Implications of Plant Density on the Resulting Community Structure of Mine Site Land

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Abstract

The relative abundances of Chenopodiaceae shrubs are different from the seed composition in the original seed mix when sown on mine waste material in semiarid regions of Western Australia. Experiments were therefore undertaken to determine what species interactions are responsible for shifts in relative abundance after seeding. The growth parameters of five members of the Chenopodiaceae were used to determine intra- and interspecific density-dependent interactions. Dominant and subordinant species were paired and grown in pots at differing densities. The growth parameters measured were height, root, and shoot biomass. Of the five species chosen for this study, *Maireana georgei* (golden bluebush) and *Enchylaena tomentosa* (ruby saltbush) do not establish well on mine site areas. These were sensitive to density in monoculture, as well as in the presence of both *Atriplex bunburyana* (silver saltbush) and *Atriplex codonocarpa* (flat-topped saltbush). Although *Maireana brevifolia* (small leaf bluebush) does establish successfully on mine sites when sown, it showed the same negative reaction when grown in monoculture and in a two-species mixture. *Atriplex bunburyana* and *A. codonocarpa*, in contrast, are dominant species and reacted differently when grown with increasing numbers of the target species (*M. georgei*, *M. brevifolia*, and *E. tomentosa*). *Atriplex bunburyana* did not exhibit any decreases in growth when grown in competition with up to four plants of the target species. However, *A. codonocarpa* did react adversely to the presence of the target species. It is thought that the resulting plant community organization reflects the original seed mixture, which is usually sown at a high density. Yet, this study has shown that the differing intra- and interspecific density responses of these chenopod species provide an indication of the resulting community organization. To maximize diversity and to prevent dominance by highly competitive species, such as *A. bunburyana*, it is important to take density-dependent effects into account during the restoration planning stage.

Key words: **Australia, Chenopodiaceae, competition, density, dominance, mine site, plant establishment, revegetation, semiarid.**

Introduction

The main aim of any restoration process is to create sustainable plant communities representative of the composition and diversity of the surrounding natural plant communities. The restoration of waste and tailings materials in the arid and semiarid areas of Australia therefore uses seed mixtures that are usually broadcast onto the soil surface with this purpose in mind (Department of Minerals and Energy 1996). The resultant revegetation is thought to be representative of the proportion of each species in the seed mixture, but this is rarely the case in many environments (Camargo et al. 2002; Gilbert et al. 2003; Kleijn 2003).

Assessments of the revegetation on mine rehabilitation sites in Western Australia have shown that one or two species may dominate several years after seeding (A. Schatral, personal communication, 1997, Curtin University of Technology). Dominance by any one species varies from one mine site to the next, and may be influenced by rainfall events in combination with environmental conditions. The dominance of one species may also occur if it is favored in the broadcast seed mixture.

This study investigated the possibility that broadcast seed mixtures contain some species-specific densities that are too high and are therefore not cost effective to the mining company. The density of organisms within a community often determines whether or not significant intra- or interspecific competition occurs (Callaway & Walker 1997; Dietz et al. 1998). Plant size is also important because it affects the outcome of competition, particularly when plants are grown in high densities. For competition to occur, plants must be large enough to interact (Weiner et al. 1997). The combination of plant density and size determines the threshold at which competition occurs in a particular environment. Beyond this threshold, plant resource requirements for optimal growth and survival exceed resource availability (Hall 1978).

When competition does occur, plants may compete for above- or belowground resources. Competition for limited

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aboveground resources, most commonly light, involves fast and significant increases in aboveground biomass. Plants that achieve the greatest height in the shortest time have a competitive advantage, giving them access to most of the available light (Newman 1973; Rhodes & Stern 1978). In contrast, competition for limited belowground resources (e.g., nutrients and water) involves fast root growth rates and greater root biomass (Aerts 1999). Some plant species have the ability to adjust their biomass allocation patterns in response to below- or aboveground competition. This adjustment is reflected in the root to shoot ratio and provides a clear indication of the type of competition (Boot & Mensink 1990; Dietz et al. 1998).

Plants of the Chenopodiaceae family are routinely used as initial colonizers on mine waste and tailings dump surfaces in semiarid Western Australia. This is due in part to the fact that they are adapted to the harsh conditions of the arid zone and also because they have a tolerance to high levels of salinity. In addition, they are represented in the natural vegetation of the surrounding areas. The genera, *Atriplex* and *Maireana*, form an integral component of the semiarid and arid shrublands of Australia (Mitchell & Wilcox 1998). Members of these two genera exhibit a variety of growth forms and mechanisms that allow them to withstand the conditions of this environment and facilitate coexistence of many species.

In this study, five members of the Chenopodiaceae were selected as examples of dominant or subordinate species on revegetation areas. They are commonly used components of seed mixtures in restoration. *Atriplex bunburyana* and *Atriplex codonocarpa* colonize mine rehabilitation sites successfully and dominate over many *Maireana* species and *Enchylaena tomentosa*, which show poor establishment success in comparison. The *Maireana* species and *E. tomentosa* are representative of the natural vegetation in the region and may contribute to the diversity of the resultant plant community. They are therefore equally as important as the *Atriplex* species in the revegetation process.

