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Are competitive effects of native species on an invader mediated by water availability?

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Location: Glasshouse facility, New South Wales, Australia.

Methods: We constructed competitive hierarchies for a representative suite of species from coastal dune communities that have been invaded by the Asteraceae shrub, bitou (*Chrysanthemoides monilifera* subsp. *rotundata*). We used a comparative phytometer approach, where the invader species was grown with or without a suite of native species in glasshouse trials. This was used to construct competition hierarchies under two water stress conditions: non-droughted and droughted. The treatments were designed to simulate current and potential future water availability respectively.

Results: We found that the invader experienced fewer competitive effects from some native species under water stress, particularly with regard to belowground biomass effects. Native species were often poor competitors with the invader, despite their adaptation to periodic water stress in native coastal environments. Of the native species with significant competitive effects on the invader, functionally similar shrub species were the most effective competitors, as expressed in below-ground biomass. The relative position of species in the hierarchy was consistent across water treatments based on below-ground bitou biomass, but was contingent on water treatment when based on above-ground bitou biomass.

Conclusions: The competitive effects of native species on an invader are affected by water stress. While the direction of response to water stress is species-specific, many species have small competitive effects on the invader under droughted conditions. This could allow an increase in invader dominance with climate change.

Keywords

invader, availability, species, mediated, native, effects, competitive, water

Disciplines

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Keywords: climate change; coastal dune community; competitive intensity; exotic species; hierarchy; invasive species

Nomenclature: Harden (1992, 1993, 2000, 2002)

Running head: Water stress affects competition with invader

Introduction

Interspecific competition is an important organizational force in plant communities (e.g. Grime 1979; Fowler 1986; Keddy 1989; Goldberg & Barton 1992). The degree to which one species affects resource availability for another species may structure plant abundance and dominance and create a competitive hierarchy in the community. Plant invaders often successfully establish and spread in novel communities due to mechanisms of competitive dominance (Levine *et al.* 2003). Successful invasion may therefore restructure hierarchies of the resident community. The competitive performance of native species against the invader will determine both the extent of invader dominance and the identity of the strongest native competitors which are likely to persist in invaded habitats. These are important considerations with respect to the regeneration potential of an area following invader control efforts.

A key challenge in contemporary ecology is understanding the dual effects of competitively dominant plant invaders on the structure of invaded communities and the effects of changing climatic conditions on competitive structures. However, few empirical studies have addressed both invader and resource availability effects on native species competition hierarchies (Thuiller *et al.* 2007). Previous research has indicated that competitive interactions are often strong under resource-rich, but not under resource-poor conditions: resource-rich habitats may select for species which readily sequester available resources, while resource-poor habitats may select for species which conserve resources and tolerate environmental stress (Grime 1979). This concept has been extended by the 'stress-gradient hypothesis' which postulates that competitive effects are more intense in low-stress environments and facilitative effects are more important in high-stress

environments (Bertness and Callaway 1994; Lortie & Callaway 2006). More specifically, comparison of species pairs across a gradient of increasing soil resource availability has indicated that the competitive effect of a species on neighbour performance is stronger with increasing resource availability (Keddy *et al.* 1997). This competitive effect of a species on the performance of a neighbouring individual may be termed “competition intensity” (Keddy 1989; Lamb and Cahill 2008). A review of competition in arid and semiarid regions by Fowler (1986) reported studies where competition was evident in watered plots only. This implies a shift from competition to survival techniques among interacting individuals under water stress.

Climate change is forecast to reduce water resource availability in many regions, including much of southern and eastern Australia (Hennessey *et al.* 2007). We may therefore predict that native and invader species may revert from competition to survival as rainfall decreases and environmental stress increases. As a consequence, the invader may experience reduced competition resulting in increased abundance or improved adaptation to novel conditions in the invaded community. Conversely, the invader may reach a physiological limit under drier conditions which may reduce its dominance (e.g. Weiss & Noble 1984) and allow greater native species representation in the community (e.g. Webster *et al.* 2008). Such biotic (competition) and environmental (drought) factors may interact, creating ecological filters which influence the process of community assembly (Funk *et al.* 2008).

There has been considerable ecological debate about the consistency of competitive ability among species in different environments or resource regimes. Some researchers have argued that there are trade-offs in competitive ability at different resource levels. So

a superior competitor at one resource level will be inferior at other supply rates compared to plants with other morphologies (Tilman 1988). Consequently, competitive hierarchies will be contingent on resource gradients. Other researchers have countered that competitive ability among plants is constant across resource gradients (Grime 1977) and that resultant competitive hierarchies are consistent across environments (Keddy *et al.* 2000; Keddy *et al.* 2002). Goldberg and Landa (1991) have suggested that these views may be reconciled by recognizing that competitive ability may be expressed in terms of competitive effect (ability of a species to suppress other individuals) or competitive response (ability of a species to tolerate or avoid suppression). Often competitive effect hierarchies are consistent across environments, but competitive response hierarchies are contingent on resource availability. Determining how invader effects and native species biotic resistance vary with resource availability is required to predict which environmental conditions increase the threat of invasion (Vila & Weiner 2004).

