The performance of progeny groups from two populations of *Phyteuma nigrum*, with particular reference to the chance of survival or extinction

J. VAN ANDEL, R. A. WESSELINGH and H. J. VAN DONK

Department of Plant Ecology, University of Groningen, Biological Centre, P.O. Box 14, 9750 AA Haren (Gn), The Netherlands

SUMMARY

Knowledge of minimum conditions for regeneration is of particular importance in estimating chances of survival and recovery of small, declining populations. In this paper, the performance of seed families from individual parents of *Phyteuma nigrum* are determined in order to investigate their potential for regeneration. It is argued that a low mean performance and a low level of variability of seed families may be of minor importance in large populations, but critical in small ones.

Key-words: Phyteuma nigrum, population size, fecundity, size inequality.

INTRODUCTION

The frequency distribution of a species in a particular area is the result of the dynamics of local populations of the species in that area. The frequency may be stable as a result of persistence of the established populations, or of a net balance between establishment and extinction of local populations. If the rate of extinction exceeds the rate of establishment, the species will decrease in frequency and may become rare or extinct. Though rarity of species has received interest from the point of view of nature conservation (Reveal 1981; Synge 1981), relatively little is known about processes concerning extinction of declining local populations (Harvey 1985; de Hullu 1985; Van Leeuwen 1987). Theories on population dynamics mainly concern establishment, growth and maintenance of populations, e.g., in terms of r- and K-strategies.

The causes of extinction of a local population may be external (change in conditions) or internal (change in plant performance or potential for regeneration), or a combination of both. A change in conditions may be natural (e.g., associated with succession of a plant community) or a result of human activity (e.g., fertilization or drainage). A change in plant performance may be due to senescence of the existing plants or to changed resistance against pests or abiotic factors. It has been shown that the potential for regeneration not only depends on the total number of seeds produced, but also on the relative contribution of each parent to the overall seed pool (Winn & Werner 1987) because of differences in both quantity and quality of the progeny from different parents. This phenomenon may be of particular importance in small declining populations of outbreeding species. In such populations, seed set may be reduced due to lack of pollination (e.g., Kwak & Jennersten 1986) and/or to a low level of genetic variation (e.g., Frankel & Soulé 1981, Van Delden 1984). This not only depends on the local population per se, but also on

the distance to other populations of the same species (the rate of isolation, cf. Loveless & Hamrick 1984) and the composition of the local flora (Kwak 1988). The potential for regeneration and the suitability of the habitat for recruitment determine the chance of long-term survival of the population. For purposes of conservation of threatened phytocoenoses and populations, we need ecological knowledge to quantify the minimum conditions for regeneration (Barkman 1984, 1985). In more general terms, criteria are needed to determine whether a community or a population is functioning 'normally' or should be considered 'disturbed' (Van Andel et al. 1987).

The present paper aims at analysing the regenerative potential of local populations of the outbreeding perennial *Phyteuma nigrum*. The frequency of this species has decreased steadily in the Netherlands (Mennema *et al.* 1985). The potential performance of progeny from individual parents from two field populations (cf. Meagher *et al.* 1978) was investigated in order to determine the dependence of fecundity as a life-history parameter on the contribution of individual parents to progeny.

MATERIALS AND METHODS

Seeds were collected from 13 plants (henceforward called parents) from each of two populations of P. nigrum F. W. Schmidt in the catchment area of the Drentse A (The Netherlands). Population Meander consisted of over a hundred plants in a meadow dominated by Filipendula ulmaria (L.) Maxim., Carex acutiformis Ehrh. and Crepis paludosa (L.) Moench. Population Diepveen consisted of about thirty plants (only 13 flowered and produced seeds) on the edge of a small, isolated ditch containing only a few species. The latter population had previously been larger (Reitsma 1979). Seeds were germinated at 15/25°C (dark/light), after 95 days pretreatment at 5°C in wet petri-dishes (dark). The percentage of germination was 48.0 ± 5.7 (n=11; 1 SE) for population Meander and 28.0 ± 5.6 (n = 13; 1 SE) for population Diepveen. Plants, one per pot, were grown from the germinated seeds of each progeny group (per parent) on two different volumes of a mixture of commercial potting soil and sand (400 g and 60 g) under glasshouse conditions. At harvest time, 10 weeks after transplantation of the seedlings, the dry weights of the roots and the shoot parts (total dry weight) of the surviving plants were determined. Statistical tests were performed to compare the progeny from the two populations and the progeny groups within each population, at P < 0.05.

