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Emex australis and the competitive hierarchy of a grazed annual pasture

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Summary

1. A neighbourhood experiment was conducted to compare magnitudes of competitive effect and competitive response using all pairwise combinations of *Emex australis*, *Trifolium subterraneum* and *Hordeum glaucum* as target and neighbour species. Neighbourhoods were established in an annual pasture set stocked at 5 dry sheep equivalents per hectare.

2. Hierarchies of competitive effect and competitive response were determined by averaging effects and responses over non-zero densities of neighbours. In addition, slopes of regressions describing the overall effect and response of each species were compared. The observed hierarchy of competitive effect was *Hordeum* > *Trifolium* > *Emex*: the inverse of the hierarchy for competitive response.

3. *Emex* was defoliated at most moderately, with plants being grazed less as the season progressed. However, this pattern of defoliation conferred no competitive advantage.

4. Since *Emex* is a relatively weak competitor, its impact as a pasture weed could be reduced by maintaining high densities of competitive, beneficial species.

Key-words: defoliation, Goldberg-Werner experiment, management, neighbourhood experiment, weeds.

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Introduction

Following its introduction from South Africa during the last century, Emex australis Steinh. (Polygonaceae, hereafter Emex) became a major weed in crops and annual pastures across southern Australia (Gilbey & Weiss 1980). Emex is responsible for substantial losses in animal production, owing in part to injuries caused by its spiny achenes (Gilbey & Weiss 1980). Because annual legume species are susceptible to damage from the herbicides used to control broad-leaved weeds, there is no economical and reliable method for selective Emex control in pastures. Seedling densities in excess of 900 per square metre have been recorded and Weiss (1981) noted densities of up to 375 established plants per square metre in pastures of south-eastern Australia. In Western Australia, Emex commonly becomes dominant in soil seed banks (Cheam 1987), largely as a result of the progressive depletion of seed stores of other species during the cropping phase of crop/ pasture rotations (Reeves 1987; Taylor & Ewing 1988). While several studies have investigated com-

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petition between *Emex* and wheat (Hawkins & Black 1958; Gilbey 1974; Williams *et al.* 1984), no information is available concerning its competitive relationships with annual pasture species. The relative competitiveness of *Emex* has a major bearing on the feasibility of renovating infested pastures, as well as on the potential for achieving biological control (Burdon, Marshall & Groves 1980).

In contrast to the competitive relationships between weeds and crops, interactions among pasture species are complicated by the activities of herbivores (Harper 1977). In particular, selective defoliation can shift the balance of interspecific competition (Cottam 1986; Forcella & Wood 1986; Van Auken & Bush 1989). Such a shift may, in turn, be reflected by major changes in community composition (Broom & Arnold 1986; Van Auken & Bush 1989). Studies investigating pasture weed competition commonly incorporate defoliation treatments. However, it is very difficult to observe, let alone simulate, natural patterns of defoliation (Greenwood & Arnold 1968; McIvor & Smith 1973). This emphasizes the desirability of conducting competition studies under field conditions (Schoener 1983).

In this paper we report an experiment which employed a neighbourhood design (Goldberg & **374** Emex *in a competitive hierarchy* Werner 1983) to investigate competitive relationships between *Emex*, *Trifolium subterraneum* L. and *Hordeum glaucum* Steud. (hereafter *Trifolium* and *Hordeum*) in an annual pasture grazed by sheep. Periodic measurements on the defoliation of *Emex* were taken in order to aid the interpretation of the experimental results.

Methods

STUDY AREA AND PLOT ESTABLISHMENT

The study took place at Wongan Hills Research Station (30°54'S, 116°43'E), approximately 200 km north-east of Perth, Western Australia. The climate here is typically mediterranean, with a winter dominant rainfall pattern (Fig. 1). The experimental site was an annual pasture on a deep loamy sand soil. *Emex, Trifolium* and *Hordeum* were the most abundant species at the site, which was last cropped in 1984. Total available N (extracted in 1 \bowtie KCl) and P (extracted in 0.5 \utimes NaHCO₃) were 40 and 19 ppm, respectively, in soil samples (n = 25) taken on 17 May 1989.

