Competition between Australian and Spanish legumes growing in seven Australian soils

María A. Pérez-Fernández[1,2] and Byron B. Lamont[1]
[1] Department of Environmental Biology, Curtin University of Technology, GPO Box U1987, Perth, Western Australia 6845, Australia
[2] Ecology Area, University of Extremadura, Avenida de Elvas s/n, 06071 Badajoz, Spain

Summary Seven south-western Australian legumes were grown in their own soils either singly or two per pot or paired with each of seven Spanish legumes. The Australian species grew the same or larger than the Spanish species in their presence (49 of 49 comparisons) or absence (87 of 98 comparisons). As our focus was the potential impact of invasives on native species, we conclude that the intensity of competition coefficient (ICC) is the most useful index of the four measures of competition used. ICC identified many instances of growth promotion (facilitation) of the Australian species in the presence of Spanish species, and a few cases of the reverse. Two Australian legumes performed relatively poorly in the presence of at least four Spanish legumes and could be susceptible to invasives

Keywords Competition, legumes, additive design, replacement design, native, exotic.

INTRODUCTION

Plant invasions have become increasingly recognised as a major threat to the functioning of natural and human-exploited ecosystems (Groves and Willis 1999). In many parts of the world, especially those characterised by a highly endemic flora, invasive plants cause serious environmental damage (Hobbs and Humphries 1995, Thresher 1999). The escalating rate of plant invasion (Rejmànek and Randall 1994) raises the question of what are the traits that enhance the probability that a species becomes a successful invader of areas where it does not occur naturally.

A plant's competitive ability is important in determining its success in undisturbed, resource-rich habitats (MacArthur and Wilson 1967, Grime 1979) where the good competitor can outgrow plants adapted to disturbed or resource-poor environments by acquiring resources more rapidly. In an environment with low resource levels, stress-tolerant plants (Grime 1979) survive longer than species adapted to resource-rich and disturbed conditions by retaining more efficiently the resources they have been able to acquire. Of the range of variables that may determine the persistence of a species in a given environment, we considered the soil to play a crucial role. The relationship between the colonising ability of a plant species and its soil substrate requirements may account for its current global distribution (Pérez-Fernández *et al*. 2000).

To quantify the level of competition between species, our experiment was conducted using the simplest replacement and additive designs. In the replacement series test (de Wit 1960), competitive ability was assessed by measuring the relative performance of two species in mixed culture, relative to their performance in monoculture at the same total density. In the additive design, mixtures of species were formed by adding plants of one of the studied species to those of plants of the other species.

Our study tested the competitive ability of seven Spanish legumes not yet considered invasive, with the exception of *C. scoparius*, growing in seven Australian soils. We compared the performance of the introduced legumes growing pairwise with seven native Australian legumes occurring naturally in those soils. We hypothesised that the Australian native legumes growing in their normal native soils would outperform the Spanish legumes growing alone or in mixture.

MATERIALS AND METHODS

Plant material Seven species of native Australian and seven of native Spanish legumes were selected, matched by plant size. The Australian species were *Templetonia retusa* (Vent.) R.Br., *Mirbelia dilatata* R.Br., *Gastrolobium villosum* Benth., *Bossiaea aquifolium* Benth., *Jacksonia floribunda* Endl. (treated as synonymous with *J. densiflora* Benth., Marchant *et al.* 1987), *Gastrolobium spinosum* Benth. and *Gompholobium tomentosum* Labill. The Spanish species were *Cytisus multiflorus* (L'Hér.) Sweet, *Cytisus scoparius* (L.), *Cytisus striatus* (Hill) Rothm., *Genista florida* (L.), *Genista hystrix* Lange, *Echinospartum barnadesii* (Graells) Rothm. subsp *dorsisericeum* G.López and *Retama sphaerocarpa* (L.) Boiss. All species (both Australian and Spanish) grow naturally on acidic soils, except *T. retusa* which grows on calcareous coastal dunes and *C. striatus* and *R. sphaerocarpa* which are able to grow on either acidic or basic soils.

