School of Chemical and Biological Science
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The biology and ecology of species of *Maireana* and *Enchylaena*: Intra- and inter-specific competition in plant communities in the eastern goldfields of Western Australia

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of the

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DECLARATION

I declare that all work presented in this thesis is that of myself alone unless otherwise acknowledged. The contents of this thesis have not been submitted previously, in whole or in part, in respect of any other academic award.

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ABSTRACT

Members of the family *Chenopodiaceae* are routinely used as colonizer plant species to rehabilitate waste and tailings materials on mine sites in the Eastern Goldfields of Western Australia. These are specifically selected for their salt and drought tolerance and also because they are representative of the surrounding natural vegetation. Where these have been sown, competition between several species has been observed. The resulting plant community structure is typically lower in species diversity than the initial seed mixture.

This study aimed to determine whether competition was occurring between five of the species commonly used and some of the mechanisms that determine community structure on the rehabilitated areas of waste material. *Atriplex bunburyana*, *Atriplex codonocarpa*, *Maireana brevifolia*, *Maireana georgei* and *Enchylaena tomentosa* were selected for the study, which was conducted in three parts.

Firstly, different plant densities and species combinations were studied in the field and in a pot trial to determine whether or not competition was occurring and to determine the resources that the plants were competing for. The results of the field trial revealed that competition was occurring, but that it formed only one component of the complex interactions between plant species, density and soil characteristics (i.e. pH and salinity). The pot trial complemented the outcome of the field trial. In addition, it showed that competition was occurring, but was even more pronounced. This was most likely due to the lack of nutrients and the limited availability of space in the pots.

In the second part of this study, the ability of each species to survive and grow when subjected to adverse environmental conditions, such as low moisture availability, high salinity and low light availability, was examined in relation to competition. All five species were treated with different water regimes and soil salinity. Salt played an important role, especially for the *Atriplex* spp. and *M. brevifolia*, in ensuring survival when moisture availability was low.

The effect of shade on the *Maireana* species and *E. tomentosa* was also researched after field observations suggested that *M. georgei* was adversely affected when growing within the canopy of *A. bunburyana*. The pot trial showed that growth of *M. georgei* was affected by progressively more shade, whereas *E. tomentosa* was facilitated by shade. *Maireana brevifolia* exhibited significant tolerance to low light intensity.

In the last part of this three-part study, all five chenopods were screened for allelopathy. Allelopathy may play an important role in determining community structure in successive plant generations. All chenopod species produced allelopathic substances, which were isolated from their leaves. The inhibition of seed germination was found to be species-specific and occurred only at certain concentrations. The seed of the *Atriplex* spp. was not affected by *M. georgei* and *E. tomentosa* extracts.

ACKNOWLEDGEMENTS

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DEDICATION

I dedicate this thesis to my Mum, Brenda Doreen Jefferson who is so special to me, who is a tower of strength and an inspiration.

Who loves a garden
Still his Eden keeps,
Perennial pleasures, plants and
wholesome harvest reaps.

AMOS BRONSON ALCOTT, 1799-1888

CONTENTS

CHAPTER 1: INTRODUCTION

The arid and semi-arid regions of Western Australia are characterised by harsh environmental conditions, such as high levels of soil salinity (Gale and Poljakoff-Mayber 1970, Caldwell 1974), low levels of nutrients and soil moisture (Caldwell 1974, Kramer 1980) and high temperatures (Caldwell 1974, Kramer 1980). Despite this, many of the plant communities in these areas are surprisingly complex. Plant species existing in these environments must have a variety of mechanisms for overcoming the potential damaging effects these environmental conditions impose, especially when disturbed.

Mining and pastoralism are the main land uses in the arid and semi-arid regions of Western Australia (Mitchell and Wilcox 1998). The disturbance of the land by mining results in large stockpiles of waste and tailings material. Revegetation of these materials is therefore ecologically important and aims to create sustainable plant communities representative of the surrounding environment (Lamont 1978, Dixon and Meney 1994). This thesis examines the role and ecological requirements of some of the most important plant species in these plant communities, with a particular focus on mine site revegetation programs.

REGULATION VERSUS LIMITATION

Plant community structure is characterised by species composition and abundance. In order to create a sustainable plant community it is important to understand what factors affect community structure. Species abundance is determined by density-dependent and density-independent factors (Sinclair 1989). In theory, a natural equilibrium point prevents populations from becoming extinct at low density and limits the population at high density. Factors causing changes in population productivity or loss are called 'limiting factors'. Limiting factors, for example, may include nutrients, soil moisture or light. Regulation is the process that facilitates a return of a population to its equilibrium. Regulatory factors, such as competition for resources, are density dependent (Goldberg *et al.* 2001).

FACTORS AFFECTING COMMUNITY STRUCTURE

Plant community structure is determined by two factors: the environmental conditions under which the plants grow (limiting factors) and the interactions between neighbouring individuals (regulatory factors) (Dale 1985, Zobel and Zobel 1988). Plant communities develop and change over time since natural selection ensures the 'fittest' group of individuals occupy a space characterised by a set of environmental conditions (Darwin 1998). Environmental heterogeneity and species tolerance limits greatly determine the size, composition and subtle boundaries of a plant community (Luken 1990).

