

Plant population processes and weed control

W.M. LONSDALE

CSIRO Division of Entomology, Campus International de Baillarguet, 34980 Montferrier sur Lez, France

Abstract. It is a hard truth that for pest plants, substantial control measures may have little impact on the population size, whereas, for endangered species, slight changes in conditions can be catastrophic. Why is this? Population size in plants is in fact often determined by an interaction between a non-linear density-dependent process - namely seed output - and various density-independent mortalities. This leads to a non-linear relationship between population size and the rate of population increase λ . The shape of this relationship is commonly such that slight changes in λ at values close to unity can produce dramatic changes in population size. By contrast, at high values of λ , such as are likely to be seen in exotic weeds, large changes in λ resulting from control measures may have little effect on subsequent population size. It is therefore essential to characterize the parameters of the various demographic curves describing a plant population if we wish to predict the results of control measures against it. This is also true if we are to investigate a plant's potential to establish at low densities and become invasive.

Introduction

Plant population size is determined by an interaction between density-dependent and independent processes (Silvertown and Lovett Doust 1993). Commonly, the density-dependent process, for example fecundity, is non-linear (Watkinson 1985), and this fact, when applied to weeds, can have profound consequences for the behaviour of the population as mortality levels shift in response to control measures.

Consider Fig. 1, which is a graphical model showing how density-dependent and independent processes interact to determine equilibrium population density. In Fig. 1a, the change in birth rate is linear with density, and thus changes in density-independent mortality produce even changes in equilibrium population density. By contrast, in Fig. 1b, there is a non-linear relationship between birth rate and population size. In this case, a minor change in mortality level can produce a major change in density, or a small one, depending on the parameters of the birth rate curve (Watkinson 1985; Fig. 1b).

Using a simple population model of the type developed by Watkinson (1980) and used by Lonsdale *et al.* (1995) to model biological control of an annual weed, I shall explore the effects of different types of control on weed population density.

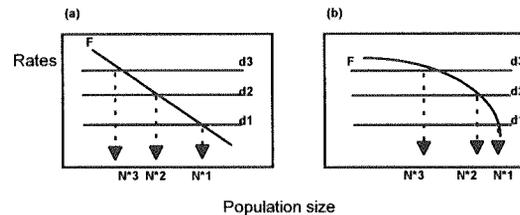


Fig. 1. The change in equilibrium population size (N^*) that results from a change in the density-independent death rate (d) when the density-dependent birth rate (F) changes (a) linearly and (b) non-linearly (Watkinson 1985).

The model

The model consists of three parts. Firstly, simple density-independent growth is expressed as

$$N_{t+1} = \lambda N_t \quad (1)$$

where λ is the finite rate of population increase, a multiplicative growth factor such that if λ is greater than 1, the population increases without regulation, and if less than 1, the population declines to extinction. The value of λ is a product of the number of offspring per plant in the absence of competition, f , and the

probability of surviving density-independent mortality, p :

$$\lambda = fp \quad (2)$$

Secondly, density-dependent fecundity per plant, F , is given by (see curve 1 in Fig. 2)

$$F = f(1 + aN_t)^{-b} \quad (3)$$

where a is the area required by a plant to produce f seeds, and b describes the effectiveness with which resources are taken up from that area (Watkinson 1980, 1985).

Thirdly, an upper limit is placed on density by density-dependent mortality, such that the relationship between the density of flowering plants N_t and the initial density of plants N_i , can be described by (Yoda *et al.* 1963) the equation (see curve 1 in Fig. 3)

$$N_t = N_i(1 + mN_i)^{-1} \quad (4)$$

where m is the reciprocal of the maximum density sustainable at flowering.

