A DEMOGRAPHIC COMPARISON OF COMMON HELIOTROPE, *HELIOTROPIUM EUROPAEUM* L.: SOUTHERN AUSTRALIA AND SOUTHERN FRANCE

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Summary The density, reproductive ecology and seedbank dynamics of *Heliotropium europaeum,* a toxic ephemeral summer-annual weed, are compared between southern Australia and southern France in an attempt to understand why heliotrope is a far more important weed in Australia. We compared the natural enemy communities as a possible explanation for demographic differences observed.

Maximum infestation densities and most basic demographic processes (e.g. seed production versus density) of the weed were similar between the two regions, although average infestation size and density were greater and their occurrence more frequent in Australia. The higher summer rainfall and more extensive rotational agriculture appeared to be the dominant causes of the plant's weed status in Australia, although 10 × larger seedbanks in Australia could not be totally explained by this. This difference in seedbank size may have resulted from either contrasting seedbank decay rates (not assessable) or differences in the rate at which seed are incorporated into the seedbank. The community of insect herbivores in each area caused slight but similar levels of damage, while differences in the prevalence of cercospora blight disease did not clearly explain the differences observed.

INTRODUCTION

Common heliotrope, *Heliotropium europaeum* L. (Boraginaceae)*,* is a summer-growing, herbaceous annual plant from the Mediterranean region to the Middle East and Australia. There is some disagreement as to whether it is native to southern Australia (Kloot 1983, Harden 1992); in the latter region it grows from November to May either dominating fallow, disturbed or ploughed land or being a significant component of annual pasture. In Australia heliotrope is considered a highly 'noxious' weed (Parsons and Cuthbertson 1992) reputed to cost Australian agriculture over $A40 million in bad years (Cullen and Delfosse 1990), while it is rarely considered an important weed elsewhere (e.g. Vasconcelos and Sa 1988). The seeds germinate on bare soil or in sparse vegetation when soil temperatures exceed 24ºC following spring and summer rainfall (Moore 1956). The plant produces flowers and seeds concurrently with vegetative growth, soon after germination, thereby creating a persistent seedbank. The weed senesces in autumn if it is not killed by drought or by cercospora blight (Brun *et al*. 1995) during the summer.

The development of weed management strategies must be supported by a thorough understanding of the dynamics of weed populations (Benoit 1987, Fernandez-Quintanilla 1988, Groves 1989, Navas 1991), and important Australian weeds often have dynamics that differ between Australia and regions where they are not considered weeds (Gill 1984, Weiss and Milton 1984, Lonsdale and Segura 1987). This paper builds on earlier studies of common heliotrope (Moore 1956, Dellow and Seaman 1987) by comparing the population dynamics of *H. europaeum* in Australia (NSW, Victoria, SA and WA) and southern France. Such studies provide an ecological basis for future control strategies.

MATERIALS AND METHODS

General surveys Over the period 1991–93, survey trips sampled infestations of the weed at 23 sites in southern France and 19 sites in southern Australia. At each site, plant density was measured and land use and soil type were recorded. The three most damaging natural enemies were also recorded at each site. All sites were revisited in the following season and plant density was re-measured.

Detailed plant monitoring Within-season population parameters were measured at nine sites in France and eleven sites in Australia in two years from 1991–93. Sites were visited at least twice during each growing season, once soon after recruitment and once close to but not after population senescence. On each visit plant density was measured using 25 randomly thrown 1 m² quadrats and 25 to 50 plants were collected at random and examined in the laboratory 2 to 3 days after collection, where cymes, and fruits (1 fruit = 4 seeds) were counted, plants dry-weighed and attack by insects and cercospora blight was assessed using a ranking system (Brun *et al*. 1995). For large plants, representative top, middle and bottom ranked branches were measured and values for the whole plant were estimated by interpolating intervening branches.

Seedbank sampling In France, from autumn 1991 until spring 1993, 100 soil cores 52 mm diameter and 68 mm depth were taken at random in each autumn and spring at three sites. In Australia, from autumn 1991 until autumn 1993, 25 soil cores 32 mm diameter and 100 mm depth (14 mm diameter after 1992) were taken at random in each autumn and spring at five sites. A greater number of samples and larger soil cores were necessary in France as exploratory sampling indicated that seed densities were much lower at these sites (Goyeau and Fablet 1982). In the laboratory the cores were sieved through stacked 2.8 mm and 0.6 mm mesh. All *H. europaeum* seeds were trapped by the lower mesh size. Seed viability was tested by placing seeds on moist filter paper at 25ºC and 16/8 hour day length for two weeks. All remaining seed were tetrazolium stained to check viability (Harper 1977).