Diversity is an important component of resilient communities. Different species may utilize unique resources, while variation in a species' environmental tolerances, physiology, morphology and life history allow for a wide range of ecosystem niches to be occupied (Luken 1990, Callaway and Walker 1997). In order to coexist, they should not make the same demands on the same resources at the same time (Luken 1990). Since resource availability changes temporally, species replacement can occur through time (Gleeson and Tilman 1990, Wilson and Tilman 1993). The tendency of plant communities to change over time is known as succession. This may involve species replacement, shifts in community structure or the biomass of particular species, and changes in the availability of resources (Callaway and Walker 1997, Fahey *et al.* 1998). Nudation, the process of plant colonisation on bare soil, for example, initiates succession. Plant survival, establishment and ability of plant colonisers to reproduce are initially determined by the prevailing physical and climatic environment (Luken 1990, Bruelisauer *et al.* 1996).

The interactions occurring between plants and their neighbours may determine community structure in a variety of ways (Tilman 1988, Callaway and Walker 1997). Positive interactions, often referred to as facilitation, occur when the survival of one species is enhanced by the presence of another. The shade of established vegetation, for example, may ensure seedling survival (Callaway 1994, Berkowitz *et al.* 1995, Holmgren

et al. 1997). Other processes that enhance neighbouring plant growth and survival include:

- modification of resources such as soil moisture, nutrients, light and temperature (Garcia-Moya and McKell 1969, Callaway 1994, Pugnaire *et al.* 1996),
- substrate modification (Callaway 1994, Pugnaire *et al.* 1996, Olofsson *et al.* 1999),
- protection from herbivory and climatic extremes (McNaughton 1978, Carlsson and Callaghan 1991),
- increased pollination success (Brown and Kodric-Brown 1979, Laverty 1992),
- provision of mycorrhizae and soil microbes (Christie *et al.* 1974, Chiarello *et al.* 1982, Amaranthus and Perry 1994),
- concentration of propagules (Day and Wright 1989, Aguiar and Sala 1994) and
- suppression of competitors (Levine 1999).

In contrast, competition occurs when one organism has a negative impact on another (e.g. consuming a resource that is in limited availability - Keddy 1989). Factors that can affect the outcome of competition include plant density (White and Harper 1969, Weiner 1980, Connolly *et al.* 1990, Goldberg *et al.* 2001), the size and age of plants competing (Wilson 1988a, Gleeson and Tilman 1990, Pake and Venable 1996, Goldberg *et al.* 2001) and the requirements of those plants (e.g. light, nutrients, pH, moisture, salinity, soil temperature) (Harris and Wilson 1970, Fahey *et al.* 1998, Williams *et al.* 1998, Cahill Jr. 1999). Interrelationships between these factors are often complex and dynamic, providing substantial challenges to the study of plant competition.

In this thesis, Welden *et al.*'s (1988) definition of competition as the "induction of physiological strain in an organism as a direct result of the use of resource items by another organism" is used. The physiological strain that one plant puts on a neighbour when competing for limiting resources is reflected by the negative effect it has on the growth parameters of the neighbour. The negative effect that one plant can have on another of the same species is referred to as intra-specific competition. Alternatively, plant competition between different species is called inter-specific competition.

COMPETITION

In many cases, plant competition is more easily understood when resource use is defined (i.e. when symmetry is taken into consideration). Absolute symmetry occurs when contested resources are divided equally amongst plants irrespective of plant size. In contrast, absolute asymmetry occurs when larger plants obtain most or all of the available resources. When contested resources are divided between plants in proportion to plant size, or "under-proportionally" with respect to size, then this resource allocation is referred to as relative-size symmetry. In contrast, relative-size asymmetry can also occur when contested resources are divided "over-proportionally" with respect to plant size (Weiner *et al.* 1997).

Competition symmetry often changes with plant age (Weiner 1988). Furthermore, it can be dependent on the limiting resources, and both above-ground or below-ground interactions. Early plant competition is symmetric, but becomes asymmetric with growth over time (Weiner 1988). Asymmetric resource competition is important in determining community structure (Kubota and Hara 1995), particularly in arid environments where below-ground resources, such as nutrients and moisture, are often limiting (Vargas-Mendoza and Fowler 1998, Pugnaire and Luque 2001). As soil fertility and moisture increase, however, competition may shift from the roots to the shoots, with light availability becoming a limiting factor (Wilson and Tilman 1995).

COMPETITIVE ABILITY

A plant's ability to acquire resources from a resource pool shared by neighbours will determine its competitive ability (Tremmel and Bazzaz 1995). The plant's competitive ability determines whether or not a negative impact on the growth and establishment of a neighbouring plant will occur, especially when a particular resource is limiting (Tilman 1988). The competitive ability of individual species is dependent on phenotypic characteristics and plant physiological requirements (Mueller-Dombois and Ellenberg 1974, Bi and Turvey 1994, Tremmel and Bazzaz 1995).

