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Combinations of stress and herbivory by a biological control mite on the growth of target and non-target native species of *Hypericum* in Australia

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Abstract. The impact of weed biological control agents on non-target native flora is an aspect of biological control which has been relatively poorly investigated. The possibility that non-target species may be affected adversely by control agents may be increased if the target and non-target species co-occur and, further, if the indigenous species is environmentally stressed and thus less able to cope with herbivory. Throughout much of its range, the non-target Australian native species, *Hypericum gramineum*, co-occurs with *H. perforatum*, a weedy species introduced from Europe and currently the subject of a biological programme employing the eriophyid mite, *Aculus hyperici*. We investigated the impact of combinations of environmental stress (nutrient-limitation, plant competition, or water stress) and herbivory by *A. hyperici* on growth of the target weed, *H. perforatum*, and the non-target native species. The alternative hypotheses that in combination, herbivory and environmental stress(es) would cause: (a) additive reductions in plant growth; (b) simple multiplicative (proportional) reductions; or (c) exert more complex synergistic reductions on growth, were examined in glasshouse experiments. Individually, stresses reduced measures of plant growth. In combination, herbivory by *A. hyperici* and environmental stress caused reductions in growth approximately equivalent to the product of the proportional growth following either herbivory or stress(es) alone. *Aculus hyperici* had relatively minor effects on growth of the non-target native, but caused severe reductions in several measures of *H. perforatum* growth.

Introduction

There are many records of reductions in plant growth and productivity caused by herbivores (e.g. Crawley 1983, 1989). Similarly, reductions in plant growth caused by abiotic stresses in the form of nutrient or water limitation, and other biotic stresses such as plant competition have been well documented (e.g. Tilman 1984).

Despite several hypotheses explaining the nature of herbivore-plant interactions, including those of Rhoades and Cates (1976), White (1984), Coley *et al.* (1985) and Price (1991), which have focused, to varying degrees, on the importance of tissue nutrients and, or, chemistry as either phagostimulants or deterrents, relatively few studies examine the combined effects of plant stress and herbivory on host-plant growth. The scarcity of such investigations is surprising given the number of studies reporting that environmentally-stressed plants frequently have higher tissue nitrogen concentrations than unstressed plants (e.g. Mitchell and Chandler 1939; Piene 1978; Stewart and Lahrer 1980; White 1984; Mattson and Haack 1987a, b; Larsson 1989; Louda and Collinge 1992; Waring and Cobb 1992), and that elevated nitrogen concentrations may lead to higher levels of herbivory, since plant herbivores are generally considered to be nitrogen limited (Mattson 1980). Moreover, the degree to which herbivore impact is modified by other plant stresses is of some practical concern. Harris (1980), for example, suggests that more effective biological control of weeds could be achieved when the target plants are environmentally stressed.

In much of southern Australia, the European perennial herb, *Hypericum perforatum* L. ('St. John's wort': Hypericaceae) is established as a weed and has been the subject of several biological control programmes (Groves 1989). The eriophyid mite, *Aculus hyperici* Liro (Acarina: Eriophyidae) is the most recent herbivore to be introduced into Australia in an attempt to control St. John's wort. Mites were released into field infestations of *H. perforatum* after host-specificity screenings indicated that their low preference for indigenous species of *Hypericum* and their reduced fecunditiy on such taxa implied that they were unlikely to have significant impacts on field populations of native 'non-target' species (CSIRO 1991).

Andres (1981) and Turner (1985) observed that post-release studies of biological control agents on 'non-target' species are generally lacking. It is therefore possible that following release of *A. hyperici* onto *H. perforatum*, the mite may move onto *H. gramineum* Forster with which *H. perforatum* commonly co-occurs in southern Australia. Clearly, the potential exists for *A. hyperici* to inflict damage on the native non-target species, particularly if it is environmentally stressed and less equipped to cope with herbivory by a novel arthropod. The possibility of damage is heightened if plant tissue quality for herbivores is enhanced by the increased availability of nitrogenous compounds during stress. In environmentally stressed plants, release of herbivores from nitrogen-limited growth may lead to synergistic reductions in plant growth. If stress also reduces the ability of the plants to tolerate herbivory, interactions between herbivores and environmental stress may lead to further decreases in plant growth.