Functional identity may be another important factor in determining the structure of competitive hierarchies. Based on theories of niche differentiation and species coexistence, we would expect that species which are morphologically and physiologically similar to each other will compete most strongly (Fargione *et al.* 2003). Consequently, invaders may experience strong biotic resistance from communities with native functional analogues. This prediction of limiting similarity among species in a community has been validated in small scale experiments (e.g. Hooper & Dukes 2010), although the strength of competitive interactions between functionally similar and dissimilar species is rarely reported. The concept of limiting similarity may aid restoration practice. For example, practitioners may reintroduce native species that are

functionally similar to existing or likely future invaders (Funk *et al.* 2008). Native competition may then exclude or limit distributions of the invader.

Competitive performance is frequently presented using both above- and below-ground biomass. Previous researchers have observed that in unproductive environments, competition is predominantly for below-ground resources such as water and nutrients, while in productive environments competition is primarily for light (Goldberg and Novoplansky 1997). We may therefore expect that water stress is more directly expressed by changes in below- than above-ground biomass in competing individuals.

Few studies investigating competitive interactions have incorporated a representative suite of species from a community. Many studies investigate mixtures involving only two species (Gibson *et al.* 1999), with very few studies addressing interactions among 10 or more species (but see Gaudet & Keddy 1995; Theodose *et al.* 1996; Rösch *et al.* 1997; Keddy *et al.* 2002; Cahill *et al.* 2008). Analysis of species pairs alone may mask general principles in competition experiments (Keddy *et al.* 1994); however logistic constraints often preclude analysis of multi-species interactions. A comparative phytometer-based approach (Gaudet & Keddy 1988) may provide some clarity as it allows concurrent analysis of interactions among a large number of species by comparing species' relative competitive effects on a common indicator or phytometer species. The comparative phytometer approach may therefore incorporate sufficient taxa to investigate realistic community competitive dynamics and relate this to functional identity and resource availability.

Here, we investigated competitive interactions under different water availabilities between a suite of native coastal fore dune species and a major invasive shrub, bitou

(*Chrysanthemoides monilifera* ssp. *rotundata*). Specifically, we took a comparative phytometer approach to determine the above- and below-ground competitive hierarchies among native grass, herb and shrub species and the invader in relation to functional identity (growth form) and water availability. Bitou, a South African shrub in the Asteraceae family, has been shown to reduce native plant species' diversity and vegetation structural complexity (Mason & French 2008) and transform ecosystems (Lindsay & French 2005). Reduced water availability, as a result of future drying trends, is expected to affect both native and invader species, however the effect on competitive hierarchies is unclear. We investigated this issue by selecting native species which may exhibit competitive advantage, particularly under water stress. Grass species were rhizomatous or stoloniferous with a C₄ carbon cycle. These characteristics provide good efficiency under water stress (Black *et al.* 1969). Herb species were prostrate and often succulent or semi succulent. Succulence may also provide an advantage under water limitation (Diaz & Cabido 1997). Shrub species were often locally abundant and dominant components of non-invaded dune communities. While the shrub growth form does not necessarily confer a competitive advantage under water stress, we reasoned that for our bitou invasion case study, shrub species were most functionally similar in growth form to bitou. Consequently, native shrub species may compete most strongly with bitou and filter this invader out of the community (see review on theory of limiting similarity in Funk *et al.* (2008)). Our study focused on seedling interactions because bitou control efforts often involve treating sections of adult bitou monoculture: in the post-control environment, it is predominantly native and invader seedlings which competitively interact.

As drought is expected to be more common under the future climatic regime (Hennessy *et al.* 2007), we investigated competitive intensity and the structure of competitive hierarchies in resource-rich (current water availability) and resource-poor (potential future low water availability) conditions. We assembled a number of predictions to investigate the potential effects of climate change on invader and native species competitive outcomes:

1. Competitive interactions between bitou and native species are evident under resource-rich (non-droughted) but not under resource-poor (droughted) conditions;
2. Bitou competes more strongly with functionally similar native shrub species than functionally dissimilar herb or grass species;
3. Species' positions in the competitive hierarchy are broadly invariant to water availability.

