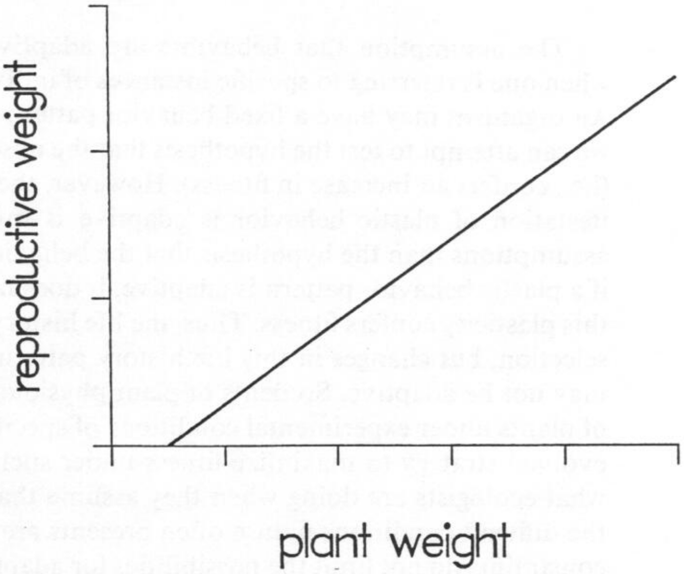

Fig. 11.3. Theoretical relationship between weight of a plant and weight of its reproductive structures (e.g., flowers, fruits, seeds).

dealing with particular problems are usually found in some organisms whenever more complex strategies for addressing the same problem are found in other organisms. Simple solutions to problems will be favored unless the selection pressure for a more complex solution outweighs the additional costs involved. Also, simple solutions are more likely to be available within the population's genetic variation. There is evidence (see below, Competition and Reproductive Allocation: A Question of Size and Allometry?) that the reproductive behavior of many plants is determined primarily by the size they achieve.

(3) The ecological responses of a genotype to different competitive regimes may indeed represent an evolved, flexible strategy that is the result of natural selection (i.e., individuals that had this capacity generally showed higher fitness than those that did not). Plants are neither responding to conditions outside their range of adaptive response, nor are they following simple fixed behavior patterns as limited by their environment. Rather, plants have evolved a suite of possible responses or tactics, each of which will tend to increase fitness in particular environments. This is the approach taken by Waite and Hutchings[62] in interpreting the results for *Plantago coronopus.* Presumably, there are costs involved in having such an ability, as there are for any developmental flexibility. Strong support for an hypothesis of adaptive developmental flexibility requires data that are not consistent with hypotheses that do not invoke flexibility because (1) Occam's razor obliges us to accept the simpler of two explanations if they are equal in other ways, and (2) because natural selection will favor a simpler (and therefore cheaper) solution when it is otherwise equal to another, more complex solution. The argument here is similar to those concerning the evolution of intelligence in animals. The benefits of developmental flexibility must exceed the increased costs over fixed behavior patterns if such flexibility is to be selected.

Thus, the hypothesis that a plant's plastic response to interference is a reflection of an evolved, flexible strategy rests upon a specific set of assumptions. The plant's ancestors must have evolved in environments with varying degrees of interference, and selection must have favored different behaviors under different competitive regimes. Individuals that showed the plastic response pattern must have had higher fitness than those that showed simpler, fixed responses.

In summary, organisms may do things not only because they have been selected to do them, but because they cannot help doing them. This may be because of direct constraints, overload and breakdown of their adaptive mechanisms, or because they have the ability to do something else that solves a more important (or more soluble) problem.

COMPETITION AND REPRODUCTIVE ALLOCATION: A QUESTION OF SIZE AND ALLOMETRY?

