Phenotypic plasticity among *Echium plantagineum* populations in different habitats of Western Cape, South Africa

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Abstract

This paper addresses phenotypic variation among Paterson’s Curse (*Echium plantagineum* L.) populations in four different habitat types (tar road verges, dirt road verges, abandoned fields and natural areas) in the Western Cape region of South Africa. The species showed significant differences in plant height, seed size and seed weight with varying habitats. The reproductive index (Ri), comprising a ratio of total number of seeds to the height of the plant, demonstrated the plastic behavior of *E. plantagineum* in the various habitats. Results indicate that plastic responses to different habitat types contribute to *E. plantagineum* invasiveness, allowing range expansion and establishment through production of lighter and heavier seeds, respectively.

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Keywords: Biological invasions; *E. plantagineum*; Phenotypic plasticity; Reproductive index; Seed size; Seed weight

1. Introduction

Many organisms respond with substantial flexibility to a changing environment, generating an array of characteristics depending on the environment in which the developing organism finds itself. A new species, when introduced into an alien environment, must become established within the constraints of site characteristics and competition with resident vegetation. Local adaptation and phenotypic plasticity, are the two strategies to cope with heterogeneous environments (MacNally, 1995; Sultan, 2000; Joshi et al., 2001; Sultan, 2001), and contribute to the success of invaders in diverse habitats (Cordell et al., 1998; Lehmann and Rebele, 2005). Richardson and Pyšek (2006) also suggested that for a species to become a widespread invader it should be plastic or evolve rapidly. Work on several colonizing species has confirmed that their populations across broad geographic and environmental ranges consisted of genetically similar populations of highly plastic genotypes (Hermanutz and Weaver, 1996). Here we define phenotypic plasticity as the ability for the same genotype to produce different phenotypes in response to different environments. Phenotypic plasticity is believed to be the primary strategy for these invaders to adapt to new and heterogeneous environments (Parker et al., 2003; Xu et al., 2003). Brock et al. (2005) have shown that invasiveness involves adaptive plasticity for traits that increase fitness while maintaining constancy for traits such as high dispersal potential. Phenotypic plasticity buffers organisms from environmental stochasticity and confers ability to function in different/new environment.

The success of an alien species depends on the degree of invasiveness, i.e. the potential to establish and spread (Rejmánek and Richardson, 1996). A few simple biological attributes can be strong predictors of potential invasiveness of a species (Rejmánek and Richardson, 1996; Sharma et al., 2005). Plant height and seed mass may act as indicators of both the establishment and regenerative phases of the life cycle (Thompson and Hodkinson, 1997; Pyšek and Richardson, 2007) and are the most relevant traits that address competitive ability (Westoby, 1998; Hodgson et al., 1999).
Numerous studies have demonstrated local adaptation in local populations (e.g. Dudley and Schmitt, 1996; Hangelbroek et al., 2003; Galloway, 2005; Becker et al., 2006; Bischoff et al., 2006). We suggest that Echium plantagineum L. (Paterson’s Curse; Boraginaceae), an invasive alien weed is mainly a “plastic generalist” (Lehmann and Rebele, 2005), but local adaptation through plastic responses may also play a role in its successful occupation of contrasting habitats.

We hypothesize that the colonizing ability of an invader is a function of plasticity for fitness-related traits, enabling it to cope with and perhaps to benefit from habitat conditions. To test this hypothesis, we evaluated the response, in terms of plant height and seed mass, of E. plantagineum to different habitats in the Western Cape, South Africa.