The experiment was conducted under glasshouse conditions. This approach has restricted relevance to field community dynamics, which may be affected by herbivory, nutrient variability and other extrinsic factors. Despite this reduced realism, we gain a detailed and direct study of competitive effects of native species on a dominant invader.

Materials and methods

Experimental procedure

In the glasshouse we used a comparative phytometer-based approach (Gaudet & Keddy 1988) to study competitive interactions of coastal dune species. This approach controlled for density, abiotic and neighbour effects. The competitive performance of native species was assessed as the relative ability of each species to suppress the performance of bitou. We therefore measured the competitive *effect* of a native species on bitou (Goldberg & Landa 1991). We selected 18 species native to coastal dune communities of New South Wales, Australia. We categorized them into three growth form functional groups: rhizomatous/stoloniferous grasses (*Cynodon dactylon*, *Imperata cylindrica*, *Ischaemum triticeum*, *Spinifex sericeus*, *Paspalum vaginatum* and *Zoysia macrantha*), prostrate herbs (*Calystegia soldanella*, *Carpobrotus glaucescens*, *Hydrocotyle peduncularis*, *Ipomoea brasiliensis* and *Tetragonia tetragonoides*) and shrubs (*Banksia integrifolia*, *Breynia oblongifolia*, *Correa alba*, *Leptospermum laevigatum*, *Myoporum boninense*, *Ozothamnus diosmifolius* and *Rhagodia candolleana*).

The glasshouse experiments were conducted in 2007 and 2008. In each year, replicates were established between May and July: replicate pots were planted up as seedlings germinated or when an individual died within the pot and a new replicate was required. For each replicate pot, the experiment ran for 140 days. Limited glasshouse space meant that a subset of different species was examined each year. However, we attempted to control for year effects by sampling two common native species and the phytometer over both years. ANOVA results indicated that year effects were non-

significant (data available on request). As a result, we assumed year effects to be non-significant for all native species and pooled results across years.

Pots were 150 mm in diameter and 400 mm deep to maximize potential rooting depths. We used a low nutrient soil mix (1:1:1 sand, vermiculite, perlite) and fertilized each pot with Osmocote PlusTM (Scotts Australia Pty Ltd) at a rate of 5 g / pot which was comparable to native dune soil conditions (Lindsay & French 2005). Pots were randomly distributed throughout the glasshouse and were encircled with mesh as required to restrict shading effects of large individuals on neighbouring pots.

We created two levels of water resource availability: a droughted regime (516 mm p.a.) based on extreme climate change projections (Hennessy *et al.* 2004), and a non-droughted regime (1032 mm p.a.) based on the current annual precipitation for coastal New South Wales (Anon. 2009). Pots were top-watered every second day with an automatic drip watering system.

All species were grown from seeds collected from coastal dune communities in New South Wales, Australia between 2006 and 2008 or sourced from seed suppliers. While we sought to include dominant, common native species, we were unable to use species with specific germination or growth requirements (e.g. *Leucopogon paviflorus*). Seeds were germinated and seedlings were transferred to pots prior to emergence of four true leaves to ensure all individuals had low initial biomass. However, we acknowledge that competitive performance in the experiment was influenced not only by interactions among species during the experimental period, but may also have been affected by initial seed and seedling sizes.

At each water resource level we set up eight replicates of bitou in combination with a native species: bitou was transplanted to the centre of the pot and three native individuals of the same species were positioned equidistantly in a triangular pattern around the bitou individual. At the commencement of the experiment, we also set up 24 (in 2008) or 32 (in 2007) replicates of bitou grown alone, where a single individual was positioned at the centre of the pot. Straight pairing of a bitou + native replicate with a bitou alone replicate would have required excessive replication of the bitou alone treatment. Instead, we increased the replication of the bitou alone treatment relative to the bitou + native treatment (3-4 times the replication). We deliberately set up a large number of replicates to account for plant mortality through the experiment.

We allowed potted individuals to establish for a week with ample watering before imposing droughting regimes, and we replaced dead individuals as required for the first six weeks of the experiment. At conclusion of the experiment, each plant was clipped at soil level and separated into above- and below-ground material. Roots were washed over a 2 mm sieve to remove soil. Root, shoot and leaf samples were oven dried at 60°C for a week and then weighed ($\pm 0.0001\text{g}$).

Statistical analyses

We assessed whether bitou experienced competition from native neighbours under droughted or non-droughted conditions using a Mann-Whitney U test. We compared bitou biomass in pots where bitou was grown alone and where bitou was grown with a neighbour. We pooled all pots of bitou with any native species because we were concerned with neighbour effects under different watering regimes, rather than individual species identities.