The chenopods selected for this study were *A. bunburyana* F. Muell., *A. codonocarpa* Paul G. Wilson, *Maireana georgei* (Diels) Paul G. Wilson, *Maireana brevifolia* (R. Br.) Paul G. Wilson, and *E. tomentosa* R. Br. *Atriplex bunburyana*, which grows to 1 m high, has slender, often straight and rigid branches, and is dioecious. *Atriplex codonocarpa* is a monoecious, short-lived perennial, or rounded annual that grows to 30 cm high. *Maireana georgei*, a perennial, has woolly branches, succulent leaves, and grows to a height of 50 cm. *Maireana brevifolia* grows to a height of 1 m, and has slender, striate, and sparsely woolly branches. *Enchylaena tomentosa* grows to a height of 1 m. The stems are soft, brittle, and usually densely woolly (Mitchell & Wilcox 1998).

The overall aim of this study was to determine whether or not increasing the densities of target chenopod species (i.e., *M. georgei*, *E. tomentosa*, and *M. brevifolia*), commonly used in seed mixtures, would increase their survival and establishment rates on mine site revegetation areas. *Maireana georgei*, *M. brevifolia*, and *E. tomentosa* were chosen as target species for the following reasons: (1) Under the usual seeding and site preparation protocols, *M. georgei* and *E. tomentosa* do not usually successfully establish in rehabilitated areas; and (2) *Maireana brevifolia* is a successful colonizer and was therefore chosen to provide contrast. All three target species were compared with *A. bunburyana* and *A. codonocarpa*, which often dominate areas rehabilitated after mining. It is expected that competition from the *Atriplex* species could be detrimental to growth of *M. brevifolia*, *M. georgei*, and *E. tomentosa*. This research had therefore three specific aims:

(1) To determine whether intraspecific competition of *M. brevifolia*, *M. georgei*, or *E. tomentosa* plants occurred when they were grown at various densities in monoculture.
(2) To determine the responses (i.e., height and biomass) of *M. brevifolia*, *M. georgei*, or *E. tomentosa* when grown with either *A. bunburyana* or *A. codonocarpa* as compared with monocultures.
(3) To determine the response of *A. bunburyana* and *A. codonocarpa* when grown with increasing densities of *M. brevifolia*, *M. georgei*, or *E. tomentosa*. This allows for an assessment of whether or not increasing densities of these chenopods restricts the growth of individual *A. bunburyana* and *A. codonocarpa* plants, thereby providing *M. georgei*, *M. brevifolia*, and *E. tomentosa* with a competitive advantage.

A study of the effects of plant density and competition will determine whether or not the resultant plant community structure is influenced by these processes. This in turn may reveal whether or not the seed mixture is effective. Recognition by land managers that some species are highly competitive at high densities will allow for an adjustment of species proportions within the seed mixture. From an operational perspective, more effective species proportions within the seed mixtures will ensure that funds are optimized.

Methods

Topsoil, representative of that of the natural environment of chenopod species, was collected from areas surrounding the Westonia open pit goldmine in Western Australia. Westonia is located on the perimeter of the Eastern Goldfields Region of Western Australia (31°20′ S, 118°40′ E). Topsoil permeability is reduced in pots, as compared with that of the natural environment. The topsoil was therefore mixed with sand at a ratio of 1 : 1 to improve permeability and to more closely mimic the soil conditions of the natural environment. The soil mixture was composed of 0.74% organic carbon, 3.5 mg/kg nitrate, 1 mg/kg ammonium, 6.9 mg/kg phosphorus, 179.8 mg/kg potassium, 5.3 mg/kg sulfur, 344.6 mg/kg iron, an $EC_{1:5}$ of 0.1 dS/m conductivity, and a pH of 8 (Wesfarmer CSBP Laboratory, Bayswater, Western Australia).

Seeds of *Maireana georgei*, *Maireana brevifolia*, *Enchylaena tomentosa*, *Atriplex bunburyana*, and *Atriplex codonocarpa* were obtained from the semiarid region of the Eastern Goldfields in Western Australia in 1997 (Nindethana Seed Services, Woogenilup, Western Australia). *Maireana georgei* seeds were extracted from the fruiting body to overcome normal dormancy mechanisms. Seeds of the other four species were not extracted from their fruiting bodies. In August 1998 (winter), seeds from all five species were sown in free draining plastic pots (26.5 cm diameter and 25 cm high) at densities greater than that required to ensure adequate seedling germination and establishment rates.

Excess seedlings were removed after germination to achieve the required densities of each trial. In the first trial, *M. georgei*, *M. brevifolia*, or *E. tomentosa* were grown in monoculture at densities of 1, 2, 4, and 10 plants per pot. In the second trial, one plant, consisting of either *A. bunburyana* or *A. codonocarpa*, was grown along with either one plant of *M. georgei*, *M. brevifolia*, or *E. tomentosa*. In the third trial, *M. georgei*, *M. brevifolia*, or *E. tomentosa* were grown at densities of one, two, or four plants together with one plant consisting of either *A. bunburyana* or *A. codonocarpa*.

All pots were kept outdoors in a field trial area at Curtin University of Technology, Perth, Western Australia. Plants were watered once daily for 15 minutes during summer by an automatic watering system. Pots were weeded as required. The plants were not watered by the automatic watering system during winter because there was adequate rainfall for their survival. Fertilizer was not applied.

Mean minimum and maximum temperatures ranged from 17 to 32°C during summer and 8–19°C during winter (Bureau of Meteorology 2002). The number of replicate pots for all three trials was 20, with half harvested at 6 months and the remainder at 12 months. The result of high seedling death after a severe storm in September 1998, however, caused the loss of some replicates in four *M. georgei* treatments, one of which had no survivors, and an *E. tomentosa* treatment under the highest plant density in the first trial. In the third trial, replicates were lost when *E. tomentosa*, *M. brevifolia*, and *M. georgei* were grown with *A. bunburyana* at the highest plant density.