On 27 April 1989, approximately 2 weeks after the first germination flush of the season, an area of $24 \text{ m} \times 24 \text{ m}$ was cultivated to a depth of 5 cm. Seeds of *Emex*, *Trifolium* or *Hordeum* were then broadcast by hand along single $8 \text{ m} \times 24 \text{ m}$ subplots and lightly incorporated.

COMPETITIVE RELATIONSHIPS

Competitive relationships within individual species and in pairwise combinations of the three species were investigated with a neighbourhood design



Fig. 1. Weekly rainfall totals and average weekly maximum ($^{\circ}$) and minimum ($^{\circ}$) temperatures at Wongan Hills during the experimental period. Total rainfall = 246 mm; 1989 annual total = 334 mm. Arrows indicate times of sowing and harvest.

described by Goldberg & Werner (1983). Their procedure entails establishing a series of neighbourhoods, all of identical size and centred upon 'target' individuals, but differing in the total number of neighbours as a result of hand thinning.

Individual neighbourhoods were established on 17 May 1989. For both single species and pairwise combinations, PVC rings (15 cm diameter and 2 cm deep) were centred upon a nominated target individual, pressed into the ground and anchored with tent pegs. All late-emerging seedlings were removed and the remaining neighbour plants were thinned so that either 0, 2, 4, 8 or 12 individuals remained, corresponding to total (including target plant) densities of 56, 157, 278, 501 and 723 plants per square metre. While the higher neighbour densities were generally located within the areas sown to individual species, other neighbourhoods were situated at random throughout the entire experimental area. Three replicates were set up at each density. 117 neighbourhoods were defined in total. Weeding was carried out at 2 and 4 weeks after neighbourhood establishment. There was no need to replace any plants early in the season, but a few target plants died in the latter part of the experiment.

The paddock was set stocked at 5 dry sheep equivalents per hectare. Towards the end of the growing season, as the seed heads of *Hordeum* plants in the surrounding paddock began to dry off, sheep tended to graze preferentially on the phenologically less advanced sward of the experimental plot. For the final weeks of the experiment, therefore, the plot was effectively stocked at a higher, but undetermined, rate. We could detect no influence of the PVC rings upon sheep grazing behaviour.

Above-ground parts of target and neighbour plants were harvested on 29 September 1989. Following oven-drying, weights (*w* in Tables 2 & 3 and Figs 2 & 3) were obtained of the target plants and combined neighbours from each neighbourhood. In addition, the number of achenes was obtained for each target *Emex* individual.

GRAZING MEAUREMENTS

At the time when the experimental neighbourhoods were defined, co-ordinates of every *Emex* plant in three fixed $20 \text{ cm} \times 50 \text{ cm}$ quadrats were determined, using a plotter following the design of Cullen, Weiss & Wearne (1978). Quadrats were positioned within the plot in locations which contained the three species in approximately equal proportions. The defoliation status of each *Emex* plant was determined in these plots at fortnightly intervals throughout the growing season.

In order to measure the intensity of grazing upon *Emex*, 60 plants showing signs of defoliation were harvested at random (excluding plants within the formal neighbourhoods and fixed quadrats) at

fortnightly intervals. These were returned to the laboratory where counts were made of the total numbers of leaves per plant and the numbers of leaves either partly or wholly removed. Partly damaged leaves were photocopied to permit estimates of percentage leaf removal.

ANALYSIS

Competitive ability in a plant species comprises two aspects: competitive effect, which is the ability of a species to reduce the performance of others, and competitive response, which is an expression of how much the performance of a species is reduced by the presence of others (Goldberg & Fleetwood 1987). In order to compare competitive effects among neighbour species and competitive responses among target species, target plant weights for each species were expressed as a percentage of the mean value for isolated plants and averaged over all non-zero neighbour densities (Goldberg & Fleetwood 1987). This procedure produced a 3×3 matrix, where rows and columns represented competitive effects and responses, respectively. The significance of individual effects and responses was determined using a Kruskal-Wallis χ^2 test.

Competitive effects and responses were also compared by regressing target weights of each species on either the density or the total biomass of each neighbour species. Since some (but not all) of these relationships appeared to be nonlinear, log-log transformations were applied in order to linearize the data. Slopes of these regressions were compared by using a t-test.