In this paper we examine the hypothesis that stressed plants are more susceptible to herbivory than healthy plants. In so doing, three alternative hypotheses are tested. These are that: (a) combinations of stresses may have simple additive effects on plant growth; (b) combinations of stresses interact in a simple multiplicative way, causing proportional reductions in plant growth; and (c) stresses might interact in more complex, synergistic ways. This paper is a synthesis of the results of previously reported experiments (see Willis *et al.* 1993, 1995) together with the results of more recent research (Willis 1994) which will be published elsewhere.

Materials and methods

Three experiments were conducted to examine combinations of herbivory and plant stress on growth of *H. gramineum* and *H. perforatum*. In the first (experiment 1), combinations of plant nutrient limitation and herbivory by *A. hyperici* on plant growth were investigated. Experiment 2 was used to examine the combined effects of plant competition and *A. hyperici* herbivory on plant growth, while experiment 3 was used to measure the effects on growth of combinations of water stress, and herbivory by *A. hyperici* and *Aphis chloris* Koch (an aphid introduced to Australia for the biological control of St. John's wort) (Briese 1989). The experiments comprised randomized blocks with all possible treatment combinations factorially applied to both *H. gramineum and H. perforatum*.

Experimental design and treatments

Details of the design and treatments employed in experiments 1 and 3 are reported elsewhere (Willis *et al.* 1993, 1995). Briefly, all experiments were conducted on pot-grown plants in a greenhouse. Experiment 1 (nutrient limitation) was set up to examine plant growth under two levels of mite herbivory (*A. hyperici* either present or absent) and two nutrient regimes, tap water (low nutrient treatment) or 100% Hoagland's nutrient solution (high nutrient treatment). Experiment 3 (herbivory and water stress) was designed to investigate plant growth under two levels of *A. hyperici* herbivory (mites either present or absent), two levels of aphid herbivory (*A. chloris* either present or absent) and two watering regimes in which plants were either watered to capacity each day (high water treatment), or maintained just above wilting point for the duration of the experiment (low water treatment).

Experiment 2 consisted of five replicate blocks, each comprising eight treatment combinations for both *Hypericum* species. The treatments were: (1) mite herbivory at two levels of intensity, plants either infested with *A. hyperici* or free of infestation; and (2) plant competition at four levels of intensity, which were achieved by growing the two *Hypericum* species free of competition and in combinations of root and, or, shoot competition with the native Australian grass, *Themeda triandra*, as follows: (i) no root competition and no shoot competition (-R-S): pots containing an individual hypericum plant; (ii) no root competition, but shoot competition (-R+S): pairs of pots, one containing three *T. triandra* plants and the other containing a single hypericum plant such that the roots of the grasses and the hypericum seedling were separated, but the shoots of all plants were together. Where hypericum shoots were not obviously shaded by *T. triandra*, they were manually inter-twined among the grass shoots; (iii) root competition, but no shoot competition (+R-S): pots containing three *T. triandra* plants and a single hypericum plant, with shoots of the former separated from those of the latter by a clear plastic screen (20x30 cm); and (iv) both root and shoot competition (+R+S): pots containing three *T. triandra* plants and a single hypericum plant with shoots of the latter growing amongst those of the grasses, and where failing to do so, manually inter-twined, as above.

In experiments 1 and 2 (nutrient limitation and plant competition), mite-free treatments were sprayed every 4-6 weeks with Omite® miticide. The negligible effect of the miticide on growth, and plant-tissue nitrogen- and phosphorus-content was established in a separate experiment. Spraying with Omite was not possible in experiment 3 (water stress and aphid herbivory) as the miticide's effect on *A. chloris* was unknown. All pots in this experiment were therefore enclosed in fine, gauze-like paper to contain mites and, or, aphids on plants. The results of a separate experiment indicated that plant growth was not affected by the gauze bags (Willis *et al.* 1993).

Infestation of plants with herbivores

In all experiments, mites were introduced to '+ mite' treatments by placing infested vegetative *H. perforatum* buds into the crown of experimental seedlings. Three buds, each infested with 5-10 mites were introduced. Plants were re-infested in the same manner after six and eight weeks. Aphids were introduced to experiment 3 in the same manner. Each of the three buds used to introduce aphids onto plants were infested with approximately 30 adults. Where establishment of either herbivore failed, the inoculation was repeated after four weeks.