Combining equations 1, 3 and 4 gives (Watkinson 1980, 1985)

$$N_{t+1} = \frac{\lambda N_t}{(aN_t)^b + m\lambda N_t} \quad (5)$$

This model can be run until it reaches an equilibrium density N^* (i.e. $N_t = N_{t+1} = N^*$). In the modelling exercises below, I used a program written in

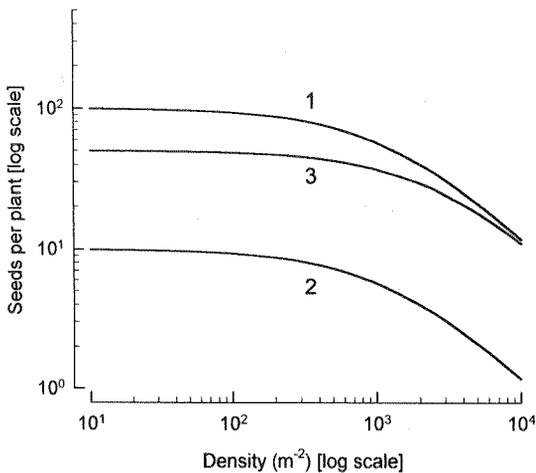


Fig. 2. Density-dependent fecundity in (curve 1) uncontrolled weed populations, (curve 2) in populations uniformly subjected to a 90% reduction in seed output (i.e. density independent control) and (curve 3) in populations subjected to a reduction in seed output that declines with increasing density.

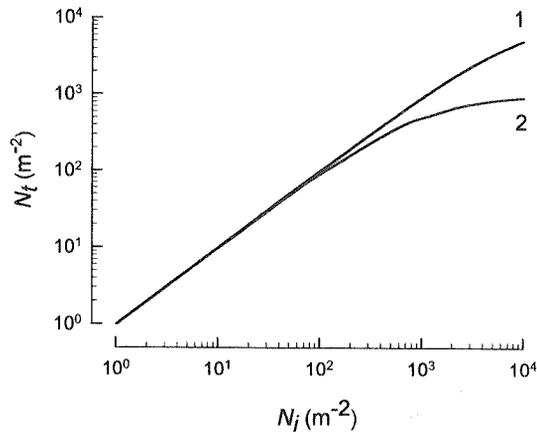


Fig. 3. The relationship between sowing density (N_i) and density at flowering (N_t) following density-dependent mortality (after Yoda *et al.* 1963). No matter how high the sowing density, final density cannot exceed $1/m$. Two curves are shown, one for uncontrolled weed populations (curve 1) and one for weed populations subject to control, such that the maximum final density is 10% of that for uncontrolled populations (curve 2).

TurboPascal by G.S. Farrell of CSIRO Division of Entomology, Darwin, Australia.

Effect of varying λ on N^*

The basic form of the curve relating N^* to λ is shown in Fig. 4a for a population that has a combination of density-dependent fecundity, density-dependent mortality at high densities, and density-independent mortality affecting λ . As the level of density-independent mortality increases, so λ declines, but this has little effect on N^* until a value of λ is reached where the surviving plants can no longer compensate for declining density by increasing the birth rate. At this point the curve starts a steep downturn and density declines steeply with any slight fall in λ .

Presumably, exotic weed populations are to be found in the flat part of the curve (Fig. 4a) - they would be expected to have high λ s but would be insensitive even to large changes in λ . Rare and endangered species, by contrast, would have low λ s and would be highly sensitive to slight changes in λ . The aim with an exotic weed population would be to push N^* below some critical economic threshold - in practice, this is likely to involve major reductions in λ , as Fig. 4a clearly illustrates.

We now have the means to investigate the effects of different weed control measures on N^* .

