Pre- and post-germination determinants of spatial variation in recruitment in the perennial herb *Helleborus foetidus* L. (Ranunculaceae)

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Summary

1 Recruitment in plant populations is a multiphase sequential process. An integrated view of the relationships between the stages and processes involved is therefore needed, but few studies have analysed the direct and indirect effects concerned. We propose a causal model of these relationships and use structural equation modelling (SEM) and path analysis to investigate the direct and indirect effects of pre- and post-germination processes on recruitment.

2 We collected information on seed production, pre-dispersal seed losses, seed removal from the ground, seedling emergence and mortality, and seedling recruitment during the first year after emergence from 1 × 1 m plots centred on reproductive individuals in three geographically distant populations of the perennial herb *Helleborus foetidus*.

3 The results suggest some congruence between the three populations and indicate that post-germination processes shape the spatial variation in recruitment more than pre-germination processes. Although between-plot variation in recruitment was mostly explained by seedling emergence and mortality, factors such as seed production and removal still have significant effects on recruitment through various, and frequently contrasting, pathways.

4 Path analysis is a powerful analytical tool for revealing important aspects of the recruitment dynamics of plant populations and the factors determining their spatial variation. Such aspects, including indirect effects, are difficult to quantify with other, more classical, approaches to recruitment.

Key-words: *Helleborus foetidus*, path analysis, recruitment dynamics, seedling, structural equation modelling

Introduction

Recruitment in plant populations is a multiphase process, with the total number of recruits and their spatial variation depending on pre- and post-germination processes. Both must be considered if we are to understand recruitment dynamics fully: seed production, seed losses due to herbivory and seed dissemination determine how many seeds move from fruits to a site where germination might occur, while post-germination processes (including emergence and seedling survival)

lead to the eventual establishment of new individuals. Establishment success depends on the dissemination pattern and on the consequences, in terms of differential emergence and survival, of the suitability of the site reached (Jordano & Herrera 1995; Schupp & Fuentes 1995; Schupp 1995).

An integrated view of recruitment has to consider these diverse processes acting sequentially, and such an approach has been adopted in several studies of the patterns and dynamics of recruitment (Reid 1989; Jordano & Herrera 1995; Clark *et al*. 1998; Dalling *et al*. 1998; Harms *et al*. 2000; Rey & Alcántara 2000; Wenny 2000; Jordano 2001). Many studies have found that recruitment dynamics are very complex: indeed, phenomena such as seed–seedling conflicts and uncoupling and spatial discordance between life stages seem

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to be the rule rather than the exception (Houle 1992; Jordano & Herrera 1995; Schupp & Fuentes 1995; Schupp 1995; Rey & Alcántara 2000). However, these studies have rarely used sampling or experimental designs that adequately explore the possibility that a process acting on early life stages (e.g. on seeds still attached to the plant) may have indirect effects on final recruitment (though see Jordano & Herrera 1995). Some processes, for example seed predation or seedling emergence, may have both direct and indirect effects on recruitment, and we need designs and analyses that are able to evaluate the relative importance of direct and indirect effects, as well as the total contribution to recruitment. Structural equation modelling and path analysis are powerful analytical tools, widely used nowadays to investigate direct and indirect effects on ecological and evolutionary processes (Pugesek *et al.* 2003, references therein), but they have rarely been used in studies of recruitment dynamics (but see Jordano & Herrera 1995). We propose here an integrative model of the determinants of recruitment in plant populations and show the usefulness of path analysis for disentangling the complex nature of recruitment.

We use *Helleborus foetidus* L. (Ranunculaceae), an ant-dispersed perennial herb, as a case study and conduct our study in three geographically distant populations located in different mountain systems in southern Spain. We included seedling emergence and survival as post-germination determinants of recruitment and pre-dispersal seed losses, number of seeds arriving at a site and post-dispersal seed removal as pre-germination factors. By considering most processes and stages from mature seed to recruited plant, we aim to explore the relative extents to which spatial variation in recruitment depends on pre or post-germination determinants and on direct and indirect effects.

We address the following questions. (i) What is the relative importance of pre- and post-germination determinants for shaping recruitment? (ii) How do processes occurring in different life stages interrelate to determine recruitment? (iii) Is there spatial concordance between seed deposition, emergence and recruitment (i.e. does the spatial variation in seed deposition determine recruitment pattern, or is it mainly affected by later processes? (iv) Is there geographical congruence in the recruitment patterns and in the processes determining them?