Measured growth parameters and analyses of data

At the completion of each experiment, after three to six months, depending on the particular trial, plants were harvested and several growth and nutrient parameters measured including root, shoot and total biomass (g) (see Willis 1994 and Willis *et al.* 1993, 1995 for discussion of other indices of plant growth). After log-transforming the data, two- and three-way analyses of variance (ANOVA), structured according to the various experimental designs, were performed for all growth parameters. It was not possible to determine directly the root mass of '+ root competition' treatments in experiment 2. For these treatments, root mass was estimated from the root:shoot ratio of samples of each species grown in a separate

Table 1. Relative (%) plant growth (total plant biomass) of *Hypericum* species in relation to various stress combinations, taking the unstressed plants to represent 100%, for the three experiments. Expected values (%) for the hypothesis that combined stresses yield the product of the proportional growth under each separate stress are presented in round brackets. Biomass of the unstressed controls are presented in square brackets. The data for *H. gramineum* and *H. perforatum* have been pooled since species differences were only marginally significant.

Experiment		*Stress combinations*			
	Mites	*High nutrients*		*Low nutrients*	
Nutrient limitation	- Mites	100 [11.6 g]		49	
	+ Mites	71		34 (35)	
		No competition -R-S		*Root and shoot competition, +R+S*	
Plant competition	- Mites	100 [11.5 g]		55	
	+ Mites	89		49 (49)	
		High water		*Low water*	
		- Aphids	+ Aphids	- Aphids	+ Aphids
Water stress and aphid herbivory	- Mites	100 [2.5 g]	80	33	22
	+ Mites	55	48	18	16 (14)

experiment, as detailed by Willis (1994). Since root growth was estimated in this way, the variable was not statistically analysed.

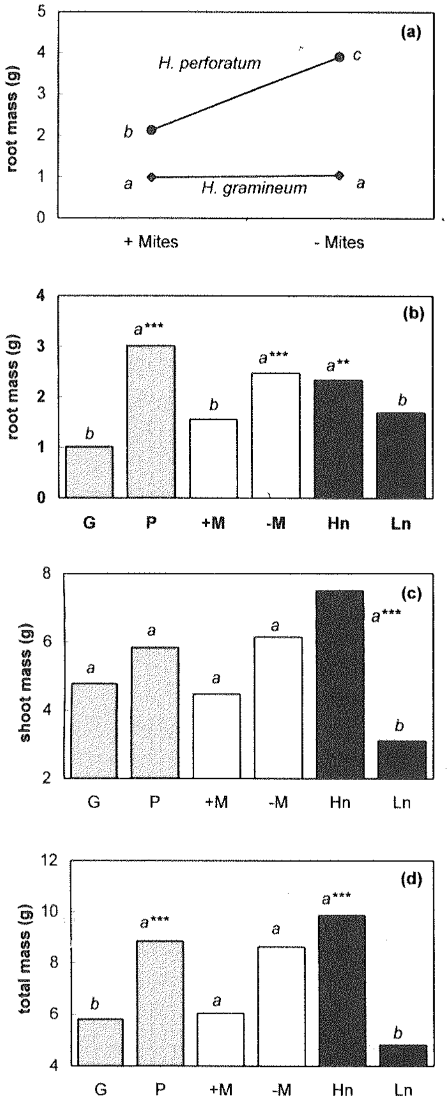

Fig. 1. (a) Interaction between mites and plant species on *Hypericum* species root mass, with significant differences indicated by points with different lettering, as suggested by a significant (P ≤ 0.001) F-test; (b-d) mean root, shoot and total biomass after experimental treatments in the nutrient-limitation experiment. Significant differences (P ≤ 0.05) between treatments of the main factors, species (lightly shaded columns; G = *H. gramineum*, P = *H. perforatum*), mites (white columns; +M = mites present, -M = mites absent) and nutrients (black columns; Hn = high nutrients, Ln = low nutrients) are indicated by columns with different lettering. The significance of F-tests between treatments of the main factors is also indicated (P ≤ 10.05*, P ≤ 0.01**, P ≤ 0.001***).

