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The interaction between natural enemies and interspecific plant competition in the control of invasive pasture weeds

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Abstract. Relative to the impact of biological control agents, plant competition has largely been ignored as an interacting factor in the success of biological weed control. This paper reviews 21 studies that have addressed this issue and draws inferences for biological control of weeds from these, based on the frequency of the different types of outcome observed. Similar studies from both Australia and from the native range of Australia's most important broad-leaved pasture weed, *Echium plantagineum* (Boraginaceae), are also summarized. The results of these studies are compared with the review to help define conditions likely to encourage maximum success for the biological control of pasture weeds.

Introduction

Weeds of permanent or semi-permanent pastures have invaded highly-similar plant communities throughout the world, resulting from the standard and ubiquitous nature of livestock practice and the numerous and now cosmopolitan pasture species introduced to support such agriculture. Within this pasture ecosystem, classical biological control is largely focused on broad-leaved weeds. The aim is to reduce the competitive ability of the weeds within the pasture community using natural enemies to reduce either the vigour or the reproductive potential of the plants to a level where they are no longer effective dominants. The interaction between the impact of control agents and pasture competition on the weed individual underlies successful population control. In pastures, at least, the complex competitive interactions between plants may be similar worldwide given the tendency of humans to homogenize the composition of these communities. Groves (1995) highlighted our extreme lack of knowledge of the dynamics of the interaction between agent impact and plant competition, suggesting that improved understanding in this area might lead to an ability to manipulate the weed's environment to increase the effectiveness of biological control. Such understanding may also help in the prevention of weed substitution following successful biological control (e.g. Burdon *et al.* 1981).

I support this view, and in this paper I review studies that have tested for interactions between natural enemies and interspecific plant competition on target plants, using examples from both the ecological and biocontrol literature. I also summarize five field-experiments on *Echium plantagineum*, Paterson's curse, which had the same basic aim. Generalities and implications relevant to weed biological control are sought from these studies.

Review of studies on the interaction between natural enemies and plant competition

A literature search was made of the *CABI abstracts* CD ROM from 1972-1995 using the keywords, "biological control of weeds" and "plant competition". The results of this search were scanned to retrieve all papers that reported experimental manipulations of both natural enemy attack and interspecific plant competition. The references within these papers were scanned for additional studies. This process identified 21 relevant studies covering 22 plant species (one annual grass, 10 annual herbs, 10 perennial herbs of pastures and one shrub; see Table 1), which, allowing for replication of species, gave 26 case histories (Table 2). Plant yield (biomass or total seed-production per plant) was the response variable most frequently used, although measuring plant survival (Parker and Salzman 1985; Müller-Schärer 1991) or subsequent seed-germination levels at the field site (e.g. Brown *et al.* 1987) also indicated strong effects, particularly for insect herbivores. Comparisons of the effects of the two factors in this review were always made at the highest

Table 1. List of plant species used in studies included in this review and the conditions (N = natural field, C = field crop, P = pot/tub) under which they were tested.

Plant species	Experimental condition	Reference
Amsinckia intermedia Fischer and Meyer	C	Pantone *et al.* 1989
Aristolochia reticulata Nutt.	P	Fowler and Rausher 1985
Capsella bursa-pastoris (L.) Medic.	N	Rees and Brown 1992
Capsicum annuum L.	C	Schroeder *et al.* 1993
Carduus nutans L	C	Kok *et al.* 1986; Cartwright and Kok 1985
Centaurea maculosa Lam.	N	Müller-Schärer 1991
Chondrilla juncea L.	P	Groves and Williams 1975
Cirsium arvense Scop.	N	Ang *et al.* 1994
Gutierrezia microcephala	N	Parker and Salzman 1985
Hypericum gramineum Forster f.	P	Willis 1994
Hypericum perforatum L.	P	Willis 1994
Hypochaeris radicata L.	C	Weiner 1993
Raphanus raphanistrum L.	N	Rees and Brown 1992
Rumex crispus L.	N	Bentley and Whittaker 1979
Rumex obtusifolius L.	N	Cottam *et al.* 1986
Senecio jacobaea L.	N	McEvoy *et al.* 1993
Senecio vulgaris L.	C	Paul and Ayres 1987, 1990; Paul 1989
Sinapis arvensis L.	N	Rees and Brown 1992
Sisymbrium offincinale (L.) Scop.	N	Rees and Brown 1992
Sorghum halepense (L.) Pers.	C	Massion and Lindow 1986
Trifolium repens L.	P	Cottam 1986
Vicia hirsuta (L.) S.F. Gray	N	Brown *et al.* 1987
Vicia sativa L.	N	Brown *et al.* 1987