Phenotypic characteristics

Phenotypic characteristics that may influence plant competitive ability include reproductive strategies such as seed production and germination (Ross and Harper 1972, Firbank and Watkinson 1985, Osborne *et al.* 1994, Bell *et al.* 1995, Schatral and Osborne 1996), germination rates (Ross and Harper 1972) and the initial growth rates of seedlings (Witkowski 1991). Other phenotypic characteristics that contribute to plant 'fitness' include plant height, longevity and rooting patterns (Mueller-Dombois and Ellenberg 1974).

Knowledge of seed germination and seedling establishment phases is more important when attempting to understand the composition and diversity of plant communities than is the response of established plants (Dixon and Meney 1994). Species co-occurrence can be promoted by differential seedling mortality, which was often due to variations in micro-topography (Battaglia 1996). In a semi-arid environment in Australia, seedling mortality rates of *Acacia* spp. and *Cassia* spp. were high (ca. 100%) within the first two months of germination (Grice and Westoby 1987). Root growth rates of surviving seedlings then determine whether plants will be competitive (Witkowski 1991). The initial growth rate of root systems is reflected in the nutrient content of the seed (Weiner *et al.* 1997). Subsequent root growth is dependent on the ability to absorb nutrients and moisture from the surrounding micro-environment (Morgan 1995). The rate of growth of the tap root of *Acacia saligna* after germination was approximately twice that of *Protea repens* (Witkowski 1991). A faster growth rate ensures greater access to soil resources and thus provides a competitive advantage.

In the arid and semi-arid environments the relative importance of competition can be inferred by the extent to which the soil is occupied by the roots of individual species (Fowler 1986). Classification of species' root systems may account for differences in competitive abilities among vegetation classes (Cable 1969). When resources such as soil nutrients or moisture are limiting, as is the case in most arid environments, the size and rate of establishment of an extensive root system is a determining factor of competitive superiority. Below-ground competition is asymmetrical, with larger root systems

extracting proportionately more available nutrients from the soil relative to smaller root systems (Weiner *et al.* 1997).

In some cases, root production may exceed shoot production (Perrson 1978). Moreover, most root zones extend much farther from the plant stem than the canopies of most individuals. In arid and semi-arid zones root systems often exhibit a wide variety of architectures both in the vertical and horizontal planes (Fowler 1986). *Atriplex saligna*, for example, has a more extensive lateral root system than legumes indigenous to the same nutrient deficient soils (Witkowski 1991). Fast initial rates of root growth provide species with a competitive advantage. Root growth of *Atriplex vesicaria* and *A. inflata* seedlings ranged from 2.2 - 2.5 cm day^{-1} (Cowling 1969). In order to quickly establish root systems, seeds require high nutrient contents (Witkowski 1991). This is particularly important for species growing in nutrient limited environments (Lee and Fenner 1989, Pake and Venable 1996).

Root excavations at different stages of plant development indicate species root system type, growth rate and an indication of relative competitive ability. Below-ground competition is determined by the overlapping root systems of competing plants (Phillips and MacMahon 1981). Partitioning of roots and shoots of plants competing in pots can provide an accurate method of determining whether or not competition is occurring below- or above-ground (Harris and Wilson 1970, Aerts *et al.* 1991, Collins and Rhodes 1993).

Physiological requirements

Common plant physiological requirements include light, heat (Harris and Wilson 1970), water (Andersen 1967, Kadmon 1995) and nutrients (Aerts *et al.* 1990, Witkowski 1991). Competition between plants, which occurs for water in arid environments, may be especially significant (Andersen 1967, Phillips and MacMahon 1981). Competition between annual grasses, perennial grasses and sub-shrubs for soil moisture is an important factor in semi-arid environments (Cable 1969). Soil temperature is also an important consideration when studying plant competition, with different species having

different soil temperature requirements for optimal growth. Increases in soil temperature from 10 to 30 °C have been shown to cause mineralisation of nitrogen and sulphur, but paradoxically, the competitive ability of *Trifolium* tended to rise with increasing temperature in the range of 10 to 22 °C (Gilbert and Robinson 1984). Soil temperature can also influence competition for available soil moisture, as determined by measuring root elongation in seedlings subjected to different moisture conditions (Harris and Wilson 1970).

Nutrient supply is another factor limiting plant growth in arid zones (Mack and Harper 1977). Soils with varying nutrient loads had significant effects on the dry weight of *Atriplex vesicaria* shoots (Malik *et al.* 1976). Plant biomass was greatest at the higher nutrient levels. Seedlings with fast growing tap roots have greater exposure to nutrients and thus a competitive edge over individuals, which grow more slowly (Witkowski 1991). A high nutrient retention capacity can, however, compensate for slow root growth. In low nutrient soils, for example, *Mollinia* sp. allocated a higher percentage of biomass to root growth (Aerts *et al.* 1991). In contrast, *Erica* sp. and *Calluna* sp. had higher retention capacities and actually out competed *Mollinia* sp. When grown in high nutrient soils, however, *Mollinia* sp. was the stronger competitor.