Results

Experiment 1 - nutrient limitation

For the three measures of plant growth considered in this paper, namely shoot, root and total plant biomass, there were few significant interactions between the main experimental factors on the log-scale used in analyses. The only significant interaction was between plant species and mites on root growth ($P < 0.001$). This significant interaction suggested that the root mass of *H. perforatum* was dramatically decreased by mites (reduced by 46%), while the decrease in the mass of *H. gramineum* roots subjected to herbivory by *A. hyperici* was minimal (6%) (Fig. 1a). Other significant effects on plant growth were generated by

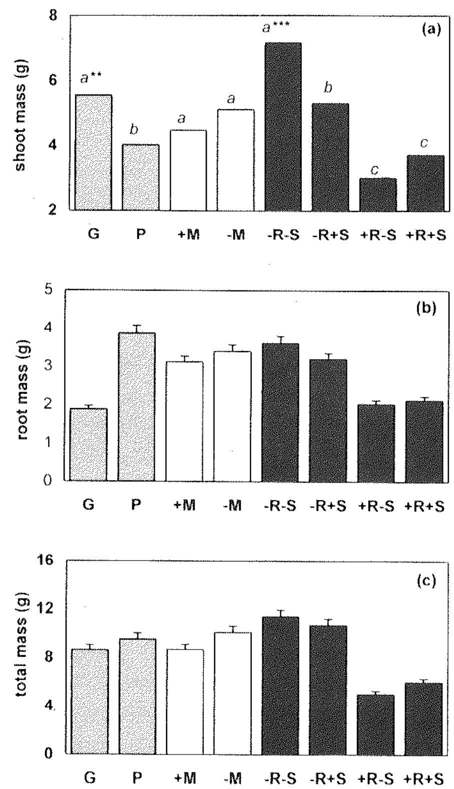

Fig. 2. (a-c) Mean shoot, root and total biomass after experimental treatments in the plant competition experiment. Error bars on figures b and c represent standard error of the arithmetic mean. Significant differences (P ≤ 0.05) between treatments of the main factors, species (lightly shaded columns; G = *H. gramineum*, P = *H. perforatum*), mites (white columns; +M = mites present, -M = mites absent) and competition (black columns; +/- R = root competition and, or, S = shoot competition) are indicated by columns with different lettering. The significance of F-tests between treatments of the main factors is also indicated (P ≤ 0.05*, P ≤ 0.01**, P≤ 0.001***).

the main experimental treatments. Root mass for example, differed between species ($P < 0.001$; Fig. 1b), thereby underlining distinct morphological differences between these taxa, while the low nutrient treatment resulted in differences in root, shoot and total mass ($P = 0.005$, $P < 0.001$ and $P < 0.001$, respectively) (Fig. 1b-d).

Table 1 summarizes the combined effects of individual stresses (low nutrients and +mites) on hypericum growth. The combination of low nutrients and the presence of mites leads to simple proportional reductions in plant mass relative to the unstressed control plants (high nutrients and -mites), close to the levels predicted from a model of proportional growth under combinations of stress (calculated as 100x the proportional growth under nutrient limitation alone x the proportional growth after *A. hyperici*-herbivory alone). Taking the high nutrient and mite-free specimens to represent 100% growth, nutrient limitation in the presence of herbivory reduced hypericum total plant weights to 34% of controls, very close to the expected value of 35%. A potential synergism between stresses leading to greater-than-proportional decreases in growth is not obvious, as is consistent with the general lack of significant ($P > 0.05$) interaction terms in the ANOVA.

Experiment 2 – plant competition

Factor interactions were not significant ($P > 0.05$) in the ANOVA. The effect of mites on shoot mass was not significant (P = 0.166), though their presence reduced this index of growth (Fig. 2a). Mites caused proportionally greater reductions in the growth of *H. perforatum* shoots than in the growth of those of *H. gramineum*. Shoot weight was reduced by 23% in *H. perforatum*, for instance, and by only 4% in the native non-target.

Shoot mass was also significantly reduced by plant competition ($P < 0.001$) (Fig. 2a). As anticipated, growth in the root and shoot competition-free controls (-R-S) was significantly higher than in any of the other treatments.

Although not analysed statistically, it is clear that the experimental treatments also affected root growth. Mites, for example, were associated with a clear decrease in root mass. Their effects appeared more pronounced on *H. perforatum* than on *H. gramineum*. Root mass was reduced by about 20% in the target weed, and by approximately 3% in the non-target native species (Fig. 2b and c).

Mites caused a 22% reduction in the total biomass of *H. perforatum* and a 4% reduction in the total biomass of *H. gramineum*. In this experiment, reductions in plant growth caused by *A. hyperici* were consistently more severe for *H. perforatum* than for the Australian native, *H. gramineum*. The trend emphasizes the host-specificity of *A. hyperici*.

