COLONIZATION BY THE ANNUAL WEED, *EMEX AUSTRALIS*

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Summary. Experimental introductions of the annual weed *Emex australis* were made in 2 consecutive years at a site in the Western Australian wheatbelt. Introductions differed in relation to the number of seeds involved and whether these were buried or surface-sown. Fates of the introductions were monitored for 30 months. The outcome of the introductions varied markedly according to the year of introduction. Successful colonizations (introductions producing at least one viable seed) were more frequent in the first set of introductions. Relationships between introduction size, seed burial status and colonization success were also different between the separate introductions. Since seedling mortality was low throughout the study, processes affecting seed burial and seed mortality are considered to be the major stochastic factors which influence the colonizing success of *Emex*.

INTRODUCTION

While some understanding has been gained of the characteristics of successful weed invaders (9), it is not possible to predict the outcome of colonizing episodes (3). The fate of an introduction depends upon the action of two groups of variables. The first includes the biological and ecological characteristics which together constitute the weed's 'preadaptation'. The other group subsumes random variables, *viz.* the environmental and demographic stochasticity which often play decisive roles in individual introductions (3). Given the importance of the latter group, it is surprising that so little attention has been paid to the role of chance in the invasion process. Weed invaders are particularly suitable subjects for this type of investigation since they are less mobile than other pests.

The object of this study was to investigate the influence of stochastic factors upon the colonization success of the annual weed *Emex australis* Steinh. (henceforth *Emex*). *Emex* is a self-compatible annual which is native to South Africa. It is an important weed throughout the wheatbelt of southern Australia, but has had the greatest economic impact in Western Australia. Undesirable effects of *Emex* include yield reduction in cereals (6,13), contamination of dried fruit (2), and lameness in sheep (4).

METHODS

Seeds of *Emex* were introduced to an annual pasture on a sandy loam at Wongan Hills Research Station (approximately 200 km north-east of Perth). Introductions varied according to the numbers of seeds (=achenes) involved (n = 1, 2, 4, 8 or 16) and whether seeds were surface-sown or buried at 2 cm. After the soil had been sieved to remove any resident *Emex* seeds, fresh seeds (>90% viability, obtained from seed cleaners in Geraldton) were sown inside 15 cm diameter PVC rings. Because a higher frequency of colonization failure in the smaller introductions was anticipated, the degree of replication decreased with increasing seed number, i.e. there were 20, 10, 5, 4, and 3 replicates, respectively, for the seed numbers given above. Treatments were distributed in a completely randomized design, comprising a block of 12 rows of seven rings with intra- and inter-row spacings of 50 and 100 cm, respectively. Introductions were made at each site during April in 1989 and 1990. The latter set of introductions was made in a separate block with twice the level of replication.

During each growing season, monthly records were obtained of newly emerged seedlings. Since the experiment was fenced in order to prevent disturbance by grazing stock, it was necessary to reduce the biomass of other species by artificial means. The area immediately adjacent to each ring was sprayed with glyphosate in early winter. Within the rings, other species were clipped periodically, but biomass reduction became more difficult to achieve as the season progressed. At the end of each growing season, *Emex* plants were harvested and the number of seeds produced by each plant was recorded.

Introductions were monitored for 30 months, at which point all remaining seeds were retrieved and tested for viability with tetrazolium chloride. Introductions were then classified as 'successful' (seedling establishment within a ring followed by the production of at least one viable seed), 'failed' (neither seeds produced nor viable seeds remaining) or 'indeterminate' (no seeds produced but at least one viable seed remaining). The effects of seed number and seed burial upon colonization at individual sites were analyzed by fitting a log-linear model (7) to the number of introductions falling within each outcome category (successful, failed or indeterminate).

RESULTS

The distribution of the fates of introductions (i.e. the proportions of outcomes in successful, failed or indeterminate categories) differed markedly between the two separate introductions (Tables 1, 2). While the effect of seed number upon introduction fate was highly significant ($P<0.001$) in the first (1989) introduction (Table 1), it was insignificant in the second. Similarly, there was a highly significant ($P<0.001$) effect of seed burial for the first introduction only (Table 2).