OUTCOME OF COMPETITION

The outcome of competition is determined by the many processes at work throughout the life cycle of a plant and is reflected in the spatial and temporal distribution of species, populations and individuals within ecosystems. Young plants often have a clumped distribution pattern while older plants are typically randomly distributed or are spaced at regular intervals (Fowler 1986). The characterisation of total pattern in unevenly aged populations, however, will often mask the patterns of age-dependent phases (Malik *et al.* 1976). Mature plants of one species can create a surrounding environment that is not conducive of other species (Fowler 1986).

The reproductive ecology of mature plants can also be affected by competition (Reichenberger and Pyke 1990, Walck *et al.* 1999, Hartvigsen 2000). The number of

seeds produced may be reduced, the timing and mode of reproduction may change as may plant resource allocation to reproduction (Weiner 1988, Walck *et al.* 1999). The number of viable seeds can decline when neighbouring plants limit water availability during the period of seed development and maturation (Bell *et al.* 1993). Natural variations in plant density, due to previous seed production, germination conditions or predation intensity, will have different effects on particular species and may induce shifts in community composition (Pantastico-Caldas and Venable 1993).

The composition of plant communities on revegetated mine site areas are initially determined by the seed mixture distributed over the area (Bell *et al.* 1990, Booth *et al.* 1999). Mine site areas chosen for rehabilitation are seeded with species density components aimed at minimising superiority and increasing diversity of species. Within several years, proportions of species in the initial seed mix are no longer reflected in the establishing vegetation. Plant competition is one of the major processes influencing community structure and was, therefore, investigated in this study.

AIMS AND CONTENTS OF THIS THESIS

Competition in arid zones, where productivity is generally low, may result from greater resource limitation (i.e. water and nutrients) compared to more productive zones (Yeaton and Cody 1976, Tilman 1982, Kadmon 1995). Most research on plant competition in arid zones has focussed on natural plant populations (e.g. Anderson 1967, Malik *et al.* 1976) and to my knowledge, there are no publications that focus on the competitive interactions of plants growing on rehabilitated mine sites.

Assessments of vegetation on rehabilitation areas of mine sites in Western Australia have revealed that one or two species may dominate several years after seeding (Brearley and Osborne 1997a, 1997b, Osborne *et al.* 1994, Osborne and Brearley 1997). *Atriplex bunburyana* and *A. codonocarpa,* for example, successfully colonise mine rehabilitation sites and dominate over *Enchylaena tomentosa* and many *Maireana* spp., which exhibit comparatively poor establishment success (Sneesby 1992, Brearley and Osborne 1997a, b). Single species dominance varies from site to site and may be

influenced by the density and composition of the broadcast seed application as well as environmental conditions (e.g. rainfall events). Natural density variations will, however, affect the outcome of competition and community structure in subsequent plant generations (Tilman 1988).

Maireana georgei and *E. tomentosa* were selected as target species and were compared with *A. bunburyana* and *A. codonocarpa* to examine competition effects within post-mining rehabilitation. In contrast to *M. georgei*, *Maireana brevifolia* successfully colonises rehabilitation sites and was studied in order to determine what characteristics make particular species successful competitors. The broad aims of this thesis were to determine whether the target species are experiencing competition. If competition was occurring, a determination of the limiting resources that have an effect on the outcome of competition and the mechanisms employed by dominant plants that give them a competitive advantage was explored.

THESIS FORMAT

Site and species descriptions are presented in Chapter 2. Chapter 3 contains a detailed field study of the establishment and spacing patterns of the species of interest after seeding at different densities on mine waste material. Chapter 4 comprises an analysis of density effects on competition. The effects of moisture availability and salinity on plant establishment are investigated in Chapter 5. The effects of shading on the target species are investigated in Chapter 6. Chapter 7 consists of a study of the effects of allelopathic leaf leachates on seed germination and seedling establishment. Chapter 8 provides a synthesis of all work conducted in this thesis, a series of conclusions and recommendations for future study. Management implications have been included at the conclusion of each chapter.

CHAPTER 2: SITE AND SPECIES DESCRIPTIONS

LOCATION

The field site was set-up on the walls of a decommissioned tailings dump at the Three Mile Hill open-cut gold mine (Herald Operations Pty. Ltd.). This mine site is located 5 km northeast of Coolgardie (30°57'S, 121°10'E), in the Eastern Goldfields region of Western Australia (Fig. 2.1). Coolgardie is located 39 km southwest of the region's mining centre of Kalgoorlie. Soil, used in the nursery trials, was obtained from the Westonia open-pit gold mine site, located on the perimeter of the Goldfields region, 320 km east of Perth, Western Australia.