Seed germination and growing conditions Germinated seeds of the Australian and Spanish species were transplanted into black plastic tubes containing soil in which the Australian species of the pair grew naturally. Each Australian and each Spanish species was also grown with another individual of its own species. For all pairwise combinations of Australian/Australian, Australian /Spanish and Spanish/Spanish species there were six replicates of every pair for the soil of each native species. In addition, there were six replicates of one seedling per pot for each Australian species in its own soil plus the seven Spanish species in each soil. Pots were randomly located within soil type on benches in a glasshouse at the Department of Environmental Biology, Curtin University, Perth, Western Australia. Pots were watered every two days from above with tap water and allowed to drain freely. Daily average maximum temperature ± SD during the experiment was 24 ± 3°C, and the daily minimum temperature was normally above 20°C. For all harvested plants the following data were recorded: shoot dry weights (index of water capture in particular) and root dry weights (index of nutrient capture in particular). These were combined to give total biomass (index of carbon capture). For each plant, shoot height and average width were also measured and multiplied (size), as an index of above-ground space capture. All plant material was oven dried for 48 h at 70°C.

Measures of competition Two indices for replacement and two indices for additive designs were used. The former were resource yield total (RYT) and relative crowding coefficient (RCC), and the latter were the aggressivity coefficient (AC) and the intensity of competition coefficient (ICC). RYT, whose expression is given in (1), measures resource use complementarity, (the extent to which components of a mixture compete for common limiting resources (de Wit 1960)):

$$\mathrm{RYT} = (\mathrm{Y}as / \mathrm{Y}aa) + (\mathrm{Y}sa / \mathrm{Y}ss) \quad (1)$$

Yaa and Yss are the yields per unit area of components *a* (Australian) and *s* (Spanish) when grown in pure stands and Yas and Ysa are the yields of the components when grown with each other in mixed culture. Values of RYT ≤1.0 indicate that the components of the mixture fully share the same resources and do not show resource complementarity; values greater than 1.0 indicate that the components compete partially for the resources and show partial resource complementarity; an extreme value of 2.0 or more indicates that the components do not compete at all and show full resource complementarity.

RCC gives a measure of the ability of one component of the mixture to obtain limiting resources, compared with its ability to utilise the same resources when grown in pure stands. Its expression for *a* when grown with *s* is:

$$\mathrm{RCC}as = (\mathrm{Y}as / \mathrm{Y}aa) / (\mathrm{Y}sa / \mathrm{Y}ss) \quad (2)$$

where all symbols are as above (Harper 1977). If the two components have equal competitive abilities, the RCC of each species growing in pairs with the other will be 1.0. This value will be >1.0 if *a* is a better competitor than *s* and <1.0 if *s* is a better competitor than *a*.

AC estimates the species aggressivity, or relative ability to maintain growth in the presence of the other. For *a* when grown with *s* the expression is:

$$\mathrm{AC}as = \mathrm{W}as / \mathrm{W}a0 - \mathrm{W}sa / \mathrm{W}s0 \quad (3)$$

where Was and Wsa represent the yields of the Australian and the Spanish components when grown with each other in mixed culture and $Wa0$ and $Ws0$ are their yields when grown in the absence of the other without replacement. When $ACas$ is positive, species *a* is less diminished by species *s* compared with its growth alone than the reverse. When $ACas$ is negative, the reverse is true. At 0, their aggressivity is the same.

ICC gives an idea of the effect of competition from adjacent plants on the performance of individual plants (Snaydon and Satorre 1989). It reflects the proportional reduction in performance of individuals under given competitive conditions, compared with their performance under conditions of no competition. The expression for the absolute intensity of competition experienced by *a* plants when grown in mixture with *s* at a given density of each is:

$$\mathrm{ICC}as = \log_{10} \mathrm{W}a0 - \log_{10} \mathrm{W}as \quad (4)$$

where the meaning of the symbols is as described above. When $ICCas$ is positive, *s* has a negative effect on *a*. At 0, *a* is unaffected by the presence of *s*. When $ICCas$ is negative, the growth of *a* is facilitated (enhanced) by the presence of *s*.

Competition indices were calculated for four plant attributes: shoot dry weight, root dry weight, total dry weight (shoots plus roots) and plant size (shoot length × width).

RESULTS

Templetonia retusa RYT for the four indices of growth was ≤1 for 1–3 of the Spanish species, >1 for 3–5 species, and ≥2 for 0–2 species (Table 1). RCC of *T. retusa* was usually or always >1 compared with the Spanish species. AC was invariably positive. Direction of ICC depended on the variable measured with competitiveness reduced by most Spanish species for shoot and root mass but facilitated for total biomass and size.

Mirbelia dilatata RYT for three of the variables was 1–2 with five Spanish species, and <1 for size with six Spanish species (Table 1). RCC was mostly <1 although it was >1 for four shoots of Spanish species. AC was mostly positive, although negative values were also observed. ICC was usually positive although shoot and total biomass production was enhanced by two Spanish species.