Results

COMPETITIVE RELATIONSHIPS

When target plant weights were expressed as percentages of the mean weights of isolated plants, a significant (P < 0.05) overall competitive effect (rows) was detected only in the case where *Hordeum* was the target species (Table 1). However, the rankings of the three neighbours in relation to the reduction of target plant weight were generally in the order of *Hordeum* > *Trifolium* > *Emex* (Table 1). All competitive responses (columns) were highly significant (P < 0.01). The rankings of the three species in terms of competitive response were *Emex* > *Trifolium* > *Hordeum*. Thus, the rankings of competitive effects and responses were complementary; *Emex* showed the weakest effect and the strongest response.

Linear regressions of target plant weight on neighbour weight were all statistically significant (Table 2). No significant differences were detected between the regression coefficients in individual rows, i.e. the per gram competitive effects did not differ significantly between neighbour species. However, significant (P < 0.05) differences were found in the competitive responses (columns) of *Emex* and *Hordeum*, with target individuals of *Hordeum* being less responsive to the presence of either *Emex* or *Hordeum* neighbours than were *Emex* targets.

Only four of the nine regressions of target plant weight on neighbour density were significant (P < 0.05) (results not presented). These all described relationships which occurred in neighbourhoods of either *Emex* or *Hordeum*.

In order to determine whether regression analysis would generate a hierarchy consistent with that derived from Table 1, the following procedure was adopted: target plant weights of species A, when growing in neighbourhoods of either species B or species C, were pooled and regressed on total neighbour biomass (or density). This regression (the per gram competitive response of species A) was compared to another regression fitted to pooled target plant weights of species B and C when grown in neighbourhoods of species A (the per gram competitive effect of species A). For *Emex*, the slope of the relationship describing its competitive response was significantly greater (P < 0.05) than that for its competitive effect (Fig. 2). This species was

Table 1. Comparison of competitive effects among neighbour species, and competitive responses among target species, averaged over all neighbour densities >0. For each target species, weight is expressed as a percentage of the mean value for isolated plants. Values are means ± 1 SE

Target species	Neighbour species			
	Emex	Trifolium	Hordeum	Kruskal-Wallis χ^2 (df = 2)
Emex	19.5 ± 6.32^{a}	13.1 ± 3.61^{a}	$8.25 \pm 2.64^{\mathrm{a}}$	2.43 ^{NS}
Trifolium	32.5 ± 9.24^{ab}	20.5 ± 3.15^{ab}	15.0 ± 3.44^{b}	2.38 ^{NS}
Hordeum	53.2 ± 6.13^{b}	33.2 ± 3.90^{b}	$38.9 \pm 13.7^{\circ}$	8.35*
Kruskal-Wallis				
$\chi^2 (df = 2)$	9.27**	10.8**	12.3**	

For within-column comparisons (among targets), values with the same letters are not significantly different by a Mann-Whitney U-test (P = 0.05). * P < 0.05; ** P < 0.01.

NS, not significant.

Emex *in a competitive hierarchy*

Table 2. Slope values for linear regressions of log target plant biomass (w) on log total neighbour biomass (w + 1). R^2 are given in parentheses; w measured in grams

	Neighbour species				
Target species	Emex	Trifolium	Hordeum		
Emex	-1.13^{a}	-1.54^{a}	-1.25^{a}		
Trifolium	$(0.586)^{**}$ -0.851^{ab}	$(0.451)^{**}$ -0.606 ^a	$(0.712)^{ab}$ -0.916 ^{ab}		
Hordeum	$(0.519)^{**}$ -0.404^{b} $(0.431)^{*}$	$(0.399)^{*}$ -0.664 ^a $(0.577)^{**}$	$(0.743)^{***}$ -0.452^{b} $(0.365)^{*}$		

Within columns, means with the same letter not significantly different P = 0.05. Means within rows not significantly different. * P < 0.05; ** P < 0.01; *** P < 0.001.

considered to be at the bottom of the competitive hierarchy (Table 1). For *Hordeum* (at the top of the hierarchy), on the other hand, the slope of the regression describing its competitive effect was significantly greater (P < 0.01) than that for its competitive response (Fig. 3). On a per-individual basis, the difference between slopes was also highly significant (P < 0.01). The corresponding slopes for *Trifolium* were not significantly different (results not presented).