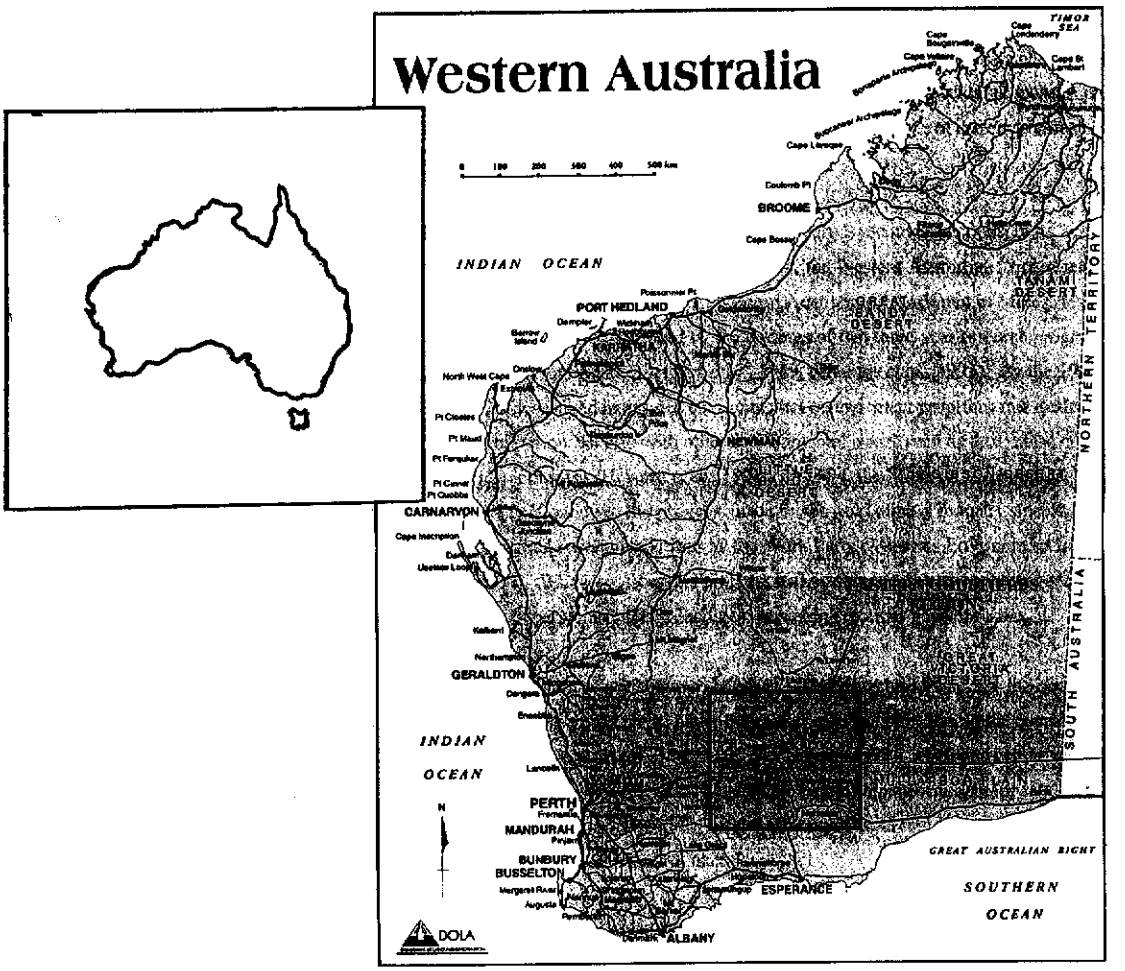


Figure 2.1 The Eastern Goldfields region of Western Australia (from Mitchell and Wilcox 1998).

SOILS

The geology of the region consists of Archaean rocks that range from 2.4 to 3 billion years old. They originally consisted of layers of shale and greywacke with layers of volcanic lava between. Over many millennia these layers have folded and eroded. Metamorphism has altered them to form slate, phyllite, schist, banded ironstone and amphibolites. Granite outcrops of tors and domes have formed in the sedimentary zones and have given rise to extensive sand plains over the western half of the region. Greenstone belts have resulted in igneous zones in the form of high abrupt ridges (Beard 1978).

The soils are usually yellow-brown loams or red-brown sandy loams (characteristic of the sand plains). The yellow-brown sands cover a sandy loam in varying depths and are often underlain by laterite. The red-brown sandy loams become finer in texture to clay with depth (7.5 cm) and overlie decomposed rock at greater depth (90 cm). Lime concretions (kunkar) are sometimes found within such profiles. Where the profile is more calcareous or the surface becomes a fine incoherent white or pink clay, lime concretions may develop into hardpans. Less calcareous soil profiles may have sandier surface horizons (Beard 1978).

CLIMATE

Average annual rainfall of the region is 240 mm but this can vary from 280 mm in the south-west to 230 mm in the north-east of the region (Bureau of Meteorology, Western Australia). Kalgoorlie's climate defines the region as a desert. Coolgardie has an average annual rainfall of 268 mm with a winter maximum consistent with the region being semi-arid with a Mediterranean tendency (Fig. 2.2). Cold fronts from the Southern Ocean produce winter (June - August) rainfall, while summer (December - February) rainfall is associated with sporadic localised thunderstorms. Temperatures range from a minimum of -3 °C in winter to summer maximums of 46 °C. Radiation frosts can occur in the winter months, but are not severe (Beard, 1978).