Table 1. Fates of buried *Emex* introductions at Wongan Hills, determined over a 3 year period

Year of introduction	Number of seeds introduced				
	1	2	4	8	16
1989	85 (10)[a]	100 (0)	100 (0)	100 (0)	100 (0)
1990	30 (62)	15 (50)	40 (40)	50 (25)	100 (0)

[a] Figures represent the percentages of successful and (failed) introduction, respectively. Indeterminate introductions can be derived by subtracting the sum of the figures from 100.

Viable seeds were detected in a substantial number of introductions which had failed to yield reproductive plants (Tables 1,2). These seeds had remained dormant for the duration of the 30 month experimental period and presumably could had germinated had the experiment not been terminated. However, most emergence occurred during the first growing season following introduction (results not presented).

Table 2. Fates of surface-sown *Emex* introductions at Wongan Hills, determined over a 3 year period

Year of introduction	Number of seeds introduced				
	1	2	4	8	16
1989	15 (50)[a]	10 (40)	40 (40)	75 (0)	100 (0)
1990	5 (88)	5 (90)	10 (30)	12 (75)	17 (67)

[a] Figures represent the percentages of successful and (failed) introduction, respectively. Indeterminate introductions can be derived by subtracting the sum of the figures from 100.

The mean reproductive output of introductions was generally low (Table 3). While the numbers of seed produced increased with introduction size in the first set of introductions, no such trend was evident for the second set.

Table 3. Cumulative number of seeds produced per introduction by burial at Wongan Hills

Year of introduction	Number of seeds introduced				
	1	2	4	8	16
1989	14 (4)[a]	13 (3)	25 (9)	39 (16)	123 (40)
1990	24 (9)	15 (8)	39 (19)	41 (17)	21 (13)

[a] Values in parenthesis are standard errors.

DISCUSSION

Results from this study show the importance of timing to the outcome of weed introductions. Since each introduction had a quantitatively different outcome, misleading conclusions could have been drawn about the colonization process if only a single introduction had been made. This work was part of a larger study involving two other sites (East Chapman and Manjimup). In an attempt to arrive at general conclusions, we will emphasize results from the 1989 introduction, since these were consistent with results from parallel introductions made elsewhere (F.D. Panetta, unpublished data).

Provided *Emex* seeds are buried, a high proportion of introductions are successful, even when few seeds are involved. While levels of seedling mortality were low (<10%), seed mortality was sometimes high (Tables 1, 2). It is clear, therefore, that the major stochastic phenomena controlling the fate of *Emex* introductions are processes which influence either seed mortality or seed burial. A degree of seed burial is required for germination (F.D. Panetta, unpublished data), but *Emex* seeds are sufficiently long-lived to take advantage of natural burial processes, e.g. the soil movement which accompanies rainsplash, erosion, grazing or trampling. Cropping activity buries many seeds, partially explaining the prominence of *Emex* in crop/pasture rotations (5).

For both buried and surface-sown seeds in 1989 introduction, the probability of colonization success increased with introduction size (Tables 1, 2). Most colonization failures occurred in the single-seeded introductions, but in natural situations, prominent dispersal vectors (r.g. contaminated agricultural products or tyre treads) could be expected to deposit seeds in small groups.

Emex is able to spread its colonizing effort over a number of seasons through seed dormancy, thus capitalizing on any interyear variations in growing conditions. Martins and Jain (8) found a similar spread of colonizing effort in their experimental introductions of *Trifolium hirtum.* There was evidence that late-emerging *T. hirtum* plants were genetically distinct (8), but such is not likely to be the case for Australian *Emex* populations (10). The presence of seed dormancy may incur costs during colonizing episodes (12). However, such costs are reduced when the probability of seed survival its high (1).

As long as the number of individuals remains small, a colony will be prone to extinction arising from either environmental or demographic stochasticity (3). A fundamental problem in the study of colonization is that some failures are easily demonstratable, but a successful outcome is considerably less so. We have defined a successful introduction as one where at least one viable seed is produced. However, colonization success for an annual species must be some positive function of its reproductive output early during a colonizing episode. Seed production by an *Emex* plant is a negative function of the biomass of its neighbours; *Emex* has been shown to be a poor competitor against such pasture associates as *Trifolium subterraneum* and *Hordeum glaucum* (11). In the present study, *Emex* survivorship and reproduction were probably enhanced, since interspecific competition was reduced through clipping and treatment with herbicides. To this extent, our estimates of its colonization success may be inflated.

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