target plant densities used in each study, as insect attack and pathogen infection levels were likely to be greatest at this density (Root 1973; Paul *et al.* 1993). Intraspecific plant effects were not considered, even though these would be strong among weed species (cf. Müller-Schärer 1991).

Table 2. Numbers of cases where a natural-enemy by interspecific-plant-competition interaction was experimentally tested, sorted by experimental condition into plant type, natural enemy type, the dominant factor and the outcome. * where dominance was equal (one case) no result was recorded. ** where one case observed more than one outcome, depending on the parameter measured, a result was allocated for each outcome.

Experimental condition	Natural field (grassland)	Managed field (crop)	Pot/ Tub	Total
Plant type:				
annual	7	3	4	14
perennial	4	3	5	12
Natural enemy:				
insect/mite	7	3	2	12
mollusc	4	1	1	6
nematode		1	1	2
pathogen		1	4	5
clipping			1	1
Dominant factor*:				
plant competition	10	6	5	21
natural enemy	2		3	5
Outcome**:				
i) substitutive	1	2	2	5
ii) multiplicative	9	3	6	18
iii) synergistic	3	2	1	6

Substitutive, multiplicative and synergistic interactions

The type of outcome was used to assess each case (Table 2). Three outcomes were recognized: (i) a *substitutive* reduction, where one factor completely smothered the other; (ii) a *multiplicative* reduction where both factors had an impact, but without an interaction; and (iii) a *synergistic* interaction.

The outcome was not related to the weed status of the target plant in these studies. Substitutive outcomes suggested that either the experiment had failed to measure an effect of one of the two factors (usually the natural enemy, e.g. Müller-Schärer 1991), or that there was a smothering effect of one factor over the other. Kok *et al.* (1986) failed to find any significant impact of weevils on *Carduus nutans* with or without competition with the grass, *Festuca arundinacea*, even though an impact had been detected in normal pasture (Cartwright and Kok 1985). *Festuca arundinacea* appeared too strong a competitor to achieve any combined result (Kok *et al.* 1986). Conversely the chosen competitor may be too weak, even when the target is attacked by a natural enemy (Paul 1989). The enemy may even govern competitor survival (Cottam 1986).

Multiplicative effects were by far the most common outcome under all experimental conditions (Table 2) and indicate that each factor will have the same relative effect on the target whether or not the other factor is present. The combined effect is termed multiplicative because the effects are most frequently additive only at the logarithmic scale of the response variable. When such factors reduce plant growth, Rees and Brown (1992) showed this can be explained using a simple plant growth model:

$$\frac{dB}{dt} = B\,[r(t) - d(t)] \qquad (1)$$

where rate of change in plant biomass B is determined by the biomass multiplied by both the plant growth rate $r(t)$ and the loss rate of biomass $d(t)$. Competition affects only the growth rate, while natural enemies may affect either the loss rate or both the loss rate and the growth rate. When natural enemies affect only the loss rate, competition and natural enemies act independently on the growth- and loss-rate functions. These will be additive when logarithms are taken (cf. Rees and Brown 1992):

$$\ln\big(B(t)\big) = \ln(B_0) + f(r) - f(d). \qquad (2)$$

where B_0 is the biomass at time $t = 0$.

Following this interpretation, a majority of multiplicative outcomes suggests that natural enemies rarely affect the plant growth rate. The effects of competition on the plant growth rate also usually outweigh any impact of natural enemies (cf. Table 2). Where natural enemies in field systems had a greater impact than competition, this effect was not on plant growth, but on subsequent seed germination (Brown *et al.* 1987). Competition was still the dominant influence on plant growth.