Gastrolobium villosum RYT for the four indices of growth was 2 with 5–6 of the Spanish species (Table 1). RCC of *G. villosum* was predominantly >1 compared with the Spanish species. AC was invariably positive and ICC was negative.

Gastrolobium spinosum RYT for the four indices of growth was 2 for most species, except it was 1–2 for size of five species (Table 1). RCC was >1 for 3–6 species, ≤1 for 1–4 species. AC was mostly positive, although negative values were observed for 1–3 species. ICC was usually negative for total size, positive for total biomass and spread through the three categories for shoots and roots.

Bossiaea aquifolium RYT for the four indices of growth was 1–2 for 2–6 species, and 2 for 1–5 species (Table 1). RCC was >1 in 5–6 Spanish species. AC was predominantly positive. ICC was usually negative, with competitiveness reduced by 0–2 Spanish species.

Jacksonia floribunda RYT for the four indices of growth was 1–2 and >2 for 0–7 species (Table 1). RCC was >1 for 4–7 Spanish species. AC was almost always positive. ICC was usually negative except size was unaffected with four Spanish species.

Gompholobium tomentosum RYT for the four indices of growth was 1–2 for 4–6 Spanish species (Table 1). RCC was usually 1 compared with the Spanish species. AC was usually positive although it was negative for size among five Spanish species. ICC was usually positive although root growth was enhanced by three Spanish species.

Spanish species The seven Spanish species showed the reverse competitive values for RCC and AC in Table 1. However, ICC*s* values do not follow from ICC*a*

Table 1. Summary of values for four competition indices for seven Australian legumes versus seven Spanish legumes and one index for the Spanish versus Australian legumes. Boundaries for RYT, RCC and AC mid-classes were taken as ±0.10, and ICC classes were ±0.05.

Attribute	*Templetonia retusa*	*Mirbelia dilatata*	*Gastrolobium villosum*	*Gastrolobium spinosum*	*Bossiaea aquifolium*	*Jacksonia floribunda*	*Gompholobium tomentosum*
RYT (<1, 1–2, >2)							
Shoot	1, 5, 1	0, 5, 2	0, 2, 5	0, 3, 4	0, 2, 5	0, 7, 0	0, 5, 2
Root	3, 4, 0	0, 5, 2	0, 1, 6	0, 2, 5	0, 6, 1	0, 0, 7	0, 4, 3
Total	2, 3, 2	0, 5, 2	0, 1, 6	0, 1, 6	0, 6, 1	1, 1, 6	0, 6, 1
Size	2, 5, 0	6, 1, 0	0, 1, 6	0, 5, 2	0, 5, 2	0, 2, 5	1, 5, 1
RCC (<1, 1, >1)							
Shoot	1, 0, 6	2, 1, 4	0, 0, 7	2, 2, 3	1, 0, 6	3, 0, 4	0, 4, 3
Root	1, 2, 4	5, 0, 2	0, 1, 6	0, 3, 4	1, 0, 6	0, 0, 7	0, 3, 4
Total	0, 0, 7	4, 1, 2	0, 0, 7	1, 0, 6	2, 0, 5	1, 1, 5	2, 1, 4
Size	0, 0, 7	7, 0, 0	1. 1, 5	1, 0, 6	0, 1, 6	1, 1, 5	3, 2, 2
AC (+, 0, –)							
Shoot	6, 0, 1	4, 1, 2	6, 1, 0	3, 1, 3	6, 0, 1	7, 0, 0	3, 4, 0
Root	6, 0, 1	3, 0, 4	7, 0, 0	4, 2, 1	6, 0, 1	7, 0, 0	5, 1, 1
Total	7, 0, 0	3, 1, 3	7, 0, 0	6, 0, 1	5, 2, 0	5, 0, 2	4, 1, 2
Size	7, 0, 0	5, 1, 1	5, 1, 1	6, 0, 1	6, 1, 0	5, 1, 1	2, 0, 5
ICC (+, 0, –)							
Shoot	2, 2, 3	4, 1, 2	0, 1, 6	2, 2, 3	1, 0, 6	0, 1, 6	5, 0, 2
Root	1, 3, 3	4, 2, 1	0, 0, 7	1, 3, 3	1, 3, 3	0, 0, 7	2, 2, 3
Total	0, 0, 7	4, 1, 2	0, 2, 5	6, 0, 1	2, 1, 4	2, 1, 4	5, 1, 1
Size	0, 0, 7	7, 0, 0	0, 0, 7	0, 0, 7	0, 1, 6	1, 4, 2	6, 0, 1
	Cytisus multiflorus	*Cytisus scoparius*	*Cytisus striatus*	*Genista florida*	*Genista hystrix*	*Echinospartum barnadesii*	*Retama sphaerocarpa*
ICC (+, 0, –)							
Shoot	4, 1, 2	7, 0, 0	7, 0, 0	7, 0, 0	2, 1, 4	7, 0, 0	6, 1, 0
Root	1, 2, 4	7, 0, 0	7, 0, 0	6, 1, 0	0, 2, 5	5, 1, 1	5, 2, 0
Total	3, 2, 2	7, 0, 0	7, 0, 0	7, 0, 0	1, 0, 6	7, 0, 0	7, 0, 0
Size	1, 1, 5	7, 0, 0	7, 0, 0	7, 0, 0	4, 0, 3	7, 0, 0	7, 0, 0