In both *H. gramineum* and *H. perforatum*, combinations of herbivory and root- and shoot-competition caused proportional decreases in plant biomass, relative to the competition- and mite-free combinations (Table 1). In combination, competition and herbivory reduced plant growth to 49% of the stress-free controls; the same value predicted by the model of proportional growth under several stresses.

Experiment 3 – water stress and aphid herbivory

The four-way interaction between mites, plant-species, water and aphids was not significant ($P > 0.05$) for any of the measured parameters and has, therefore, been omitted from further discussion. In the only significant interaction ($P = 0.008$, but see Willis *et al.* 1993) for any of the growth parameters considered in this paper, the combination of +mites and +aphids caused a severe reduction in *H. gramineum* shoot weight, while in *H. perforatum*, the combined effect of both herbivores was the same as each acting alone (Fig. 3). Nevertheless, relative to unstressed controls, the high stress combination of +mites and +aphids caused proportionally greater reductions in the mass of *H. perforatum* shoots than in those of *H. gramineum*. This trend was consistent for decreases in root and total plant biomass., indicating the host-specificity of the biological control agents.

Overall, the main experimental factors (plant-species, mites, water and aphids) had highly significant ($P \leq 0.016$) effects on shoot, root and total plant weight (Fig. 3a-c). Where such differences were found, high stresses (low water, +mites and +aphids) reduced the magnitude of growth.

In this experiment also, the combined effect of individual stress factors on total plant growth was roughly multiplicative. The combination of mites, aphids and water stress was, therefore, expected to yield a total plant biomass approximately 14% of the biomass of unstressed hypericum. In fact, the stresses resulted in a reduction in plant biomass to 16% of controls.

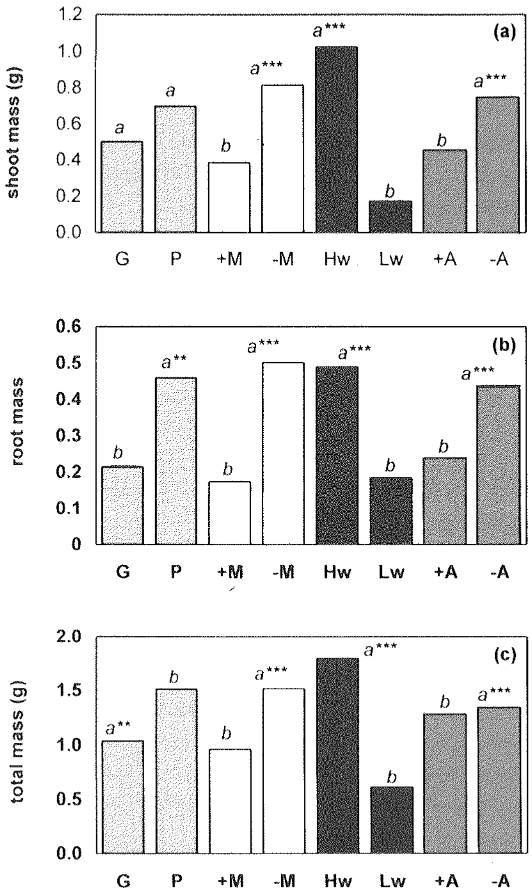

Fig. 3. (a-c) Mean shoot, root and total biomass after experimental treatments in the water-stress experiment. Significant differences ($P \leq 0.05$) between treatments of the main factors, species (lightly shaded columns; G = *H. gramineum*, P = *H. perforatum*), mites (white columns; +M = mites present, -M = mites absent), water stress (black columns; Hw = high water, Lw = low water) and aphids (darkly shaded columns; +A = aphids present, -A = aphids absent) are indicated by columns with different lettering. The significance of F-tests between treatments of the main factors is also indicated ($P \leq 0.05$*, $P \leq 0.01$**, $P \leq 0.001$***).

Discussion

The results of this study demonstrate that growth of nutrient-limited and competitively- and water- stressed hypericum seedlings may be severely retarded relative to unstressed controls, consistent with the result of other plant growth/stress experiments. In general, the stresses reduced measures of plant growth such as shoot, root and total biomass. Herbivory by *A. hyperici* and, in experiment 3, by *A. chloris*, also caused reductions in plant growth, though the effects were generally more severe on *H. perforatum* than on *H. gramineum*.