In many cases, changes in time of flowering and seed production in plants grown at different densities can be explained in terms of plastic growth and size-dependent reproduction of individuals. Many plants must achieve a minimum size if they are to produce flowers and fruits.[43,59,71,76] Above this threshold size there may be a relatively simple relationship between size and seed production (Fig. 11.3). This could account for the "parabolic" response of reproductive yield to density and the decrease in reproductive allocation of individuals grown at higher densities. At higher densities individual plants are smaller and, because the *x*-intercept of the relationship between reproductive biomass and vegetative biomass is positive, they have a smaller proportion of their biomass in reproductive tissues. As examples of an allometric view of reproductive allocation, I have reanalyzed the data on reproductive allocation in field populations of *Verbascum thapsus* presented by Reinartz,[50] and that of experimental populations of *Plantago major* presented by Hawthorn and Cavers.[23,24] Reinartz's data on 12 field populations of *Verbascum thapsus* (Fig. 11.4a) show a trend of increasing fraction of plant biomass in seeds with increasing mean plant size. When replotted, the data show a simple linear relationship between vegetative biomass and seed biomass: there is a minimum vegetative biomass required for reproduction and above that minimum a constant proportion of the additional biomass is in seeds. A linear regression of seed weight on vegetative weight accounts for 96% of the variation in weight of seeds produced (Fig. 11.4b), and the residuals are consistent with the assumptions of regression analysis. If there is a minimum size for reproduction and the relationship between reproductive weight and vegetative weight is linear, the relationship between percent reproductive allocation and total or vegetative weight will not be linear: it will shown an ever-decreasing slope approaching a constant percent allocation to reproduction.

Similar results are obtained from reanalysis of data on reproductive allocation in density experiments on *Plantago major*[22,23,24] (Fig. 11.5). Data that would be curvilinear if percent allocation were plotted against weight appear to be linear when reproductive weight is plotted against plant weight (or, more appropriately, against vegetative weight). Ninety-eight percent of the variation in mean spike weight produced by individuals with different neighbor conditions[23] (Fig. 11.5a) and 72% of the variation in seed weight produced by *Plantago major* individuals that did produce seeds in monocultures grown at three densities,[22,24] (Fig. 11.5b) can be accounted for by this simple model. A similar relationship accounts for almost all the variation in repro-

