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Annual Review of Ecology and Systematics, Vol. 11. (1980), pp. 411-452.

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THE ECOLOGICAL AND GENETIC CONSEQUENCES OF DENSITY-DEPENDENT REGULATION IN PLANTS

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INTRODUCTION

Plants stand still and wait to be counted.

J. L. Harper (1977)

Understanding the mechanisms of population size regulation is of vital importance to both the pure and applied ecologist. Throughout the history of ecology one school of thought has maintained that populations of plants and animals are in some way regulated by “density-dependent factors”—i.e. processes that either increase mortality or decrease fecundity as the density of the population increases (133). Thus there would be a density-dependent feedback that holds the population within certain limits. A second school of thought has maintained that “density-independent factors” (e.g. weather conditions or disturbance) are more important in determining population size.

Whether populations are regulated by density-dependent or density-independent factors has been the subject of intensive debate and controversy over the past twenty-five years, especially in the zoological literature (10,

41, 146). In part, the basis for this controversy may lie in different spatial and temporal scales of reference, as well as in differing expectations about the presence of equilibrium vs nonequilibrium states in natural populations (37). Yet much of the controversy stems from a lack of adequate information about density-dependent regulation, particularly with regard to its frequency of occurrence, intensity, spatial pattern, and interactions with density-independent factors. Technical problems in censusing populations, particularly those of animals, and in studying the operation of the phenomenon itself contribute to the paucity of information. Paradoxically, density-dependent factors may operate during seasons when population numbers are low, as when the regulating force is the number of refuges or "safe-sites" available to tide the population over the harsh season. The operation of density-dependent factors may be sporadic, will interact with density-independent factors, or (in populations undergoing unpredictable fluctuations in time and space) may only be one component necessary for the continuing long-term persistence of those populations (37). Indeed, such fluctuating populations have been cited as paradigms of density-independent regulation (e.g. 9).

The tractability of plants for population studies contrasts markedly with that of animals. As a consequence, future understanding of the nature of density-dependent regulation, and of its mode of operation with regard to predictability, spatial and temporal scale of action, severity, and biological basis, is likely to come from studies on plants. A clearer understanding of the ecological, genetic, and evolutionary consequences of different kinds of density dependence is also likely to be forthcoming.

This review describes the manifold causes and consequences of density-dependent regulation, formulates new conceptual frameworks for their study, and offers a predictive synthesis of ecological genetics as related to plant density. This synthesis will, we hope, stimulate further research on the process of density regulation. We review density-dependent processes in natural populations; studies on experimental and agricultural plant populations have recently been reviewed extensively by Harper (76). We focus on natural plant populations, but many of the concepts developed here are equally relevant to animal populations, though perhaps harder to apply in practice.

DENSITY-DEPENDENT REGULATION IN NATURAL POPULATIONS

Density dependence in natural plant populations is poorly documented, presumably because plant population biology is still a young science. We first consider the evidence from descriptive studies, much of which is of

necessity circumstantial. We then examine the more rigorous lines of evidence from perturbation experiments.

Intraspecific Competition

DESCRIPTIVE STUDIES *Neighbor effects* One of the most important density-dependent effects is competition among individuals of the same species. In sessile organisms such as plants, competition for resources occurs primarily between closely neighboring individuals (132). Thus in any population that is not uniformly dispersed, the effective density experienced by an individual depends on the number, size, and position of neighboring individuals. In this situation we may expect several outcomes: (a) Where competition results in plants of different sizes, plant size and distances among individuals will be positively correlated. (b) Where competition results in mortality, either the overall spatial pattern will shift to a more regular (over-dispersed) distribution or there will be fewer individuals than expected by chance in the immediate proximity of other individuals.

These effects have been documented in natural populations. Pielou (155) showed a positive correlation between the distance between nearest neighbors and the sum of the diameter of trees in a population of *Pinus ponderosa*. A similar relationship was obtained in a mixed population of *Pinus ponderosa* and *Pseudotsuga menziesii* (156), though in this study intraspecific neighbors were not distinguished from interspecific neighbors. Yeaton & Cody (244) showed a significant correlation between log of photosynthetic surface area and distance between individuals in the desert cacti, *Opuntia acanthocarpa* and *O. racemosa*, and between an index of plant size and distance between individuals of *Yucca shidigera*. Similar correlations were present in *Larrea tridentata*, *Franseria deltoidea*, *Carnegiea gigantea*, *Opuntia fulgida*, and *Fouquieria splendens* from an Arizona desert (243) and in *Acacia caven* from a Chilean savannah (73).

Over-dispersed plant distributions as the outcome of competition among individuals have frequently been observed among desert plants (21, 25, 87, 109, 238). Shifts from clumped to random, or from random to over-dispersed distributions have also been detected when populations were followed over a season or over a number of years. Thus Hutchings (95, 96) showed that shoots of *Mercurialis perennis* commenced growth in a clumped distribution that then moved towards a random distribution throughout the season. Similar trends were observed by Kitamoto (110) in *Solidago altissima*. Shifts toward a spaced distribution pattern in populations over a number of years have been observed in two stands of *Ceanothus megacarpus* studied over twelve and sixteen year periods (183), in a number of species of forest trees over a thirty year period (42), and in stands of the

sand pine *Pinus clausa* (115). That the scarcity of close neighbors in a plant population might indicate a mortality effect of competition has been discussed by Pielou (157), who failed to find such an effect in a pure stand of *Pinus ponderosa*, but did find the effect in a pooled population of *Pinus ponderosa* and *Pseudotsuga menziesii*. Both populations had previously shown evidence of competition in correlations between plant size and distance between neighbors (156, 157). Skellam (191) showed trends toward a scarcity of close neighbors in a population of *Plantago major*. The most direct demonstration that neighbor effects can influence mortality comes from the work of Sagar (cited in 76), who showed that the survival probability of *Plantago lanceolata* seedlings was decreased if they were growing near mature individuals.

Unfortunately, the evidence for density effects obtained by plant population mapping is at best circumstantial, since the effects of spacing may be confounded with microenvironmental differences. Thus plants growing in poor conditions may be small and have a low survivorship, yet be far apart; while those growing in good conditions may be close together, but large and with a high survivorship. Such a positive relationship between density and survivorship was found in a series of naturally occurring stands of *Vulpia fasciculata* (225). Perhaps a more serious problem with neighbor analyses is that failure to find a positive relationship between size and spacing may be readily dismissed by invoking confounding effects of site differences: Failure to find density-dependent effects tells us nothing about whether such effects are really present or not.

Density effects Comparisons of plant size and population dynamics in plots or sites of different density can be another source of evidence for density-dependent effects, but again the confounding effects of possible microenvironmental differences among sites make clear interpretation difficult. Thus a two year study of *Ranunculus repens* (180) showed a negative relationship between the life expectancy of ramets and the density of plants at different sites on a grazed pasture. Yet a continuation of this study over an additional two year period (I. D. Soan, personal communication) showed a reversal in the relative densities of some of the study sites that was not reflected in reversal of the relative risks of mortality. The difficulties inherent in interpreting between-site differences are further illustrated in the case of *Spergula vernalis* on a dune system in Poland, where Symonides (203) studied populations from 5 sites. At each site he subdivided a 10 m² area into one hundred 1 m² quadrats. He then examined the relationship between density and plant weight among the hundred quadrats at each site. This relationship was strongly negative in three of the sites and strongly positive in two others. The sites where the density/weight relationship was negative

had about twice the density (20 plants/0.1 m²) of those where the relationship was positive. Yet the effect was not one of density alone since densities overlapped considerably in the quadrats within the high- and low-density sites. It is clearly possible to explain away the results by invoking density dependence in the three high-density sites but microenvironmental differences in the low-density sites. From such data the correct alternative cannot be determined.

Evidence from site differences must therefore be regarded with a fair degree of skepticism. Nevertheless when numerous sites are compared, and particularly when support for density effects comes from additional lines of evidence, then demonstrations of negative relations between density and plant size or reproductive output can be convincing (225).

In a relatively pure stand, further evidence for the effects of density can be inferred if the log plant weight/log density approximates a slope of -1.5 as predicted by the self-thinning law (76, 79, 231, 245). Evidence that this law operates in natural populations was first cited by Yoda et al (245). Numerous stands of *Plantago asiatica* investigated at two different localities and on different dates all closely fitted the expected -1.5 self-thinning line. A similar relationship was found in the herbaceous species *Erigeron canadensis*, *Ambrosia artemisifolia* *elatior*, *Amaranthus retroflexus*, and *Chenopodium*. Other workers have found the same relationship in pedunculate oak (22), *Prunus pennsylvanica* and *Abies balsamea* (136), *Ceanothus megacarpus* (183), and *Pinus* spp. (153). In all these cases the presence of intense density effects was further supported by observations of overcrowding and death.