Methods

Helleborus foetidus, hereafter hellebore, is a perennial herb distributed in western and south-western Europe (Werner & Ebel 1994). In the Iberian Peninsula it typically occurs in mountain forests, especially in clearings and at forest edges. Each plant consists of one to several ramets that, in the field, develop a terminal inflorescence after four to seven seasons of vegetative growth, although plants become reproductive in 3–5 years under garden conditions. Flowers are apocarpous, with one to five carpels (most commonly two or three) each containing eight to fifteen elaiosome-bearing seeds that are dispersed by ants. Fruit maturation and seed shedding take place in June and early July. Flowers, and especially developing fruits, are frequently consumed by rodents (mainly *Apodemus sylvaticus*) and lepidopteran larvae (*Noctua* spp. and *Trigonophora flammea*, Noctuidae). Details of the floral biology and seed dispersal of *H. foetidus* in the Iberian Peninsula can be found in Herrera *et al.* (2001, 2002a,b), Garrido *et al.* (2002) and Fedriani *et al.* (2004). Most of the seeds germinate after 2 years of dormancy (Herrera *et al.* 2002a; Garrido 2003), and only 5% of seeds germinate after 3 years. Seed germination and seedling emergence occur from late December to early May, with a peak in March (Garrido 2003). Population dynamics are strongly variable within and between regions, with some large and continuous populations of thousands of individuals showing persistence for many years, while other more fragmented populations persist locally for only a few decades (Garrido 2003). Seedling recruitment thus becomes a key process in population dynamics.

We monitored three populations in three different mountain systems in south-eastern Spain (Jaén Province): Sierra de Mágina (Mediterranean open scrubland, 1650 m a.s.l., 37°44′ N, 3°28′ W), Sierra de Cazorla (*Pinus nigra* forest, 1270 m a.s.l., 37°56′ N, 2°52′ W), and Sierra de Segura (Mediterranean open scrubland, 1550 m a.s.l., 38°16′ N, 2°32′ W) (see Garrido *et al.* 2002 for further vegetation and climate details). We used a regular (systematic) sampling design consisting of 100 1×1 m plots, 10 m apart from each other, set along 10 parallel transects in each population. However, as seedling emergence never occurred more than 1 m from an adult (reproductive) hellebore (see Garrido 2003), data analyses considered only the 88 plots that contained adult plants ($n = 34$ in Mágina, $n = 17$ in Cazorla, and $n = 37$ in Segura). The 1×1 m plots were permanently marked and monitored for seedling emergence and survival from January 1999 to December 2001. In each plot we quantified seed production by any existing adult hellebore, fruit losses due to pre-dispersal herbivory, and seed removal from the ground by ant dispersers or rodent predators. Thus, each sampling unit provided all the information required to link the processes occurring from seed production to seedling recruitment.

Seed production was measured by directly counting the number of carpels releasing mature seeds. Pre-dispersal losses were obtained by directly counting the total number of flowers consumed by rodents and caterpillars. To estimate seed removal on the ground, two open Petri dishes were placed in each plot, each containing 20 fresh seeds (with elaiosome attached) and some litter to simulate natural conditions. A previous study suggested that hellebore seeds become much less attractive to and/or difficult to detect by ants and rodents after 24 hours (Fedriani *et al.* 2004) and the number of seeds remaining was therefore counted after 36 hours.
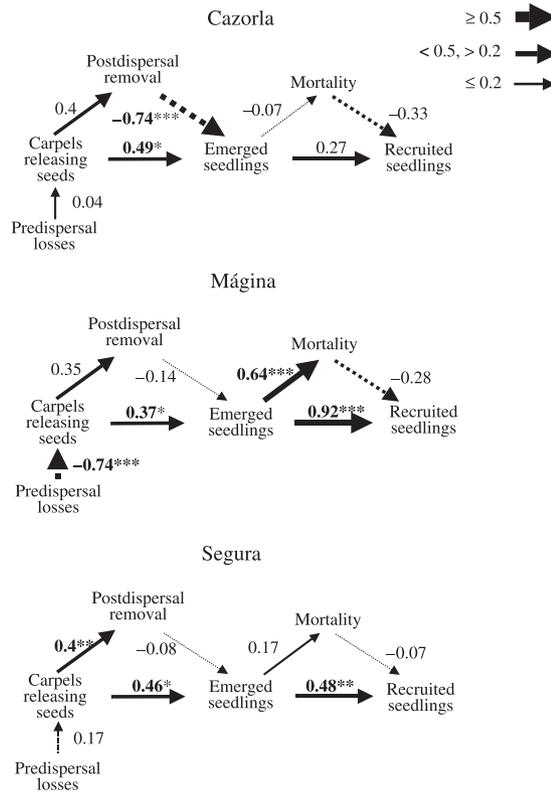
Fig. 1 Structural equation model for each population (Cazorla, *n* = 17; Mágina, *n* = 34; Segura, *n* = 37) of the influence of different processes on recruitment (recruited seedlings) of *H. foetidus*: seed production (estimated as the number of carpels releasing seeds), pre-dispersal herbivory (pre-dispersal losses), seed removal on the ground (post-dispersal removal), emergence density (emerged seedlings), and seedling mortality probability (mortality). Standardized path coefficients significantly different from 0 are marked with asterisks (*$P < 0.05$, **$P < 0.01$, ***$P < 0.0001$). Continuous lines indicate positive effects and dashed lines negative effects, with the magnitude of the coefficient determining their width.