RESULTS AND DISCUSSION

Surveys In France, few sites were found with large *H. europaeum* populations (65% of populations had weed densities less than 1 m^{-2}), while in Australia all sites contained greater than one plant m^{-2}. Germination and recruitment took place following significant summer rainfall (i.e. anytime from November to April in Australia and from May to August in France). Crop harvesting and/or cultivation during this period also appeared to stimulate recruitment (cf. Vasconcelos and Sa 1988). Regional rainfall data suggest that a minimum of 10 mm rain was necessary for germination, but about 25 mm was required to ensure population establishment.

Only two French sites had *H. europaeum* in two successive years, while in Australia half the populations had weed present in both years. In France 43% of populations were in ploughed fields, 43% in fallow fields and 13% in pasture, while in Australia, 45% of infestations occurred in fallow fields following cereal harvest, 35% in pasture, 18% in ploughed fire breaks and 2% in fodder crops. In France, flowering plant density ranged from 0.05 to 700 per m^{-2}. Low density populations were found in all habitat types, but the site with the highest density was an overgrazed pasture in 1992. This site, Moulès-1 (see Brun *et al.* 1995), was still fairly devoid of vegetation in spring 1993, but only two seedlings were observed, despite a large viable seedbank and sufficient rainfall (L. Brun unpublished). In Australia, flowering plant density ranged from 1 to 980 m^{-2}. The highest density infestation was also in a grazed pasture (the density of seedlings started at 5,300 m^{-2}). The largest individual plants were found in fallow fields in both countries. In France, 14 populations were on calcareous/clay soils, eight on a neutral sandy soil, and one on acid volcanic soil, while in Australia most populations were on sandy soil (variable pH). Clearly *H. europaeum* can infest a range of soil types (cf. Moore 1956).

The relative frequency of the most damaging natural enemies found on *H. europaeum* in Australia and France (Table 1) show that cercospora blight was the most damaging in both regions during this study, with natural disease epidemics being observed in both regions (Brun *et al.* 1995).

Table 2. Mean (range) values for different parameters measured from France and Australia.

Parameter	France 92 and 93 (9 sites[A])	Australia 91/92 + 92/93 (11 sites)
Seedling density m^{-2}	15 (0.3–700)	125 (20–892)
Fl plant density m^{-2}	14 (0.3–700)	120 (20–892)
Plant dry weight (g)	(0.5–8.6)	(0.3–7.5)
Cymes plant^{-1}	64 (0.5–170)	23 (8–48)[B]
Fruits plant^{-1}	628 (1.2–1104)	234 (32–755)[B]
Seed rain m^{-2}	78 323 (17–235 200)	271 183 (187–1 456 101)
Seedbank m^{-2} (autumn)[D]	21 759 (17 408–43 478)	177 852 (71 627–426 100)
Seedbank m^{-2} (spring)[D]	9950 (1325–40 242)	119 251 (31 224–251 384)
% Leaf surface eaten by insects[C] (median)	7.3	10.8[B]
% Leaf surface lost to cercospora (median)	8.0	26.0[B]

[A] n=10 as one site used in two years.
[B] Data only available from 5 sites and only in 92/93.
[C] See Table 1 for species involved.
[D] Calculated from both sites plus years, see methods for sample sizes.

Table 1. Natural enemies of *H. europaeum* in Europe and Australia in order of damage importance (% of sites in top three natural enemies) from surveys. [A] The most damaging from 1991 to 1993, [B] the most damaging in 1992/93 only.

France	% Sites	Australia	% Sites
Longitarsus albineus (flea beetle)	86	*Utethesia pulchelloides* (heliotrope moth)	92
Cercospora heliotropii-bocconii (blight fungus)[A]	55	*Longitarsus* sp. 'Victoria' (native flea beetle)	69
Pachycerus cordiger (root weevil)	29	*Cercospora taurica* [B] (native blight fungus)	61
Uromyces heliotropii (rust fungus)	4	*Nysius vinitor* (Rutherglen bug)	23

Demographic studies   The results from nine French sites followed in detail in 1992 and 1993 and from the eleven Australian sites followed in 1991/92 and 1992/93 are summarized in Table 2. Mean plant density and seed production per metre squared were lower in France, while mean plant size and seed production per plant were larger at French sites.