The thinning law almost certainly does not apply to single species considered singly within mixed stands (24, 106) and, therefore, cannot be used as supporting evidence for density effects in complex communities. Nor does the law appear to apply to natural populations of ramets of plants with clonal growth. Hutchings (96) showed that in nine clonal species, as the size of the ramets increased throughout a growing season their number decreased (see also 97, 135). The precise relationships were complex and species-specific, as might be expected where the units undergoing self-thinning are not physiologically independent.

That greatest mortality often occurs during periods of most rapid growth might be construed as evidence for density effects, since then the effects of competition for resources are likely to be most severe. This relationship has been reported in two populations of *Plantago lanceolata* in grazed grassland (76), in *Plantago major* and *P. rugelii* from old fields (83), in *Anthoxanthum odoratum* on a zinc mine (12), in *Ranunculus repens*, *R. acris*, and *R. bulbosus* from a pasture (180), and in *Plantago lanceolata* from a coastal dune grassland (227). Such evidence for density dependence is clearly very

circumstantial, however, since during active growth periods plants may also be subject to greater mortality from predators or pathogens (which may or may not act in a density-dependent manner).

Density may influence the progression of plants through various developmental stages. Symonides (204) studied the phenological development within five annual dune species growing at three different density levels. The time of seedling emergence and the duration of the seedling phase depended primarily on weather conditions, and afterward the increase in density was accompanied by an acceleration of the developmental phases preceding flowering and a shortening of the life cycle. The shorter the life cycle of a species, determined by its biological properties, the more pronounced the phenological acceleration. Acceleration of development in high-density populations of annual plants also has been observed by Palmblad (151a). In contrast to ephemeral annuals, the phenological reaction of biennial and perennial plants to overcrowding is an elongation of the life cycle and the retardation of successive phenophases (130, 151a, 168).

An acceleration in development and concomitant earlier flowering period in density-stressed annuals may have important ramifications for seed-set if the shift in flowering draws a population away from its pollinators in time. For example, Rust & Clement (177) estimated that the probability that a *Collinsia sparsiflora* flower would be cross-pollinated by bees in an early flowering population was 0.40 versus 0.62 for mid- and late-season blooming populations. In general, early flowering populations may be at a disadvantage because of competitive relationships with other species or because the prime pollen vectors are sparse or absent (86, 138).

PERTURBATION STUDIES "Clearly, one could not demonstrate density dependence in a population which was exactly numerically constant" (142). Because site effects may be confounded with density effects, descriptive studies provide at best only circumstantial evidence for density dependence. Where such descriptive studies include a detailed demographic component, the circumstantial evidence for density dependence may be very strong (e.g. demonstration of changes in pattern among different age classes), yet since confounding effects are still present, quantifying the spatial and temporal scales of these effects remains difficult. It has become increasingly apparent that precise demonstration and quantification of density-dependent effects requires manipulation or perturbation of the density of natural populations (30, 75, 142, 202).

Removal experiments Watson (227) removed *Plantago lanceolata* from a 5 X 0.5 m strip of dune grassland during the course of sampling individuals for a genecological study. An adjacent strip was left undisturbed. The strip

where the plants were removed was only partially recolonized and therefore a population was reestablished at a much lower density. Plants in both the removal strip and the undisturbed strip were mapped at three-monthly intervals for over two years. In the low-density strip the plants had a much greater survivorship, and somewhat greater fecundity, than in the adjacent high-density strip. Putwain & Harper (166) studied the effect of adding seeds of *Rumex acetosella* and *R. acetosa* to areas where adults of these species had been removed by spot herbicide treatment. Establishment of seedlings was significantly greater in plots where *Rumex acetosella* had been removed than in those where they had not. Removal of adults appeared to have no effect on establishment of *R. acetosa* from seed.

Addition experiments Two approaches are possible with addition experiments. One can measure either the demography of individuals added to populations of different densities or the performance of the existing population following addition of individuals. The former approach was used by Fowler (62) in a study of the survivorship and reproduction of *Plantago lanceolata* and *Salvia lyrata* seedlings transplanted into a mown field in areas with different background densities of the two species. Rates of transplant survivorship and reproduction were lowest in areas where the background density of the conspecifics was high; they were highest in areas where initial density was low but natural invasion also occurred. Although the treatments were not replicated, very similar responses were seen in both species. See also (225).

Increasing and decreasing densities Watkinson & Harper (225) thinned existing field populations of the sand dune winter-annual *Vulpia fasciculata* at the seedling stage and added seed to other plots to provide an extremely wide range of densities. The results showed marked density dependence with regard to number of seeds per plant, but relatively little with regard to survivorship. The values for these experimental plots of *Vulpia* were remarkably congruent with those obtained from naturally occurring plots of various densities. From these density-response data, Watkinson & Harper (225) constructed a model of density-dependent regulation that predicted seed-to-adult survivorship. The values observed in the field corresponded closely to those predicted from the model.

DENSITY-DEPENDENT REGULATION IN EXPERIMENTAL POPULATIONS An experimental plant population biologist, unfamiliar with the literature on natural populations, would be incredulous that there could still be question about the importance of density-dependent effects in nature. The ease with which plants can be grown at different spacings and the relevance of such studies to agricultural and forestry practice have resulted

in a wealth of studies, all of which have shown that density can drastically affect growth, mortality, and reproductive output. The many examples have been extensively reviewed by Harper (76), and it will suffice here to summarize the major generalities to emerge from such experiments, and to emphasize points of relevance to later discussion.

In experiments where plants are grown over a range of densities, three or perhaps four phases in the response of the population to density can be recognized. These phases also reflect a time course of behavior of individuals within a single pure stand as they increase in size from seedlings to adults.

1. *Low-density phase.* At extremely low densities, individuals do not compete for resources. Increasing density has no effect on dry weight per plant but results in a direct linear increase in yield per unit area.

2. *Medium-density phase.* Plants generally respond to moderate density by a reduction in growth rate (and consequent reduction in size and reproductive output). Such "plastic responses" are seen as a decrease in dry weight per plant with increasing density. Yield per unit area rapidly approaches a constant value, equivalent to the "carrying capacity" of the area under consideration [see (49) for formal comparison with K]. Such a plastic response can be approximated (49, 76, 187) by a density/yield relationship of the form:

$$(1/w) = A\rho + B,$$

where w = weight per plant, ρ = density of plants sown, and A , B = species-specific constants. This has been termed the "density effect law" (187). At high densities (such that the value of B is relatively small), this relationship gives a line of slope of about -1 when log weight per plant is plotted against log of density.

3. *High-density phase.* At high densities mortality effects become important. Mortality due to density effects within a pure stand has been termed "self-thinning." This response may not be evident when yield per unit area is plotted against initial density, since overall yield often remains constant in spite of mortality within the stand. Only when we plot plant size against the density of *surviving* plants do we find a different relationship—the "3/2th power law of self-thinning" (245) such that:

$$w = C\rho^{-3/2}$$

where w = weight per plant, ρ = density of *surviving* plants, and C = a species specific constant.

This relationship applied for a large number of experimental populations (76, 231, 245) and for several natural populations (see previous section).

The three phases of density effects and some exceptions are well documented (76). A fourth phase reflects the effects of high density on seed

output, but this is not well understood (particularly in biennial and perennial species). Extremely high densities may suppress flowering and seed production while producing no reduction in dry weight yield per unit area. This response was described in the "biennial" *Digitalis purpurea* by Oxley (cited in 76) and in the perennial *Tussilago farfara* by Ogden (cited in 76). In annual plants, high-density effects on reproductive output per unit area may well be less marked.

"Safe-sites" (i.e. locations ideal for germination and establishment) also may be a function of density (80). Given that they are about the size of a single seed, the occupation of such sites will be analogous to a system of sampling without replacement, the probability of occupancy being determined by the hypergeometric distribution. Occupation of sites reduces the number available for the remainder of the population. The greater the density of seeds falling on an area with a certain number of safe-sites, the less likely it is that a particular seed will land in one. The resulting density response has never been quantified, but will probably be a simple function of number of safe-sites and number of seeds. Alternatively, we may readily imagine safe-sites that permit the germination of more than one seed, especially if the seeds are small. Under such circumstances, intensive competition will ensue among the seedlings within a site, resulting most often in thinning to a single plant or to one dominant and a few suppressed plants. Given that safe-sites are discontinuous, dense multiple germination in safe-sites may be followed by one episode of thinning early in development, and another later as the plants from different microsites begin to interact.

In contrast to the attention given to the importance of density-dependent factors in determining the fate of established plants, scant attention has been given to the effect of seed density upon germination. Ballard (19) and Palmblad (151a) reported both positive and negative response to sowing density among certain weedy species. Based on his own tests of 11 species and on tests of 11 other species reported in the literature, Linhart (129) found that positive density-dependent responses appeared to be characteristic of species of closed habitats, while neutral or negative responses occurred in weedy species of open habitats. Recently, Waite & Hutchings (222) reported that germination and salinity tolerance of *Plantago coronopus* seeds are enhanced when seeds are sown in clumps. The extent of the positive density-dependent response, and the optimum clump size for maximum germination are dependent on the salinity level and the nature of the substrate. Symonides (205) found neutral responses to seed density in three dune annuals.

