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Abstract

To investigate the effect of increased nutrient availability on competition amongst invasive and native plants, I measured changes in above and below ground biomass of *Chrysanthemoides monilifera* spp. *rotundata* (bitou bush) and *Asparagus aethiopicus* (asparagus fern) competing with two native species, *Banksia integrifolia* and *Ficinia nodosa*, under high and low-nutrient regimes. Bitou bush, as a primary invader, was competitive under all conditions lowering the growth of native species in both high and low nutrients. Asparagus fern as a secondary invader, did not influence growth of native species but responded, like bitou bush, to high nutrients. Native species were generally negatively affected by increases in nutrients. With bitou bush soils often providing higher nutrients, the chance of secondary invasion by asparagus fern is more likely, although asparagus fern is unlikely to invade low nutrient soils quickly. The invasive species, therefore, differed in their competitive ability in these coastal dune communities.

Keywords

competition, dunes, strength, two, significant, invasive, species, coastal

Disciplines

Life Sciences | Physical Sciences and Mathematics | Social and Behavioral Sciences

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Competition strength of two significant invasive species in coastal dunes

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Abstract

To investigate the effect of increased nutrient availability on competition amongst invasive and native plants, I measured changes in above and below ground biomass of *Chrysanthemoides monilifera* spp. *rotundata* (bitou bush) and *Asparagus aethiopicus* (asparagus fern) competing with two native species, *Banksia integrifolia* and *Ficinia nodosa*, under high and low nutrient regimes. Bitou bush, as a primary invader, was competitive under all conditions lowering the growth of native species in both high and low nutrients. Asparagus fern as a secondary invader, did not influence growth of native species but responded, like bitou bush, to high nutrients. Native species were generally negatively affected by increases in nutrients. With bitou bush soils often providing higher nutrients, the chance of secondary invasion by asparagus fern is more likely, although asparagus fern is unlikely to invade low nutrient soils quickly. The invasive species, therefore, differed in their competitive ability in these coastal dune communities.

Key words: asparagus, biomass, bitou bush, growth, nutrients, resource competition

Introduction

Exotic plant species differ in their invasiveness (Williamson and Fitter 1996): while some dominate habitats quickly, others appear to remain in low abundance. Increased resource use efficiency and superior competitive ability may be important characteristics enabling exotic plants to dominate invaded areas. Exotic species with high resource use efficiency can grow larger using limited resources available (Witkowski 1991). Daehler (2003) showed that invaders tended to have lower construction costs for leaves than co-occurring natives. Improved resource use efficiency will promote early reproduction and increased size that may eventually result in overgrowing surrounding plants. Highly competitive species, that gain limited nutrients or water at the expense of native species, are likely to win available spaces in the landscape. Interference competition, through allelopathy, may also promote invasiveness (Heirro and Callaway 2003). A release of compounds from plants may slow growth of neighbours. In classic competition experiments where nutrients are not followed closely, this mechanism is indistinguishable from resource competition. Slower growth of competing species may indicate resource competition or interference competition, or both.

Competitive ability and efficiency are likely to vary with resource availability (Wedin and Tilman 1993, Sharma *et al.* 2010). Invasion increases following nutrient or water addition (Huenneke *et al.* 1990, Burke and Grime 1996). Increased nutrients provide new opportunities for establishment of exotic

species which may not normally be invasive under lower nutrient conditions. Nutrient addition can be from human pollution or from a primary invader causing improved soil nutrients (Lindsay and French 2005, Hagos and Smit 2005, Magesan *et al.* 2012, Gonzalez-Munoz *et al.* 2012). These changes may encourage the establishment of secondary invasive species which further disturb the ecosystem (Vitousek and Walker 1989, Gonzalez-Munoz *et al.* 2012). Establishment of secondary invasive species can be promoted through weed control activities (Mason and French 2007, Blanchard and Holmes 2008) which cause significant disturbances, opening up bare ground and tilling the soil. Understanding the competitiveness of different species under a range of nutrient conditions will be important to guide effective management.