We quantified the intensity of competition on the phytometer for each native species using the Relative Competitive Performance (RCP) index (Gaudet & Keddy 1988, 1995). The RCP was expressed as the mean percent reduction in bitou biomass by the native species and calculated as:

$$\text{RCP} = [(B_{\text{control}} - B_{\text{mix}}) / B_{\text{control}}] \times 100$$

where B_{control} was the biomass of bitou when grown alone and B_{mix} was the biomass of bitou when grown with a native species. As the numbers of replicates for bitou alone (droughted $n = 49$ and non-droughted $n = 53$) and bitou + native treatments (n ranged from 3-16 across water treatments) differed considerably, we used a bootstrapping program to estimate mean Relative Competitive Performance and standard errors for competitive hierarchy analyses (above and below-ground dried biomass). We performed 10 000 resamplings using R version 2.7.1 (R Development Core Team 2008). In each resampling, n values were selected with replacement from the bitou alone and bitou + native samples respectively, and the difference between the averages of these new samples was calculated. The mean of the 10 000 differences estimates the mean Relative Competitive Performance, while the standard deviation of these 10 000 differences estimates the standard error of the mean (Davison and Hinkley 1997, p. 16).

The comparative approach allowed construction of competitive hierarchies under droughted and non-droughted conditions. We formally tested competitive relationships by calculating whether RCP confidence intervals overlapped with zero. If $|\bar{x}| > 1.96 \times SE$ (Davison & Hinkley 1997) then we rejected the null hypothesis and concluded that competitive or facilitative interactions between bitou and native species were significant.

The influence of watering regime on bitou biomass when grown alone was assessed using a one factor ANOVA. The influence of watering regime along with the functional and species identity of neighbours on bitou above- and below-ground biomass were examined using three factor ANOVAs. Droughting level and native species functional identity were treated as fixed effects. Species identity was treated as a nested fixed factor within functional identity. Tukey HSD tests were used to perform focused comparisons between pairs of means. Normality and homoscedasticity of data were graphically assessed. Where appropriate, we used square root data transformations. Finally, we assessed whether species maintained their relative positions in the competitive hierarchy under different water regimes by using correlation analysis. We used Pearson's correlation coefficient when data were normal, and Spearman's rank correlation coefficient when data were non normal. All analyses were conducted using SPSS (2008).

Results

When grown alone, bitou biomass was significantly reduced under droughted compared with non-droughted conditions. This was true for both above-ground biomass ($F_{1,100} = 126.255$; $P < 0.001$; droughted mean \pm SE: $5.478\text{g} \pm 0.235$; non-droughted: $9.139\text{g} \pm 0.226$) and below-ground biomass ($F_{1,100} = 46.268$; $P < 0.001$; droughted mean \pm SE: $4.596\text{g} \pm 0.371$; non-droughted: $7.885\text{g} \pm 0.356$). Consequently, the negative effect of water stress was evident on the invader without any neighbour competition. We then investigated the effect of competitors on bitou performance.

Competitive interactions under droughted and non-droughted conditions

Above- and below-ground bitou biomass was significantly higher when grown alone (droughted $n = 49$; non-droughted $n = 53$) than with native species neighbours (droughted $n = 87$; non-droughted $n = 117$) under non-droughted conditions only (Table 1; Fig. 1). We did not detect a significant difference in bitou biomass across treatments under droughted conditions (Table 1).

Competitive effects of functional groups

The competitive effects of native species on below-ground biomass of bitou were significantly different amongst species within functional groups (Table 2). In addition, below-ground competitive effects were dependent on the type of functional group grown with bitou (Table 2): shrub species were significant competitors with bitou (Tukey HSD: $P = 0.003$; bitou biomass with shrub: mean \pm SE: 5.172 ± 0.308 ; bitou biomass alone 6.241 ± 0.246). Shrub species were also significantly more competitive against bitou than grass species (Tukey HSD: $P = 0.04$; bitou biomass with grass: mean \pm SE: $5.970 \pm$

0.336; bitou biomass with shrub 5.172 ± 0.308). All other functional group comparisons were non significant.

These findings were consistent with the relative competitive performance results. Under droughted conditions, most species were poor below-ground competitors with bitou. Only one shrub species, *Rhagodia candolleana*, had a significant competitive effect on bitou below-ground biomass (Table 3; 29.44 % reduction in bitou below-ground biomass). In contrast, the grass *Paspalum vaginatum* facilitated below-ground growth in bitou (Table 3; 46.77 % increase in bitou below-ground biomass). Under non-droughted conditions, shrub species proved the most competitive with four of the seven species being significant below-ground competitors with bitou (Table 3; 21.66 - 60.20 % reduction in bitou below-ground biomass). Two herb species, *Tetragonia tetragonoides* and *Carpobrotus glaucescens* had a significant competitive effect (Table 3; 80.75 % and 17.28 % reduction in bitou below-ground biomass respectively). However, none of the grass species were significant below-ground competitors with bitou under non-droughted conditions.