2. Materials and methods

2.1. Plant species

E. plantagineum (Boraginaceae) is an erect annual (occasionally biennial), commonly 30–60 cm in height (maximum height=1.5 m), that reproduces by seed. It is commonly known as Patterson’s Curse and is native to southern Europe (Grigulis et al., 2001). E. plantagineum has a hairy, dark green, broadly oval rosette 30 cm long leaves and produces several seeding stems that develop branches with age. The inflorescence is conical to somewhat loosely branched with few to many spreading unbranched monochasia and sessile flowers arranged in 2 rows. Fruits are 8–11 mm long (maximum=15 mm), with fine spreading hairs. Although generally a spring-flowering annual, E. plantagineum is highly adaptable and given suitable rainfall some plants germinate out-of-season and persist for longer than one year. It is a very prolific seed producer; heavy infestations can yield up to ≈ 10,000 seeds per square metre (Piggin, 1978). Such levels of seed production are likely more than adequate to permit persistence and potential dominance. Seeds are brown to grey, 1 mm long (maximum=15 mm), with fine spreading hairs. Although generally a spring-flowering annual, E. plantagineum is highly adaptable and given suitable rainfall some plants germinate out-of-season and persist for longer than one year. It is a very prolific seed producer; heavy infestations can yield up to ≈ 10,000 seeds per square metre (Piggin, 1978). Such levels of seed production are likely more than adequate to permit persistence and potential dominance. Seeds are brown to grey, 1–3 mm long; three sided and strongly wrinkled and pitted. Seeds are dispersed through animal fur, through the alimentary tracts of birds and grazing animals, via water, and in particular as a hay or grain contaminant (Grigulis et al., 2001).

2.2. Data collection

Richardson and Pyšek (2006) suggested that invasive species establish and proliferate across a range of environmental conditions through their plastic responses. So, we sampled E. plantagineum across a range of habitats and landscapes to observe the possible plastic response of this species. We identified four habitat types: tar road verges, dirt road verges, abandoned fields and natural areas in the Western Cape, South Africa. E. plantagineum population densities were sampled during its peak growth period (October–early November, 2007) using twenty four 1×1 m quadrats randomly located within each habitat. Each E. plantagineum population was sampled for height, number of spikes, number of flower on each spike, seeds on each spike, total no of seeds, seed size and weight per 100 seeds, for an average individual in each quadrat. The Reproductive Index (Ri) was estimated as the ratio of total number of seeds to the height of the plant (Regehr and Bazzaz, 1979; see Aronson et al., 1993).

3. Results and discussion

E. plantagineum populations exhibited substantial differences in plant height in different habitat conditions ($F_{3,92}=161.22, p<0.001$). The average height ranged from 55–102 cm in different habitats, with maximum sizes observed around tar roads and minimum in natural habitats (Table 1). Interestingly, ANOVA also indicated significant differences in number of spikes per plant ($F_{3,92}=88.79, p<0.001$), number of flowers on each spike ($F_{3,92}=57.35, p<0.001$), number of seed on each spike ($F_{3,92}=80.96, p<0.001$), total number of seed per plant ($F_{3,92}=81.43, p<0.001$), average seed size ($F_{3,92}=79.98, p<0.001$) and average seed weight ($F_{3,92}=76.53, p<0.001$). E. plantagineum density also differed significantly among the habitats ($F_{3,92}=38.99, p<0.001$). Table 1 summarizes the vegetative and reproductive characteristics of E. plantagineum in different habitats.

Table 1

|                   | Tar road | Dirt road | Abandoned landscapes | Natural areas |
|-------------------|----------|-----------|----------------------|---------------|
| Height (cm)       | 102 (2.38) | 85.1 (0.94) | 67.1 (1.19) | 55 (1.63) |
| Number of spikes  | 32.3 (1.28) | 24 (0.46) | 18.6 (0.45) | 15.5 (0.62) |
| Number of flower on each spike | 22.1 (0.74) | 14.3 (0.53) | 15 (0.31) | 14.3 (0.30) |
| Number of seeds on each spike | 93.5 (2.85) | 57.2 (2.11) | 60 (1.23) | 57 (1.23) |
| Number of seeds per plant | 3091 (199) | 1390 (75.5) | 1121 (43.9) | 889 (44.8) |
| Seed size (mm)    | 1.38 (0.01) | 1.58 (0.02) | 1.67 (0.01) | 1.88 (0.03) |
| Mean weight per 100 seeds (g) | 0.62 (0.01) | 0.77 (0.01) | 0.79 (0.01) | 0.99 (0.03) |
| Density in 24 ($1 \times 1$ m) | 18 (0.67) | 17.3 (0.49) | 22.3 (0.42) | 24.8 (0.66) |
| Reproductive index (Ri) | 29.7 (1.42) | 18.64 (0.76) | 16.21 (0.49) | 16 (0.45) |

Values in a row with different letters are significantly different from each other according to Tukey’s HSD test at $p<0.05$.
A correlation matrix among the vegetative and reproductive traits is presented in Table 2, and indicates the influence of plant size on seed production and proportion of energy allocated to seeds. Large plants seem to have reproductive advantage, as they produced large number of seeds (Annapurna and Singh, 2003a; Ollerton and Lack, 1998). Height is an indicator of relative size and may explain the greater ability of larger plants to extract resources (Niklas, 1993). Not surprisingly, larger individuals occur in resource rich areas along the verges of tar roads (Spellerberg, 1998; O’Farrell and Milton, 2005).