The plant height in approximately half of the pots of each of the target species was measured 6 months after seedling emergence, after which the plants were harvested. The roots were washed of soil. Each plant was then divided into shoot and root components. Shoots and roots were dried in an oven at 60°C for 3 days, before weighing. Root to shoot ratios were calculated for each replicate for each species. The same procedure was repeated after the 12-month harvest. *Atriplex codonocarpa*, an annual, was harvested at 6 months whereas the perennial, *A. bunburyana*, was harvested at 12 months.

Homogeneity of variances was tested using Levene's test (Ott 1988). Data that were not normally distributed were log transformed. Plant height and shoot and root weights at the different density treatments were analyzed using one-way analysis of variance (ANOVA) using SPSS 10.0 for Macintosh (1989–2000, SPSS Inc., Chicago, IL, U.S.A.). All means were compared using Tukey's compromise post hoc test. Where homogeneity of variances could not be corrected by $\log_{10}$ transformation of data, the nonparametric Kruskal–Wallis test was used. This test approximates the parametric ANOVA procedure (Ott 1988).

Results

Experiment 1: Chenopod Growth in Monoculture

Enchylaena tomentosa. The height of all 6-month-old *E. tomentosa* plants significantly decreased when densities exceeded two plants per pot ($p < 0.001$). The height of 12-month-old *E. tomentosa* plants, however, did not significantly differ between density treatments ($p = 0.138$; Fig. 1A). The root and shoot dry weight of individual plants decreased at increased plant densities for both 6-month-old ($p < 0.001$) and 12-month-old ($p = 0.006$ and $p < 0.001$, respectively) plants (Fig. 1B & 1C). The root to shoot ratios were at a maximum at densities of 10 plants per pot at the 6-month ($p = 0.012$) and 12-month ($p < 0.001$) harvest (Fig. 1D). All 6-month-old plants at all densities had greater shoot than root biomass. At 12 months old, however, plants at higher density (4 or 10 plants per pot) had more root than shoot biomass.

Maireana brevifolia. There was a visible correlation between the height of *M. brevifolia* and plant density. Six-month-old *M. brevifolia* plants were shorter in height as plant density increased ($p < 0.001$; Fig. 2A). By 12 months, there were no differences in height between planting densities of one, two, or four plants per pot. Plants at densities of 10 per pot, however, were significantly shorter ($p < 0.001$). The root and shoot dry weight decreased as plant density of 6-month-old ($p < 0.001$) and 12-month-old ($p < 0.001$) plants increased (Fig. 2B & 2C). The root to shoot ratio increased as planting density of 6-month-old *M. brevifolia* plants increased ($p < 0.001$), but there was no significant difference in this ratio at 12 months ($p = 0.259$; Fig. 2D). Individuals had approximately equal root and shoot biomass when grown at densities of one, two, or four plants per pot, but had greater root than shoot biomass when grown at a density of 10 plants per pot for both the 6-month-old and 12-month-old *M. brevifolia* plants.

Maireana georgei. The height of *M. georgei* plants was unaffected by planting density at 6 months ($p = 0.037$) or at 12 months ($p = 0.489$) of age (Fig. 3A). The root and shoot dry weights of both 6-month-old ($p < 0.001$; Fig. 3B) and 12-month-old ($p < 0.001$; Fig. 3C) plants decreased as plant density increased. Root to shoot ratios did not significantly differ with increasing density of 6-month-old *M. georgei* plants ($p = 0.252$). In contrast, at 12 months, all