Factors responsible for density-dependent seed germination may involve the release of germination stimulants by germinating seed, or differences in the movement and absorption of water and ions (222). The adaptive advantages of a positive density-dependent germination response are diffi-

cult to envision since it will lead to high levels of seedling competition. However, some possible advantages include stabilization of the seedling microenvironment, facilitation of root penetration in hard soils, and occupation of favorable microsites to the exclusion of other species (129). The density effects noted above occurred under laboratory conditions. The issue of prime importance is whether seed clumps in natural seed banks germinate in a density-dependent manner.

Interspecific Competition

In single-species stands, density-dependent reduction in survivorship and/or mortality is the result of a decrease in resources available per individual with increasing density. How the presence of another species influences population regulation is frequently misunderstood, so much so that interspecific competition is often quite erroneously equated with a density-dependent effect. This is most easily seen if we consider that the total amount of resources available to, say, species A, may be reduced by the presence of another species, B. This, of itself, is not a density-dependent effect since the amount of resources removed from the system in no way relates to the density of species A. The presence of heterospecifics becomes a density-dependent effect only if the intensity of competition (i.e. the proportionate effect of species B on the survivorship and reproduction of species A) increases with increasing density of A. Otherwise, the presence of species B may simply lower the survivorship and reproductive output of species A in a manner analogous to a density-independent abiotic factor. If so, regulation will be the result of an intraspecific density dependence.

The demonstration of interspecific competition in natural populations therefore tells us little about density-dependent processes. We need to know whether competition effects become more severe with increasing density; otherwise a purely intraspecific perspective on density-dependent regulation will suffice.

Perhaps because its nature seems so obvious, competition among different members of a plant community has only been clearly demonstrated (let alone quantified) in a few instances. Plant ecologists have been reluctant to move beyond descriptive community analysis into perturbation analysis [for exceptions see (6, 61, 166, 188)]. Perturbation analysis by means of species removals or additions is an essential prerequisite for unambiguous demonstration of species interactions; otherwise it is impossible to say whether co-occurrence is due to the lack of competition or whether it leads to competition.

Because we know so little, it is impossible to clarify how competitive effects are density-dependent. Unfortunately, experimental systems give remarkably little insight into density-dependent regulation. Most competi-

tion experiments have held density constant, varying relative frequencies of the competitors and comparing yields in mixtures in relation to yields in pure stand. Such "replacement series" experiments provide an elegant basis for the analysis of competition (49); however, they are carried out at constant overall density and so provide insight into frequency-dependent, rather than density-dependent effects. To gain insight into the latter, the density of species A should be varied while the density of species B is kept constant. Calculating the yield of species A over a range of densities in the presence of species B, relative to the yield of A in pure stand at the same range of densities, would provide information on density-dependent changes in competition coefficients.

Experiments where density responses have been investigated with and without a background of associated species suggest that such approaches may be fascinating and fruitful. For example, Harper & Gajic (77) studied the density responses of *Agrostemma githago* in pure stand and in the presence of different densities of wheat and sugar beet. Whereas in pure stand the mortality rate was density-independent over a wide range of seed densities, the curves became density-dependent in the presence of the background species. Curiously, the greatest density-dependent effects were seen when beet was at low densities and wheat was at high densities. In other experiments where one species is kept constant and the frequency of the other is varied [termed "additive experiments" (76)], the density of the species measured is held constant while the density of surrounding individuals is varied. Such experiments are relevant in an agronomic context since they mimic a situation where a crop is subjected to different levels of weed infestation, but they are the reverse of what is required for an understanding of density dependence.

In a study of *Papaver* (78), one of the few where both density and proportion were varied, each species was grown at two densities against a background of every other species. In most instances (17 out of 20) the density response (as measured by a seed's chance of producing a mature plant) is either less or unchanged when the background species is at a high rather than low density. This suggests that the presence of the other species makes density-dependent effects less pronounced rather than more severe. Unfortunately, it is not possible to calculate competition coefficients because the appropriate pure-stand densities were not grown. Similar difficulties apply to the interpretation of other experiments where both density and frequency have been varied (29, 38).

We know little about density-dependent regulation and its interaction with interspecific competition in natural or artificial populations because we fail to conceptualize density dependence as a process in its own right and therefore as worthy of singular investigation. Moreover, most competition

studies have been carried out either explicitly or implicitly in an agricultural framework and not with a view to understanding regulation of natural populations.

Predators and Pathogens

Herbivores and pathogens may have a devastating effect on agrocommunities (especially monocultures) and natural ecosystems. The pathogen *Phytophthora cinnamoni*, for example, kills plants in 444 species in 131 genera of 48 families and has devastated complex forest woodland and heath communities on more than 100,000 hectares in western Australia (145, 230). In the Brisbane Range of Victoria, at least 50% of the common understory species were exterminated, as were 40% of the overstory species within a period of 6–8 months from species invasion by the pathogens. The fate of species subjected to intense pathogen or herbivore pressure is also illustrated by the success in controlling, and in some cases eradicating, weed species by biological control methods (8, 233, 237). Two spectacular examples among many of equal success are the destruction of over 60 million acres of *Opuntia* spp. in Australia by the imported moth, *Cactoblastis cactorum* (53) and the control of *Hypericum perforatum* in the western United States by the beetle *Chrysolina quadrigemina* (93).

Of all plant assemblages, agrocommunity monocultures are the most vulnerable to the ravages of insects and pathogens. These simple systems are so susceptible to the outbreaks of herbivores or epidemics of pathogens that sustained production is nearly impossible without extensive use of chemical pesticides (5, 99, 112, 113). Even recently introduced species may be severely damaged by organisms that had been previously inconspicuous on wild native plants (201, 215, 226).

Well-documented outbreaks of insects in the northern temperate and coniferous forests occur in areas where a single tree species forms extensive monocultures of even age. The spruce budworm, *Choristoneura fumiferana*, causes the most damage in pure, old stands of balsam fir (137, 214). Spruce budworm outbreaks are most frequent in high-density stands. The European pine looper, *Bupalus piniarius*, is much more destructive in pure pine stands than in mixed woods (56). Damage by white pine weevil, *Pissodes strobi*, is insignificant where its major host grows as a subdominant in mixed forests (67).

These trends appear to be characteristic of simple, natural communities as well. Thus in subarctic regions, where vegetational diversity is naturally low, outbreaks frequently occur in primeval forests (147, 184). The highly diverse forests of the tropics, on the other hand, are believed to be relatively free of herbivore outbreaks if the vegetation is not simplified by cutting (54, 218). Greater abundance and effectiveness of insect predators and parasites

plus a lower concentration of available food seem to account for lower herbivore pressure on plants of complex communities (160, 172, 173, 193, 217).

Epidemics in natural forest ecosystems are not infrequent but are limited in time and space by functional diversity of host, pathogen, and environmental parameters. The reduction of diversity through silvicultural practices often results in widespread epidemics or pandemics. For example, southern fusiform rust (*Cronartium fusiforme*), a rarity in forests before 1900, is now pandemic in loblolly and slash pine plantations through much of the southern pine forests (72, 198). The distribution and incidence of this pathogen have increased dramatically in recent decades, coincident with intensive forest management of southern pine (52).

"Where too many plants of one species are grown together, they are apt to be attacked by some pest, insect, or fungus" [Ridley, as quoted by Janzen (100)]. Root (172) formalized this notion in the form of a "resource concentration hypothesis": "Herbivores . . . are more likely to find and remain in a pure or dense stand of a host plant than in a sparse or diverse stand." The effects of density and diversity are often confounded in empirical studies because a reduction in diversity is almost invariably accompanied by an increase in the density of the remaining species (159, 206). The effect of density per se may also be confounded by total population size, which is usually a positive function of density.

Although we might expect higher density to be associated with higher levels of herbivory per plant, this seems not to be the pattern. Pimentel (160) showed that the density of herbivores in sparse plantings of *Brassica oleracea* was more than 5 times that in dense planting. Inverse correlations of density and herbivore numbers have also been described with aphids on field beans (228), kale and cocksfoot (4), and sugar beet (84), with lepidopteran larvae on *Aster umbellatus* (48), in *Brassica oleracea* (47) and *Pastinaca sativa* (212, 213), in cabbage white butterflies (102), and in rosette disease in groundnuts (47a). The agricultural literature shows that increased pest control has been achieved by increased crop plant density (2, 3, 94, 120, 223, 228).

Data on density-dependent grazing by large herbivores are fewer. Grazing of clover by pigeons was density-independent when clover leaves were above a certain density, but at very low densities grazing was clearly reduced (143a).