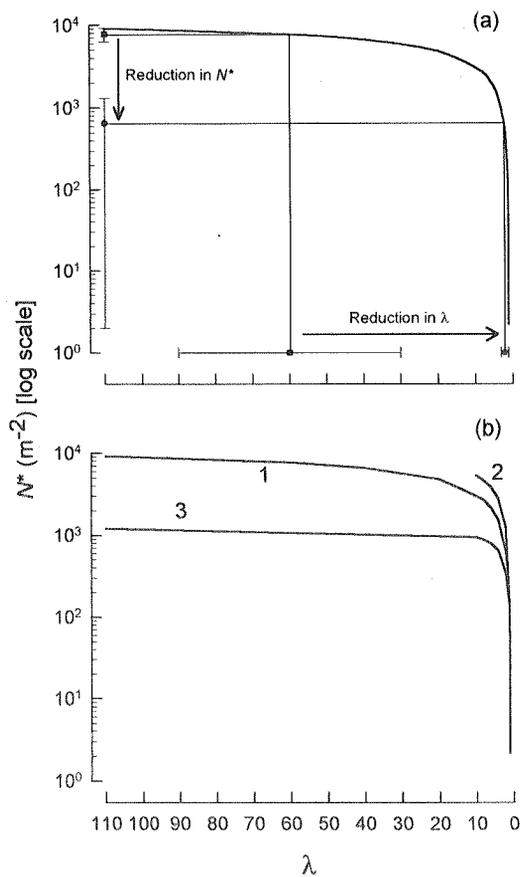


Fig. 4. The relationship between the equilibrium population size in plants (N^*) and the net rate of population increase λ . In (a), it is shown that a reduction in λ from 60 down to 2.02 not only reduces N^* , it also markedly increases the variability of the population size (assuming that the CV in λ stays constant, in this case at 50%). In (b), the effect of density-dependent suppression of seed output (curve 2), and of increasing the intensity of density-dependent mortality (curve 3), are shown in comparison with the basic curve (curve 1). (Parameter values are, for curve 1: $a = 7.57 \times 10^{-4} \text{ m}^2$, $-b = -1.63$, $m = 8 \times 10^{-5} \text{ m}^2$; for curve 2: $a = 3.57 \times 10^{-4} \text{ m}^2$, $-b = -1.63$, $m = 8 \times 10^{-5} \text{ m}^2$; and for curve 3: $a = 7.57 \times 10^{-4} \text{ m}^2$, $-b = -1.63$, $m = 8 \times 10^{-4} \text{ m}^2$).

Density-independent control

Density-independent control would not change the shape of the curve in Fig. 4a - it would simply lower λ and move the population along the curve. Whether it would have a major effect on N^* would depend on how low λ was depressed (see Fig. 4a). Note that, if we assume a certain amount of random variation in λ , maintaining the same proportional variation at a lower λ would produce, not only lower densities, but also greater proportional variation in densities than would be seen in the uncontrolled populations (Fig. 4a).

The assumption of density-independent control is

simplistic, yet is generally essential in modelling weed biological control because we have as yet no clear idea of the basic shapes of herbivore response curves, or of the effects of the herbivores on the plant demographic parameters. For example, Lonsdale *et al.* (1995) chose density-independent depression in seed output to model biological control of the malvaceous annual shrub *Sida acuta* (see curve 2 in Fig. 2). This contrasts with the insect biocontrol literature in which the characterization of the mutual interaction of predator and prey has been well studied (e.g. Hassell 1978, 1981). The prevalence of density-independent control of weeds, where a constant proportion of plants survive the control effort, remains unclear. For example, one might think of herbicides as fairly indiscriminate, but even here, rather than killing a constant proportion of plants, the proportion killed might in fact increase with density as plants become weakened by intraspecific competition. (Surprisingly, however, there seems to be little or no evidence on this topic).

Density-dependent control

One can identify two forms of (potentially) density-dependent control.

Control of fecundity

Control of fecundity might be achieved in a variety of ways: seed and flower feeders (e.g. Hoffmann and Moran 1991), seed pathogens (e.g. the head smut *Sporisorium ophiuri* on itch grass *Rottboellia cochinchinensis*; CABI 1995), or through fitness-suppressing insects. The simplest form of density-dependent depression in fecundity is shown by curve 3 in Fig. 2. It differs from curve 2 in Fig. 2 (density-independent depression of fecundity) in that it converges on the uncontrolled populations (curve 1, Fig. 2) at high densities - for example, because of saturation of the predator population. As a consequence, it changes the shape of the N^* - λ curve (curve 2 in Fig. 4b), such that the equilibrium density climbs more steeply with increasing λ . However, it is similar to density-independent depression in that it alters f , the fecundity at low densities, and thus lowers λ (see Eqn 2), holding the maximum λ closer to the all-important value of 1 (Fig. 4b).