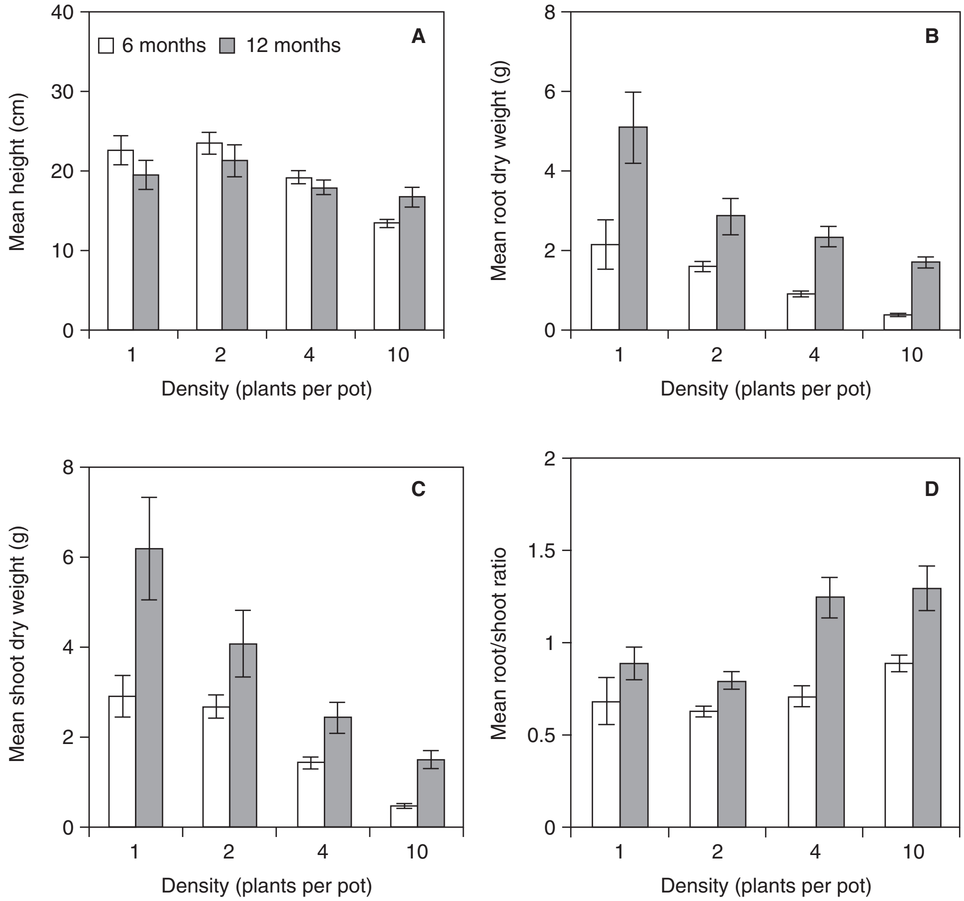

Figure 1. *Enchylaena tomentosa* mean height (A), root dry weight (B), shoot dry weight (C), and root to shoot ratio (D) at 6 (no shading) and 12 months (shaded) when grown in monoculture at differing plant densities. Bars indicate standard errors.

plants revealed significantly increased ratios at a density of 10 plants per pot compared with densities of one and two plants per pot ($p < 0.001$). Generally, plants had greater shoot than root biomass, regardless of plant density, for both the 6-month-old and 12-month-old *M. georgei* plants.

Mortality. For *E. tomentosa*, *M. brevifolia*, and *M. georgei*, there was little or no mortality observed at 6 months of age across all planting densities. However, there were some plant deaths during the 6- to 12-month period. For example, 30 and 19% of *E. tomentosa* and *M. brevifolia*, respectively, did not survive to the 12-month harvest when grown at a density of 10 plants per pot. *Maireana georgei* exhibited 35 and 16% mortality, at a density of 2 and 10 plants per pot, respectively, by the 12-month harvest. Pots in which plant mortality occurred were removed as a repetition.

Experiment 2: Selected Chenopods Grown with *A. bunburyana* or *A. codonocarpa*

The growth parameters of *E. tomentosa*, *M. brevifolia*, and *M. georgei* grown in monoculture were compared with that of plants grown in two-species mixtures (with *Atriplex bunburyana* or *Atriplex codonocarpa*) at a density of two plants per pot (Tables 1–3). No mortality was recorded when these plants were grown in association with either *A. bunburyana* or *A. codonocarpa*.

Enchylaena tomentosa. There was no significant difference between the height of 6-month-old *E. tomentosa* plants when grown in monoculture or along with *Atriplex* species (Table 1). Shoot dry weight of *E. tomentosa* was significantly greater in association with *A. codonocarpa* than compared with *A. bunburyana*. There was no significant difference, however, between 6-month-old *E. tomentosa* monocultures with *Atriplex* species combinations. The root dry weight of 6-month *E. tomentosa* plants was significantly greater when grown together with *A. codonocarpa*. At 12 months, plant height and shoot and root dry weight of *E. tomentosa* were significantly greater if grown with *A. codonocarpa* than with *A. bunburyana* or in monoculture.

Maireana brevifolia. Six-month-old *M. brevifolia* plants exhibited similar plant heights and shoot dry weights when grown in monoculture and with the *Atriplex* species (Table 2). Root dry weight of *M. brevifolia* was, however, reduced when grown alongside *A. bunburyana* plants. At