As far as pathogens are concerned, the incidence of infection and the rate of spread are not well understood. In *Lepidium sativum* the advance of damping-off disease in inoculated seedling stands is positively correlated with density (34, 36). The incidence of damping-off in pine seedlings is also positively correlated with density (65). Likewise, there is a positive correla-

tion between *Apium graveolens* density in experimental plots and infection incidence by *Cercospora* species (27). On the other hand, infection rate of rice blast disease is not dependent on host density (105, 111). Pielou & Foster (158) compared the incidence of *Armillaria mellea* in isolated and crowded Douglas fir trees and found that tree spacing did not affect the incidence of root rot. Bloomberg (31) found that isolated seedlings of Douglas fir were more prone to attack by *Fusarium oxysporum* than those in clumps.

Plant density also influences both microclimate within a plant canopy and the patterns of spore dispersal. Hirst & Stedman (89) found that as the density of potato populations increases, the microclimate is made more favorable for an epidemic of *Phytophthora infestans*. Dense stands of many crops reduce the wind speed enough to diminish the detachment of spores. Dense stands also tend to be warmer and have higher humidity, both of which inhibit spore dispersal (178, 220). The relationship between plant density and rate of spread of pathogens is poorly understood. When a density-dependent relationship is found we do not know whether to attribute it to host plant proximity or to the influence of the host on the microenvironment.

The developing or predispersed seed presents an especially nutritious food source for insects, and predation of these seeds is extensive. Platt et al (161) investigated the level of predispersal seed predation of *Astragalus canadensis* by curculionid beetle larvae. About 37% of the pods were attacked in high-density arrays, versus 61% in low-density arrays. A similar pattern was found for predispersal squirrel predation on ponderosa pine (117) and lepidopteran larvae predation on lupines (32). The effect of host-plant density on seed predation is not similar in all cases, as seen in the study of the interaction between *Asclepias syriaca* and the seed-sucking bug, *Onocopeltus fasciatus*. Ralph (169) found a significant positive correlation between bug and pod density at several sites; high bug density was associated with high levels of damage. A positive correlation between pod infestation and plant density was found by Vandermeer (216). The pattern of infestation and damage for postdispersal seed may be the converse for vegetative material and predispersed seeds. The survival probabilities of seeds are often greater in low-density arrays than in high ones (98, 100, 101, 124, 234). Seed density can also influence both foraging distances and extent of group foraging by ant species (28).

Pollinators

Pollen receipt will in turn be a function of, among other things, population density. Consider first self-incompatible zoophilous species. When pollinators forage they apparently "maximize" net energy and nutrient yields per

unit foraging time (124, 125, 167). Some, for example, exhibit flower constancy: individual pollinators forage within one plant species for a period of time (18, 64, 68, 86, 165). In a large population, where pollinators' rewards will not be depleted in a short time, the higher the density, the less the energy expended by pollinators to obtain the same caloric and nutritional reward, and thus the higher the level of flower constancy. Conversely, as density declines, the profitability of foraging upon a given species declines, and pollinators will seek alternative food plants (125).

Density-dependent flower constancy has interesting implications for interspecific cross-pollination. Given that a species of pollinator feeds from flowers of two cross-incompatible plant species that are obligate outcrossers and grow in mixed populations, the incidence of interspecific flights would probably be greater as the density of the joint population declined. Correlatively, pollen wastage would also increase and we may expect seed set per flower in both species to decline with decreasing density. If the two plant species were cross-compatible, differences in density might be accompanied by differences in hybrid seed production. The lower the density the greater the likelihood that a given seed will be hybrid. To our knowledge, the actual relationship between density and interspecific hybridization has not yet been explored.

Plant density and seed production per flower are often positively correlated. For example, seed production in *Astragalus canadensis* was about 20% higher in high density arrays than in low density ones within the same population (161). Within a population of *Cassia biflora*, seed set was positively correlated with density (189). The highest-density populations are not necessarily those with the highest percentages of fertilized eggs. For example, in *Phlox drummondii* seed set per flower is lower than the norm in populations with relatively high or relatively low densities (D. A. Levin, unpublished data). The lowest mean seed-set per flower is found in populations with few, but large, individuals. Competition for pollinator service between flowers on the same plant apparently reduces the level of interplant pollination compared to that when each plant has only a few flowers.

In wind-pollinated plants the amount of pollen deposited per flower is a positive function of the amount of pollen per volume of air, which in turn is a positive function of plant density (71, 170, 171, 200). As the density of a population declines, the density of the conspecific pollen cloud (and hence pollen deposition per stigma) also declines. These relationships have not been studied in a wide variety of species; the forestry literature provides the most substantive evidence (200).

We may ask also whether pollen density, through its effect on pollen-tube competition, influences the quality of seed produced. Ter Avanesian (207–210) pollinated two populations each of *Gossypium hirsutum*, *Vigna catjang*,

and *Triticum aestivum*, one with little pollen and the other with excessive quantities of pollen. The coefficient of variation among the resultant sporophytic generation was lower with large than with small pollen quantities. The influence of gametophytic selection on sporophyte quality has also been demonstrated in *Dianthus chinensis* (139) and *Petunia hybrida* (140, 141).

Conclusions

Both direct and indirect evidence indicates that density-dependent processes have an impact on natural plant populations. However, the evidence is sparse, often circumstantial, and primarily from populations of dominant or abundant species. Our greatest insights into the mechanisms of density dependence have come from the study of experimental populations. Generalizations such as the density-yield relationship of Shinozaki & Kira (187) and the self-thinning law of Yoda et al (245) have provided us with theoretical models with great synthetic and predictive potential. These empirically derived relationships emphasize that the classical Lotka-Volterra models of regulation, which have played such a large part in the development of theoretical ecology, are oversimplistic for plant populations because they fail to take into account individual plasticity and because they assume a linear relationship between density and number of offspring per individual. More realistic models based on generalizations about density response in experimental populations have recently been produced (224a) and are an important step for the development of models for natural populations.

The experimental studies have serious deficiencies in the context of the natural world. First, these experiments have been concerned predominantly with "yield" rather than with life-history parameters. In only a few of the studies is it possible to relate density of seeds sown and number of seeds produced per individual. Having such input/output data in comparable units is essential for the development of recursive models of population growth and regulation [cf (225), where such a model was developed for a natural population]. Second, the emphasis on a high degree of replication and "tidy" experimental designs in density experiments has resulted in accurate estimates of performance at a few but not at a wide range of densities. It is imperative for predictive modelling that the general form of the input/output (seed sown/seed produced) relationship be obtained over as wide a range of densities as possible. Third, there have been no experiments on population growth over several generations, like those on *Tribolium* (152) or *Drosophila* (16).

With regard to the effects of heterospecifics on density-dependent regulation, little information exists either on how the density response of a particular species is influenced by the presence of another species, or, more critically, on how competition coefficients vary with density in two- or multi-component mixtures.

The inadequacies of the existing literature on density dependence are by no means obvious, and they are therefore worth emphasizing as pointers to future research. Nonetheless, we can already visualize dimensions whereby the phenomenon of density dependence might be quantified. It is clear that density effects have a spatial aspect, a temporal aspect, and are themselves a function of the age or size of the individuals comprising the population. Regulation by intraspecific competition will occur on a much finer spatial scale than regulation by a highly dispersed pest or mobile predator. Moreover, there will be a limit to the distances over which such density effects are "felt." Thus one can manipulate density in different plots in the same general area (225) or even in adjacent plots (166, 227); yet these plots behave as essentially independent "populations." Thus Harper (76) has stated that "The fixed positions of plants makes it easier to think about distance, meetings, and neighbors than it is with animals. Neither plants nor animals react to the density of their populations, but to the effects of the number and proximity of their neighbors. The term 'density' is an abstraction removed from the level of cause and effect."

The temporal aspects of density-dependent regulation have rarely been considered explicitly in studies of natural or experimental populations (142). The response time to changes in density may be a matter of days, as in the greater mortality rate of seedlings germinating near existing adults, or it may be extremely slow and extend over many decades, as in the case of self-thinning during the growth of stands of forest trees. The responses of predators or parasites to increased plant density may be behavioral and rapid, or they may be relatively slow if they are contingent on the growth, reproduction, and subsequent increase in population size of the predator. There is every reason to expect that many combinations of temporal and spatial scales will be found in natural populations.

Density effects will be a function not only of numbers per se but also of the age and size of the individuals. For example, in most plants density effects may only become apparent as the plants increase in size or age. Or certain components of a plant's life-history may be subject to the action of one kind of density-dependent factor (e.g. seed predation) whereas other parts of the life-history may be subject to a quite different factor (e.g. interspecific competition).

We can therefore envisage the dimensions of age, size, and numbers interacting with a range of density-dependent factors at different spatial levels and at different rates. We can predict that these interactions will lead to a complex sequence of events where regulation is shunted from one factor to another, where the operation of one effect is induced (or retarded) by the operation of another, and where a population may be subjected either simultaneously or sequentially to a wide array of effects. Description and clarification of such complex situations are likely to be difficult, but we feel

they can be aided considerably by the introduction (in a later section) of two concepts: the ecological neighborhood area, and ecologically effective density.

