

A deterministic model to study the importance of density-dependence for regulation and the outcome of intra-specific competition in populations of sparse plants

P.G.L. KLINKHAMER and T.J. DE JONG

*Department of Population Biology, Research Group Ecology of Plants and Herbivores,
P.O. Box 9516, 2300 RA Leiden, The Netherlands*

SUMMARY

The importance of density-dependence is addressed by discussing the results of a simple deterministic model for plant populations. The model takes into account that plants, once germinated, do not move. It is shown that density-dependence can keep sparse populations sparse. Also, it is shown that density-dependence, even if it affects only a minority of the individuals, can determine the outcome of competition. The effect of density-dependence on selection for a specific seed size and generation time are discussed.

Key-words: annual plants, density-dependence, deterministic model, intra-specific competition.

INTRODUCTION

Harper's famous encouragement to study plant population dynamics was 'plants stand still and wait to be counted'. Indeed, one of the most characteristic features of terrestrial plants is that they do not move over great distances during all but two phases of their life (pollen dispersal, seed dispersal). This makes classical logistic models on regulation inappropriate for modelling plant populations, because they are based on the assumption that all individuals interact with all others. Relatively recently, models have been explored that take into account that plants only interact with their nearest neighbours (Agren & Fagerstrom 1984; De Jong *et al.* 1987; Geritz *et al.* 1988). All these authors used so-called 'safe-site' models; a type of model first proposed by Skellam (1951). In this paper we will use such a model to study the effect of density-dependence (DD) in sparse plant populations.

Amongst theoretical population biologists there seems to be no doubt about the existence and the importance of DD in plant populations. Without it a population would either become extinct or overflow the planet (Hastings 1978; Levin *et al.* 1984; Cooper 1984). Environmental fluctuations may obscure the pattern but even in highly fluctuating environments a population will follow a random-walk which brings it to extinction (if the geometric growth average is smaller than one) or to infinity (if the geometric growth average exceeds one) (Reddingius 1968). To field biologists, the matter is not all that clear. There are of course many, well documented, examples of populations that reach very high densities of both seedlings and adults and in which DD is clearly operating on seed

survival, seedling establishment, individual plant growth, seed production and so on (Harper 1977). There are also examples in which populations never seem to reach high densities, and in which it is questioned whether DD ever occurs or in which it seems to affect only a minority of the plants in the population (Antonovics & Levin 1980). Recently, Strong (1984, 1986) introduced the concept of density-vague regulation for fluctuating populations. If populations are fluctuating in a random-like fashion, DD might be operating only in the exceptional occasions when density is extremely high. Mostly the population will behave as if it is fluctuating stochastically. Yet DD is keeping it from drifting to infinity. Sometimes, however, even in populations that do not show strong fluctuations, detailed studies may fail to show strong DD in any of the plant's life-stages, the population density at the same time being at some kind of equilibrium, or at least not showing clear signs of declining or increasing over some period of time. A good example of this are the *Carlina vulgaris* populations from chalk grassland, studied by Grubb (1986) and by Schenkeveld & Verkaar (1984). Antonovics & Levin (1980) stated: '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'. The importance of DD is, therefore, still open to debate and researchers studying plant-population dynamics are highlighting questions such as: 'Does DD have any significant effect on keeping sparse populations sparse?', and 'If DD affects only a minority of the individuals in the population, does this mean that we can neglect DD in predicting the outcome of natural selection?'.

In this paper, we will address these questions by discussing the results of a simple deterministic model for plant populations. Most of this paper will be on annual plants. The effect of DD on selection for generation time will be shown by means of numerical simulation of competition for safe-sites between an annual and a biennial type. Although DD may evolve from factors other than intra-specific competition (like seed predation or herbivory) only DD effects that arise from intra-specific competition were studied.

THE MODEL

It is very difficult to detect the level of DD in sparse plant populations. To study the effect of DD on natural selection is even harder, because it is virtually impossible to conduct field experiments on a relevant time scale. In many cases modelling is the only solution, though a model cannot do justice to the complexity of interactions among plants and to the overwhelming variation found in nature. In analogy to field or laboratory experiments, in modelling too, as few factors as possible should be varied.

This paper concentrates on the effects of DD and leaves out stochastic variation in reproductive output or safe-site density. Furthermore, it is assumed that seeds are dispersed randomly within the population. This may be true for some wind dispersing species, e.g. *Senecio jacobaea* (Poole & Cairns 1940; Van der Meijden *et al.* 1985). Also density-dependent seed predation may lead to a more random distribution pattern of the seeds. In other cases, however, the distribution of seeds may be clumped. The introduction of stochastic variation and of different dispersal patterns will be the goal for future research.