Watering regime was a significant main effect (Table 2) with bitou below-ground biomass significantly higher under non-droughted compared with droughted conditions (non-droughted mean \pm standard error: $6.851\text{g} \pm 0.234$; droughted: $4.347\text{g} \pm 0.270$). In general, total biomass results reflected below-ground more closely than above-ground biomass results (data not shown).

There was a significant interaction among water treatment, functional group type and native species identity for the above-ground bitou biomass analysis (Table 2). While the shrub, *Rhagodia candolleana*, was a consistent competitor with bitou under both

droughted and non-droughted conditions (Table 3), the effect of species within functional groups varied with water treatments. The interaction was driven by variable bitou above-ground biomass responses when grown with a number of native species. Both the grass *Cynodon dactylon* and the herb *Carpobrotus glaucescens* were significant competitors with bitou under droughted conditions, but not under non-droughted conditions (Table 3). In addition, the shrub *Leptospermum laevigatum* significantly facilitated bitou shoot growth under non-droughted conditions, while the shrub *Breynia oblongifolia* significantly facilitated bitou shoot growth under droughted conditions (Table 3).

Two native species, *Digitaria didactyla* (grass) and *Acaena novae-zelandiae* (herb), could not be grown in competition with bitou for the duration of the experiment: most replicates died prior to completion of the experiment regardless of the imposed watering regime. In addition, the herb *Hydrocotyle peduncularis* and shrub *Correa alba* had insufficient replication under droughted conditions to allow measurement of their effects on bitou.

Effects of water availability on competitive hierarchy structures

Species positions in competitive hierarchies based on below-ground bitou biomass were relatively consistent regardless of water availability ($r = 0.620$, $P = 0.010$). This result was corroborated by the non-significant interaction between water treatment and species nested within functional groups in the ANOVA for below-ground bitou biomass (Table 2). However, the competitive effect of several native species within each functional group on bitou biomass was non-significant under both droughted and non-droughted conditions (non-bolded species in Table 3). The rankings of these species are

indistinguishable in statistical terms. Consequently, a subset of species drove the significant positive correlation across watering regimes for below-ground bitou biomass.

In contrast, hierarchical structure was contingent on water availability for above-ground bitou biomass. Data were non normal, so we used Spearman's rank correlation coefficient which indicated that the rankings of the competitive scores shifted depending on water availability ($r_s = 0.303$, $P = 0.254$). This finding was validated by the significant interaction between water treatment and species nested within functional groups in the ANOVA for above-ground bitou biomass (Table 2) (Goldberg & Scheiner 1993).

Discussion

Our results indicate that the environmental stress of reducing water availability, which is predicted to affect sections of the New South Wales coast, may change competitive interactions between bitou and native dune species: some native species may be less effective competitors and provide less resistance to invasion under water stress. As individual species' fitness decreases under water stress, native plant strategies may revert from competition and growth to tolerance and survival. While bitou biomass may be reduced under the environmental stress of drought, concomitant relative weakening of competitive interactions with native species may allow bitou to maintain and perhaps compound its invasion status under climate change. A full assessment of invader status in a future water-stressed climate will require analysis of native species effects: both competitive effects of the invader and environmental effects of water stress on native species. The present study has focused only on invader effects. However, this study does provide some indirect evidence that the invader will be advantaged relative to native species. Firstly, we were unable to achieve sufficient replication to measure the effect of native individuals on bitou for two species (*Digitaria didactyla* and *Acaena novae-zelandiae*) regardless of the watering regime. Two further species (*Hydrocotyle peduncularis* and *Correa alba*) had insufficient replication under the droughted regime. While glasshouse limitations such as lethal physical stress of transplanted seedlings or an incompatible mycorrhizal environment cannot be discounted, these native species may also be particularly poor competitors against bitou or may reach physiological limits under droughted conditions.