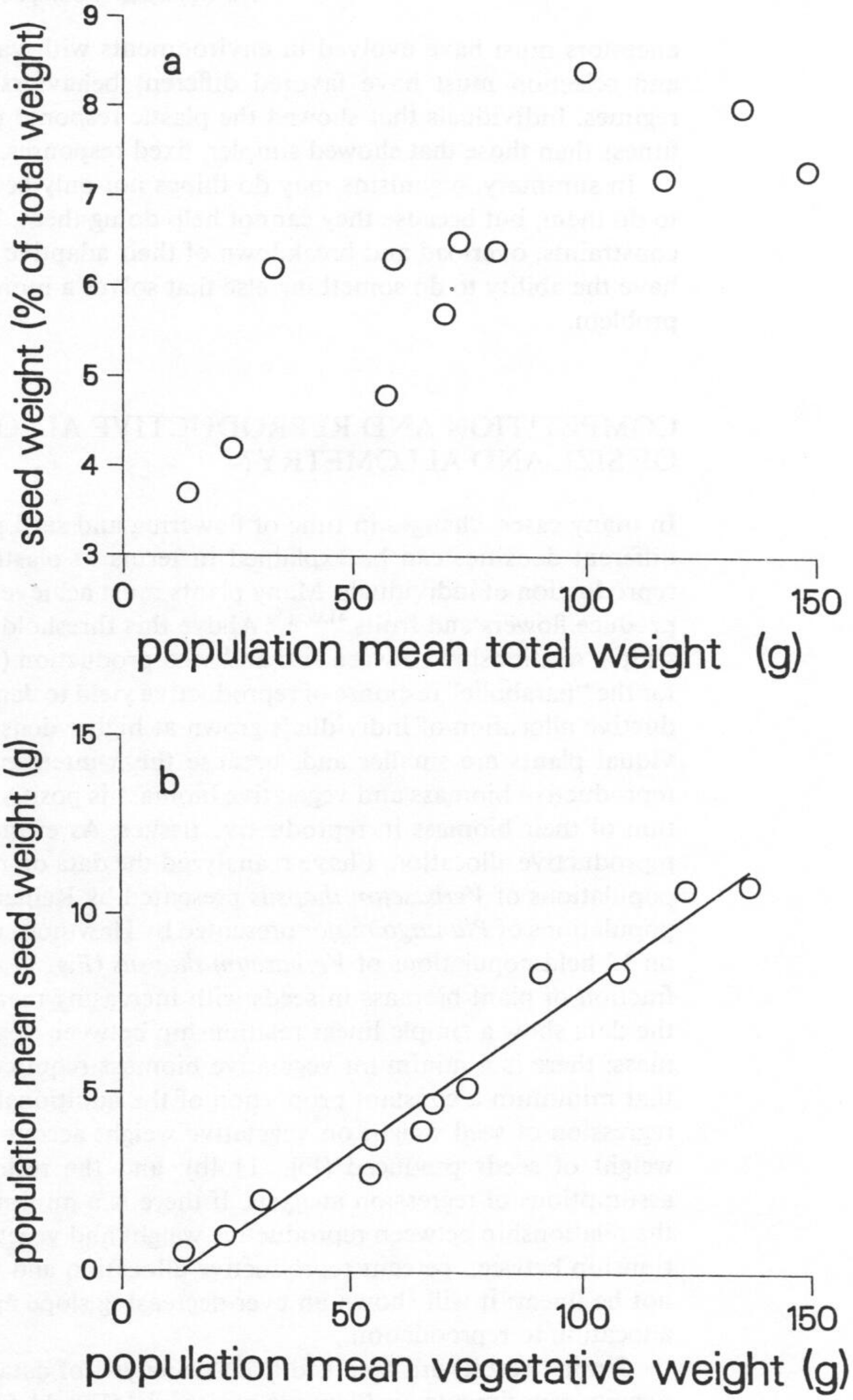

Fig. 11.4. (a) Relationship between mean total plant weight and the mean percentage of dry matter in seeds in 12 field populations of *Verbascum thapsus* from North America (after Reinartz[50]). (b) Same data replotted as mean vegetative plant weight versus mean seed weight ($r^2 = 0.96$).