The model is based on the assumption that the habitat can be subdivided into sites that are suitable for establishment and reproduction and sites that are not. Each year suitable sites (here after referred to as safe-sites) occur at density d , and let the surface area of a site be c . In the next section the results for a single type of plant are discussed, ignoring genetic

diversity of the local population. Each established individual produces z seeds. A fraction o of the seeds dies during seed production and thereafter (e.g. by seed predation) z and o will be combined in one parameter s ($s = z(1 - o)$), the number of seeds at the time of germination produced by one individual.

All density-independent mortality after germination effectively reduces the density of safe-sites (d). Seeds are dispersed randomly within the habitat. If there is no density-dependent mortality or growth, all seeds present in safe-sites at the time of germination will produce seeds. The chance of a seed landing in a safe site equals $d c$. The one-step transformation for the density-independent case is, therefore:

$$N_{t+1} = N_t s d c,$$

$$N_{t+1}/N_t = s d c.$$

The density of the population (N) will increase if $s d c > 1$, the population will become extinct if $s d c < 1$.

To study the effect of density dependence we will assume that in each safe-site only one individual can establish itself (an alternative interpretation is that the seed production of a safe-site equals s for any number of seeds in the site > 1).

The number of seeds in a site will follow a Poisson distribution with mean $N_t s c$.

The chance of a site having no seeds is:

$$P(n=0) = \exp(-N_t s c)$$

The chance of a site having seeds is, therefore:

$$P(n \geq 1) = 1 - \exp(-N_t s c)$$

The one-step transformation being:

$$N_{t+1} = d(1 - \exp(-N_t s c))$$

A convenient way to study the dynamics of this system is by plotting N_{t+1} versus N_t . If N_t is very large $N_{t+1} \rightarrow d$; if N_t is very small:

$$\lim_{N_t \rightarrow 0} \frac{N_{t+1}}{N_t} = \lim_{N_t \rightarrow 0} \frac{d(1 - \exp(-N_t s c))}{N_t} = d s c.$$

From (1) it can be seen that the population will become extinct if $d s c < 1$ (not surprisingly this result is the same as in the density-independent case). If $d s c > 1$ the population will reach some equilibrium density (N^*) at the intersection of the curve relating N_{t+1} to N_t and the line $N_{t+1} = N_t$ (Fig. 1). The level of DD-mortality can be calculated from the difference between the number of seeds present in safe-sites at the time of germination and the number of seedlings that eventually becomes mature.

EQUILIBRIUM DENSITIES

At the equilibrium:

$$N^* = d(1 - \exp(-N^* s c)). \quad (2)$$

The equilibrium density will be smaller than d , if seed production is high $N^* \rightarrow d$. Interestingly, the proportion of safe-sites occupied with seeds depends on the number of safe-sites itself. If d is high, N^* will be high and $N^*/d \rightarrow 1$ (see 2). In other words, in the equilibrium, the proportion of sites occupied will increase with the density of available sites. This means

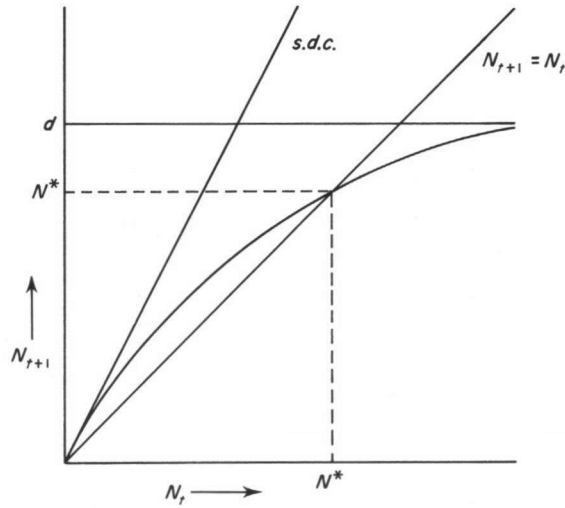


Fig. 1. The relation between N_t and N_{t+1} ; the dashed line indicates the equilibrium density. The line $s d c$ gives the rate of increase of the population if there is no density-dependence. N^* gives the equilibrium density; s = seed production per flowering individual, d = density of safe-sites, c = surface area of a safe-site.