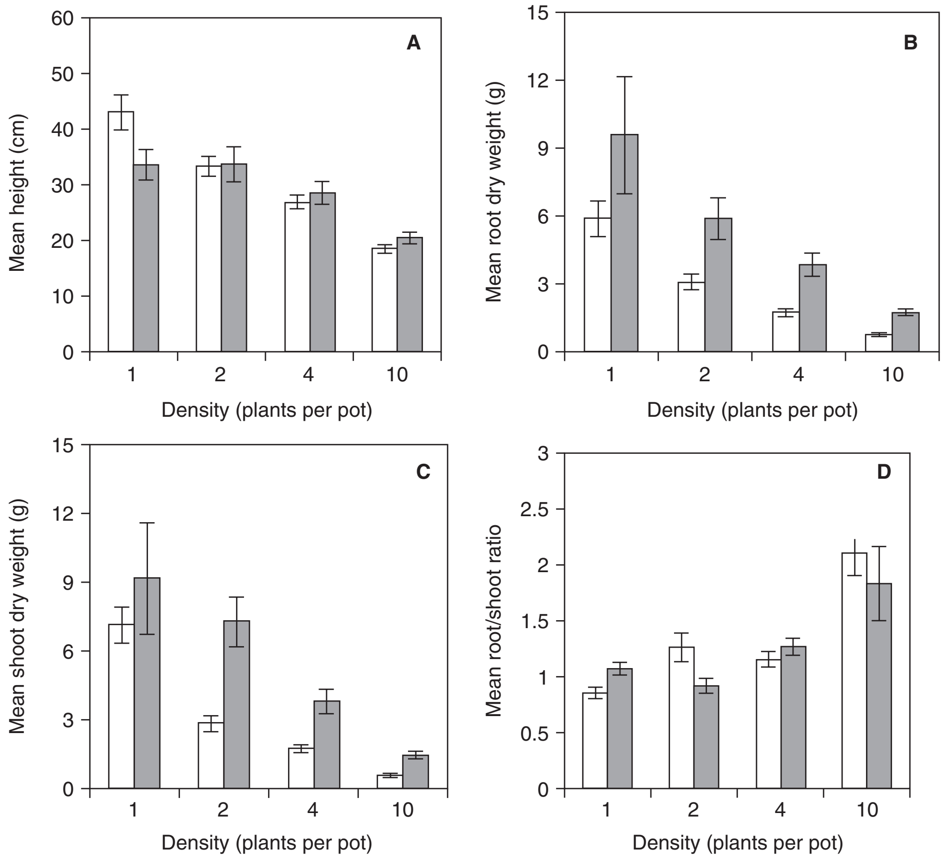

Figure 2. The mean height (A), root dry weight (B), shoot dry weight (C), and root to shoot ratio (D) of *Maireana brevifolia* at 6 (no shading) and 12 months (shaded) when grown in monoculture at differing densities. Bars indicate standard errors.

12 months of age, plant height and shoot and root dry weights of *M. brevifolia* did not differ in association with *Atriplex* species or in monoculture.

Maireana georgei. The height of 6-month-old *M. georgei* plants in association with *A. bunburyana* was significantly greater than that of plants in monoculture or with *A. codonocarpa* (Table 3). Twelve-month-old *M. georgei* plants also exhibited increased plant height when grown with *A. bunburyana*. Shoot dry weights of 6-month-old *M. georgei* plants were significantly greater when grown with *A. codonocarpa* than with *A. bunburyana* or in monoculture. At 12 months, however, *M. georgei* shoot dry weight was greatest in monoculture. Root dry weight of 6-month-old *M. georgei* plants was significantly lower when grown with *A. bunburyana* compared with plants in monoculture. At 12 months, there was no significant difference in root dry weight between *M. georgei* in monoculture or with *Atriplex* species.

Experiment 3: Growth of *A. codonocarpa* and *A. bunburyana* When Grown with the Three Target Chenopods

Atriplex codonocarpa. Plant height and root and shoot dry weight of 6-month-old *A. codonocarpa* plants decreased as the density of the target plants increased (Fig. 4). The root to shoot ratio of 6-month-old *A. codonocarpa* plants inversely correlated with the density of *E. tomentosa* or *M. georgei*. There was no mortality of *A. codonocarpa* plants, regardless of plant age or density of co-planted target species.

Atriplex bunburyana. There were no significant differences in plant height or root or shoot dry weight of *A. bunburyana* plants grown with different plant densities of the three competing chenopod species (Fig. 5). Root to shoot ratios of *A. bunburyana* did not differ when the plant density of either *E. tomentosa* or *M. brevifolia* was increased. *Atriplex bunburyana* root to shoot ratios decreased significantly, however, when grown with one *M. georgei* plant. There was no mortality of *A. bunburyana* plants, regardless of plant age or density of co-planted target species.

Discussion

Competition plays an important role in determining the botanical composition of plant communities (Wilson 1988*a*). Interactions between plants growing at different densities in the same location are dependent on species

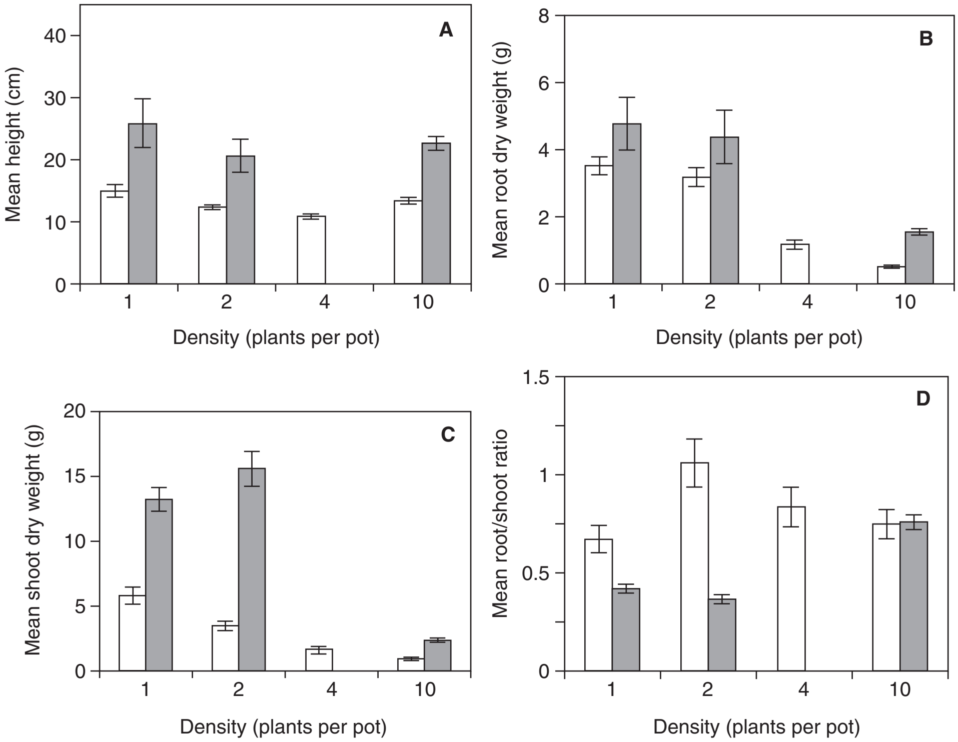

Figure 3. *Maireana georgei* mean height (A), root dry weight (B), shoot dry weight (C), and root to shoot ratio (D) at 6 (no shading) and 12 months (shaded) when grown in monoculture at differing densities. Bars indicate standard errors.