DATA ANALYSES

The variables considered in the analyses were: the number of carpels releasing seeds in each plot in 1999 (a relative estimate of seed production, see above); pre-dispersal losses (proportion of carpels eaten by rodents and caterpillars in 1999); seed removal on the ground (cumulative proportion of seeds disappearing from Petri dishes in each plot, averaged for 1999 and 2000); seedling emergence (number emerging in each plot in 2001, i.e. the year when most 1999-produced seeds germinate; Garrido 2003); seedling mortality (cumulative proportion for 1999 and 2000); and recruitment (cumulative number of seedlings after first year for 1999 and 2000).

Causal relationships between these variables were analysed with a structural equation model (SEM), using the SEPATH Module of STATISTICA (Statsoft Inc. 2000, Tulsa, USA) and log-transformed data. As recruitment is a multiphase sequential process, we built a model (Figs 1 and 2) that explicitly assumes this sequential structure, rather than considering
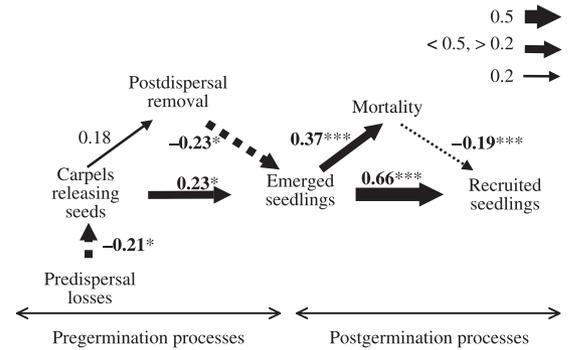
Fig. 2 Structural equation model derived from the pooled data for all three populations (*n* = 88). Model and symbols as in Fig. 1.

alternative non-sequential models (for example, with direct paths from seed production to established seedlings).

The hypotheses of causal relationships between processes were tested by a goodness-of-fit test between the observed covariance matrix and that expected if the model was correct. Because, even after transformation, some variables did not show a normal distribution, the discrepancy function used to fit the model was GLS (generalized least squares), which is preferred to others (e.g. maximum likelihood) in cases of lack of multi-variate normality (Tomer & Pugesek 2003).

One SEM was constructed for each population and subsequently compared with the other populations through multigroup comparison (see Bentler 1989; Bishop & Schemske 1998; Grace 2003) to test the hypothesis of total equality of path coefficients in the three populations.

Results

Although close to significance, the between-population comparison of SEMs did not reject the null hypothesis of total equality of the path coefficients (χ^2 = 52.09, d.f. = 38, P = 0.07). There was therefore no reason to look for between-population differences in path coefficients (Bishop & Schemske 1998) and we have to assume that causal relationships between stages and processes determining the recruitment patterns were similar in the three populations (Fig. 1). Pooling samples from different localities, which improved the statistical power of the model, was thus statistically reasonable. The goodness-of-fit tests for the merged data set indicated that the model adequately described the relationships between variables (χ^2 = 7.35, d.f. = 8, P = 0.5; Joreskog GFI = 0.972; McDonald Noncentrality Index = 0.95–1.000), thus corroborating the underlying hypothesis of causal relationships between the processes involved in recruitment.