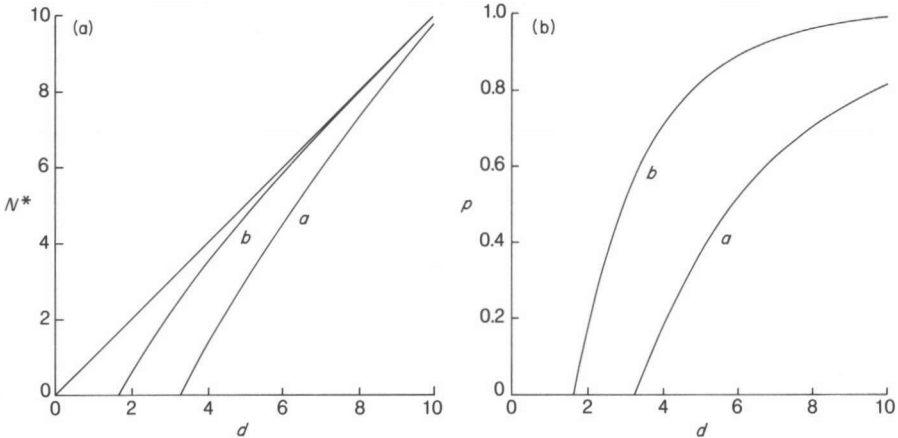


Fig. 2. (a) The relation between the equilibrium density (N^*) and the density of safe-sites (d). The surface area of a safe-site = 0.01, a : seed production = 30; b : seed production = 60. (b) The proportion of seedlings suffering from density-dependence (p). d = density of safe-sites, the surface area of a safe-site = 0.01, a : seed production = 30; b : seed production = 60.

that there can exist an equilibrium at which only a small proportion of the available number of sites is occupied and only a small proportion of the total number of seedlings will suffer from DD. Yet DD is essential for the existence of an equilibrium density, because without it a population would slowly but steadily increase. Therefore, DD can keep sparse populations sparse. In Fig. 2 examples are given of species producing 30–60 seeds per plant that are still alive at the time of germination. This number of seeds is well within the range found for sparse populations of monocarpic plants (Schenkeveld & Verkaar 1984; Grubb 1986). The surface area of a safe-site is 0.01 which, if we scale in m^2 ,

equals 100 cm^2 . This approximates the size of, for example, a footstep or a rabbit scrape and is assumed to be the area an adult individual can occupy. The fact that the equilibrium density is sometimes much lower than the density of available sites has some interesting consequences.

- (a) If only a small proportion of the seedlings suffers from intra-specific competition, this does not necessarily mean that intra-specific competition is unimportant for determining the number of plants.
- (b) Some authors found an increase in population density after adding seeds to the population and concluded that the number of available sites does not limit the population density (e.g. Schenkeveld & Verkaar 1984). Such a conclusion would be justified with the logistic model in mind but not with the safe-site model. An increase in the density of available sites would also have resulted in a higher population density (see 2). It is the chance that sites and seeds coincide which determines the equilibrium density. Seeds and safe-sites can be limiting at the same time. This is in agreement with Bullock (1976) who stated: 'Stable population size, at any life stage, is not environmentally fixed, e.g. by the number of safe-sites, but is also a function of reproductive capacity and dispersal'.
- (c) A second species (M) which produces more seeds that are less competitive compared to the first species (N) may occupy the sites that are left over by species one. If species N is competitively superior to species M , the density of sites available to M will be $d - N^*$. Species M may, therefore, coexist with species N if $S_m c (d - N^*) > 1$. Coexistence can occur on the basis of differences in seed production and competitive ability only (Skellam 1951; Agren & Fagerstrom 1984; Geritz *et al.* 1988).

DENSITY-DEPENDENT REGULATION

We will now examine whether DD, even if it affects only a minority of the population, determines the outcome of intra-specific competition by looking at two traits: seed size and generation time.

- (1) Although there can be strong phenotypic variation in both the number of seeds and the seed size (e.g. Winn & Werner 1987), it is believed that there is a trade-off between the number of seeds produced and seed size (e.g. Salisbury 1942; Harper *et al.* 1970; Baker 1972; Primack 1979; Kawano 1981; Primack & Antonovics 1982; Kromer & Gross 1987). Seed mass is positively correlated with seedling size in many cases and can also influence seedling competitive ability, growth and establishment (e.g. Gross 1984; Stanton 1984; Winn 1985; Marshall 1986; Wulff 1986). Under DD one would expect there to be a selective advantage to producing larger seeds because they produce larger seedlings that may outcompete the conspecific seedlings in the site. Without intra-specific competition the latter is not important and we might expect selection for smaller seeds. In Fig. 3 an example is worked out of the competition between two types, one type producing 20% more seeds than the other at the cost, however, of its seedlings always losing in competition with the other type. In the density-independent situation, the relative frequency of the type producing fewer seeds will decrease towards zero. If only one seedling can establish per site the relative frequency will go to one. Note that in the equilibrium of the DD-case, the proportion of individuals that suffers from DD is 17%. With other parameter values the two types or species may coexist (see section on Equilibrium Densities, Geritz *et al.* 1988).