Table 1. Growth parameters (means and the standard errors in brackets) of plants aged 6 and 12 months.

	Et	*Et (Ab)*	*Et (Ac)*	*p*
6 months				
Height (cm)	23.45[a]	18.79[a]	23.84[a]	0.216
	(1.30)	(2.43)	(3.04)	
Shoot dry weight (g)	2.70[ab]	1.61[b]	3.59[a]	**0.011**
	(0.26)	(0.41)	(0.57)	
Root dry weight (g)	1.59[b]	0.98[b]	1.94[a]	**0.014**
	(0.13)	(0.31)	(0.32)	
12 months				
Height (cm)	21.25[b]	21.67[b]	33.47[a]	**0.010**
	(1.97)	(1.11)	(3.64)	
Shoot dry weight (g)	4.09[b]	2.82[b]	6.75[a]	**0.025**
	(0.74)	(0.56)	(0.90)	
Root dry weight (g)	2.86[b]	2.67[b]	5.19[a]	**0.009**
	(0.45)	(0.70)	(0.61)	

One-way ANOVA summaries compare *Enchylaena tomentosa* (Et) (at a density of two plants per pot) grown in monoculture with those grown in two-species mixtures (one plant of *E. tomentosa* and one plant of *Atriplex bunburyana* [Ab] or *Atriplex codonocarpa* [Ac]) ($p < 0.05$). Similar letters indicate means, which are not significantly different, based on Tukey's compromise test ($p < 0.05$).

Table 2. Growth parameters (means and the standard errors in brackets) of plants aged 6 and 12 months.

	Mb	*Mb (Ab)*	*Mb (Ac)*	*p*
6 months				
Height (cm)	33.32[a]	33.25[a]	27.62[a]	0.126
	(1.61)	(2.88)	(1.85)	
Shoot dry weight (g)	2.84[a]	2.38[a]	2.81[a]	0.675
	(0.35)	(0.42)	(0.28)	
Root dry weight (g)	3.10[a]	1.6[b]	2.79[a]	**0.007**
	(0.30)	(0.30)	(0.29)	
12 months				
Height (cm)	33.71[a]	28.05[a]	31.15[a]	0.442
	(3.02)	(2.70)	(2.74)	
Shoot dry weight (g)	7.29[a]	3.30[a]	4.26[a]	0.082
	(1.10)	(0.75)	(0.63)	
Root dry weight (g)	5.88[a]	3.47[a]	4.62[a]	0.171
	(0.92)	(0.72)	(0.64)	

One-way ANOVA summaries compare *Maireana brevifolia* (Mb) (at a density of two plants per pot) grown in monoculture with those grown in two-species mixtures (one plant of *M. brevifolia* and one plant of *Atriplex bunburyana* [Ab] or *Atriplex codonocarpa* [Ac]) ($p < 0.05$). Similar letters indicate means, which are not significantly different, based on Tukey's compromise test ($p < 0.05$).

characteristics and the conditions under which they grow (Wilson 1988*a*). Conditions that may influence the outcome of plant interactions include available soil volume (pot size) (McConnaughay & Bazzaz 1991), time (age of plants) (Wilson 1988*b*), and resource availability (Bi & Turvey 1994). Different species may also exhibit different sensitivities to these conditions (Pantastico-Caldas & Venable 1993). Although the environmental conditions experienced by a pot trial are different from those in the field, they provide valuable insight into the mechanisms of competitive interaction of plants (Gibson et al. 1999).

Table 3. Growth parameters (means and the standard errors in brackets) of plants aged 6 and 12 months.

	Mg	*Mg (Ab)*	*Mg (Ac)*	*p*
6 months				
Height (cm)	12.51^{c}	24.73^{a}	15.20^{b}	**<0.001**
	(0.34)	(1.52)	(1.02)	
Shoot dry weight (g)	3.41^{b}	3.04^{b}	5.40^{a}	**0.006**
	(0.36)	(0.60)	(0.54)	
Root dry weight (g)	3.19^{a}	1.69^{b}	2.34^{ab}	**0.007**
	(0.28)	(0.36)	(0.34)	
12 months				
Height (cm)	20.81^{b}	39.20^{a}	21.32^{b}	**<0.001**
	(2.69)	(2.71)	(1.50)	
Shoot dry weight (g)	15.61^{a}	6.83^{b}	10.21^{b}	**<0.001**
	(1.35)	(0.63)	(0.97)	
Root dry weight (g)	4.39^{a}	2.97^{a}	4.79^{a}	0.055
	(0.8)	(0.37)	(0.33)	

One-way ANOVA summaries compare *Maireana georgei* (Mg) (at a density of two plants per pot) grown in monoculture with those grown in two-species mixtures (one plant of *M. georgei* and one plant of *Atriplex bunburyana* [Ab] or *Atriplex codonocarpa* [Ac]) ($p < 0.05$). Similar letters indicate means, which are not significantly different, based on Tukey's compromise test ($p < 0.05$).

Root competition is the main mode of competition determining plant community structure in arid and semiarid environments. Belowground competition occurs in these environments because resources such as nutrients and water are limiting. In this trial, nutrients were limiting. However, space may also have contributed to intra- and interspecific competitive effects in this study.