The analysis of the pooled data is shown in Fig. 2 and Table 1. These results indicate many significant direct and indirect effects on recruitment, and complex relationships between the processes involved. Total effects were lower for pre- than post-germination processes, although all the processes considered had a significant

Table 1 Direct and total effects on dependent variables in the structural equations model. Significant direct effects are shown in bold type and marked with asterisks (*$P < 0.05$, **$P < 0.01$, ***$P < 0.0001$). Total effects cannot be evaluated as significant or not as they include all the pathways, both those statistically significant and those not. The model explained 39% of the variance in recruitment. r^2 indicates the proportion of variation in the dependent variable explained by the model in each case. DE = direct effects, TE = total effects

	Dependent variables									
	Seed production		Post-dispersal removal		Emergence		Mortality		Recruitment	
Independent variables	DE	TE	DE	TE	DE	TE	DE	TE	DE	TE
Pre-dispersal losses	**−0.21***	−0.21	–	−0.04	–	−0.04	–	−0.01	–	−0.02
Seed production	–	–	0.18	0.18	**0.23***	0.18	–	0.07	–	0.11
Post-dispersal removal	–	–	–	–	**−0.23***	−0.23	–	−0.08	–	−0.14
Emergence	–	–	–	–	–	–	**0.37*****	0.37	**0.66*****	0.59
Mortality	–	–	–	–	–	–	–	–	**−0.19*****	−0.19
r^2	0.05		0.04		0.09		0.14		0.39	

effect on recruitment. There was a direct positive effect of emergence and a weaker direct negative effect of mortality on recruitment. Emergence was equally affected by seed production and by seed removal, although in opposite directions. Seedling mortality was directly and positively affected by emergence (i.e. density dependent) and therefore indirectly by factors affecting emergence (seed removal (−) and seed production (+)). Seed removal on the ground indirectly affected recruitment both negatively, via its effect on emergence, and positively, via the positive effect of emergence on mortality. This suggests that the negative effect of seed removal on recruitment may be buffered by reducing density-dependent mortality (indirect effect = 0.02). The negative indirect effect of seed production on recruitment via mortality (indirect effect = −0.02) was more than compensated for by a positive effect via emergence (indirect effect = 0.15) so that the total balance of its effects was positive (see Table 1). Pre-dispersal losses affected recruitment less than seed removal (total effects of −0.02 and −0.14, respectively). Finally, seed production did not have a significant effect on seed removal on the ground.

Discussion

GEOGRAPHICAL VARIATION IN RECRUITMENT PATTERNING

Exploration of geographical variation in recruitment patterning has rarely been attempted for a single species (though see Rooney *et al*. 2000). Although the between-population comparison of the fitted SEMs from the different localities suggested that there was geographical congruence in the determinants of the spatial variation of recruitment, these results should be interpreted cautiously. The number of sampling units per population was low for optimal SEM comparison (Bentler 1989; Bishop & Schemske 1998) and the test was, in fact, close to significance. In addition, Fig. 1 shows that path coefficients in Mágina were rather different to those at the other two localities, at least in

terms of the effect of emergence on mortality and the effect of pre-dispersal losses on seed production. On the other hand, the apparent congruence may reflect the relatively small geographical range studied (all three localities are in southern Spain): this hellebore is found throughout Western Europe and greater differences in determinants of recruitment may arise on wider geographical scales.

AN INTEGRATED SEQUENTIAL VIEW OF RECRUITMENT PATTERNING

Studies of seedling recruitment can be approached from three major perspectives: (i) the demographic perspective, focusing on transition probabilities between stages, allowing the identification of critical life stages and processes for recruitment (Jordano & Herrera 1995; Clark *et al*. 1999; Rey & Alcántara 2000; Traveset *et al*. 2003); (ii) the recruitment limitation perspective, focused on clarifying whether plant populations and communities are seed- or microsite-limited (Eriksson & Ehrlén 1992; Clark *et al*. 1999; Turnbull *et al*. 2000; Zobel *et al*. 2000); or (iii) the recruitment patterning perspective, which addresses the factors shaping spatial variation in recruitment (Houle 1992, 1994; Jordano & Herrera 1995; Wada & Ribbens 1997). Data from the present study fall into the third category and results should be interpreted in these terms. From this perspective, our study shows that post-germination determinants (emergence and survival) had a stronger effect on patterning of recruitment than pre-germination determinants such as the total number of seeds reaching the ground or their removal by rodents and ants (see total effects in Table 1). We opted for a model that realistically described the multiphase sequential nature of the recruitment process, but alternative models are possible and might lead to different conclusions.

Post-germination determinants of recruitment pattern

The most important determinant of spatial variation in recruitment was the number of emerged seedlings, and

thus pre-germination processes (including germination) become important through indirect effects. Hence, the small proportion of variation in the emergence pattern (9%) explained by seed production and removal on the ground suggests that germination and processes affecting the seed bank (not explored here) may have a strong influence on recruitment patterning. In hellebore, available data suggest that these processes entail long-term seed losses mainly due to the activity of rodents and pathogens during the prolonged seed dormancy of this species (Garrido 2003).