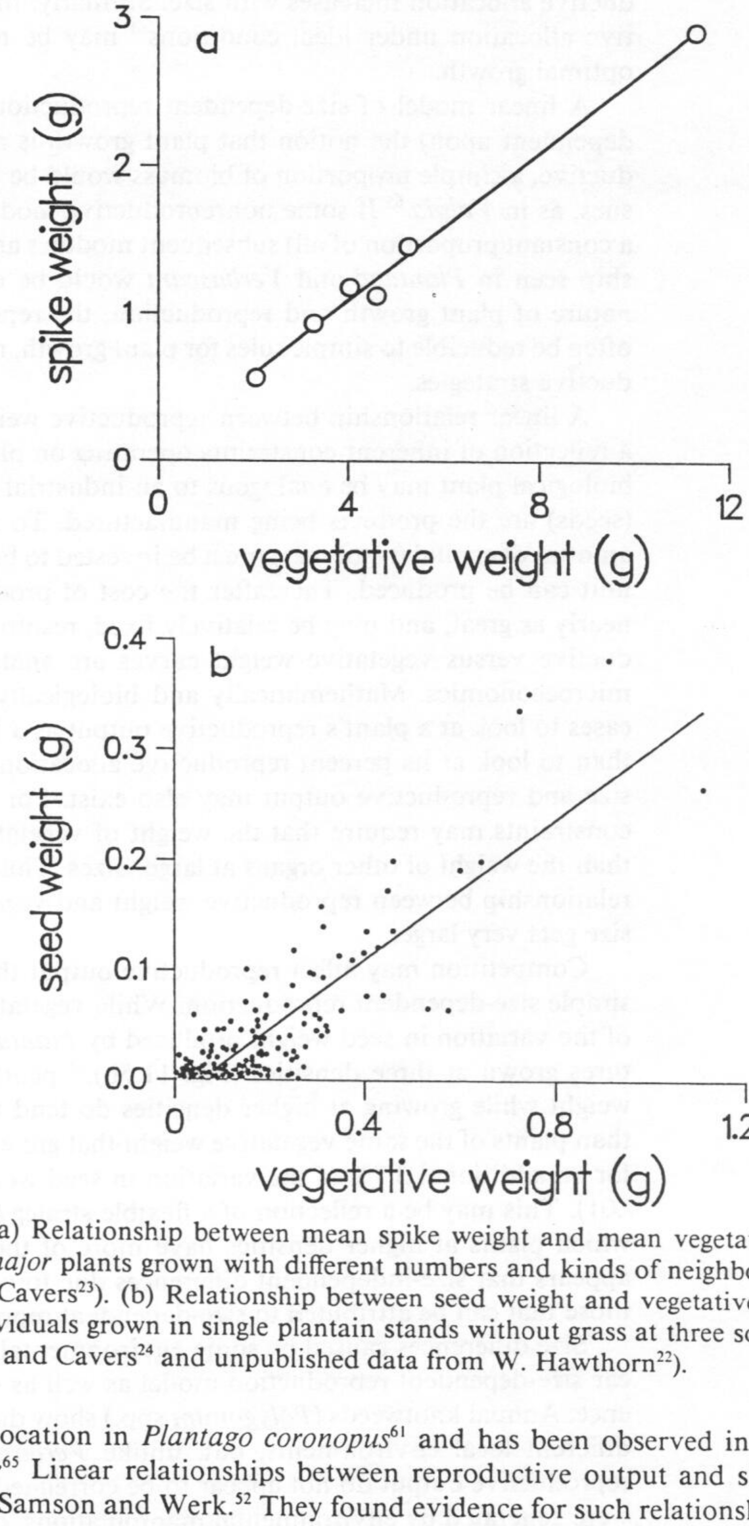

Fig. 11.5. (a) Relationship between mean spike weight and mean vegetative weight for *Plantago major* plants grown with different numbers and kinds of neighbors (after Hawthorn and Cavers[23]). (b) Relationship between seed weight and vegetative weight for *P. major* individuals grown in single plantain stands without grass at three sowing densities (Hawthorn and Cavers[24] and unpublished data from W. Hawthorn[22]).

ductive allocation in *Plantago coronopus*[61] and has been observed in several other studies.[25,63,65] Linear relationships between reproductive output and size have been studies by Samson and Werk.[52] They found evidence for such relationships in 18 species of desert winter annuals, and in published studies on 8 annual and 4 perennial species.

Changes in reproductive allocation with size may be seen in terms of simple allometric relationships. Since there is a minimum size for reproduction, percent reproductive allocation increases with size. Similarly, the concept of maximum reproductive allocation under ideal conditions[60] may be nothing more than a reflection of optimal growth.

A linear model of size-dependent reproduction is consistent with (although not dependent upon) the notion that plant growth is modular. If all modules are reproductive, a simple proportion of biomass would be expected to be in reproductive tissues, as in *Vulpia*.[65] If some nonreproductive modules are produced first, and all (or a constant proportion of all) subsequent modules are reproductive, the linear relationship seen in *Plantago* and *Verbascum* would be expected. Because of the modular nature of plant growth and reproduction, the reproductive behavior of plants may often be reducible to simple rules for plant growth, rather than complex, flexible reproductive strategies.

A linear relationship between reproductive weight and vegetative weight may be a reflection of inherent constraints operating on plant growth and reproduction. The biological plant may be analogous to an industrial plant, a factory in which offspring (seeds) are the products being manufactured. To build such a factory, a significant amount of capital (resources) must be invested to build machinery, etc. before the first unit can be produced. Thereafter the cost of producing each additional unit is not nearly as great, and may be relatively fixed, resulting in a linear relationship. Reproductive versus vegetative weight curves are analogous to marginal cost curves in microeconomics. Mathematically and biologically, it may be more useful in most cases to look at a plant's reproductive output as a function of size or other variables, than to look at its percent reproductive allocation. Nonlinear relationships between size and reproductive output may also exist. For woody perennials, biomechanical constraints may require that the weight of vegetative support tissues increase more than the weight of other organs at larger sizes. Thus, we might expect the slope of the relationship between reproductive weight and vegetative weight to decrease as plant size gets very large.

Competition may affect reproductive output through mechanisms in addition to simple size-dependent reproduction. While vegetative weight alone accounts for 72% of the variation in seed weight produced by *Plantago major* individuals in monocultures grown at three densities (Fig. 11.5b),[22] plants that achieve a given vegetative weight while growing at higher densities do tend to have slightly lower seed weight than plants of the same vegetative weight that grew at lower density. Density accounts for an additional 3.7% of the variation in seed weight produced by individuals ($p < .01$). This may be a reflection of a flexible strategy or constraints on growth through which plants at higher densities have more of their weight in vegetative tissues. It appears that size-independent differences due to competition are small compared to those that can be attributed to size-dependent reproduction.