RESULTS

Analysis of variance of the log-transformed total dry weights revealed that the mean dry weight of progeny from population Diepveen (the smaller one) was significantly lower than that from population Meander, independent of whether they were grown in large or small pots (Table 1). Biomass production of the Diepveen progeny in large and small pots amounted to 75 and 79%, respectively, of that in the Meander progeny. The growth reduction due to the small volume of soil was equal in both populations: 37 and 39%, respectively, of the production in large pots. In conclusion, progeny from the small population (Diepveen) did not perform as well as that from the large population (Meander), as far as the mean total dry weight per plant is concerned.

Within population Meander, no significant differences were detected between the mean total dry weights of progeny groups (Duncan's multiple range test), whereas the progeny from population Diepveen showed two or three significantly different clusters (Fig. 1).

Table 1. Mean total dry weight $(mg \pm 1 \text{ SE})$ of progeny from two field populations of *Phyteuma nigrum*, after 10 weeks growth in the glasshouse in different sized pots (with 400 and 60 g soil, respectively)

Treatment	Population	
	Meander	Diepveen
Large pots	1167.5 ± 62.8	876·4±47·2
Small pots	434.5 ± 20.2	342.5 ± 19.7

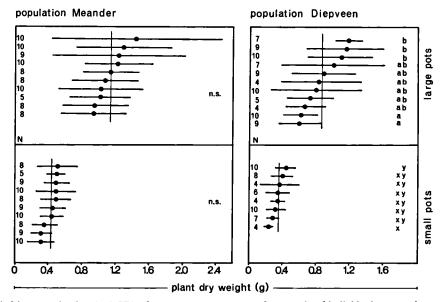


Fig. 1. Mean production $(\pm 1 \text{ SD})$ of progeny groups, grown from seeds of individual parents in two field populations. The plants were grown individually in pots of two different sizes. Mean value per treatment is given by a vertical bar. Significant differences between the progeny groups are indicated (a vs. b, x vs. y).

Whether or not differences exist in the performance among progeny groups within a population depends on the variation in response of each group (Fig. 1). A great deal of overlap in response among progeny groups in population Meander was found, mainly due to the higher variation (s.d.) in groups with a higher mean dry weight. In progeny from population Diepveen, the variation in response tends to be highest in groups with an intermediate mean dry weight, and lower at both extremes so that they differ from each other. In conclusion, the phenotypic performance (total dry weight) of progeny from the large population (Meander) does not depend on the individual seed-producing parent, whereas the performance of progeny from the small population (Diepveen) depends on the parent.

DISCUSSION

The mean production of progeny from the small population was lower than that of progeny from the large population. Only in progeny from the small population could we

detect differences in performance among progeny groups (per parent), leading to the conclusion that the potential regeneration in this population depends on the parental seed source. It should be emphasized that these results need not necessarily be related to the differences in abundance between the two populations. Unfavourable habitat conditions, either for a population or for individual plants in a population, may cause the production of inferior seeds, both in large and small populations. The fecundity of parents also appeared to differ in large populations of the common species *Lychnis flos-cuculi*. However, we should not exclude an effect of population size.

A relatively low variable response of progeny from a small population may be due to a reduction of the genetic variation in this population. Whether or not this is true in the present experiment can be answered only after further experimentation on the gene-flow network and consequences for the performance of the progeny (Ouborg 1988).

The point here is whether the results presented in this paper on the performance of progeny groups from different parents can be used as phenotypic symptoms to estimate the chance of survival or extinction of a given population, either large or small. Many recent papers have emphasized the importance of studying phenotypic variability (whether or not based on genetic variability), in addition to the mean performance of a population (e.g., Ernst 1981, 1983; Van Andel et al. 1984, 1986; Weiner & Solbrig 1984; Biere 1987; Ernst et al. 1987). Competitive pressure, for example, may influence the frequency distribution or inequality of plant size in a population (Weiner 1985), which has consequences for the relative contribution of individual plants to the progeny. Nevertheless, the suppressed population may be able to capture a larger part of the resources if its component individuals show a higher size inequality (Biere 1987). Similarly, Westoby & Howell (1986) have shown that in self-thinning stands of radish, mixed-age stands had a higher biomass yield than uniform stands grown from similar biomass-density combinations. These results indicate that size variability, due either to genetic variation or to differences in individual plasticity, may enlarge the chance of survival of a population under selective pressure. Progeny groups from P. nigrum parents having produced a relatively low mean biomass with a low level of variation might have a lower chance of regeneration. The overall effect on the survival of a population in the long run may well depend on the size of the population.

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