The Ri showed a decreasing trend from tar road > dirt road > abandoned fields > natural areas, and a similar trend was observed for plant height. Although, significant differences in Ri were observed only among tar road, dirt road and other habitats (Table 1). Habitat induced variability in Ri is indicative of differential colonization response of *E. plantagineum* (*F* 1,92 = 58.7, *p* =< 0.001). A significant increase in Ri was observed with increasing plant height (*r*² = 0.5365; *p* = 0.02), although the seed size and seed weight were significantly and negatively related to plant height (Table 2) and Ri (Fig. 1) respectively. The disparity within the seed size and seed weight also demonstrates the plastic behavior of *E. plantagineum* to different habitats (Table 1).

Light seeds are more dispersible (Weihre et al., 1999) compared to heavier seeds (Fenner, 1985) and production of numerous light seeds in *E. plantagineum* around the road verges may thus facilitate further spread and colonization to new sites. Strategically, substantial seed output (propagule pressure) along road sides may ultimately lead to the invasion of adjacent land, and further spread of this species across the landscape (Richardson et al., 2000; Von Holle and Simberloff, 2005). Hansen and Clevenger (2005) also suggested that the invasive species are dominant along the road verges due to their high colonization ability and high seed production. In contrast, production of larger seeds (i.e. with greater reserves), although fewer, would confer an added benefit to *E. plantagineum*, Navie et al. (1998) argued that the less dispersible heavier seeds produced in natural areas would likely form a persistent seed bank. These observations also support the proposition that the availability of seed reserves can have important impact on seedling establishment (Leishman, 1999), and thus the persistence or invasiveness of a species. Large seed size can potentially improve a seedling’s competitiveness because seedlings from large seeds typically have a lower probability of mortality (Daws et al., 2005) — seedlings are more tolerant of shade, drought, low nutrient availability and defoliation (Leishman et al., 2000).

Plasticity of plant traits in different habitats highlights contrasting strategies that could make *E. plantagineum* a successful invader. Tall plants with small seed mass are appropriate for a rapid population expansion around the road verges. The second strategy is for short plants with high seed mass to persist in an otherwise less favorable habitat. This strategy leads to a slow population build-up, with a gradual increase in the size of the seed bank in abandoned fields and natural areas. Daws et al. (2007) also suggest that shift in seed mass may contribute to invasiveness. *Parthenium hysterophorus*, for example, shows plastic response to soil quality leading to contrasting strategies that contribute to its success as an invader (Annapurna and Singh, 2003a,b). Wood and Degabriele (1985) observed that *E. plantagineum* exhibits substantial phenotypic plasticity in response to localized environmental factors in South-Eastern Australia.

In addition to variable habitats, soil characteristics and the presence of other species in natural habitats may also bring out a plastic response by influencing the growth performance of *E. plantagineum*, through competition and other indirect effects. These need to be further investigated through *in-situ* experimentation as results may have important implications for the management of the species.

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**Table 2**

| Number of spikes | Number of flower on each spike | Number of seeds per plant | Seed size (mm) | Weight per 100 seeds |
|------------------|-------------------------------|---------------------------|----------------|---------------------|
| Height (cm) | 0.95 | 0.72 | 0.87 | -0.89 | -0.85 |
| Number of spikes | 1 | 0.82 | 0.94 | -0.86 | -0.81 |
| Number of flower on each spike | 1 | 0.94 | -0.71 | -0.65 |
| Number of seeds per plant | 1 | -0.77 | -0.73 |
| Seed size (mm) | 1 | 0.94 |
| Weight per 100 seeds | 1 |

All the correlations in bold are significant at the level 0.01.
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