I investigated differences in competitiveness between a primary invader *Chrysanthemoides monilifera* subsp. *rotundata* (Asteraceae, hereafter bitou bush) and a secondary exotic scrambler *Asparagus aethiopicus* (Asparagaceae, hereafter asparagus fern) which is increasing in abundance in native habitats, perhaps promoted through increased disturbances and soil nutrients. In Australia, both are listed nationally as Weeds of National Significance. I compared their final biomass and effects on native species when grown under different nutrient levels to investigate if one can be considered more invasive than the other.

Bitou bush is a primary invader of coastal dune communities on the east coast of Australia. Invasion and management both negatively influence native vegetation (Mason and French 2007) and there is evidence that bitou bush releases allelopathic compounds which influence germination of native species (Ens *et al.* 2009a,b). Decomposition rates of leaf litter are faster and nitrogen levels tend to be higher in the soil under bitou bush infestations (Lindsay and French, 2004, 2005). Few native species can negatively influence growth rates of bitou bush in conditions of normal water availability or in drought, suggesting competitive superiority over native species (Mason *et al.* 2012).

Asparagus fern is becoming a significant problem in many coastal areas, dominating dune habitats particularly disturbed patches or areas following bitou bush control. This suggests that it may respond positively to changes associated with disturbances, such as increased nitrogen, and may be more invasive near these resource-rich patches. Little is known about the invasion pattern of this species.

Methods

For each invasive species, competition was investigated with two native species: *Ficinia nodosa* (Cyperaceae) and *Banksia integrifolia* subsp. *integrifolia* (Proteaceae). *Ficinia nodosa* is a rhizomatous perennial that occurs commonly in coastal sand habitats. *Banksia integrifolia* is a small tree that occurs from coastal areas to the mountains on the east coast. On the fore dune it grows to 5 m, but it is taller within woodland behind fore dunes.

Two levels of nutrients were applied in a factorial experiment. A low nutrient treatment (0.02%N) was based on N found in foredune soils by Lindsay and French (2005, 0.02-0.1%N). A high nutrient treatment (0.09%N) was based on N found in bitou bush-invaded dunes (Lindsay and French 2005, 0.04-0.09%N). A native slow release fertilizer (Osmocote® Native Gardens) was applied once to achieve these levels.

Seeds were germinated in seedling trays with 2:1:1 river sand: vermiculite: perlite and seedlings were transplanted at cotyledon or early first leaf stage into 23 cm diameter pots using the same soil mix and placed in a glasshouse with daily watering. Pots were moved regularly to avoid positional effects in the glasshouse. Interspecific competition between the invasive plant and a native was measured by planting one of each native with one of each invasive species. Plants were placed 3 cm apart. Intraspecific competition was measured by planting two of each species into each pot. To determine maximum growth and resource use efficiency, a single individual of each plant was planted into each pot. Separate experiments were run with bitou bush and asparagus fern. For each experiment, up to 8 replicates of each combination were planted. New seedlings were replanted into pots for the first couple of weeks if seedlings died. After this point, pots where one seedling died were not analysed.

Each experiment was concluded after 5 months and all plants were harvested, with roots and shoots separated and dried in an oven at 60°C for at least 4 days. Only one individual from pots with two conspecifics was measured. I ensured that the experimental design was balanced by using the same number of replicates for each combination in analyses; n was always between 4 and 6 for each nutrient by competition category. Two factor ANOVAs were used to investigate the effects of nutrient and competition on root and shoot dry weight (JMP 9.0.2, SAS Institute Incorporated, 2010). Where significant tests occurred, Tukeys HSD tests were used to identify where differences lay.

Results

Effect of bitou bush on native biomass

Banksia integrifolia seedlings had lower root biomass when grown with bitou bush seedlings ($F_{2,29} = 9.07$, $p \leq 0.001$, Fig. 1, Table 1). While high nutrients favoured shoot growth overall (Table 1), shoot biomass was significantly negatively affected by the presence of bitou bush in both high and low nutrients (interaction, $F_{2,30} = 4.47$, $p = 0.020$). For *F. nodosa*, both intraspecific and interspecific competition with bitou bush resulted in reduced shoot growth but root growth was only affected by bitou bush (root, $F_{2,18} = 10.63$, $p \leq 0.001$; shoot, $F_{2,18} = 6.39$, $p = 0.008$, Fig. 1). Shoot growth was also reduced at high nutrients ($F_{1,18} = 17.14$, $p \leq 0.001$).