Seedling mortality was the second most important determinant of recruitment (see total effect in Table 1), and was directly influenced by emergence density. Studies showing density-dependent seedling mortality are frequent in the literature (Janzen 1970; Augspurger 1983; Watkinson 1987; Wills *et al*. 1997; Hanley 1998; Kitajima & Fenner 2000), and this has frequently been related to pathogens such as damping-off fungi (Augspurger & Kelly 1984; Kitajima & Fenner 2000) and bacteria (Pedersen *et al*. 1999). In the present study, symptoms of infection were scarce, with desiccation during the summer drought being the major cause of mortality (Garrido 2003). Thus, the observed density dependence may be due to competition for water. The final consequence of this density-dependent mortality was that the best sites for emergence were the worst for survival.

Pre-germination determinants of recruitment

All pre-germination processes had statistically significant pathways towards emergence, mortality and recruitment, indicating a certain predictive power over these patterns. Contrary to other studies (see Kitajima & Fenner 2000; Jordano 2001, and references therein), the pattern of recruitment depended only slightly on the total number of seeds deposited *in situ*. In fact, there was no significant concordance between the spatial variation in number of carpels releasing seeds and the number of recruited seedlings (Spearman correlation, $r_s = 0.07$, $P = 0.46$, $n = 88$), indicating that processes acting after seed deposition substantially modified the pattern of recruitment and suggesting that recruitment is strongly site dependent. The potential of post-dissemination processes, particularly of seedling-related processes, to modify the pattern of recruitment, which has mainly been demonstrated for woody plants (e.g. Jordano & Herrera 1995; García 1998; Castro 2000; Rey & Alcántara 2000; Jordano 2001), is not surprising as seedlings are more vulnerable to the abiotic environment than seeds (Kitajima & Fenner 2000 and references therein).

The effect of removal of seeds on the ground highlights the ecological significance of the ant–seed interaction. Removal of seeds from the ground was very high and rapid, averaging 76% in 36 hours and, as ants remove hellebore seeds faster than rodents (Fedriani *et al*. 2004), was probably more closely related to

secondary dispersal than to consumption. Seed removal had a direct negative effect on emergence and a negative total effect on recruitment. Whilst it is not surprising that a high seed removal leads to an *in situ* reduction in emergence, efficient seed dispersal by ants should have promoted high recruitment in patches away from reproductive hellebores. Our initial systematic sampling did not, however, detect emergence or recruitment in any of the 1×1 m plots lacking reproductive hellebores (≥ 63 plots without reproductive individuals in each locality). Surprisingly therefore we found no evidence in favour of efficient dispersal by ants, and the overall effect of seed removal on both emergence and recruitment was negative. Very few studies have demonstrated a total positive effect of ant dispersal on plant fitness or population recruitment and explorations like those reported here, together with experimental tests of the apparent causal relationships detected by SEM analyses (Bentler 1989; Bishop & Schemske 1998), are needed to determine whether such benefits actually exist.

THE USEFULNESS OF PATH ANALYSIS IN RECRUITMENT DYNAMIC STUDIES

Path analysis allowed us to treat the different processes involved in recruitment dynamics in an integrative sequential way. We were therefore able to elucidate complex relationships between processes such as the different pathways by which seed production affected seedling recruitment (positive, via the direct effect of emergence on recruitment, or negative, due to the dependence of mortality on density of emerged seedlings). Some relationships were even more complex: although the total effect of post-dispersal removal on recruitment was negative, the positive result of reducing density-dependent mortality represented a compensation pathway (Crawley 2000), reducing the size of the overall effect. Such tangled relationships may be impossible to elucidate using more classical approaches to the analysis of recruitment.

It is also important to note that the causal relationships demonstrated by path analysis need experimental validation. Some of the effects shown in our study have already found some experimental support. For example, experimental evidence from our three populations suggests that ant exclusion increases recruitment *in situ*, but that the increase is insignificant (Herrera *et al*. 2002a), supporting the observation that dispersal, if any, is over very short distances (less than 1 m). Furthermore, although pre-dispersal losses due to herbivory affected seed production, they had a slight negative effect on recruitment. Herbivore- and pollinator-exclusion experiments on hellebore have corroborated that floral herbivores decrease *in situ* seedling recruitment in the presence of effective pollination (Herrera *et al*. 2002a).

In conclusion, path analysis has revealed important aspects of early plant recruitment dynamics and the

factors determining its spatial pattern. Though these insights need experimental verification, our results highlight the fact that for a full comprehension of recruitment processes, we need to use analytical tools that consider all stages and processes (and their direct and indirect causal relationships) in an integrated way. We suggest that a research program combining monitoring of natural recruitment, path analysis and experimental testing would greatly improve our understanding of natural recruitment processes.

Acknowledgements

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