The growth form and correlated traits determine the competitive ability of plants (Dietz et al. 1998). Both *Atriplex bunburyana* and *Maireana brevifolia* had a greater overall height and biomass, in comparison with other species. These traits show a competitive advantage over smaller species. In addition, *Maireana georgei* seeds were removed from their fruiting bodies during this study to overcome dormancy. During restoration practices, *M. georgei* seeds are not extracted and therefore germination is delayed. The size differences between *M. georgei* and the other species will be greater on restored areas than shown in this study. Size differences will likely cause asymmetric competition, where larger plants obtain more of the available resources (Weiner et al. 1997). There is sufficient evidence to suggest that asymmetric competition regulates the growth of plants in semiarid and arid environments (Cable 1969; Yeaton & Cody 1976; Goldberg & Novoplansky 1997; Vargas-Mendoza & Fowler 1998; Pugnaire & Luque 2001).

Is Intraspecific Competition Occurring Between Plants of the Three Target Chenopod Species?

The negative impact expressed in the growth attributes of the three chenopod species with increasing plant density is indicative of competition (Weiner et al. 1997; Vargas-Mendoza & Fowler 1998). This was particularly evident

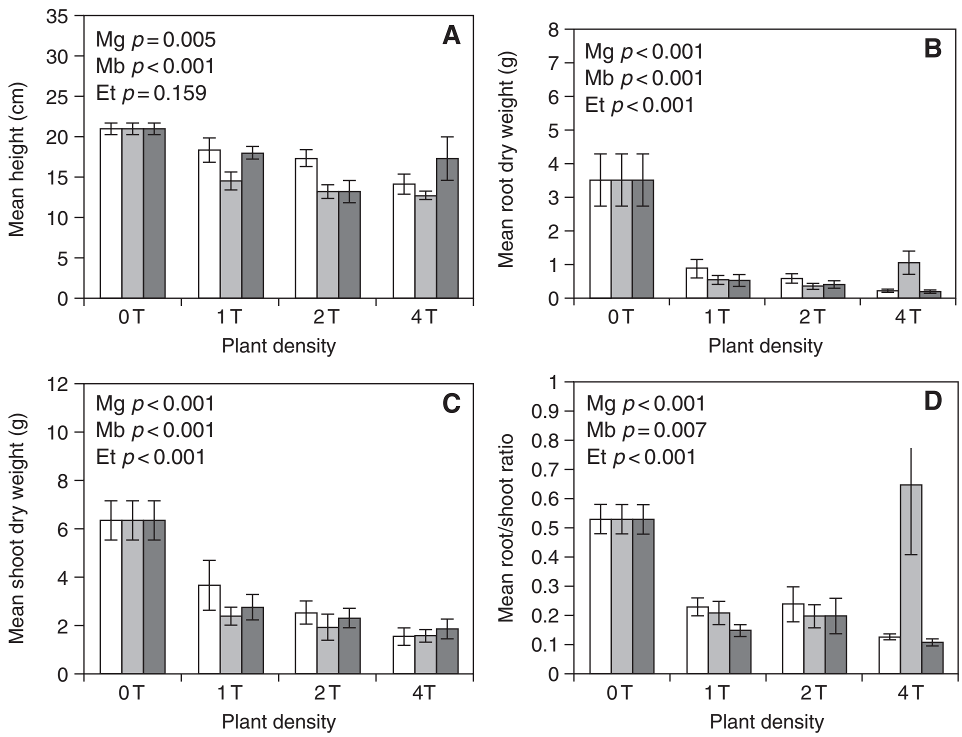

Figure 4. Mean *Atriplex codonocarpa* (Ac) plant height (A), root dry weight (B), shoot dry weight (C), and root to shoot ratio (D) when grown with increasing numbers of the three target species (T); *Maireana georgei* (Mg) (no shading), *Maireana brevifolia* (Mb) (light shading), or *Enchylaena tomentosa* (Et) (dark shading). The control consisted of one plant of *A. codonocarpa* per pot. Bars indicate standard errors.