The addition of nutrients improved growth of both roots and shoots of bitou bush seedlings. There was no evidence of competitive effects for shoots ($F_{1,24} = 20.27$, $p \leq 0.001$), however for roots, biomass decreased in the high nutrients when seedlings were grown with another plant, irrespective of identity (interaction, $F_{3,24} = 3.19$, $p = 0.040$, Fig. 1).

Effect of asparagus fern on native biomass

Banksia integrifolia seedlings were unaffected by the presence of asparagus fern, and were only negatively affected by high nutrients (roots, $F_{1,24} = 7.97$, $p = 0.009$, shoots $F_{1,24} = 8.24$, $p = 0.008$, Fig. 2). *F. nodosa* seedlings showed a similar response where roots were negatively influenced by high nutrients ($F_{1,30} = 5.95$, $p = 0.021$, but shoot biomass was not affected ($F_{1,30} = 2.24$, $p = 0.145$, Fig. 2). In contrast, asparagus fern seedlings responded positively to nutrient addition, having greater shoot growth ($F_{1,32} = 9.25$, $p = 0.020$) but no change in root biomass ($F_{1,32} = 0.05$, $p = 0.820$).

Discussion

Bitou bush was able to increase biomass to a greater extent than the two native species, indicating that it is more efficient in using available nutrients for growth. Under both high and low nutrients, the biomass of roots and shoots at the end of the experiment were higher for bitou bush seedlings growing alone than seedlings of either native. In fact, under high nutrients, bitou bush root biomass was over four times greater (dry mass 8.4 g bitou vs 0.7 g for both *B. integrifolia* and *F. nodosa*, Fig. 1), indicating that in nutrient rich areas, bitou bush is likely to significantly dominate open spaces.

Not only is there evidence of high resource use efficiency, but our results also suggest that bitou bush is competitively superior to the two native species at both nutrient levels. Bitou bush negatively influenced native species by reducing root and shoot growth. Previous studies have found that native species were more competitive than invasive species at some nutrient levels (Daehler 2003). Daehler (2003) found only five species that were highly competitive across a range of conditions. These were two herbs and three grasses. This study has added a new growth form to this highly successful weed group; a shrub. Bitou bush appears to be another of these highly competitive invasive species over a range of conditions.

The results could be a consequence of two competitive mechanisms. First, competitive resource use may have prevented the native species from gaining adequate nutrients to maintain growth. Secondly, allelopathic compounds may have caused interference competition, stunting growth. Bitou bush is allelopathic (Ens *et al.* 2009a,b) and both forms of competition may be operating to ensure reduced growth rates of competing species. As this experiment cannot distinguish the contributions of each of these mechanisms, further work is needed.

Bitou bush was unaffected by the presence of either *B. integrifolia* or *F. nodosa* as it grew equally large alone and with either of the natives. Similarly, in experiments investigating how competition varied with water limitation, bitou bush was highly resilient to neighbouring plants (Mason *et al.* 2012). Only six of 18 different native species had an effect on the growth of bitou bush marginally and only in low water availability (Mason *et al.* 2012). Competitive superiority in the use of nutrients and water, and higher resource use efficiency makes this invader a formidable problem for native ecosystems, even in areas that are undisturbed.

In contrast, asparagus fern had no impact on either native species, suggesting nutrient competition is not facilitating invasion. This is interesting given that root biomass was considerably greater than either native species in both high and low nutrients. However, above ground biomass responded positively to higher nutrients indicating that increased nutrient levels are likely to facilitate the invasion of this species. Effective conversion of nutrients into biomass at high nutrients is likely to facilitate the invasion of this species into dune communities, particularly as the plants grow. However, unless aided by increases in nutrient levels, asparagus fern appears unlikely to invade native ecosystems at the same rate as bitou bush as it does not compete well during early seedling stages. Nutrient addition is known from a number of systems to influence invasion (Huenneke *et al.* 1990, Burke and Grime, 1996, Li and Norland, 2001) often in association with disturbance (Hobbs and Huenneke 1992, Lake and Leishman

2004). In South Africa, invasive *Acacia saligna* can outperform a native shrub when nutrients are high, while at normal nutrient levels, there is little competitive advantage (Witkowski 1991).