We now couch our findings within the wider invasion ecology framework. Reduced competitive effects of native species on the invader as a mechanism of invasion is consistent with the biotic resistance hypothesis which states that potential invaders may fail to spread in communities where native species have strong competitive interactions (Elton 1958; Maron & Vila 2001). The converse implication is that weak competitive interactions within the recipient community may facilitate invader spread and dominance. The mechanism of invader dominance via reduced native competitive intensity may complement the theory of fluctuating resource availability, which states that a plant community is more susceptible to invasion when resource availability increases (Davis *et al.* 2000). While the theory predicts that water supplementation will increase invasibility, it is unclear how water restriction will affect community invasibility. Davis *et al.* (2000) noted that severe drought may cause plant mortality and create gaps in the vegetation which may then enhance invasibility. In our study, two native species (*Hydrocotyle peduncularis* and *Correa alba*) may follow this scenario. However, most native species were able to survive the drought conditions, albeit with few competitive effects on the invader. This may increase invasibility of dune communities by improving invader fitness relative to native species in a drought-stressed environment. Field observations of invader and native species size, dominance and reproductive fitness may confirm our inferences. Our results show that few native species had significant competitive effects on bitou, and of these species, few were able to reduce bitou biomass by more than 50% regardless of water availability. This result indicates that active restoration strategies are necessary in bitou invaded habitats.

Native functional groups had variable competitive effects on bitou. Shrub species were the most effective competitors with bitou as expressed by below-ground biomass. The native shrub growth form is functionally most similar to bitou, indicating that traits associated with resource capture strongly affect relative biomass in this community. Initial replanting efforts should include competitive native shrub species such as *Rhagodia candolleana*, *Correa alba*, *Myoporum boninense* and *Banksia integrifolia* following bitou removal. These native species are likely to provide the strongest competitive resistance to bitou recruitment and re-establishment. Two herb species, *Tetragonia tetragonoides* and *Carpobrotus glaucescens*, had significant competitive effects on bitou above- and / or below-ground biomass. These species exhibit succulence which often provides an advantage under water limitation (Diaz & Cabido 1997). However, both species were competitive under non-droughted as well as droughted conditions, which may indicate that both of our treatments imposed some limitation on water availability, or that other traits allow these species to significantly compete with bitou. Grass species had minimal competitive effects on bitou. Two species, *Cynodon dactylon* and *Imperata cylindrica*, were significant above-ground competitors with bitou under droughted conditions, albeit with relatively small above-ground biomass effects (<25% reduction in bitou biomass). It appears that the C₄ carbon strategy is insufficient to strongly affect bitou performance regardless of water availability.

The consistency of competitive hierarchies across different water availabilities was dependent on the measure of competitive effect. The below-ground biomass hierarchy remained consistent under droughted and non-droughted conditions. However, the structure of the above-ground biomass hierarchy was contingent on water availability.

While shoot and root biomass values are interdependent, they may not respond to environmental change at the same rate or magnitude (Brouwer 1962, 1983). Certainly, when soil water is a limiting resource, root biomass allocation is expected to increase relative to shoot allocation (Wang & Taub 2010). Where moisture, rather than light, is a limiting resource, and where neighbours are in early stages of development (i.e. leaf canopies do not overlap), interactions may be stronger and expressed more directly in below than above-ground biomass. But our results have also shown that above-ground allocations of bitou biomass vary depending on neighbour identity and environmental conditions. This finding may indicate that bitou and/or native species have greater flexibility in shoot than root allocations. The consistency of competitive hierarchies between environments has important implications for emergent species compositions: if species positions change between environments then competition may drive alternate community structures (Novoplansky & Goldberg 2001). It is unclear from our study whether below- or above-ground interactions structure plant hierarchies under field conditions. Field observations of species dominance and the contribution of above- vs. below-ground biomass are required to predict whether hierarchies will remain consistent under future climate change.

Our study has addressed, in part, the critical question of whether climate change could increase the susceptibility of vegetation communities to invasion (Dukes & Mooney 1999). We found that native competitive effects were evident under non-droughted but not under droughted conditions and this may allow maintenance or expansion of the invader's range with future prolonged drought. Several studies have modeled the response of invaders to novel abiotic factors under climate change (e.g. Kriticos *et al.*

2003; Thuiller *et al.* 2007; Bradley *et al.* 2009), however few studies have addressed the response of invaders to altered biotic interactions under climate change (but see Nui & Wan 2008). Our research provides some insight into how biotic interactions may structure future invaded communities. Inclusion of other components of climate change such as temperature changes and carbon dioxide enrichment in construction of competitive hierarchies may further improve our ability to predict invader distributions and abundance in a changing world.