VEGETATION

Plant communities of the Goldfields region, Western Australia have been classified into formations based on physiognomy and further subdivided into plant communities according to their floristic composition (Table 2.1) (Beard 1978).

PLANT SPECIES DESCRIPTIONS

Chenopodiaceae

Throughout the world, chenopod communities are found in environments containing extreme temperatures. In Eurasia and the Great Basin of North America, for example, the main chenopod areas are subject to severe winter snows and freezing temperatures (Goodall 1975). The Chenopodiaceae cover 5 - 10 % of the arid and semi-arid areas of Australia (Goodall 1975). Countries that occur in similar latitudes to Australia's arid zones, also have chenopod communities that grow under high temperatures and very saline soils.

Chenopods occur within four main land systems in Western Australia according to Oxley (1975). These are:

- Nullarbor Plain (complex mosaic of species),
- the perimeter of the Nullarbor Plain (mixed chenopod community),
- the coastal communities near Canarvon (mostly *Maireana polypterygia*, *M. aphylla*, *Atriplex bunburyana* and *A. vesicaria*) and
- the riverine and drainage systems of the Gascoyne and Murchison catchments (perennial chenopod shrublands).

However, chenopods have also been observed growing in the valley floors of the lower south-west (pers. comm. Barrett-Lennard).

Chenopods vary in the type of mechanisms they employ to withstand drought. The depth of root systems, tolerance of defoliation and the rate of recovery from defoliation differ among species (Sharma 1982, Fowler 1986). *Atriplex* and *Maireana* spp. attain high water use efficiency by having low transpiration rates and the C_4 photosynthesis pathway (Sharma 1982). Chenopods are capable of extracting water from the soil at low soil water

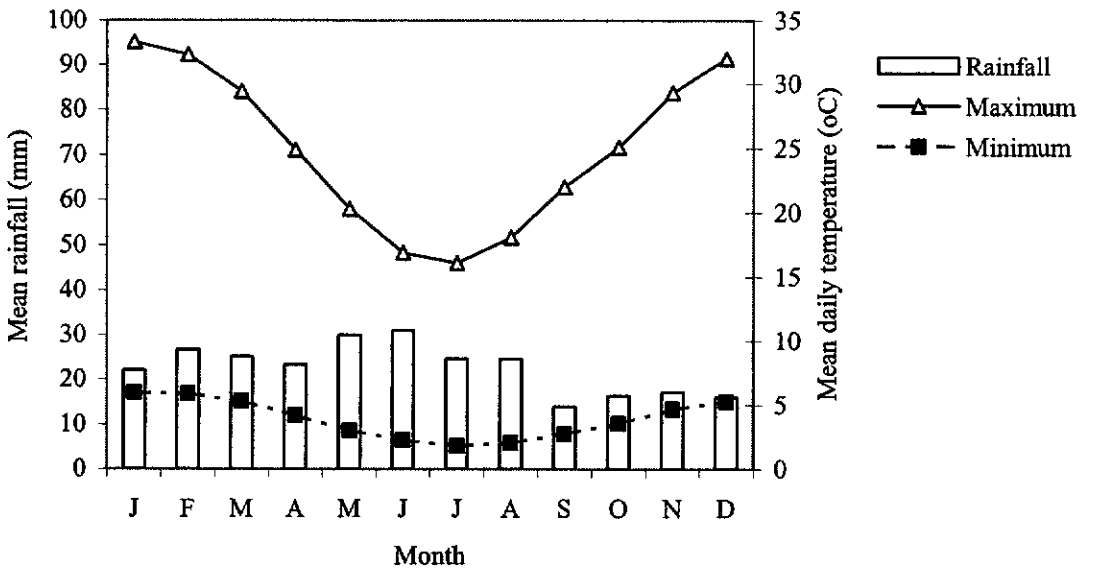


Figure 2.2 Mean monthly rainfall and temperature of Coolgardie, Western Australia (Bureau of Meteorology, Western Australia).

Table 2.1 Plant communities and associations of the Goldfields region (Beard 1978).

Community	Associations
A. Woodland - sclerophyll	12 sp. *Eucalyptus*, 1 sp. *Casuarina*
B. Low Woodland (trees <10 m tall) - mulga	Mulga (*Acacia aneura*) with *Eucalyptus* and *Casuarina* associations
C. Shrubland - thicket (dense 1- or 2- layered shrub communities)	3 different *Acacia-Casuarina* associations
- scrub (open shrub communities)	2 *Acacia* associations
D. Shrub Steppe - mallee and spinifex	1 association
E. Succulent Steppe - unwooded succulent steppe	2 associations
- lightly wooded succulent steppe	3 associations

potentials by accumulating solutes within their leaves, which maintains lower leaf water potentials compared to that in the soil (Sharma 1982).