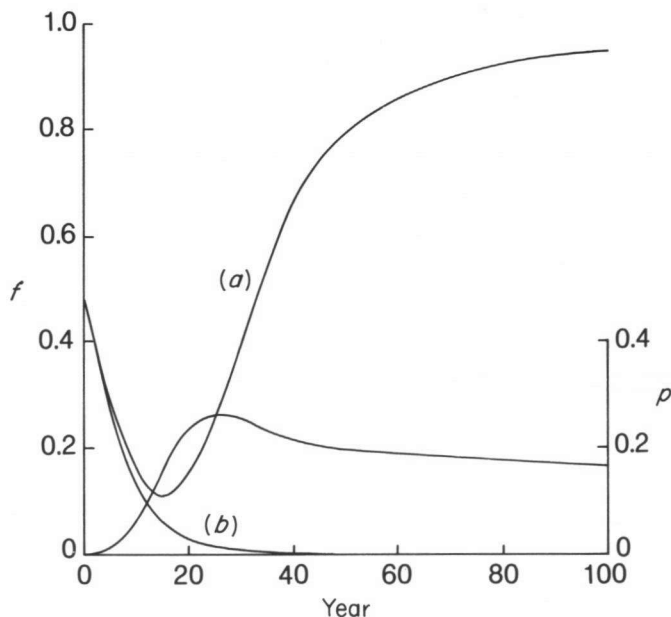


Fig. 3. The relative frequency (f) of a type producing 30 seeds per flowering plant growing together with another type that always loses competition in a site but produces 20% more seeds. The density of safe-sites = 4. The surface area of a site is 0.01. The starting density for both types = 0.01. (a) The density-dependent situation, (b) the density-independent situation. The proportion of individuals suffering from density-dependence (p) is given on the right axis.

- (2) It is generally believed that short generation times are advantageous under density-independent conditions (e.g. Lewontin 1965) because of the compounding of interest in growing populations. In a DD situation generation time is not important for determining the outcome of selection and selection will be for increasing expected life-time seed production (De Jong *et al.* 1987). In Fig. 4 an example is given of the competition between an annual (producing 30 seeds) and a strictly biennial type (producing 65 seeds, and suffering 50% additional mortality in the second year of growth). According to Hart (1977) biennials produce about twice the number of seeds produced by annuals. The second year mortality is chosen according to what is commonly found in biennial species (e.g. Gross 1981; Verkaar & Schenkeveld 1984; De Jong & Klinkhamer 1988). Without intra-specific competition the relative frequency of the biennial decreases towards zero, with intra-specific competition (even though only 22% of the individuals suffers from it) the relative frequency of the biennial increases to one and the annual becomes extinct. With lower levels of DD we obtain similar results but extended over a larger period of time.

DISCUSSION

In this paper random seed distribution within the population is assumed, a requirement not always met. Another distribution pattern of the seeds will, however, not alter the main conclusions in this paper qualitatively. If seed dispersal is clumped, the seeds will sample a