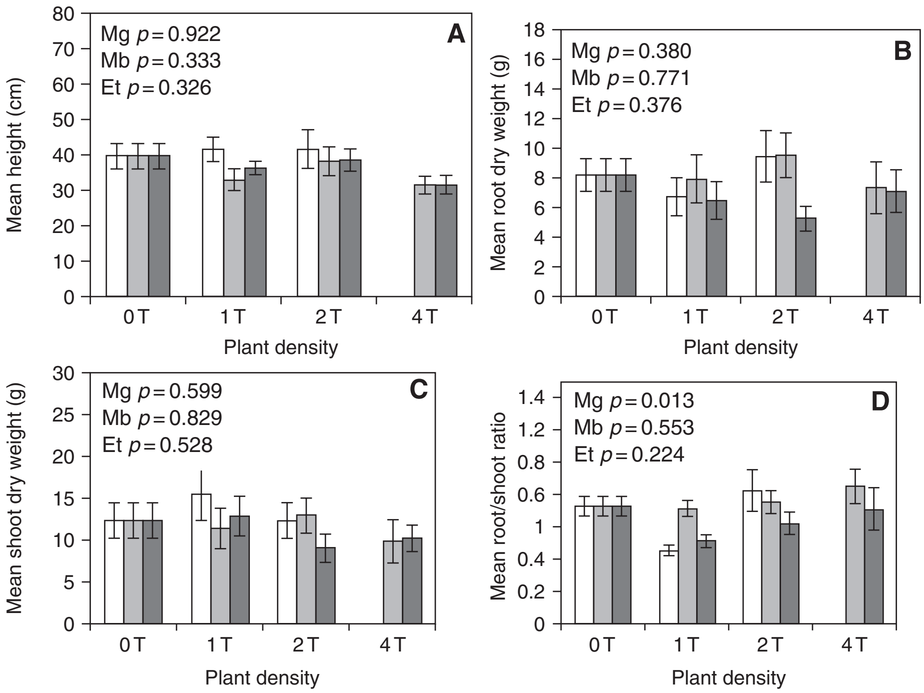

Figure 5. Mean *Atriplex bunburyana* (Ab) plant height (A), root dry weight (B), shoot dry weight (C), and root to shoot ratio (D) when grown with increasing numbers of the target plants (T); *Maireana georgei* (Mg) (no shading), *Maireana brevifolia* (Mb) (light shading), or *Enchylaena tomentosa* (Et) (dark shading). The control consisted of one plant of *A. bunburyana* per pot. Bars indicate standard errors.

when the chenopod species were grown in monoculture. It was also independent of plant age. The change in allocation of resources to roots and shoots indicated the type of competition occurring (Dietz et al. 1998). Increases in the root to shoot ratios of the chenopod species, when responding to increased plant density, indicates that there is belowground competition (Boot & Mensink 1990). Restrictions imposed by available soil volume (pot size) and soil nutrients were likely to have increased with time and become increasingly limiting, especially as the plants grew larger.

Of all the species, *M. brevifolia* had the greatest root biomass. This species also allocated more resources to its roots compared with other species, suggesting that it may be superior when competing for nitrogen (Gleeson & Tilman 1990; Witkowski 1991; Dietz et al. 1998). Larger root systems are beneficial when competing for nutrients, particularly in the nutrient-poor soil of many semiarid environments (Aerts 1999). This may provide an explanation for the better establishment success of *M. brevifolia* compared with that of *Enchylaena tomentosa* and *M. georgei*, especially on mine site revegetation areas.

Is Interspecific Competition Occurring When the Target Chenopods Are Grown with *Atriplex bunburyana* or *Atriplex codonocarpa*?

Enchylaena tomentosa, when grown with *A. codonocarpa*, exhibited significant increases in both root and shoot dry weight in comparison with the monoculture. This may indicate growth of *E. tomentosa* has been facilitated when grown in the presence of *A. codonocarpa*. Plants of *A. codonocarpa* allocated more of their biomass to their shoots, especially when in the presence of the target species. The aboveground biomass would appear to be of greater importance to this annual. This may provide considerably more available space in the pot for *E. tomentosa* roots in comparison with the available space when grown in monoculture or in the presence of an *A. bunburyana* plant.

Atriplex bunburyana and *A. codonocarpa* had a negative impact on the growth of *M. brevifolia* and *M. georgei*. *Maireana georgei* plants increased in height when grown with *A. bunburyana*. Newman (1973) suggested competition for light was a key causal factor of increased plant height when plants are grown in the presence of another plant. Small height differences often determine plant ability to obtain optimal light intensities required for survival, growth, and reproduction. Slightly taller plants should have a competitive advantage, which increases over time until shorter plants are totally suppressed (Newman 1973; Rhodes & Stern 1978).

Is the Growth of *A. bunburyana* or *A. codonocarpa* Affected When Grown with Increasing Numbers of Either *E. tomentosa*, *M. brevifolia*, or *M. georgei* Plants?

The growth of the perennial, *A. bunburyana*, did not differ when grown with plants of the selected chenopod species, illustrating the strength of this competitor and its ability to avoid being suppressed at least under the conditions imposed during the pot trial. *Atriplex bunburyana* shoot to root ratio remained relatively unchanged when grown alongside *E. tomentosa* and *M. brevifolia*. Bi and Turvey (1994) showed that aggressiveness of *Acacia melanoxylon* was reflected by its relatively unchanged shoot to root ratio in response to interspecific competition. In our study, the growth of the annual, *A. codonocarpa*, in contrast, decreased when the density of the three target species was increased. As indicated by increased shoot biomass, the allocation of resources to shoots increased in *A. codonocarpa* when grown with *M. georgei* or *E. tomentosa*. The effects of competition were expressed by increased growth of the aboveground plant tissues (Dietz et al. 1998), and in this instance, may have resulted from the relatively short lifecycle of *A. codonocarpa* and its need to reproduce within a short period.

Conclusion and Recommendations

The results outlined in this article provide an indication that intra- and interspecific competition does occur between the five chenopods studied. Revegetation programs should take into account the competitive aggressiveness of *Atriplex bunburyana*. The ability of this species to outcompete both *Maireana* species and *Enchylaena tomentosa* provides evidence of its ability to dominate revegetation areas several years after sowing. When determining the composition, and the respective densities of the seed mixture to be broadcast, it is important to take into account the competitiveness of the component species. In particular, *A. bunburyana* should be sown at reasonably low densities to ensure the resulting plant community is diverse and not dominated by this species.

Future research would include a collation of species with potential to dominate revegetation areas in the Eastern Goldfields region. Environmental reports, showing the composition and density of the broadcast seed mixtures, as well as revegetation assessments showing plant diversity indexes and species abundance, can be used to provide an indication of which species are likely to become dominant. A list of these species can be used as a guide for land managers during the revegetation process. This information can be used to optimize species densities in seed mixtures and thus make the revegetation process more cost effective. Finally, more research is required to determine which plant–plant interactions are occurring between listed dominant species and those that do not establish well on restored sites.

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