Australian *Atriplex* spp. have adapted to highly saline conditions by storing salt in salt glands or in vesiculated hairs on the leaves (Carrodus and Specht 1965). Vesicle density is greater in young leaves compared to more mature leaves. One explanation for this is that when the salt content reaches a critical level, cell walls collapse and the resulting salt crust on the leaf surface reflects light (Sharma 1982). Aslam et al. (1986), however argue that the greater density of vesicles on young leaves play an important role in ion regulation during leaf expansion. Once expansion has occurred, salt is stored and the leaves become more succulent. Redirected salt also plays a role in the reproductive biology of *Atriplex* spp. Most *Atriplex* seeds have bracteoles that contain high levels of salt. Germination will generally not occur until significant amounts of salt are leached away (Anderson 1982).

Atriplex bunburyana F.Muell.

Distribution of *A. bunburyana* populations is shown in Figure 2.3. *Atriplex bunburyana*, commonly known as Silver Saltbush, has very similar foliage to *A. stipitata* making it difficult to distinguish between the two species. Both are small erect shrubs with long-pedicellate fruit. More bluish leaves, a slightly different bracteole shape and the presence of antler-like appendages on some specimens distinguish *A. bunburyana* from *A. stipitata* (Parr-Smith and Calder 1975, Parr-Smith 1982). Silver Saltbush grows to 1 m in height, has slender, often straight and spinose branches and is dioecious (Fig. 2.4A). The leaves are elliptic to broadly elliptic, entire, with a thin, bluish scaly covering. Male flowers grow in small disjunct glomerules forming slender panicles. Female flowers grow in disjunct clusters arranged in slender panicles (Mitchell and Wilcox 1998). The root system consists primarily of a taproot and several fine lateral roots within the top 15 cm of the soil (Short 1998) (Fig. 2.4B).

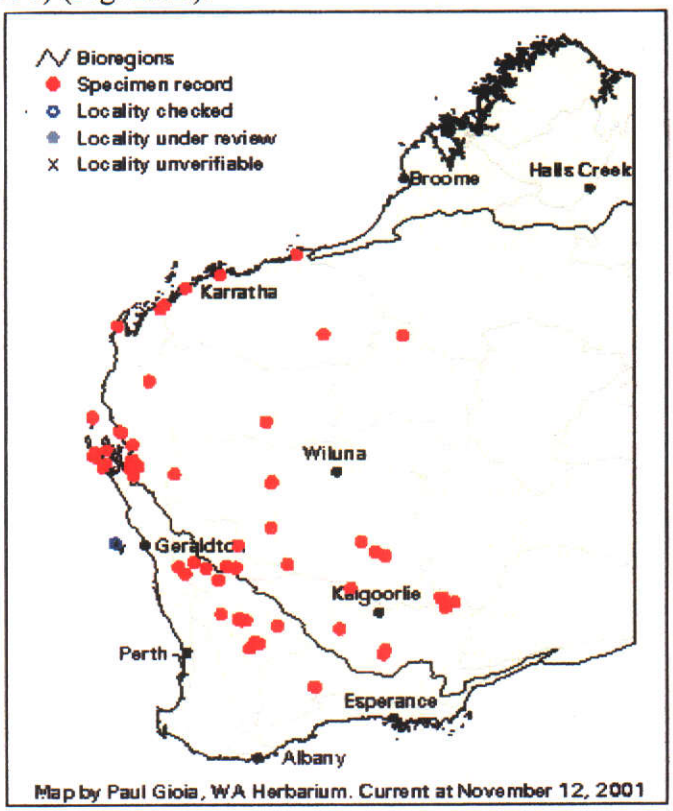


Figure 2.3 Distribution of *A. bunburyana* populations in Western Australia (reproduced with permission from the authors of Florabase).