Synergy between the factors is observed when the effect of one of the factors considered changes the absolute or relative effect of the other factor, which is detected on analysis as an interaction between the natural enemy treatment and the competition treatment. Synergy was an uncommon result. Two basic types of synergy were observed. In the simplest type (1-factor synergy) the second factor is observed to have an impact only in the presence of the first. Given the usual overriding effect of competition, the second factor was usually the natural enemy. Two cases of this were found: one on a pasture weed, *Rumex obtusifolius*, in native pasture (Cottam *et al.* 1986) and a second on a grass weed of alfalfa (Massion and Lindow 1986).

Referring back to Eqn 1, the interaction in these cases results from a natural enemy effect on the loss of biomass, *d(t)*, only while plant growth *r(t)* is being depressed by competition. The natural enemy need not be affecting plant growth rate in such cases.

The converse of this synergy can occur if a weak plant-competitor is used and competition is only evident when the target is suppressed by the natural enemy (e.g. Pantone *et al.* 1989). In this case, the natural enemy may have been reducing plant growth-rate, even in the absence of competition, because the natural enemy, a flower gall-forming nematode, was clearly physiologically linked to the weed.

Classic, or 2-factor, synergy where both factors have an impact on the weed in isolation but the combined effects of the two factors is more than the multiplication of each single factor effect, appears to be most elusive, but potentially the most effective outcome for weed biological control systems. Only one study registered 2-factor synergy: the impact of *Puccinia chondrillina* and *Trifolium subterraneum* on skeleton weed growth in pots (Groves and Williams 1975). It would be important to confirm whether this synergy occurs in the field and whether the underlying mechanism is a joint effect of the rust and the competitor on plant growth-rate. The only other example of 2-factor synergy was the doubling of the mortality of one-year-old *Gutierrezia microcephala* saplings by grasshoppers with surrounding vegetation (Parker and Salzman 1985). Plant growth rate of survivors was not affected in this instance and the effect of vegetation cover on the ability of the grasshopper to locate seedlings was an identifiable mechanism for the synergy.

Case study of *Echium plantagineum*

Echium plantagineum is an introduced, toxic pasture weed in areas with wet summer temperate and Mediterranean climates in Australia, South America and South Africa. In southern Australia, where *E. plantagineum* infests some 33 M ha, it is abundant because of affinities for soil type (improved acid soils), climate and land management. A lack of abundant, strongly competitive, pasture species and natural enemies, however, is considered to be the reason for its dominance in some areas (Piggin and Sheppard 1995). *Echium plantagineum*-rich pasture is often a mixture of a low diversity of introduced European species (Smyth *et al.* 1992) with only *T. subterraneum* and other weeds in competition for germination sites (Piggin and Sheppard 1995). The same is not true within its native Iberian range where, in addition to natural enemies, the plant competes with many other winter annual species. In this region the plant is dominant in only some recently cultivated pastures and then only for a season (A. Sheppard and G. Forrester unpublished). CSIRO's Paterson's curse project has been operating in both Australia and in the native range over the last five years.

Native range

In experiments carried out at Agde (southern France) during 1990 and at Evora (Portugal) during 1992, natural enemies were manipulated using insecticides and fungicides. The experiments included one crude perturbation of the pasture community, namely post-emergence cultivation in autumn. This treatment disrupted the normal plant interactions following germination and allowed survivors to grow under much reduced competitive pressure from neighbours.

Experiment 1. In France, the owner ploughed one half of his horse paddock only and advantage was taken of this fortuitous event by selecting 40 plants in each half of the paddock at random, half of the plants in each section were treated with an insecticide/fungicide application. The number of flowers and seeds produced were counted, seed production being correlated with plant size. Horse grazing was light and about the same across the field and there was no visible difference between the ploughed and unploughed halves. Untreated plant roots were attacked by *Mogulones* spp. or *Longitarsus echii* (10%), and *Phytoecia coerulescens* (25%). The opportunist circumstances of this experiment resulted in no treatment replication, thereby precluding statistical analysis; however, the logged data presented per plant (Fig. 1) tend to indicate no impact of natural enemies between treated and untreated (attacked) plants in the unploughed area, while the untreated plants in the cultivated area produced 37% fewer flowers and 53% fewer seeds. The outcome, therefore appeared to be substitutive as competition smothered any effect of natural enemies.