Control of survival

There are many examples in the biological control literature of agents killing whole plants, but there is

little evidence to demonstrate a change in the rate of plant mortality with density. I will investigate the possibility very simplistically by varying m in Eqn 4. The effect of more intense density-dependent mortality is expressed by increasing m , so that the asymptotic density declines (curve 2 in Fig. 3) - a simplistic approach because it takes no account of predator satiation. This is where the proportional mortality declines with increasing prey density because the predator population is saturated. Though mostly exemplified in the arthropod predator-prey literature, it is known to occur in herbivory (e.g. Islam and Crawley 1983, Watkinson *et al.* 1989), though there are few specific examples. In the absence of information on this phenomenon, the obvious over-simplification will have to serve us here. The effect of this form of control, then, is to depress the plateau of the $N^*-\lambda$ curve (curve 3 in Fig. 4b). Thus, this form of mortality increases the range of values of λ over which low, stable values of N^* can be attained.

Invasion potential

Something of a 'holy grail' for quarantine authorities the world over is the possibility of being able to predict invasion potential in newly-introduced or genetically modified organisms. It is an important requirement of the proposed new quarantine protocol in Australia, for example. Can we use an understanding of population dynamics to seek predictors of weediness? In a recent extremely interesting study by Crawley *et al.* (1993), the population dynamics of two lines of transgenically modified canola plants were compared to that of their unmodified relatives at a range of habitats, to see if the genetically modified lines had a greater invasion potential. The key variable for comparison was the finite rate of population increase λ . In fact, there were no significant differences in λ values between the lines. More interesting from the present point of view, however, were the absolute values of λ , because we have little information on field-measured values of λ with which to compare values we might obtain for potential new weeds. In fact all the mean values were less than unity.

Clearly, this would imply that all the lines would decline to extinction if left to their own devices in the field, but what value of λ does it take to make a weed? Crawley *et al.* (1993) assumed that values >1 meant the plant had invasion potential, because the population would increase in size. Now, although the terms

population density and population size can sometimes be safely interchanged, it is important here to distinguish between them. For, no matter what the value of λ , the local population *density* eventually has to reach some equilibrium value, even as overall regional *abundance* continues to increase through the dispersal of seeds to new habitats. Both density and abundance represent different aspects of weediness, but both are positively dependent on λ . Thus, all values of $\lambda > 1$ would result in plants that increase in abundance, but values close to 1 are likely to mean a plant that is always at low density, and perhaps unlikely to be a serious weed.

One way of predicting the invasion potential of unknown plants might be by measuring the density of the species at well-contained sites, under specified environmental conditions, maintained and allowed to self-seed for several generations. A high mean mature density would imply a potential for weediness, in that the plant could become locally dominant. Moreover, if this density turned out to be very stable over time it would also suggest that the plant was in the flat, stable part of the $N^*-\lambda$ curve (see Fig. 4a), with a rather high λ that would result in a rapid rate of increase in abundance if it were to escape. Such a type of study would have to be set in context with studies of known weeds, but it does suggest that large numbers of species might be reliably screened by simply censusing their densities at flowering over a few generations.

It would be a mistake to assume that, by simply dividing the density of plants in one generation by that in the previous one, we were obtaining a true estimate of λ . If the plant is in the stable part of its $N^*-\lambda$ curve, its density will be held roughly constant by density-dependent factors from generation to generation (giving an apparent λ of 1), but the very fact of this stability indicates that λ in reality is likely to be quite high (Fig. 4a).