One mechanism by which herbivory combined with other stresses may interact to cause reductions in plant growth is by decreasing root growth, thereby constraining the plant's ability to access a limited resource. The experiments above generally indicated that *H. perforatum*'s root mass is severely reduced by *A. hyperici*, and that the biological interaction of herbivory and environmental stress caused roughly proportional reductions in growth. The effects were similar, but less severe for *H. gramineum*.

In the above experiments, changes in the size and structure of populations of *A. hyperici* were not monitored except to confirm their presence at the end of the experiments. Nevertheless, it appears that well-fertilized, well-watered and vigorous hypericum plants are able to 'out-grow' the negative effects of *A. hyperici* herbivory. The observation that growth of environmentally-stressed plants is more severely retarded than in the vigorous plants supports Harris's (1980) argument that biological control of some weeds may be more effective if agents are released onto stressed plants. Our results provide little evidence, however, for a synergism between environmental stress and herbivores.

Combinations of herbivory by *A. hyperici* and other biotic or abiotic stresses caused few significant interactions, thereby lending little support to the hypothesis that combinations of stress and herbivory cause synergistic reductions in plant growth. Rather, the results suggest that combinations of stresses cause multiplicative (proportional) reductions in growth, approximately equivalent to the product of the proportional growth under individual stresses (Table 1).

In a study of the combined effect of the fungal pathogen *Puccinia chondrillina* on growth of skeleton weed (*Chondrilla juncea*) competitively stressed by clover (*Trifolium subterraneum*), Groves and Williams (1975) found slightly greater than proportional reductions in growth. Cottam *et al.* (1986) reported synergistic reductions in plant growth following competition and invertebrate herbivory. Re-examination of their data, however, suggests that they too observed simple proportional reductions. The model of simple proportional reductions outlined above predicts that in their system, herbivory and competition would decrease root and rosette dry weights to about 13% and 24% of ungrazed, noncompeting controls. In fact, these parameters decreased to 12.4% and 21.5% of the controls, respectively, approximating proportional reductions.

Confusion about interactions between factors, and possible synergistic effects on plant growth, stems from interpretation of the term 'interaction' and, to a large extent, whether the data being compared have been logarithmically transformed. As in this study, Parker and Salzman (1985) use the term 'interaction' to mean the statistical non-additivity of effects, most usually arising when plants respond non-linearly to combinations of treatments. They found no such interaction between herbivory and plant competition on growth in their plant-herbivore system. In a study of the combination of slug-herbivory and competition on plant growth, Rees and Brown (1992) found no interactions and concluded that, on the logarithmic scale, the factors were additive. Importantly, however, they note that on a linear scale, the combined effect of such biotic stresses is multiplicative (proportional) and conclude that it is more sensible to view combinations of herbivory and competition in this way.

The results of this study and those of Groves and Williams (1975), Cottam *et al.* (1986) and Rees and Brown (1992) imply that proportional (multiplicative), or slightly greater than proportional reductions in plant growth may characterize plant stress-herbivore interactions. If generally true, this is an important and simple way to predict effects of stress in complex systems and suggests that complex factorial experiments may not be essential.

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References

Andres L.A. (1981) Conflicting interests and the biological control of weeds. In: *Proceedings of the V International Symposium on Biological Control of Weeds,* pp. 11-20. E.S. Delfosse (ed.). 22-27 July 1980, Brisbane, Australia. CSIRO, Melbourne.

Briese D.T. (1989) Host-specificity and virus-vector potential of *Aphis chloris* (Hemiptera: Aphididae), a biological control agent for St. John's Wort in Australia. *Entomophaga*, 34: 247-264.

Coley P.D., Bryant J.P. and Chapin F.S. (1985) Resource availability and plant antiherbivore defense. *Science*, 230: 895-899.

Cottam D.A., Whittaker J.B. and Malloch A.J.C. (1986) The effects of chrysomelid beetle grazing and plant competition on the growth of *Rumex obtusifolius*. *Oecologia*, 70: 452-456.

Crawley M.J. (1983) *Herbivory: The Dynamics of Animal-Plant Interactions.* University of California Press, Berkeley, California.

Crawley M.J. (1989) Insect herbivores and plant population dynamics. *Annual Review of Entomology*, 34: 531-564.

CSIRO (1991) *The Host-specificity of* Aculus hyperici *(Liro) (Acarina: Eriophyidae) in Relation to Different Species in the Genus* Hypericum. CSIRO Division of Entomology Application to the Australian Plant Quarantine and Inspection Service: Canberra.