Experiment 2. In an unimproved Portuguese cattle/sheep pasture eight 2x2 m subplots were used inside two fenced and two unfenced plots (see Forrester 1992). In autumn, cultivation and insecticide/fungicide treatments were applied in a fully randomized block design (two replicates per plot) with untreated blocks as controls. In summer, two *E. plantagineum* plants were chosen at random from each subplot and the numbers of flowers and seeds produced per plant were counted. In this experiment grazing was the overriding factor causing a three-fold reduction in plant seed-production (cf. Smyth *et al.* 1996). Cultivation also increased plant size and seed production by 25%, but only in the ungrazed plots (G. Forrester and A. Sheppard unpublished). There was no effect of natural enemies on seed production in any treatment combination, due to very low levels of attack by root/stem-feeding weevils (<5%).

Australia

Experiments 3, 4 and 5. These experiments were conducted in a mown field at CSIRO's Black Mountain site in Canberra in 1993, 1994 and 1995. In each experiment 200 *E. plantagineum* were planted out in a 20x10 grid, each line and row 1.5 m apart. In experiments 3 (1993) and 4 (1994), eight-week-old identically-grown rosettes were planted out into the field plots prior to winter. In experiment 5 (1995), naturally-occurring seedlings were transplanted from within the experimental field into the grid design. This modification gave a more natural range of plant sizes. Plants were grouped as 50 square blocks of four and alternate blocks were either continually weeded to 30 cm from the central meristem or left as control blocks. Within each block, one plant, selected at random, was treated with insecticide, two other plants received

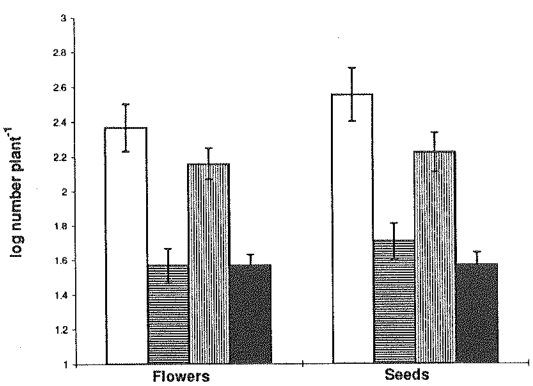

Fig. 1. Mean number of flowers and seeds per *E. plantagineum* plant (log values) from the four treatments in experiment 1 in France (±SE); grazed plants on cultivated ground with insecticide+fungicide (white), grazed pasture plants with insecticide+fungicide (horizontal hatch), grazed plants on cultivated ground (vertical hatch), and grazed pasture plants (black).

augmented levels of insect biological control agents and the fourth plant was an untreated control. In experiment 3, the leaf-mining moth *Dialectica scalariella* was used, although high damage levels were not achieved. The experiment demonstrated, however, that the insecticide (Rogor®) did not alter plant growth. In experiment 4, the insect treatment was one pair of the root-crown weevil, *Mogulones larvatus,* caged per plant for one week. In 1995, when *M. larvatus* had become established at the site, the four plant treatments became: (i) insecticide control; (ii) two plants with natural levels of *M. larvatus;* and (iii) one plant with one pair of a taproot weevil, *Mogulones geographicus,* caged per plant for one week. All mature seeds produced per plant were counted. Log-transformed data were used for all the analyses.

In experiment 4, the insecticide and unsprayed-control treatments were combined as no significant difference was found between the two. Seed production per plant was reduced by both the pasture competition and *M. larvatus* treatments. However, only the combination of *M. larvatus* and pasture competition caused a significant reduction of 62% with respect to the controls (ANOVA $P<0.03$; Fig. 2). In 1995, the two weevil-treatments were not significantly different, allowing the combination of results from these treatments. The preliminary results (number of cymes, Fig. 3) show clear multiplicative reductions resulting from both weevils and pasture competition which is in agreement with the only other similar study recording an impact of a root-herbivore on a pasture weed (cf. McEvoy *et al.* 1993). In experiment 5, root-crown damage by the weevils caused a significantly greater reduction in cyme number than competition. Plants in experiment 4 grew much larger than those in the pasture surrounding the experiment and those used in experiment 5. This accounted for the differences in the treatment effects between experiments.