Within coastal dune in eastern Australia, bitou bush can increase nutrient levels in the soil (Lindsay and French 2005). As a result, there will be good opportunities for asparagus fern to establish as a secondary invader following bitou bush control activities, given its positive response to nutrients and the negative response by both native species. Establishment may be particularly effective given that these dune communities suffer from recruitment limitation, especially after bitou bush invasion (French *et al.* 2011). Following weed control, native seedlings may compete for opportunities to establish with both asparagus fern and bitou bush. The presence of asparagus fern in these open spaces is likely to result in the establishment of some plants, increasing the success of secondary invasion.

These two species differ in their ability to affect native species at the seedling stage. While the primary invader, bitou bush, is a superior competitor, the secondary invader is only likely to invade disturbed areas, particularly where nutrient addition has resulted. This experiment has identified different invasion mechanisms by these two species which clearly predict differences in rates of invasion into dune communities.

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Table 1. Probability values of F ratios from 2 factor ANOVAs investigating dry root and shoot biomass for the two native species, *Banksia integrifolia* and *Ficinia nodosa*, grown in competition with bitou bush and asparagus fern. Tukeys HSD tests were used to identify where differences lay (multiple comparisons).

| Species | | Nutrients | Competition | Nutrient x competition | Main comparisons |
|------------------------------|-------|-------------------|-------------------|------------------------|--|
| Bitou bush trials | | | | | |
| Banksia | Root | 0.968 | 0.008 | 0.183 | Banksia alone and with conspecific > with bitou bush |
| | Shoot | <0.0001 | <0.0001 | 0.020 | Higher nutrients > low nutrients except when grown with bitou bush |
| Ficinia | Root | 0.001 | 0.001 | 0.179 | Ficinia alone and with conspecific >with bitou bush |
| | Shoot | 0.968 | 0.001 | 0.183 | Low nutrients > high nutrients Ficinia alone and with conspecific > with bitou bush |
| Bitou bush | Root | 0.023 | 0.034 | 0.042 | Bitou bush alone in high nutrients>all others |
| | Shoot | 0.0001 | 0.111 | 0.126 | High nutrients > low nutrients |
| Asparagus fern trials | | | | | |
| Banksia | Root | 0.009 | 0.431 | 0.540 | Low nutrients > High nutrients |
| | Shoot | 0.008 | 0.468 | 0.383 | Low nutrients > High nutrients |
| Ficinia | Root | 0.021 | 0.407 | 0.245 | Low nutrients > High nutrients |
| | Shoot | 0.145 | 0.427 | 0.342 | |
| Asparagus | Root | 0.820 | 0.921 | 0.824 | |
| | Shoot | 0.005 | 0.057 | 0.288 | High nutrients > low nutrients |

Figure legends

Figure 1. Average biomass (\pm sd) of a) roots and b) shoots of *Banksia integrifolia* (banksia), *Ficinia nodosa* (Ficinia) and *Chrysanthemoides monilifera* (Chrysanthemoides) grown in high and low nutrients across different competition treatments: alone, with a conspecific (con) and with *Chrysanthemoides monilifera* (Chrys). n=6, Banksia, n=4 Ficinia, n=4 Chrysanthemoides.

Figure 2. Average biomass (\pm sd) of a) roots and b) shoots of *Banksia integrifolia* (banksia), *Ficinia nodosa* (Ficinia) and *Asparagus aethiopicus* (Asparagus) grown in high and low nutrients across different competition treatments: alone, with a conspecific (con) and with *Asparagus aethiopicus*. n=5, Banksia, n=6 Ficinia, n=5 Asparagus.

