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## Short communications

# Population cycles caused by overcompensating density-dependence in an annual plant

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**Summary.** We analyse demographic data from a seven-year study of the annual crucifer *Erophila verna* which showed two-year cycles of abundance in the field. The unusual behaviour of this population is shown to be the consequence of overcompensating density-dependence. Very local differences in germination success between plots can account for observed differences in their population dynamics over the long term.

**Key words:** *Erophila* – Demography – Density-dependence – Germination

It is well known that, theoretically, some forms of density-dependence may cause fluctuations in single-species populations (May 1975). However, in reality, density-dependence is usually a stabilizing process in the dynamics of populations of insects (Hassell et al. 1976, Thomas et al. 1980) and of plants (Watkinson and Harper 1978; Antonovics and Levin 1980; Silvertown 1982; Crawley 1983; Watkinson 1985). In this note, we draw attention to the first case known to us of a natural plant population in which density dependence appears to be responsible for cycles in abundance.

Symonides (1983 a, b, 1984) reports a seven-year demographic study of a population of the sand dune annual *Erophila verna* (Cruciferae) in Poland. She censused individuals in 10 cm × 10 cm plots of larger quadrats and, on the local scale, found that the abundance of *E. verna* cycled between extreme densities of 1–2 and 55–65 individuals 0.01 m<sup>-2</sup> plot with an exact two-year period (Fig. 1a, b). We show here that these cycles result from the relationships Symonides (1983 a, b) found between plant density and fecundity which indicate that seed production per plot showed an overcompensatory reduction with density (Fig. 2).

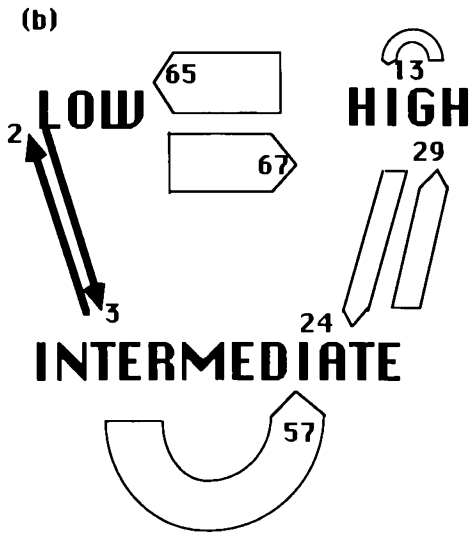
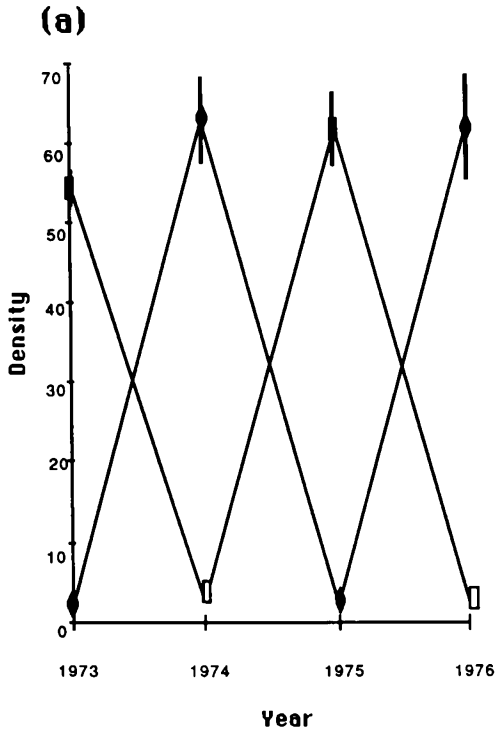
In Fig. 3 we have plotted the total viable seed production per plot against initial seedling density. Since no significant numbers of viable seeds survived in the soil after the main flush of germination in the spring following their production (Symonides 1984), we can use the number of viable seeds produced in a plot to predict the number of seedlings in the next season. A set of germination percentage curves intercepting the seed production curve turn the graphs in Fig. 3 into a graphical analog of a difference equation model which may be iterated by cobwebbing. Iterating the model for different values of germination percentage (Fig. 3a, c, e) shows that the dynamics of this population (Fig. 3b, d, f respectively) may be radically altered by changes in only this parameter, and that 2-year cycles of the kind observed in the field occur when germination is between 0.5% and 1%. Actual germination in the cycling field plots varied from year-to-year, between mean values of 1 and 3%.

Although our model (Fig. 3c, d) produces cycles of the same period as those observed in the field, the model's cycles are of smaller amplitude. We believe this is due to the averaging procedure involved in obtaining Fig. 2, combined with the sensitivity of the populations' dynamic behaviour to the shape of the right-hand end of the seed production curve.