Although no significant differences in per gram competitive effect were observed between species, the basis of *Hordeum*'s strong competitive effect was apparent in the biomass of *Hordeum* neighbour plants when compared with the pooled neighbour weights of *Emex* and *Trifolium* (Fig. 3); *Hordeum* neighbour biomass was significantly greater by a Mann-Whitney test (Z = 3.24, P < 0.01).

Emex seed production was linearly related to target plant biomass (y = -1.38 + 14.7x, r = 0.99, n = 42, P < 0.001) for data combined over all neighbour species. Relationships between log seed numbers and either neighbour density or log total biomass



Fig. 2. *Emex*: overall competitive effect (on pooled *Trifolium* and *Hordeum* targets) (\circ) (y = 0.692 - 0.656x, $R^2 = 0.32$, P < 0.001) and competitive response (pooled *Trifolium* and *Hordeum* neighbours) (\bullet) (y = 0.874 - 1.29x, $R^2 = 0.55$, P < 0.001); *w* measured in g.



Fig. 3. Hordeum: overall competitive effect (on pooled *Emex* and *Trifolium* targets) (\circ) (y = 0.752 - 1.09x, $R^2 = 0.69$, P < 0.001) and competitive response (pooled *Emex* and *Trifolium* neighbours) (\bullet) (y = 0.726 - 0.487x, $R^2 = 0.40$, P < 0.001); w measured in grams.

were described by linear models, although better fits were generally obtained with biomass as the independent variable (Table 3). None of the differences between the effects of neighbour species upon *Emex* seed production were statistically significant.

PATTERNS OF DEFOLIATION

Emex seedlings were not grazed until they reached the three true leaf stage. Thereafter, individual plants escaped defoliation for short periods only; approximately 80% of the sampled population suffered some degree of defoliation during the period spanning 4-8 weeks after emergence (Fig. 4). Less than 5% of the population escaped defoliation over the entire experimental period.

Generally, more leaves were partly rather than wholly removed (Fig. 5). Whole leaf removal peaked at 10 weeks after emergence. At this time, the majority of defoliated individuals had fewer than 30% of their leaves wholly removed and only one plant in 20 lost more than 50% of its leaves. Part leaf removal decreased linearly with time ($y = 46 \cdot 6 - 1 \cdot 99x$, r = 0.954, P < 0.001). The loss of leaf area from partly eaten leaves was relatively low at week 10 (mean percentage loss \pm SE = $36 \cdot 0 \pm 1 \cdot 7$, n = 100).

Table 3. Slope values for regressions of log *Emex* seed numbers on (a) log total neighbour biomass (w + 1), and (b) neighbour density (thousands of plants per square metre). R^2 given in parentheses; w measured in grams

	Neighbour species		
	Emex	Trifolium	Hordeum
(a) Biomass	-0.980	-1·340	-1.054
	(0.658)**	(0·484)**	(0.618)***
(b) Density	-1.618	-1·618	-1·704
	(0.490)**	(0·288)*	(0·471)**

* P < 0.05; ** P < 0.01; *** P < 0.001.



Fig. 4. Time course of grazing escape by *Emex*.

Discussion

In his review of field experiments on competition, Schoener (1983) stated that the major reason for conducting competition experiments in the field is to determine whether (and how) competition operates in the presence of possible overriding factors. One such factor might be the grazing animal; the use of exclosures significantly increased the fraction of species showing competition (Schoener 1983). Our study, on the other hand, has revealed the existence of a well defined competitive hierarchy in a simple annual community which was grazed. While we are not in a position to comment upon possible mechanisms of competition, it is probable that competition for light did not occur, since at no point during the season was sward thickness greater than 30 mm.