Discussion

One hidden assumption in the account given above has been that the density-independent mortality happens before density-dependence sets in to compensate. This assumption is not necessarily wrong, but the timing of mortality does have a profound influence on the dynamics of the population in the long term. If density-independent mortality acts before the onset of density-dependence, then compensatory growth by the

surviving plants can muffle the effects of that mortality. If, however, density-independent mortality follows the action of density-dependence, late in the growing season, then little opportunity for compensatory growth exists and the impact of the mortality will be felt strongly in the next generation (R.P. Freckleton and A.R. Watkinson unpublished results).

It is often said that we need to model weed populations to understand and predict their behaviour under control measures of various kinds. As shown above, however, it must be emphasized that for plants, density-dependence can be so strong, and the form of it so important (see Fig. 1), that it is critical for the success of any model that we should understand the density response of the population processes. Besides the plant, the biocontrol agent too is likely to exhibit a response to plant density, though the strength of this generalization is hampered by the fact that we have few measurements of density dependence in herbivores or pathogens (see e.g. Augspurger and Kelly 1984; Burdon *et al.* 1992).

Acknowledgements

I thank S. Böttcher, J. Coupland and C. Smith for critically reading the manuscript.

References

- Augspurger C.K. and Kelly C.K. (1984) Pathogen mortality of tropical tree seedlings: experimental studies of the effects of dispersal distance, seedling density, and light conditions. *Oecologia*, 61: 211-217.
- Burdon J.J., Wennstrom A., Ericson L., Muller W.J. and Morton R. (1992) Density-dependent mortality in *Pinus sylvestris* caused by the snow blight pathogen *Phacidium infestans*. *Oecologia*, 90: 74-79.
- CABI (1995) *International Institute of Biological Control Annual Report 1994* pp.57-58. CABI, Ascot, Berks, UK.
- Crawley M.J., Hails R.S., Rees M., Kohn D. and Buxton J. (1993) Ecology of transgenic oilseed rape in natural habitats. *Nature*, 363: 620-623.
- Hassell M.P. (1978) *The Dynamics of Arthropod Predator-Prey Systems*. Princeton University Press, New Jersey.
- Hassell M.P. (1981) Arthropod predator-prey systems. In: *Theoretical Ecology*, Second edition, pp. 105-131. R.M. May (ed.). Blackwell Scientific Publications, Oxford.
- Hoffmann J.H. and Moran V.C. (1991) Biocontrol of a perennial legume, *Sesbania punicea*, using a florivorous weevil, *Trichapion lativentre*: weed population dynamics with a scarcity of seeds. *Oecologia*, 88: 574-576.
- Islam Z. and Crawley M.J. (1983) Compensation and regrowth in ragwort (*Senecio jacobaea*) attacked by cinnabar moth (*Tyria jacobaeae*). *Journal of Ecology*, 71: 829-843.
- Lonsdale W.M., Farrell G. and Wilson C.G. (1995) Biological control of a tropical weed: a population model and an experiment for *Sida acuta*. *Journal of Applied Ecology*, 32: 391-399.
- Silvertown J.W. and Lovett Doust J. (1993) *Introduction to Plant Population Biology*. Blackwell Scientific Publications, Oxford.
- Watkinson A.R. (1980) Density-dependence in single species populations of plants. *Journal of Theoretical Biology*, 83: 345-357.
- Watkinson A.R. (1985) On the abundance of plants along an environmental gradient. *Journal of Ecology*, 73: 569-578.
- Watkinson A.R., Lonsdale W.M. and Andrew M.H. (1989) Modelling the population dynamics of an annual plant: *Sorghum intrans* in the wet-dry tropics. *Journal of Ecology*, 77: 162-181.
- Yoda K., Kira T., Ogawa H. and Hozumi K. (1963) Self-thinning in overcrowded pure stands under cultivated and natural conditions. *Journal of Biology (Osaka City University)*, 14: 107-129.