GENETIC CORRELATES OF DENSITY

Gene Flow Within Populations

In both insect- and wind-pollinated plants, increased density usually results in decreased pollen dispersal and consequently decreased gene flow distances. In the case of insect-pollinated plants, the search distances of pollinators are smaller in a dense population as a result of behavioral adjustments of the insects, whose search patterns are determined by resource availability. Levin & Kerster (126, 127) have shown a highly significant linear relationship between plant spacing and mean bee flight distance for three populations in each of nine herbaceous plant species. Similar effects are likely in wind-pollinated plants. At higher densities, wind speeds will be reduced, and the pollen will be more likely to hit plant parts other than the stigmas. Few attempts have been made to quantify these density effects in wind-pollinated species.

In general it is therefore likely that as a population becomes denser, pollen dispersal distances become smaller. This has two consequences. First, given that near neighbors may be closely related (55, 182), the levels of inbreeding will rise, and inbreeding depression effects may be evident (162). Second, the neighborhood size (i.e. genetically effective number of individuals) will not be a direct function of increasing density. Indeed it has been argued (126) that because of the offsetting effects of increased density on decreasing gene flow distances, the neighborhood size may not change with plant density.

The effects of density on gene flow by seed dispersal are less well understood. Where seeds are wind-dispersed, general principles similar to those for pollen dispersal probably apply: Increased density may result in decreased dispersal because of reduced windspeed, increased probability of impaction, or decreased plant size (224b). Where seeds are dispersed by frugivorous birds (91, 154), high postdispersal densities may occur around fruit bearing trees, near perch sites, and on migration routes between trees. Where seeds are dispersed by fruits that become attached to animals, the distance a propagule is carried will be a function of probability of attachment to the animal, the saturation limits for attachment sites on the animal, the distance the animal travels, and the probability that the propagule will eventually be dislodged or fall. Pioneering approaches to quantifying these aspects have been made (33, 197). Fruits may be more easily dislodged in stands of a different species than in stands of the species producing those

fruits (33). This will lead to a higher probability of dispersal away from high-density patches, and hence to an "overdispersed" rather than clumped distribution of propagules. In general, we know little about the quantitative aspects of seed dispersal in plants, and even less about how such dispersal distances are related to density.

Pollen- and seed-dispersal schedules may be influenced directly by the impact of density on stature. As a consequence of intraspecific competition, plants in high-density arrays may be substantially shorter than those in sparse arrays. Differences in stature are important for airborne pollen and seed flow because the distance traveled by these units is a function of the height of reproductive structures. The greater the elevation, the greater will be the mean and variance of the dispersal distance, and the longer will be the tail of the distribution (71). A significant fraction of a pollen cloud may be expected to travel more than 10 times source height (70). Seed dispersal distances would be more difficult to predict because of the various dispersal adaptations. For the genera of Compositae with a plumose pappus, a 3-fold increase in plant height may be accompanied by a 2-fold increase in maximum dispersal distance under a given set of wind conditions (186).

Gene Flow Among Populations

Because of the reduced gene flow distances with increased density, the propensity for microdifferentiation will be greater in high- than in low-density populations. Levin & Kerster (127) have remarked that "high-density arrays will be able to maintain many alleles at each locus at a moderate frequency and will resemble a graded patchwork in general structure . . . [that] bears a strong affinity to the structure which Wright [240a] deems most conducive to rapid evolution." Where there are contrasting densities in populations among which there is divergent selection and gene flow, absolute migration distances between the habitats may be asymmetrical, and "swamping effects" of gene flow from a habitat with a high plant density to another of lower density may retard genetic divergence of the latter (11, 13, 69). Such swamping effects may be severe even though dispersal profiles may indicate that dispersal per se decreases rapidly with distance. Conversely, high-density "pockets" will suffer much less from gene flow than dispersal profiles would indicate (66); as a consequence, high-density pockets may readily undergo genetic differentiation (46). For these reasons, density must be taken into account when quantifying the forces determining patterns of genetic divergence.

Effect of Density on Mating Systems

As density declines, a progressively larger proportion of pollen deposited on a stigma will be from the same plant. This is especially evident in

zoophilous and anemophilous trees that produce enormous amounts of pollen (15, 63, 181, 200). If a species is self-compatible but principally outbreeding, declining density will result in increased levels of self-fertilization. In cotton, for example, the outcrossing rate was about 25% when plants were grown close to each other, whereas it was only 4% when plants were grown 25 ft apart (190). Increased self-fertilization is likely to be accompanied by inbreeding depression as evidenced by increasing proportions of abnormal progeny. For example, in *Betula pendula* and *Betula pubescens*, the percentage of germinable seed declines as the percentage self-pollination increases (181). A broad spectrum of recessive lethal and harmful genes affecting newly germinated seedlings have been described in species of *Pinus*, and the frequency of expression of these increases as self-pollination and spatial isolation increase (20, 199).

If the species is largely self-incompatible, infrequent conspecific pollination in low-density populations may select for greater self-compatibility. This process may be important in the evolution of self-fertility in early flowering populations of *Leavenworthia* (131), pioneering populations of *Pinus ponderosa* (20), and in isolated tropical trees (17), in which connection the phenomenon has been termed Baker's Law.

Where a single genotype can become large, as in trees or clonally propagating species, the abundance of flowers on one genotype may severely limit pollinator movement away from that genotype, so reducing cross pollination in self-incompatible [e.g. *Asclepias tuberosa* (241)] or heterostylous [e.g. *Houstonia caerulea* (242)] species. In clonally propagating species, the impact of density on mating system can be properly quantified only if population density is expressed in terms of both genet (genotype) and ramet (physiological) individuals.

Density may influence the breeding structure of a population through its effect on development. In *Lithospermum caroliniense*, which produces obligately outcrossing (chasmogamic) flowers and obligately selfing (cleistogamic) flowers, the proportion of the seed production from self-fertilization is positively correlated with the density of this species in natural populations (123). The balance between sexual and asexual reproduction likewise may be influenced by density. Increasing plant density in natural population is accompanied by greater emphasis on asexual reproduction in *Tussilago farfara* (149), *Rubus hispidus* (1), *Hieracium floribunda* (211), and *Fragaria virginiana* (87).

In dioecious species, density may also affect the sex ratio. In a field experiment, Onyekwelu & Harper (150) found that the growth of male and female plants of the annual *Spinacea oleracea* was affected differentially by population density, males forming an increasing fraction of the population. In their low-density treatment (120 seeds per 50 × 50 cm plot), survivorship

was 55% and the sex ratio was roughly 1:1. In their medium-density treatment, survivorship was 38% and the ratio of males to females shifted to 1.5:1. In their high-density treatment, survivorship declined to 14%; however, the sex ratio remained at roughly 1.5:1. Natural populations of *Chamaelirium luteum* contain a greater proportion of males in high density areas (135b).

Genotypic Differences in Density Response

Most studies of intraspecific variation in density response have been carried out in an agricultural context. Varietal differences in response to spacing have been investigated with a view to determining optimum planting density (23, 45, 57, 60, 103, 104, 116, 144, 164, 176, 185, 239). In forage crops, performance of plants grown as spaced individuals was compared with that in swards (119, 174). The implication of genotype-density interactions in plant breeding have been discussed by Lazenby (118). Most agronomic studies have been limited, in terms either of the range of spacings and characters measured, or of analytic detail. Many studies have gone little beyond demonstrating the existence of a significant genotype-density interaction component in spacing or seed-rate trials.

Khan & Bradshaw (108) showed large varietal differences in density response; in general, seed yield showed a greater response to spacing in linseed than in flax. This could be related to the fact that linseed has been bred for seed production under relatively wide spacing, while flax has been bred for fiber production under close spacing. Similar large varietal and character differences in density response were observed in soybeans (88). Fery & Janick (60) compared various density-response models to observed density responses of different corn varieties. Response to spacing was shown to be highly heritable in flax and linseed (107).

Studies on density response differences among genotypes within natural populations, or among populations have been far fewer. Antonovics (14) demonstrated genetic changes during self-thinning in artificial populations of *Plantago lanceolata*, which suggest differential mortality responses of genotypes to density. Genetic changes during self-thinning have also been demonstrated in artificial populations of *Phlox drummondii* composed of different cultivars and variants from natural populations (F. A. Bazzaz, D. A. Levin, unpublished). Differential mortality is implied in the rapid genetic changes in pastures following establishment from seed [see (195) for discussion]. Solbrig & Simpson (196) studied two apomictic biotypes of *Taraxacum officinale* from a single population and obtained evidence suggesting that biotypes from disturbed areas showed greater response to increased spacing than biotypes from denser stable areas.