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Tables

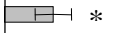

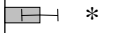





























Table 1: Mann-Whitney U Test results of neighbour effect on bitou above- and below-ground biomass under droughted (bitou alone: $n = 49$; bitou with neighbours: $n = 87$) and non-droughted (bitou alone: $n = 53$; bitou with neighbours: $n = 117$) conditions

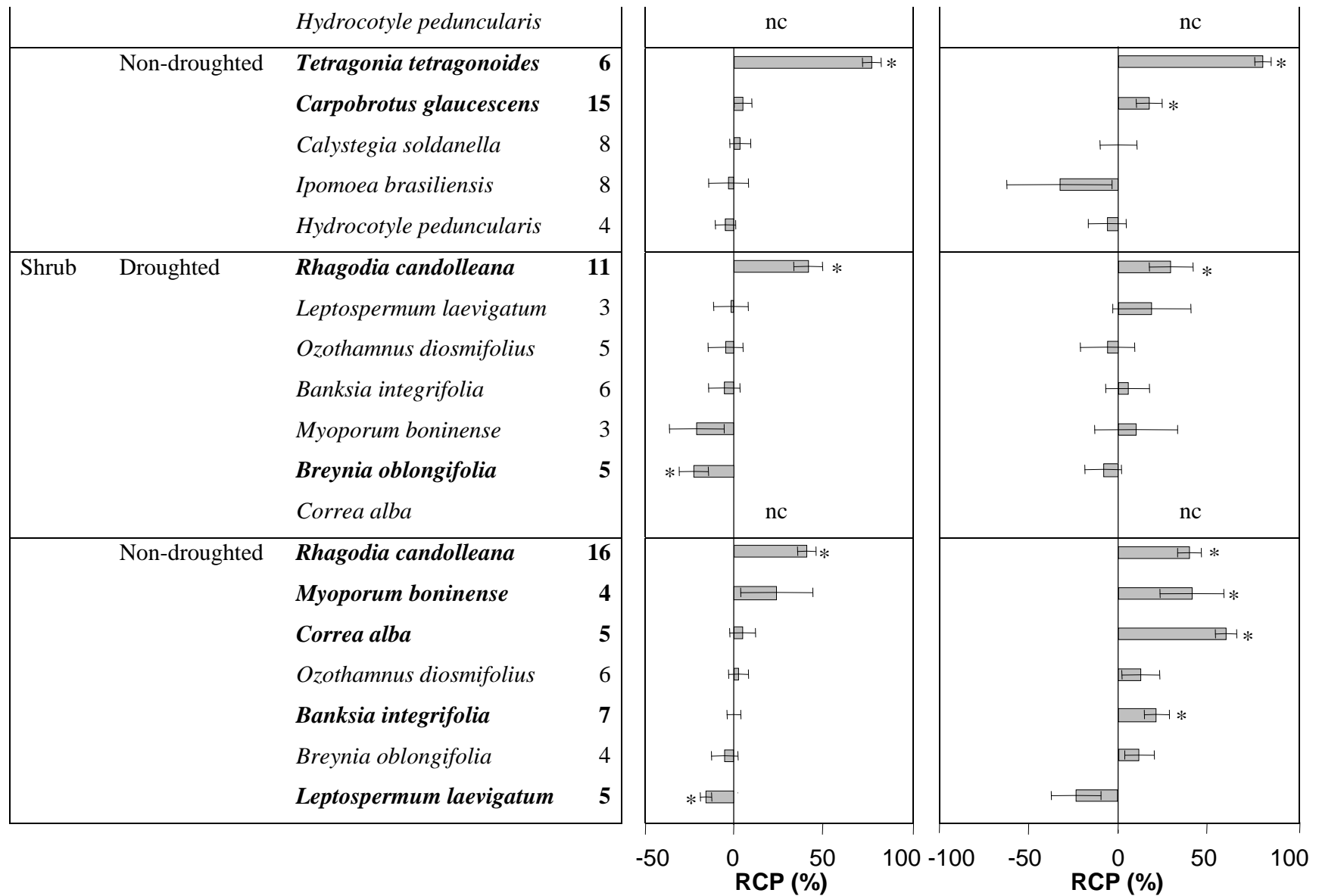
	U	P
Droughted		
Bitou above-ground biomass	1866.500	0.230
Bitou below-ground biomass	2088.000	0.844
Non-droughted		
Bitou above-ground biomass	2483.000	0.038
Bitou below-ground biomass	2420.000	0.022

Table 2: ANOVA results for the influence of water availability (W), neighbour functional group identity (F) and neighbour species within functional group S[F] on bitou above- and below-ground biomass

Factor	df	MS	<i>F</i>	<i>P</i>
Bitou above-ground biomass				
W	1	620.423	236.723	<0.001
F	3	14.632	5.583	0.001
S[F]	15	26.604	10.151	<0.001
W x F	3	5.604	2.138	0.096
W x S[F]	13	6.387	2.437	0.004
Error	273	2.621		
Bitou below-ground biomass				
W	1	15.224	69.799	<0.001
F	3	0.856	3.926	0.009
S[F]	15	1.231	5.643	<0.001
W x F	3	0.351	1.609	0.188
W x S[F]	13	0.263	1.206	0.274
Error	273	0.218		

Table 3: Relative competitive performance (\pm one standard error) for each native species under droughted and non-droughted conditions as expressed by the mean percent change in bitou above- and below-ground biomass when grown with 18 dune species (see tabular values for n) compared with bitou above- and below-ground biomass when grown alone (droughted; $n = 49$; non-droughted: $n = 53$). * and bold text indicates significant competitive (positive RCP value) or facilitative (negative RCP value) effect of native species on bitou; $P < 0.05$; nc = not calculated.