Groves R.H. (1989) Ecological control of invasive terrestrial plants. In: *Biological Invasions: A Global Perspective - SCOPE 37,* pp. 437-461. J.A. Drake, H.A. Mooney, F. di Castri, R.H. Groves, F.J. Kruger, M. Rejmanek and M. Williamson (eds). John Wiley, Chichester.

Groves R.H. and Williams J.D. (1975) Growth of skeleton weed (*Chondrilla juncea* L.) as affected by growth of subterranean clover (*Trifolium subterraneum* L.) and infection by *Puccinia chondrillina* Bubak & Syd. *Australian Journal of Agricultural Research*, 26: 975-983.

Harris P. (1980) Stress as a strategy in the biological control of weeds. In: *Biological Control in Crop Protection - Beltsville Symposia in Agricultural Research (BARC) Symposium 5,* pp. 333-340. G.C. Papavizas (ed.). Allanheld, Osmun Publishers, New Jersey.

Larsson S. (1989) Stressful times for the plant stress - insect performance hypothesis. *Oikos*, 56: 277-283.

Louda S.M. and Collinge S.K. (1992) Plant resistance to insect herbivores: a field test of the environmental stress hypothesis. *Ecology*, 73: 153-169.

Mattson W.J. (1980) Herbivory in relation to plant nitrogen content. *Annual Review of Ecology and Systematics*, 11: 119-61.

Mattson W.J. and Haack R.A. (1987a) The role of drought in outbreaks of plant-eating insects. *BioScience*, 37: 110-118.

Mattson W.J. and Haack R.A. (1987b) The role of drought stress in provoking outbreaks of phytophagous insects. In: *Insect Outbreaks: Ecological and Evolutionary Perspectives,* pp. 365-407. P. Barbosa and J.C. Schultz (eds). Academic Press, San Diego.

Mitchell H.L. and Chandler R.F. (1939) The nitrogen nutrition and growth of certain deciduous trees of northeastern United States. *Black Rock Forestry Bulletin*, 11: 94.

Parker M.A. and Salzman A.G. (1985) Herbivore exclosure and competitor removal: effects on juvenile survivorship and growth in the shrub *Gutierrezia microcephala. Journal of Ecology,* 73: 903-913.

Piene H. (1978) Effects of increased spacing on carbon mineralisation and temperature on young fir. *Canadian Journal of Forest Research*, 8: 398-406.

Priçe P.W. (1991) The plant vigour hypothesis and herbivore attack. *Oikos*, 62: 244-251.

Rees M. and Brown V.K. (1992) Interactions between invertebrate herbivores and plant competition. *Journal of Ecology*, 80: 353-360.

Rhoades D.F. and Cates R.G. (1976) Toward a general theory of plant antiherbivore chemistry. *Recent Advances in Phytochemistry*, 10: 168-213.

Stewart G.R. and Lahrer F. (1980) Accumulation of amino acids and related compounds in relation to environmental stress. In: *Biochemistry of Plants Volume 5. A Comprehensive Treatise on Amino Acids and Derivatives,* pp. 609-635. B.J. Miflin (ed.). Academic Press, New York.

Tilman D. (1984) Plant dominance along an experimental nutrient gradient. *Ecology*, 65: 1445-1453.

Turner C.E. (1985) Conflicting interests and biological control of weeds. In: *Proceedings of the VI International Symposium on Biological Control of Weeds*, pp. 203-225. E.S. Delfosse (ed.). 19-25 August 1984, Vancouver, Canada. Agriculture Canada, Ottawa.

Waring G.L. and Cobb N.S. (1992) The impact of plant stress on herbivore population dynamics. In: *Insect-Plant Interactions. Volume 4*, pp. 167-226. E. Bernays (ed.). CRC Press, London.

White T.C.R. (1984) The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. *Oecologia*, 63: 90-105.

Willis A.J. (1994) *The Ecology of* Hypericum gramineum *with reference to the biological control of* H. perforatum *by the mite*, Aculus hyperici. Ph.D. Thesis, The Australian National University, Canberra.

Willis A.J., Ash J.E. and Groves R.H. (1993) Combined effects of two arthropod herbivores and water stress on growth of *Hypericum* species. *Oecologia*, 96: 517-525.

Willis A.J., Ash J.E. and Groves R.H. (1995) The effects of herbivory by a mite, *Aculus hyperici*, and nutrient deficiency on growth in *Hypericum* species. *Australian Journal of Botany*, 43: 305-316.