THE ECOLOGICAL NEIGHBORHOOD

In this section we introduce the concept of an ecological neighborhood in order to discuss the way density effects influence ecological processes and the way they interact with genetic processes within populations. We first define an ecological neighborhood, then discuss its operationality and relationship to similar concepts, and finally consider how it can be interfaced with other ecological ideas.

Conceptualization

Consider an idealized population in which a large number of even-aged plants are uniformly spaced over an extensive homogeneous landscape. The interplant distance beyond which effects of density are absent may be referred to as the ecologically effective distance. With this distance as radius, we can draw a circle around a plant, outside which the effects of density are absent. This area will be designated the ecological neighborhood. Vis-à-vis a given density-dependent factor, all plants within the idealized population will have the same neighborhood area, and the density of the population as a whole will be termed its ecologically effective density. The ecologically effective area and density describe the highest densities that can be attained before a particular density-dependent factor begins to take its toll. At this point the number of plants per ecological neighborhood will be one. If higher densities are reached the number of plants per ecological neighborhood is increased proportional to the density. The greater the numbers per neighborhood, the greater the impact of regulatory factors. The numbers per neighborhood will be large in situations where adjustment to density is by plastic response in individual size, or where the effects of predators are not felt by impact on mortality but by impact on fecundity. Even where the impact of density is felt through mortality, the numbers per neighborhood will be large if the density-dependent processes are slow and their effects are as yet incomplete. Yet if density response is rapid and entirely by mortality then on average there may be only one individual per control area.

Consider a population whose density is below that which evokes a density-dependent response. Each plant would be within a neighborhood discontinuous from that of other plants. At higher densities, neighborhoods would be closer together; at a certain density they would touch, forming a continuum; at higher density neighborhoods would overlap, eliciting density-dependent responses from the plants. The area of the neighborhood would remain the same even though density varied. We can therefore visualize any species continuum as consisting of a series of overlapping circles, one per plant, such that plants with overlapping radii will influence each other

through density-dependent effects, whereas plants not overlapping in this way will be density-independent. The ecologically effective area is therefore analogous to the "neighborhood area" of the population geneticist (240). However, since one is defined from density effects and the other from gene flow distances, their magnitudes may be very different. The relationships between the ecological and genetic neighborhood areas form the subject of the next section. We suggest that "control area" and "control distance" might be useful shorthand terms for "ecological neighborhood area" and "ecologically effective distance."

Our model of a population provides a means of describing interplant distance in functional terms. We are used to measuring distances between plants on a linear scale: The information that two plants are 1 meter apart does not in itself elucidate the ecological relationships between the plants or how those relationships would be altered if the density were altered. In an idealized population, distance can be expressed in terms of neighborhood radii. When plants are less than a neighborhood radius apart they are subject to density-dependent effects. If the distance is greater than one radius, the plants are not affected by density. For more detailed theoretical or field studies, the precise form of the density-vs-fitness relationship could be used to quantify the probability and magnitude of individual interplant effects. The ecological neighborhood should therefore not be seen as a unit with qualitatively distinct properties, but rather as a useful generalization from the spatial scale of density-dependent effects. The "genetic neighborhood" is similarly a generalization based on the spatial extent of gene flow.

Measurement of Ecological Neighborhood Areas

In any population it is possible to measure the approximate density below which density-dependent effects no longer operate. At such densities, the spacing between plants would define the radius of the neighborhood.

In experimental monocultures, where density-response curves approximate the Shinozaki & Kira (187) density yield relationship, the point intersection of the two asymptotes of the plot of log plant weight against log of density can be used as a cutoff point defining the radius of the neighborhood area. Given a relationship, $w^{-k} = A\rho + B$, (where A , B and k are constants, w = weight, and ρ = density) this intersection occurs at a point $\log \rho = \log B/A$. This density therefore formally represents a turnover point from no density-dependent effects to severe density-dependent effects. The value B/A also appears directly in the reparameterization of the density-yield relationship suggested by Watkinson (224a). We may expect this turnover point to be precise in the case of regular plant spacing and much less precise in the case of a random plant distribution.

The measurement of ecological neighborhood areas in natural populations is likely to be considerably more difficult. The examples given in previous sections show clearly that demonstration of density effects from purely descriptive data is fraught with problems. If we know the nature of the controlling agent (e.g. intraspecific competition) we may be able to assess intuitively at what point density-dependent effects are likely to operate, but frequently such intuition will be misleading. Thus in situations where we suspect intraspecific competition to be the major controlling agent, it is difficult to know whether the size of the individuals (and hence our guesses at their distance of interaction) are the results of density per se or of density-independent site effects. This dilemma is illustrated most clearly in studies on forest trees. Here measurements of tree root and crown diameter can be used to estimate "influence zones" (see next section for discussion), yet studies have shown that the degree of overlap between such influence zones is a poor predictor of tree growth. Often the best predictor is trunk diameter, which in turn reflects "influences of other factors, such as tree history, genetic characteristics, microsite, and climatic variation" (26). Before descriptive analyses of neighbor effects can be used in even a limited way to study density effects, their validity must be tested against experimental systems where density effects can be manipulated. At present we know too little about how a density-response curve translates into neighbor effects and vice versa; moreover, it is important to know how environmental heterogeneity will influence these relationships.

Thus until descriptive methods are refined and tested against experimental sources of evidence, they should be abandoned as a means of obtaining useful information about the scale of density dependence in natural populations. Instead, the estimation of ecological neighborhood areas will depend on some form of perturbation analysis. Studies on the addition and removal of individuals from plant and animal communities are in their infancy both technically and interpretively. Many populations are not amenable to such analyses for either technical or conservational reasons. Nevertheless, perturbation analysis may often be the only means of understanding the causal factors in community structure (75, 128, 142). The difficulties in applying a perturbation and following its consequences are far fewer with plants than with highly motile animals. The few such experiments that have been done have proved to be a powerful means of understanding density dependence. Watkinson & Harper (225) altered densities of natural stands of the dune annual grass *Vulpia membranacea* by addition of seed and removal of individuals. At densities below about 100 plants per 0.25 m², the number of spikelets produced was almost entirely independent of density. In dune habitats, this annual therefore has an ecological neighborhood of about 3 cm radius. Watson (227) removed all the individuals of *Plantago lanceolata*

from a 0.5 m $\times$ 5 m plot of vegetation and studied the demography of plants in a directly adjacent plot of the same size. The results showed that the effect of the removals on the demography of the plants in the adjacent plot was localized: Beyond 25 cm no effects on survivorship, reproductive output, or rates of recruitment were detectable. Clearly this population is also characterized by a small ecological neighborhood, yet one somewhat bigger than *Vulpia*'s.

Such experiments have been too few to provide generalizations about the tactics and technology of perturbation analysis for measuring density effects. Nevertheless it is possible to propose a series of guidelines regarding such experiments and their execution.

1. Ideally the perturbations should generate a range of densities both below and above those currently present in the population. Where additions are not feasible, removals would be adequate if density effects are currently present in the population.
2. Such perturbations should avoid drastic shifts in density. There may be nonlinearities in the density responses representing complex stable and unstable equilibria with regard to density regulation. Only a few of these equilibria may be relevant to the current dynamics of regulation within a particular population. For example, a drastic reduction in density may increase plant-to-plant distances such that pollinator service is no longer effective; or a large increase in density may bring the threshold of the population to a point where particular predators are now attracted into the area. Clearly the changes in density should be a compromise between those large enough to detect effects (particularly to detect distances over which control ceases to be effective) and those so large that they disturb the natural context within which the results are to be applied.
3. Experiments could be carried out either by increasing or decreasing density over particular areas, or by changing neighbor relationships by adding or removing individuals around particular "tester" individuals. The former is likely to be preferable where the control is via pathogens and herbivores since presumably they respond to more than just localized density. On the other hand, where control is via intra- or inter-specific competition, direct study of neighbor effects may be adequate.
4. The effects of density should be measured in terms of parameters that can be used for predicting population growth. These may be the classical age-dependent life-history parameters normally used in population projection (121, 179), or measures of size-class transition and size-dependent mortality and fecundity (81, 229).
5. Density effects should be measured on the same time scale (generation, breeding interval, year) used in projecting population growth. The time

scale of the perturbation should correspond to this time interval of measurement; ideally, density should remain unchanged over this period.

6. Since we are concerned with population projection, the size and age class distributions must be taken into account. Results will be altered by changing the density of juveniles rather than that of adults. Similarly a particular stage of the life history (e.g. dormant seed) may not be effective in contributing to density response; population predictions will be correspondingly more complicated.