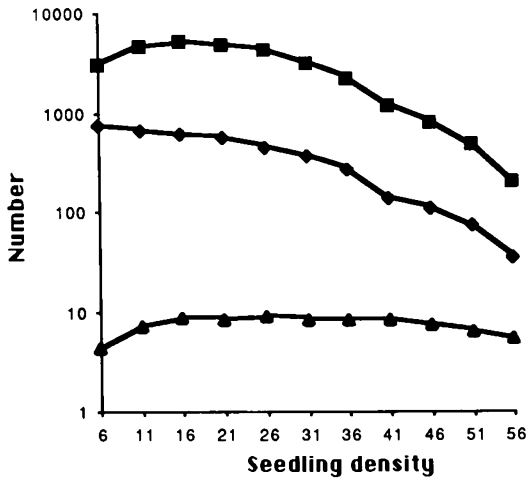
Some of the 10 cm × 10 cm plots in the study tended to remain at a stable, intermediate density and did not show cycles in abundance (Fig. 1b). We suggest that the difference between these and the cycling plots may be due to persistent differences in germination conditions on a local scale. According to our model (Fig. 3a, b) non-cycling plots are predicted to have consistently poor germination conditions (<0.5%) and cycling plots should have relatively good germination conditions (between 0.5% and 1%). The profound consequences of such differences between plots are a further example of the importance of spatial heterogeneity in understanding plant population dynamics.

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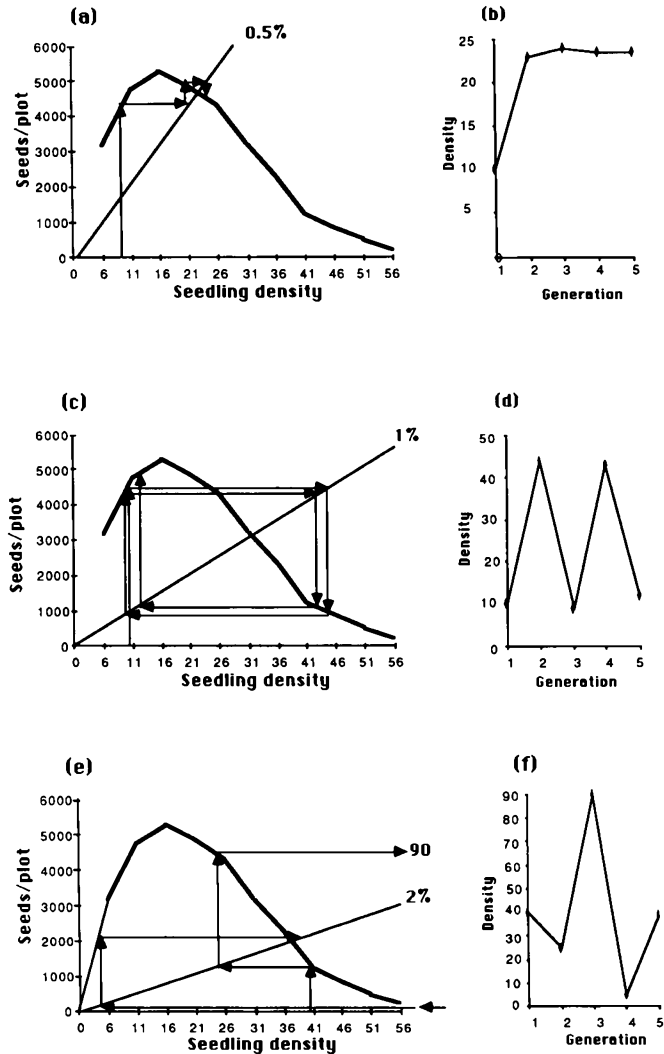
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**Fig. 1a.** The mean density of seedlings of *E. verna* in ten  $0.01 \text{ m}^{-2}$  plots over four generations. *Open symbols* are plots beginning at a high density in 1973, *closed symbols* are plots beginning at a low density in 1973. Standard deviations are shown for high densities by a *vertical bar*. **(b)** The number of transitions between low, intermediate and high density classes (1–4, 5–10, 11–56 seedlings per  $0.01 \text{ m}^{-2}$  respectively) in 31 plots continuously occupied by *E. verna* over seven years. There were no transitions low→low. Data from Symonides (1983a) Fig. 2



**Fig. 2.** Components of seed yield per  $0.01 \text{ m}^{-2}$  plot graphed against the initial seedling density per plot recorded at the beginning of the season. Data are seven-year average relationships. (Data from Symonides 1983a and b, corrected for drawing errors in the original publications). —■— Seeds/plot; —◆— Seeds/plant; —▲— No. Fruiting



**Fig. 3a–f.** Graphical models of the population dynamics of *E. verna*. The *heavy curve* is the same as the “seeds per plot” curve in Fig. 2, but here is plotted on a linear scale. The dynamics of plots with different germination conditions are derived by iteration of the graphical model, with the numbers predicted per plot over five generations shown alongside. **a, b** germination = 0.5%, **c, d** germination = 1%, **e, f** germination = 2%

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