In France, 1993 was a bad year for *H. europaeum* as only three populations were found over the 16 000 km² of the region surveyed. The Mediterranean dry summer was not broken by the usual thunder storms. Recruitment only occurred in late August which appeared to prevent insect attack and gave little time for cercospora blight to have any impact (cf. Brun *et al.* 1995). Seed production was still high by the end of the season (1993 data: fruits pl^{-1} = 731 ± 214, seed rain m^{-2} = 56 962 ± 46 170).

Heliotropium europaeum populations could be grouped into three broad categories;

(a) high competition, medium density sites on weedy fallow land, characterized by poor plant growth, high mortality and low seed production; 10s to 100s seeds m^{-2} (2 Fr. and 1 Au. sites).

(b) intermediate, sparsely weedy sites, characterized by low densities of large plants (>100 cymes) producing 10 000s seeds m^{-2} (5 Fr. and 3 Au. sites).

(c) bare ephemeral sites, characterized by ploughed or bare pasture and high densities of *H. europaeum* producing 100 000s seeds m^{-2} (3 Fr. and 7 Au. sites).

In French fallow-field sites changed from (c)-type to (a)-type within a season where 35–50% of plants appeared to die from plant competition. These rapid
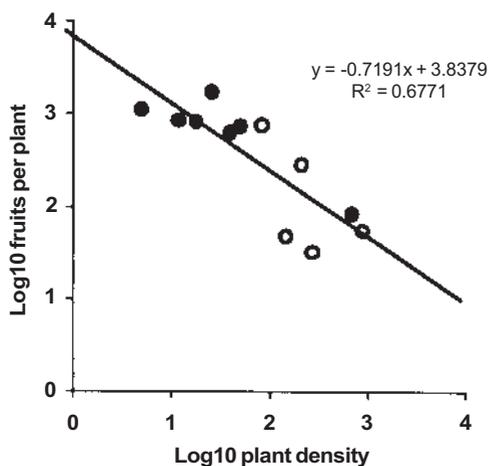

$$y = -0.7191x + 3.8379$$
$$R^2 = 0.6771$$

Figure 1. Regression of plant density against fruit production for all populations not considered affected by interspecific competition in both France (●) and Australia (○).

changes in site quality did not occur in Australia, but may not have occurred with grazing anyway.

The Australian infestations were mostly (c)-type and showed dynamics similar to populations in France of matching type. Out-break populations of the weed in France approached maximum densities recorded in Australia, while seed production per plant and seed rain were also similar in these situations (Brun *et al.* 1995). Over all (b) and (c) type sites, plant density was negatively correlated with fruit production per plant (Figure 1). The Australian population subset were at the high density end of the relationship, but had a slope (-0.90) not significantly different from the French subset. Australian populations, therefore, did not appear to be a distinct group that might be typical of a weed escaping biotic constraints such as natural enemies. The slope for the combined data in Figure 1 was not significantly different from -1 (P>0.05), indicating perfect density compensation, i.e. the populations use all resources freed by declining density. A shallower slope for the French populations (-0.54, significantly greater than -1) suggests that these populations may be less able to exploit such resources (due to, e.g. interspecific competition, lower soil fertility or disease).

Pachycerus cordiger attack was observed at only two French sites and typical damage levels by *Longitarsus albineus* decreased through the season as plants grew exponentially. Cercospora blight occurred at all French sites with large plants increasing to epidemic levels at sites with very high plant density (Brun *et al.* 1995). The levels of foliar damage by insects and pathogens did not appear to be lower at sites in Australia. If *H. europaeum* is alien to Australia and thus relatively free of natural enemies, then this result is contrary to expectation. The combination of a far higher overall weed abundance and two abnormally wet summers (1991/92 and 1992/93) in Australia, however, did lead to above-average abundance of natural enemies. For example, the moth *Utethesia pulchelloides* uncharacteristically decimated southern Australian populations of the weed in 1993. Abundance of the alternative host, *Echium plan-tagineum,* early in the season may have contributed to this. The wet seasons also led to uncharacteristically high levels of cercospora blight in most regions of Australia except for northern NSW (R.C. Lewis personal observation).