Other Neighbor Concepts in Ecology

COMPETITIVE RADIUS The concept of an ecological neighborhood distance may seem superficially similar to the terms "competitive radius" or "zone of influence" (26, 151), but brief consideration will reveal that there are fundamental differences. First, competitive radius rather obviously refers only to situations of competition, and excludes regulation by other trophic levels. Second, the term is usually used in a post-facto manner, since it generally refers to the space occupied by an individual *after* it has undergone density-dependent regulation, and therefore to its current rather than potential interactions. For example, consider a species that responds to density by largely plastic responses. In such a case each plant's ecological neighborhood will contain numerous small individuals. The immediate "zone of influence" of any one individual, on the other hand, may be quite small, simply because high density has limited the plant's size. In a sense, we can say that the competitive radius of an individual represents its "realized space," whereas the neighborhood area represents its "fundamental space."

TRAIT GROUP Wilson (236) has introduced another ecological analog of the genetic neighborhood: the "trait group." This is defined as "a group of individuals within which interactions occur with respect to the trait under consideration" (235). Such interactions include "competition, aggression, mating, defense against predation, or any other process of ecological interest" (236). The concept is close to that of the ecological neighborhood but differs in two important respects. First, it is defined from existing rather than potential interactions. Second, the interactions need not be density-dependent, nor is any particular density dependence invoked in the models. The kinds of interactions postulated by Wilson (235, 236) often act in a density-dependent manner; but we can envisage a situation where, for example, two individuals interact with regard to pollinator attraction, yet pollinator service in no way limits population growth. The conceptual and biological independence of selective agents from regulatory agents has fre-

quently been emphasized (39, 74). The concept of the trait group is therefore useful for describing a set of individuals among which interactions are actually occurring, but it does not denote the scale of action of density-dependent factors.

Correlates of the Ecological Neighborhood

DENSITY-DEPENDENT REGULATION We can predict that intraspecific competition, interspecific competition, and the actions of predators and parasites will result in different control areas. The distance of action of density effects due to intraspecific competition will be closely related to the potential size of the individuals of a given species in a given environment, particularly to the extent of the canopy and root systems. There is reason to believe that ecological neighborhoods may be smaller under interspecific competition than under intraspecific competition, in a way that is again related to plant size. When the potential size of the individual is limited by the second species, the intraspecific density effect will occur within a much smaller radius. Thus in communities of ecologically similar populations (guilds), the ecological neighborhoods may be quite small. If the species use different resources the effect will be less severe. If the species differ in competitive ability, the neighborhood of the weakest competitor will be smaller than that of the stronger competitor; the latter will be affected less and its behavior in mixture will resemble its behavior in pure stand.

Where population regulation is mediated through a higher trophic level the scale of the density effect will depend on the mobility of the predator or the dispersal capacity of the disease agent. In general we would expect such density effects to occur over a distance greater than that of density effects resulting from inter- or intraspecific competition among sessile components. The precise pattern will also depend on behavioral responses and host specificity of the regulating agent. In animal populations predators aggregate in areas of high prey density [e.g. see (114)]. The scale of density-dependent effects is itself a function of density. How general this phenomenon is in herbivores is not clear. There is often an inverse correlation between plant density and herbivore attack. Aggregative predator responses are only clearly seen for postdispersal seed. The reasons for this are not clear: Perhaps such responses are only strongly favored where the prey themselves have substantial mobility (e.g. animal prey or dispersed seeds). Aggregative responses may be an "unnecessary luxury" where the prey are sessile and located with a high degree of predictability.

Where predators have a short generation time, predator concentration may result from population growth rather than from behavioral shifts leading to aggregation. In such cases the predator dispersal distances must be considered over the several predator generations equivalent to the time

span of the iterative component of the life history used to estimate plant density response.

If the predator is a generalized one, then it may respond to the total density of all suitable host species, thus increasing the area and magnitude of the density effect. Any plant species susceptible to such a generalized predator will therefore suffer more severe reductions in numbers and have a larger neighborhood area. In introducing the concept of "apparency" as a general term for vulnerability of a plant species to discovery by herbivores, Feeny (58) has stated "It may be that there exists a maximum density which can be reached by a plant species in any given region in ecological time, corresponding to a certain level of apparency of the plants to their adapted herbivores and pathogens present in that region." Apparency will be a function of, among other things, the nature of the associated species. Non-host plants can have the converse effect of inhibiting infestation by predators and pathogens. This has been called "associational resistance" in plant-insect herbivore systems (172, 173), and has been reviewed in plant pathogen systems by Burdon (35).

Associated species can therefore affect the abundance of the predator or pathogen either directly, by providing it with another food source, or indirectly, by influencing its behavior. In both instances the dimensions of the ecological neighborhood will be dependent on the community composition, though the precise mechanisms of such dependence are not understood and will require critical study.

AGE The mechanism of density-dependent regulation may be age-dependent. In estimating neighborhood areas it is important to sum the various density effects over an organism's entire life cycle. This age dependency may arise from changing size, changing concentrations of defense chemicals and morphology, or from development of organs that may be susceptible to particular pathogens (e.g. inflorescence parasites). Thus if there is seed or seedling predation, the density may be so reduced that the adults grow under negligible intraspecific density constraint (100). Measurement of density-dependent effects at only one stage in the life cycle will therefore result in a misleading estimate of neighborhood area.

However, such age-dependent regulation becomes important in life-history evolution, where age-specific mortality and fecundity shifts lead to compensatory changes in other life-cycle components. Moreover any changes in age-specific density-independent effects will result in differential weighting of age-specific density effects. The net evolutionary result will be changes in the neighborhood areas and neighborhood numbers. The increasing interest in density-dependent life table construction and modelling will give added impetus to the study of the consequences of such age-dependent density effects.

DISPERSAL The frequent suggestion that the “function” of dispersal is to get the seed “away from” the parent plant has rarely been examined critically. In perennials, at least, it would seem advantageous for both the parent and its offspring if the latter fell outside the neighborhood area of the parent, and one might predict that species with widely different-sized ecological neighborhoods will have correlatively different dispersal profiles. Alternatively, dispersal profiles may be a function of colonization of new habitats or avoidance of inbreeding. At present there have been few critical studies of the selective advantages of particular dispersal profiles; whether such profiles relate to ecological neighborhood size remains an open question.

Nevertheless, the relationship between the dispersal profile and the scale of density-dependent effects will still be important in several evolutionary processes. Thus where several progeny from one parent fall within each other’s ecological neighborhood, sib-sib interactions and kin selection forces become important since close relatives then influence each other’s fitness (192). Sib competition has also been regarded as a crucial factor in accounting for the evolution of sexual reproduction (59, 135a, 232). Plants sometimes have compound dispersal units which ensure that two or more related seeds will land in the same ecological neighborhood; the selective advantage of this is not clear.

NUMBERS A major determinant of the numbers of individuals in a neighborhood will be the relative importance of mortality response (i.e. survivorship) versus plastic response (i.e. fecundity) to the density-dependent agents: the greater the plastic response the greater the numbers in the neighborhood. Plastic responses have been demonstrated frequently in experiments on intraspecific density response (76). The mortality rate in *Agrostemma* (77) was constant up to densities of 10,000 plants m^{-2} . If one guesses the ecological neighborhood area to be 0.1 m^2 , then over a thousand individuals may be present in a single neighborhood! Where there is appreciable mortality, the number of surviving individuals will depend on environmental factors as well as the growth form of the plant. Frequently under “good” environmental conditions (e.g. high fertility) the size of individual plants is larger yet the number of survivors is smaller (79, 245).

RELATIONSHIP BETWEEN ECOLOGICAL AND GENETIC NEIGHBORHOODS

“The lack of correspondence of ecological, genetic, and evolutionary populations is both a bother and a challenge” (90).

Numerical and Spatial Relationships

There is no necessary *a priori* relationship between the area of a neighborhood defined in ecological terms (on the basis of distances over which density-dependent effects operate) and that of one defined in genetic terms (on the basis of distances over which genes travel). Separate biological phenomena underlie these two concepts. Other biologists have perceived a distinction between the genetic and ecological views of population cohesion. Wilson (235) introduced the general concept of a "trait group" (discussed previously) as a group of individuals that interact biologically, regardless of their degree of gene exchange. Harper & McNaughton (78) distinguished (a) situations where closely related species interact ecologically and are in "such proximity that a struggle for existence would be possible" from (b) situations where they interact through potential gene exchange ("effective range of genetic interference"). They suggested the terms "synectic" and "sympatric" to distinguish between these situations, but they did not extend their ideas to the intraspecific level. Horn (90) suggested that in many plants the ecologically effective population may be smaller than the genetic neighborhood. He also suggested the idea of an "evolutionary population," this being defined by the distance over which genes spread during a particular period of evolutionary time.