Other studies have indicated that the separate components of competitive ability, namely effect and response, are inversely correlated (Goldberg & Fleetwood 1987; Miller & Werner 1987), although theoretically these components could be uncorrelated or even negatively correlated (Goldberg & Fleetwood 1987). The absence of significant differences in per gram competitive effect between



Fig. 5. Part-leaf (\circ) and whole-leaf (\bullet) removal from *Emex* plants. Values along top of graph give mean number of leaves per plant. Bars indicate ± 1 SE.

species of a similar life form (Table 2) has been observed elsewhere (Goldberg 1987; Goldberg & Fleetwood 1987), and was predicted in the original exposition of the experimental design (Goldberg & Werner 1983). This implies that plant size is a critical determinant of competitive ability; combined neighbour weights of *Hordeum*, the most competitive species in the present study, were significantly greater than those of the other two species (Fig. 3). In a study designed to measure the relative competitive ability of 44 herbaceous wetland species, Gaudet & Keddy (1988) found that plant biomass explained 63% of the variation in competitive ability.

The weak competitiveness of Emex is not likely to have resulted from heavy grazing. Emex was defoliated to moderate levels at most and defoliation decreased as the growing season progressed (Fig. 5). Meadly (1965) stated that *Emex* was grazed only 'accidentally', but our findings are more in agreement with the observation of Gilbey & Weiss (1980) that sheep readily graze its seedlings. Weiss (1976) experimentally defoliated isolated Emex plants either by removing entire leaves or by excising discs (similar to partial defoliation in the present study). He found that reducing the total leaf area by removing whole leaves had a greater effect upon growth than did the removal of an equivalent amount of leaf area by discs. However, plants showed considerable resilience; 4 weeks after the cessation of defoliation treatments (excised discs), there was no significant difference in total dry weight between plants which had experienced repeated weekly losses of 50% of their leaf area and undefoliated controls (Weiss 1976).

While no measurements were obtained on the defoliation of either *Trifolium* or *Hordeum*, it appeared that the latter species was heavily grazed, at least until it began to produce seeds. Thus, the most competitive species in this community was possibly the most highly defoliated as well. Any overall decrease in grazing pressure would probably further disadvantage *Emex*. Several studies have found the effects of defoliation and competition upon plant growth to be additive (Fowler & Rausher 1985; Pendery & Provenza 1987; Jaramillo & Detling 1988). If such is the general case, then the divergence of artificial from natural defoliation regimes should be a less serious drawback to experiments conducted outside natural settings.

In their assessment of the limitations of neighbourhood models, Firbank & Watkinson (1987) maintained that these models are unlikely to be effective in predicting individual plant performance unless plants emerge synchronously. We promoted synchrony in our experiment through cultivation and by removing plants which were obviously late emergents. However, one cause of asynchrony is especially pertinent to the problem of managing *Emex* in annual pastures. Although infrequent, substantial rainfall events occur during the otherwise dry, hot summers of south-western Australia (Panetta 1988). These events usually trigger some germination of winter annual species (Rossiter 1966), but only relatively drought-tolerant seedlings such as those of *Emex* (Gilbey & Weiss 1980) survive for long afterwards. It is not uncommon, then, for established populations of *Emex* to be present when later rains initiate the growing season *per se*.

Since *Emex* is a weak competitor, its dominance in the vegetative component of annual pastures would appear to depend upon low numbers of more competitive species such as Trifolium and Hordeum. The weed control measures employed during cropping sequences largely prevent seed production by these species, while *Emex*, with its relatively long-lived seeds (Cheam 1987), comes to dominate the seed bank. This suggests that Emex could be managed more effectively by tolerating weedier crops, by using pasture legumes which develop more persistent seed banks or by resowing pastures after a series of crops. In the short term, the presence of interspecific competition should reduce seed production by Emex (Table 3). Further work is required to assess the effect of reducing seed production upon the abundance of Emex in subsequent pastures. However, the longevity of preexisting *Emex* seeds could be expected to dampen any reductions in its numbers.

Considerable effort has been devoted in Western Australia to the achievement and evaluation of grass-free pastures. Among the documented benefits are reductions in the weed and disease burdens of subsequent cereal crops (Thorn & Perry 1983). The present study has shown, however, that a widespread annual grass species is highly competitive against *Emex.* Although assessment of the relative competitiveness of other grasses has not been completed, we predict that the use of annual grasses will be central to the effective management of this weed. Furthermore, the weak competitiveness of *Emex* should promote a synergism between the results of agronomic and biological control methods (Groves & Williams 1975; Burdon, Marshall & Groves 1980).

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