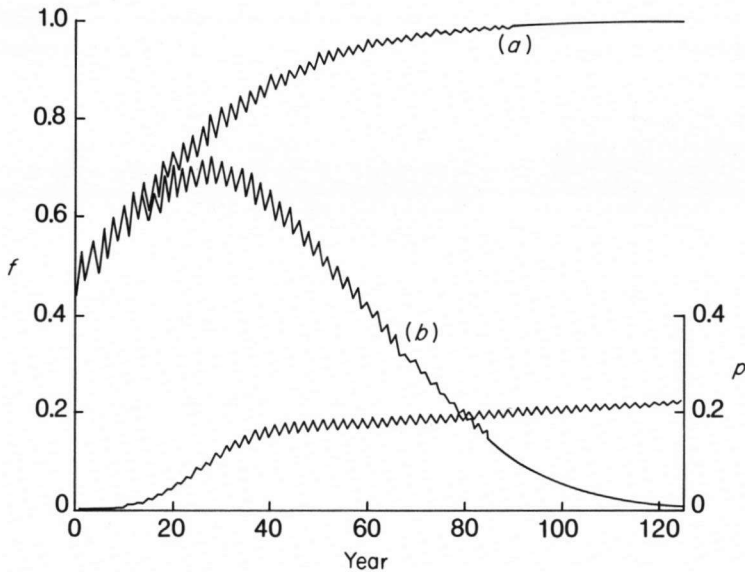


Fig. 4. The relative frequency of an annual type (f) growing together with a biennial type. The density of safe-sites = 4. The surface area of a safe-site = 0.01. The seed production of the annual = 30; the seed production of the biennial = 65; the rosette survival of the biennial = 0.5; the starting density for both types = 0.01. (a) The density-independent situation; (b) the density-dependent situation. The proportion of individuals suffering from density-dependence (p) is given on the right axis.

smaller area. This effectively reduces the number of available sites. From Fig. 1 it can be seen that smaller d reduces the rate of increases at low levels of N_t . The curve relating N_{t+1} to N_t will intersect the line $N_{t+1} = N_t$ at a lower level of N^* . Therefore, if seed dispersal is clumped, N^* will be lower and the number of empty sites will be higher. Because the chance of seeds landing in the same site will be increased, the level of DD will be higher. If both seeds and sites show a clumped distribution the situation depends upon the occurrence of yearly variation of the areas with a high safe-site density. If such areas stay in place from year to year, limited dispersal will be advantageous. If such areas are on different places from year to year, random dispersal will be more profitable.

From the examples given it is clear that even low levels of DD can be important in determining the number of plants and the outcome of competition. It is also clear, however, that when this is the case it takes a long time, after starting at low densities, before the equilibrium density is reached. During the build up of the population, initially, another type (the one with smaller seeds in example one, the one with the shorter generation time in example two) may increase in relative frequency than the type that will eventually be selected for as a result of the intra-specific competition. The importance of DD can, therefore, only be estimated if growth rate of the population and longevity of the habitat are known. It should be known whether the population is increasing or decreasing (which by itself may be the result of selection) or has reached an equilibrium density. The effect of low rates of DD on selection in growing populations is quite different from the effect of low rates of DD in equilibrium populations. Also, if the population is increasing, it should be known whether it is likely ever to reach the equilibrium. This may seem trivial but shows that sometimes neither of the two basic approaches used in life-history models may be appropriate. On the one hand the expected geometric-growth average is used as a selection

criterion. This measure can, for purely logical reasons, not remain constant. On the other hand, in the case of intra-specific competition, the Evolutionarily Stable Strategy (ESS) approach (that is, to search for a strategy which cannot be invaded by mutants having an alternative strategy, Maynard Smith 1976) is used, which assumes that the resident population is at equilibrium density, a situation that perhaps will never be reached. If stochastic population fluctuations occur, the complexity of the situation increases. We may then have a situation of density-vague regulation (Strong 1984, 1986). DD occurs only once in a while but keeps the population from drifting towards infinity. Therefore, DD is important for population regulation. The question whether DD, in a stochastic environment with low levels of DD, is also important in determining the outcome of natural selection is one of the major challenges for both theoretical and field population biologists. For only one specific set of cases it is definite that density-independent selection occurs. If, before reaching the equilibrium density, two competing types are set proportionally to a much lower density because of some disaster (e.g. fire, flooding, herbivory etc.), and this process repeats itself frequently, then selection always operates in an increasing population, making DD relatively unimportant (De Jong *et al.* 1987).

The study of DD presents some problems to population biologists in the field. Although we all intuitively know what is meant by a safe-site these can almost never be counted in the field. An idea about the fraction of the total area that consists of safe-sites (dc) can, however, be gained from experiments in which seeds are sown at low densities. In addition, we need to know at what distance individuals influence each other and what proportion of the seedlings grow next to a conspecific within that distance (c.f. Watkinson & Harper 1978). Such evidence may be gained from descriptive studies but is necessarily circumstantial. Plants growing in poor microhabitats may be small, have a low survivorship, and yet be far apart, while those growing in good conditions may be close together, but large, and with a high survivorship (Antonovics & Levin 1980). To decouple the effects of microhabitat and plant density, experiments should be done in which seeds and/or seedlings are planted at known densities. For sparse populations the problem remains that the environmental variation may be large in relation to the DD-effects, making the detection of DD difficult.

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