values so these are given separately in Table 1. These show that five species were always suppressed by the presence of Australian species independent of growth index, while growth of two species was unaffected or facilitated by the presence of Australian species.

DISCUSSION

On the basis of relative yield total, *Templetonia retusa* was the only species with a tendency to fully exploit the resources available, while all other combinations showed a mixture of competition for the same resources and use of different resources. Minimal overlapping to maximise access to light is a likely explanation for the latter. *Gastrolobium villosum* and *Jacksonia floribunda* tended to show full complementarity These two species may have used the water and nutrients available sparingly and without overlap for light. Comparing inter- with intraspecific competition, the relative crowding coefficient (RCC) showed that five Australian species invariably or usually responded more favourably than their Spanish partners. The exceptions were *Mirbelia dilatata* and *Gompholobium tomentosum* that tended to show the reverse or a greater mixture of responses, depending on the index.

When comparing the density effect of adding another species to the pot, the aggressivity index gave an almost identical pattern to RCC (Table 1). The intensity of competition coefficient (ICC) was the only one of the indices used that did not include responses of the competing species in the formula. It simply compares growth of the target species alone in relation to its growth when the other species is added. Since this simulates the invasive process, and our focus was not on how this compares with the reverse effect, we conclude that this is the most useful index for our study.

In conclusion, most or all of the seven Spanish species studied would not displace at least five of the seven Australian species during establishment in their own soils. The only vulnerable species were *Mirbelia dilatata* and *Gompholobium tomentosum*. While five Australian species showed a superior interspecific competitive ability compared with intraspecific competition (replacement design) or when alone (additive design), only *Genista hystrix* showed similar properties, including facilitation in the presence of other species. The results were sensitive to the index of growth/resource capture used as well as the index of competition, although there was a strong relationship between RCC and AC, with ICC appearing the most useful.

REFERENCES

de Wit, C.T. (1960). On competition. Verslagen van Landboukundige Onderzoekingen 66, 1-82. PUDOC, Wageningen, The Netherlands.

Grime, J.P. (1979). *Plant strategies and vegetation processes*. (John Wiley, New York, USA).

Groves, R.H. and Willis, A.J. (1999). Environmental weeds and loss of native plant biodiversity: some Australian examples. *Australian Journal of Environmental Management* 6, 164-171.

Hobbs, R.J. and Humphries, S.E. (1995). An integrated approach to the ecology and management of plant invasions. *Conservation Biology* 9, 761-770.

MacArthur, R.H. and Wilson, E.O. (1967). *The theory of island biogeography.* (Princeton University Press. Princeton, New Jersey, USA).

Marchant, N.G., Wheeler, J.R., Rye, B.L., Bennett, E.M., Lander, N.S. and Macfarlane, T.D. (1987). *Flora of the Perth region*. Part Two. (Western Australian Herbarium. Department of Agriculture, Western Australia).

Pérez-Fernández, M.A., Gómez-Gutiérrez, J.M., Vicente-Villardón, J.L. and Martín-Berrocoso, A.M. (2000). Germination of nine legumes indigenous to the Iberian Peninsula in relation to soil substratum characteristics. *Journal of Mediterranean Ecology* 1, 141-153.

Rejmànek, M. and Randall, J.M. (1994). Invasive alien plants in California: 1993 summary and comparison with other areas in North America. *Madroño* 41, 161-177.

Snaydon, R.W. and Satorre, E.H. (1989). Bivariate diagrams for plant competition data: modifications and interpretation. *Journal of Applied Ecology* 26, 1043-1057.

Thresher, R.E. (1999). Diversity, impacts and options for managing invasive marine species in Australian waters. *Australian Journal of Environmental Management* 6, 137-148.