We can envisage situations where the magnitudes of the ecological and genetic neighborhoods differ greatly. Thus in herbaceous wind-pollinated plants, density may be regulated by intraspecific competition acting over extremely small distances, whereas pollen may be carried over much larger distances; here the ecological neighborhood may be much smaller than the genetic neighborhood. In populations of self-incompatible species, where there is intense competition for pollinator service, the two types of neighborhood may be congruent. In populations regulated by a free-ranging herbivore, the ecological neighborhood may be much larger than the genetic neighborhood, especially if the plants are self-fertilizing. Indeed, the greater the level of selfing, the larger will be the ecological neighborhood relative to the genetic. We can envisage similar cases in animal populations. Where distances for foraging are similar to search distances for mates, ecological and genetic neighborhood areas may be essentially alike. In other cases, as in moths where pheromones attract mates over long distances yet density is determined by foraging of caterpillars (or search distances of their parasites), genetic neighborhoods may be far larger than ecological neighborhoods. In order to make predictions that are more than intelligent guesses, we clearly need more data on gene-flow distances and on distances over which density-dependent factors operate. With regard to the consequences of selection in natural populations, expectations based on the ecological neighborhood differ from those based on the genetic neighborhood.

Selection

We commonly recognize different types of selection (namely directional, stabilizing, and disruptive) on the basis of the relationship between the phenotypic distribution of a character and the fitnesses of individuals with those phenotypes (134). These well known types of selection are conceptually clear if we consider a population as a "bean bag" with definite bounds within which phenotypes are distributed at random. In nature, however, the bounds of a population are not clear for several reasons. First, the genetic and ecological neighborhoods of a population may be very different. Second, these areas, defined as zones of genetic and ecological influence, do not necessarily coincide with the overall spatial extent of the group of organisms under consideration: Neighborhoods are functional interacting units located at arbitrary positions in a continuum. Third, important genetic correlates of density must be taken into account when considering population processes.

Given the varying spatial relations among genetic and ecological neighborhoods, what are the consequences if we superimpose selection on this system? The answer depends on the spatial variation in the fitness of the phenotypes. It is perhaps appropriate to focus on a particular example before generalizing the relationship between genetic neighborhood, ecological neighborhood, and the area over which selection acts in a uniform manner ("selection area"). This example concerns the distinction between disruptive selection and multiple-niche selection. The confusion about this distinction has been pointed out by other authors (143) and it serves therefore as a useful example.

As originally defined by Mather (134), disruptive selection operates when, in a single "population," phenotypes that deviate more from the mean have higher fitness. However, note how selection in favor of extremes may occur; (a) regardless of spatial variation in selection pressures—e.g. when there may be two optimal character combinations, or where hybrid intermediates are less fertile; and (b) with spatial variation such that one extreme of the phenotypic range is favored in one microsite and a different extreme is favored in another. Is the latter disruptive selection? If we consider the individuals in each microsite to be the "populations" to which we apply Mather's definitions, then within each such microsite selection is directional, not disruptive. On the other hand, if we consider the "population" to be a genetic neighborhood whose area spans several such microsites, then we may perhaps infer (as is frequently done) that the case is one of disruptive selection. Which view is correct depends not only on the relative scale of the selection area and the genetic neighborhood but also on the scale of the ecological neighborhood. This follows from the basic formu-

lation that whereas selection for two extreme homozygotes (and against the heterozygote) cannot maintain a stable gene frequency equilibrium, selection for the two homozygotes in different "niches" (where the numbers in each niche are independently controlled) can, under certain conditions, result in a stable polymorphism (122). Such a "multiple niche model" as it is termed, maintains polymorphism because there is a limit to the number of each genotype that can exist in each niche, such that the one at low frequency has an implied density advantage in its own niche. Such "niches" are really our ecological neighborhoods, except they have been conceptualized much more rigidly as population segments between which there is absolutely no interaction as far as population regulation is concerned. "Multiple niche selection" is therefore the result of (a) ecological neighborhoods' being smaller than genetic neighborhoods, and (b) the occurrence of differential selection on a spatial scale equivalent to the scale of an ecological neighborhood. So, although we can superficially draw the analogy between "multiple niche" and "disruptive selection," we are really describing a situation more complex, more realistic, and therefore more interesting than the simpler view of selection types based on phenotypic scales alone. Indeed, in "multiple niche models" there is no reason to suppose that within each niche selection is opposite and directional: Selection may even be directional in one niche and stabilizing in another (50).

In order to understand selection in natural populations and its consequence for population genetic structure (microdifferentiation, maintenance of polymorphisms, and levels of heterozygosity), it is essential to conceptualize the spatial extents of fitness values, of density effects, and of gene exchange. Here we conceptualize the processes in terms of selection areas, ecological neighborhoods, and genetic neighborhoods. We do not mean to imply an atomistic view of these areas; we use these terms only because we do not have the mathematical expertise to consider changes in selection, density effect, and gene flow as functions of distance, and then examine the consequences of these more complex functional relations. In Table 1 we therefore generalize the consequences of qualitatively different relations among selection areas (S), ecological neighborhoods (E), and genetic neighborhoods (G). The more important cases are described in detail below.

1. $E < G < S$. In this case selection occurs uniformly over the genetic neighborhood, and all the members within an ecological neighborhood interbreed at random. This is equivalent to the classical assumptions of selection. Selection is in this case one of the regular Matherian types (stabilizing, disruptive or directional), depending on how fitness varies with phenotype.

2. $S < G < E$. In this case different levels of selection occur within a genetic neighborhood, and the numbers within each ecological neighborhood are

Table 1 Relation between genetic neighborhood area (G), ecological neighborhood area (E), and selection area (S), and their interpretation in terms of classical views of patterns and types of selection. Blank regions are logically inconsistent combinations.

		G < E	G > E
S < G	S < E	<u>S < G < E</u> Regular disruptive selection with ± random breeding [Case 2 in text]	<u>S < E < G</u> Multiple niche selection with ± random breeding [Case 3 in text]
	S > E		<u>E < S < G</u> Multiple niche selection with limited gene exchange; resembles clinal selection
S > G	S < E	<u>G < S < E</u> Uniform selection over genetic neighborhoods, but different in different ecological areas; re- sembles multidirectional selection	
	S > E	<u>G < E < S</u> Uniform selection over many ecological and genetic neigh- borhoods [Case 4 in text]	<u>E < G < S</u> Regular “bean bag” model of selection [Case 1 in text]

not individually controlled. This case represents “regular disruptive selection” (i.e. as originally conceived) with more or less random breeding.

3. $S < E < G$. In this case a random breeding population comprises several niches (areas of ecological independence) which may contain different selection regimes. This case represents “multiple niche selection” with random breeding between the niches.

4. $G < E < S$. In this case the selection regime is the same over a “large” area that spans ecologically and genetically independent units. This type of selection may be climatic, may be the result of biotic interactions with a widespread species, or may be “organizational”—i.e. selection that increases organizational efficiency (such as selection for warm-bloodedness) but that is not directly related to environmental effects.

Within such overall schemes the interactions of selection and density will add further complications, either as a result of selection intensities’ varying with density or as a result of genotype–density interactions. If density-dependent effects are genotype-specific then there will be complex interac-

tions between the effects of selection and factors determining population size (7, 40, 44, 74, 224). In a multiple-niche situation, the effects of selection in each niche are confounded with the size of the population that each area can support (122), and the range of genotypes falling in a particular niche may itself be a function of density (51). In such instances both density-dependent factors and selection *per se* determine gene frequencies within the genetic neighborhood.

CONCLUSIONS

In this review we have explored the relations between the density of plant populations and their ecology and genetics. We hope to have established the importance of investigating density-dependent effects explicitly to determine both their frequency and their consequences. We have shown that the spatial and temporal patterns of density-dependent regulation are likely to be complex, with important and sweeping consequences for populations. We have formulated predictions and generalizations about such consequences; these await detailed exploration. Plant population biology as a field is ripe for such explorations since plants not only "stand still and wait to be counted" but also stand still and wait to be removed or planted!

We hope to have challenged field biologists to explore the rates, levels, and spatial extents of different kinds of density control in plants. This challenge can be met by biologists willing to manipulate populations rather than simply describe their pattern or demography (though such descriptions are also seriously wanting). We have also thrown down the gauntlet to those population geneticists and population ecologists who have yet to see an intimate connection between their two disciplines. When do genotypic factors or ecological factors alone sufficiently describe populations? When must both be considered in concert? We expect the latter is usually the case. Our final challenge goes to the theoretical population biologist to develop models that are more realistic extensions of the concepts developed in this paper.

ACKNOWLEDGMENTS

The conversations that led to this paper were initiated while Janis Antonovics was on a Visiting Professorship at the University of Texas, Austin. We are extremely grateful to Dean Paul Olum of The College of Natural Sciences for Academic Development Funds that made this visit possible. We also wish to thank the many people who have contributed over the years to a discussion of the ideas presented here. Special thanks go to the Duke Pop Gen Group and Hall of Fame for their resigned tolerance of "new

dynamic ideas in ecology," and to the following for their comments and input on the manuscript: Norman Ellstrand, Norma Fowler, John Harper, Tom Meagher, Mark Rauscher, Carl Schlichting, Ruth Shaw, Brian Trenbath, Andrew Watkinson, Henry Wilbur, and David Sloan Wilson.

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