Seedbanks   Mean soil seedbank estimates for autumn and spring under three French and five Australian *H. europaeum* populations are given in Table 2. Seedbanks were lower in spring, and in Australia were mostly 10^5 m^{-2}, while those in France were 10^3–10^4 m^{-2}. These differences may have resulted from higher mean seed production m^{-2} (Table 2), or the more frequent 'heliotrope
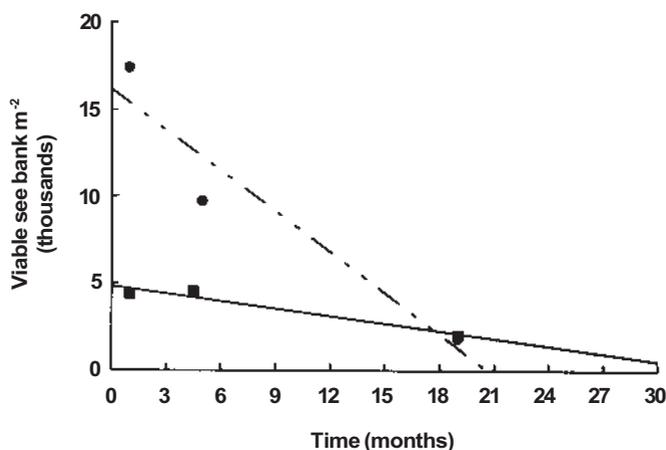
Figure 2. The decay of *H. europaeum* seedbanks at Triadou (■), and Moulès-2 (●), in southern France over time with fitted regression lines. Both sites cultivated in month 12.

years' per site observed in Australia; this does not seem sufficient, however, to explain a ten-fold difference in seedbank size. Differences might be explained by a lower rate of seedling recruitment from the seedbank, increased losses between seed production and incorporation into the seedbank, and/or reduced seed longevity in the seedbank in France.

Seedling recruitment from the spring seedbank was estimated as 0.4% at Moulès-2 in France in 1992 (spring seedbank 9717 ± 1928 seeds m^{-2} (95% C.I.)), while estimates from three Australian sites were 0.20–0.35%. This parameter does not, therefore, clearly explain the differences observed. The component of seed production subsequently detected in the seedbank was estimated as 20% at Moulès-1 in 1992 when seed rain was 235 200 seeds m^{-2}. Cercospora blight was also rife at this site (Brun *et al.* 1995). In Australia this parameter was estimated to be between 79–87% from three sites in 1991/92, where seed rain was about a third that at the French site.

The third possible explanation for the differences in the seedbank sizes observed between France and Australia may be contrasting seedbank longevity. At two French sites no seeds were produced in the 2.5 year sampling period following 1991. Recruitment of 36 seedlings m^{-2} occurred at one site in 1992, but these died without flowering. Both sites were sown to winter wheat in autumn 1992 and soil treatment prior to this would have altered seedbank survival. Seedbank decay curves are given in Figure 2 (cf. Vasconcelos and Sa 1988). Seedbank longevity in Australia has not been measured directly, because all Australian sites had some seed production in most years. Unpublished data collected by

CSIRO Division of Entomology in the 1980s suggest that the seedbank decay rates for Australian sites may be similar.

CONCLUSIONS

The principle reason why common heliotrope is more abundant in Australia may be that the climate, with frequent but irregular summer rains, and land management practices of extensive rotational agriculture over large areas, favour summer-annual weeds. Ploughing of fire breaks in Australia also stimulated *H. europaeum* infestations. Most demographic differences observed appeared to result from underlying differences in the size of the seedbanks in the two regions and the effect this had on recruitment density. This may lead to larger and more frequent infestations of this weed in Australia, but it seems unlikely that the ten-fold difference in the sizes of the seedbanks observed is wholly explained by increased environmental favourability. One explanation appeared to be differences in losses between seed production and incorporation into the seedbank in the two regions. The highly damaging cercospora blight epidemics might provide some explanation for this, but existing data offer little support (Brun *et al.* 1995, Hasan *et al.* 1995). Alternatively, there may be differing levels of post-dispersal seed predation by ants, other insects or rodents between the two regions (Paynter *et al.* in press). Further comparative studies are needed to fully explain the differences identified.

This study has also shown that, contrary to popular belief (Crawley 1989), demographic differences between plants as weeds and natives do not simply result from differences in fecundity. Factors that also influence

seedbank dynamics can be equally important in determining the abundance of a weed and the problem it causes.

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