Group	Water stress	Native species	n	Above-ground biomass	Below-ground biomass
Grass	Droughted	<i>Cynodon dactylon</i>	4		
		<i>Imperata cylindrica</i>	5		
		<i>Ischaemum triticeum</i>	6		
		<i>Spinifex sericeus</i>	4		
		<i>Zoysia macrantha</i>	4		
		<i>Paspalum vaginatum</i>	3		
	Non-droughted	<i>Imperata cylindrica</i>	6		
		<i>Paspalum vaginatum</i>	8		
		<i>Spinifex sericeus</i>	5		
		<i>Ischaemum triticeum</i>	5		
		<i>Cynodon dactylon</i>	4		
		<i>Zoysia macrantha</i>	4		
Herb	Droughted	<i>Tetragonia tetragonoides</i>	4		
		<i>Carpobrotus glaucescens</i>	9		
		<i>Calystegia soldanella</i>	8		
		<i>Ipomoea brasiliensis</i>	7		



Figures and figure legends

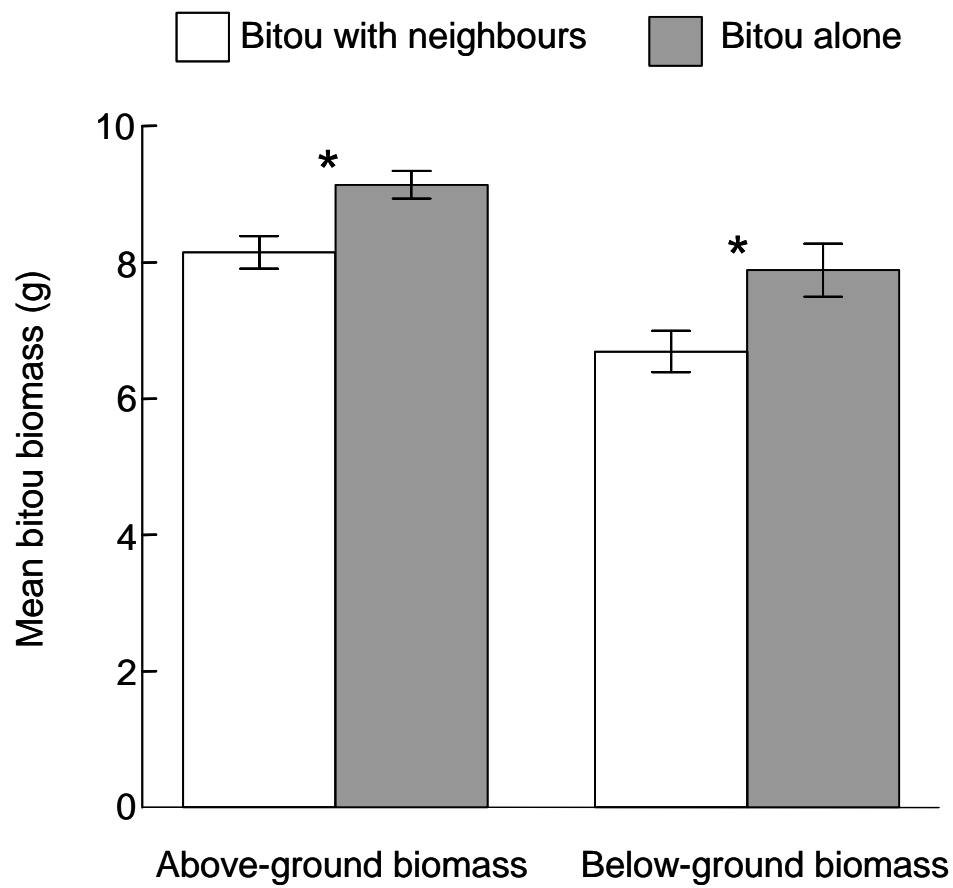


Figure 1: Mean above-and below-ground bitou biomass for bitou grown alone and with native neighbours under non-droughted conditions (\pm one standard error) * $P < 0.05$.