Size differences caused by some environmental factors may not always fit the linear size-dependent reproduction model as well as size differences caused by interference. Annual knotweeds (*Polygonum* spp.) show differences in reproductive output in different local environments, but, unlike *Verbascum thapsus*, these differences in reproductive output do not appear to be correlated with size.[26] When size differences were generated by environmental manipulations, only 56% of the variation in reproductive weight of *Diplacus auranthiacus* stems could be accounted for by differences in size. Shaded plants had greater vegetative weight than plants that were watered or fertilized, but the former group showed lower reproductive weight.[4] This could be because the levels and ratios of mineral nutrient, light, and water have direct physiological effects on growth and development (e.g., nitrogen surplus will increase growth and suppress flowering). Density does not change the relative concentrations of these resources available to the population, rather, it determines the number of individuals among which these nutrients will be (equally or unequally) divided. Pitelka et al.[44] have argued that it is not size but the accumulation of some critical store of resources (or the attainment of a physiological state indicating that adequate resources will be available) that determines if *Aster acumunatus* plants flower. Pitelka et al. used height as a measure of size and evaluated reproduction in percent allocation. But a regression of mean reproductive weight versus mean vegetative weight for the different environmental treatments accounts for over 70% of the variation in reproductive weight (and it accounts for 80% if the one case in which reproductive allocation was not significantly different from zero is excluded). The correlation between number of flower heads per ramet and ramet weight is 0.96. If the resource being stored before a plant will reproduce is photosynthate, the level of accumulation will be reflected in plant weight, although not necessarily plant height. In plants, size may be a measure of stored resources, and an indication of future available resources.

If reproductive output is a function of size, the allometric relationship between vegetative weight and reproductive weight may be considered as an essential part of the plant's reproductive strategy. Different life histories may be a reflection of different reproductive allometries, which are the products of natural selection. This may be true whether or not the allometric relationship between size and reproductive output is as simple as it appears to be for *Plantago coronopus* or *Verbascum thapsus*. Alternatively, different allometries may be the result of constraints imposed by different growth forms, and may be merely satisfactory, rather than optimal.

As discussed above, the effects of density on reproduction may be closely related to the time and rate of growth and development. As plants grow, at any given point they will have a certain size and a certain reproductive yield (Fig. 11.3). At higher densities plants may grow more slowly and they will have a smaller size, and therefore be at a point of lower reproductive allocation than plants grown at lower density for the same period of time. There is considerable evidence[15,56,71] that fecundity and other demographic parameters are better viewed as functions of size rather than age. Thus, within limits, if plants growing at higher densities are given a longer period to develop so that they could achieve the same size, they might show reproductive behavior similar to plants grown at low density for a shorter period. Ideally, one would like to compare the effects of density at equal mean plant weights, as well as equal time for development. At high densities, however, high mean plant weights cannot be achieved because of the constraints imposed by density-dependent mortality. Also, even if high- and low-density populations show similar size-dependent reproductive allocation, density may change the population size structure and therefore the distribution of reproduction among individuals within the population.

Hypotheses based upon flexible strategies may yield the same predictions as an allometric hypothesis. For example, Hickman[26] has suggested that competition may result in more assimilate being allocated to structures that increase competitive ability, leaving less assimilate for reproduction. While the allometric approach has the advantage of simplicity, if weight-independent changes in energy allocation in response to density can be demonstrated, this would provide strong support for an hypothesis of flexible reproductive strategy. Hutchings and Waite[30] see the effects of competition on the timing of reproduction in *Plantago coronopus* as independent of the effects of competition on size. They looked at life history in *Plantago coronopus* as a function of the proximity of neighbors, as measured by nearest neighbor distance, mean distance to several neighbors, and area of Thiessen polygons based upon neighbor locations. They found that individuals that had fewer and distant neighbors tended to reproduce earlier than those with more and close neighbors. Plants that failed to reproduce had the smallest territories. They report that these differences in phenology could not be attributed to differences in plant size as measured by rosette diameter, although they present very little data on size differences and rosette diameter is probably not a good measure of size. Even if a plant's response to neighbors is a reflection of an evolved, flexible reproductive strategy, plant size may be the mechanism through which variation in environmental conditions (including neighbor proximity) is detected and translated into variation in reproductive behavior.

Future research into the effects of competition (or other factors) on plant reproduction should (1) include data on individuals of different sizes, (2) emphasize reproductive output, rather than allocation, and (3) look at size-dependent effects. Such data may help us to distinguish between nonadaptive responses, simple size-dependent effects, and flexible reproductive strategies.

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