Interaction of factors in pasture weed control

The review of studies indicated that the type of outcome, whether substitutive, multiplicative or synergistic, was related to the relative magnitude and type of natural enemy impact and competition, and the competitive ability of the target weed. Substitutive effects tend to result from one dominant and one weak factor, usually an over-suppressive competitor and an innocuous natural enemy. Such studies are of little consequence for weed control systems, where the weed

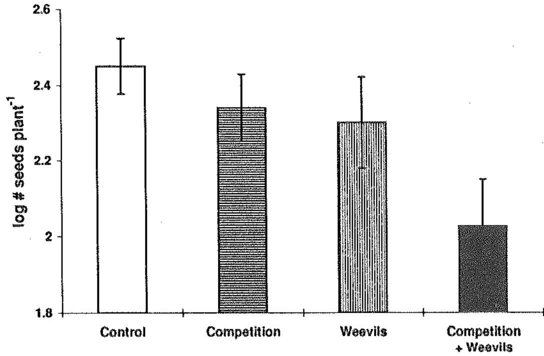

Fig. 2. Seed number per plant, for *E. plantagineum,* from four treatment combinations in experiment 4, in Australia (log values ±LSD).

dominates weaker competitors. This may differ in the native range of the weed. For example, the results from the *E. plantagineum* experiments 1 and 2 showed that competition in this environment is the main factor depressing plant vigour. Nonetheless, biological control agents may be highly effective once released into Australia where weed abundance is higher and plant competition lower.

Simple multiplicative effects of natural enemies and competition were the norm in most studies (Table 2). As well as being easier to measure, interpret and perhaps predict, such effects also provide effective weed control. The successful control of *Carduus nutans* and *Senecio jacobaea* in North America appear to have resulted from multiplicative effects of these factors (Cartwright and Kok 1985; McEvoy *et al.* 1993).

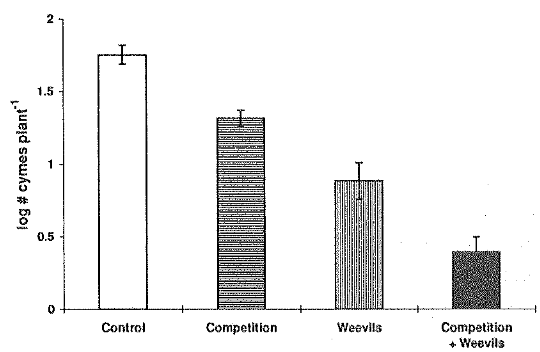

Fig. 3. Number of cymes per plant, for *E. plantagineum,* from four treatment combinations in experiment 5, in Australia (log values ±LSD).

Synergistic interactions may be the basis of a few classic cases of highly successful biological control, where the value of competition in weed control has been accredited (e.g. Goeden *et al.* 1967; Groves and Williams 1975). Field data for the existence of synergy, however, are still lacking and even if demonstrated, such interactions occur too rarely to be of importance in the control of most pasture weeds (Table 2). Any plant competitor of an important invasive weed certainly starts at a disadvantage, and the impacts of natural enemies on the weed are, in general, small relative to plant competitive forces (Table 2). Synergy may occur when the weed's closest competitor is sufficiently strong to allow the presence of a natural enemy to change the competitive balance in favour of the competitor. The growth model discussed here suggests that natural enemies must affect the weed growth rate (i.e. not just reduce plant size) for a synergistic outcome. This should be tested in the field when synergistic results are observed.

The predominance of multiplicative effects of agent(s) and pasture competition, however, suggests that these should receive priority for research on the biological control of pasture weeds. With the relative similarity of plant species in introduced pastures throughout the temperate world, comparing absolute and relative effects of pasture competition and biological control agents for weeds, where control success is known, may help to predict the likely outcome of existing programmes. Successful biological control may seem more likely where agent impact is great, dominating any effect of pasture competition (as in *E. plantagineum* experiment 5). Alternatively this may simply imply that the weed has few competitors and can dominate with or without the agent. Introduced pastures provide an ideal environment to explore such alternatives.

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