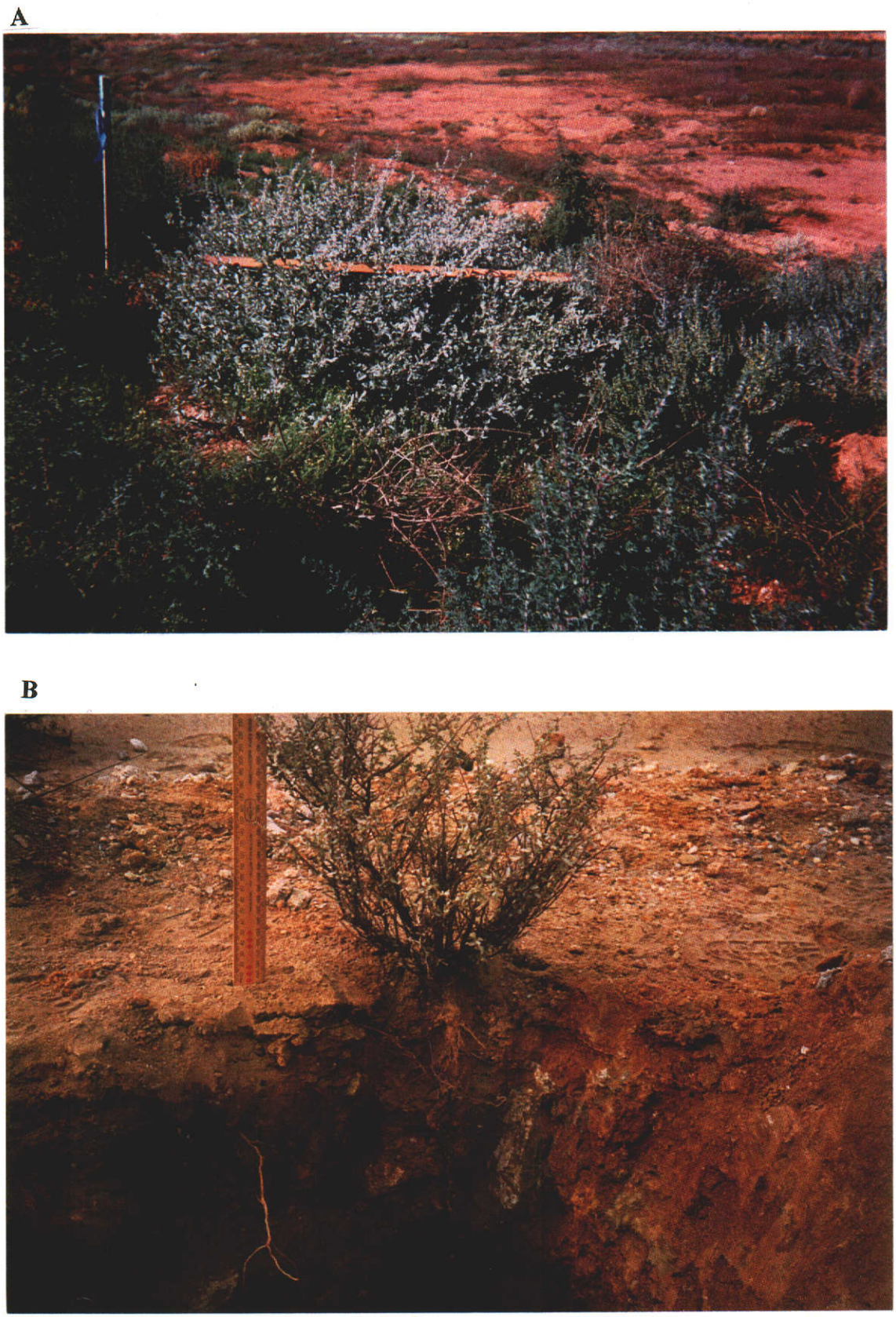


Figure 2.4 The above-ground (A) and below-ground (B) form of *A. bunburyana.*

Atriplex codonocarpa Paul G. Wilson

Distribution of *Atriplex codonocarpa* populations is shown in Figure 2.5. Flat-topped saltbush, or *A. codonocarpa*, is a monoecious, short-lived perennial, or rounded annual, that grows to 30 cm in height (Fig. 2.6). The leaves are rhomboid-orbicular, thin, with sinuate-dentate margins and a scaly sheen. Male and female flowers are mixed in small sub-terminal clusters. Female flowers also occur in scattered axillary clusters. The fruiting bracteoles are sessile, soft and spongy, completely united, turbinate to cup-shaped with a flat top. Seed have a horizontal, basal radicle (Mitchell and Wilcox 1998).

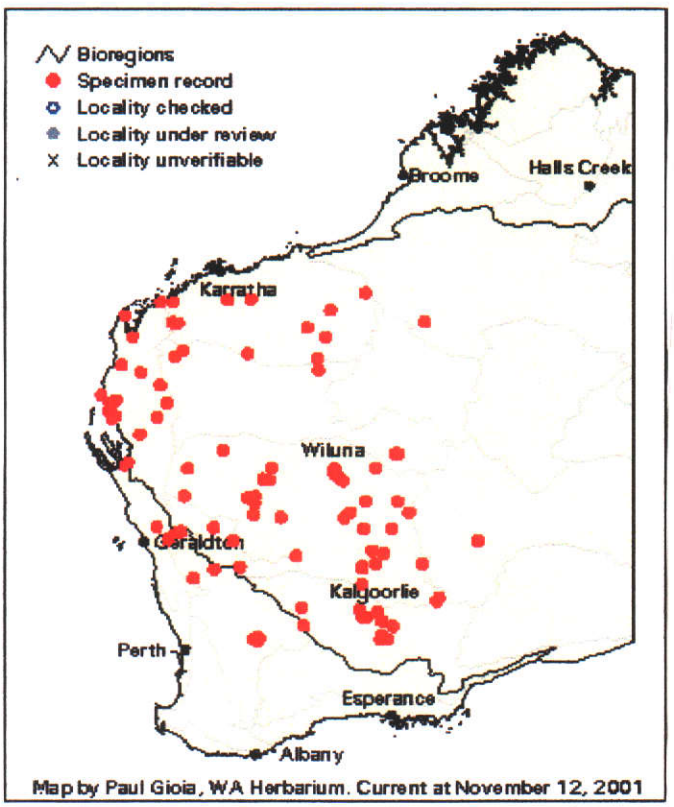


Figure 2.5 Distribution of *A. codonocarpa* populations in Western Australia (reproduced with permission from the authors of Florabase).

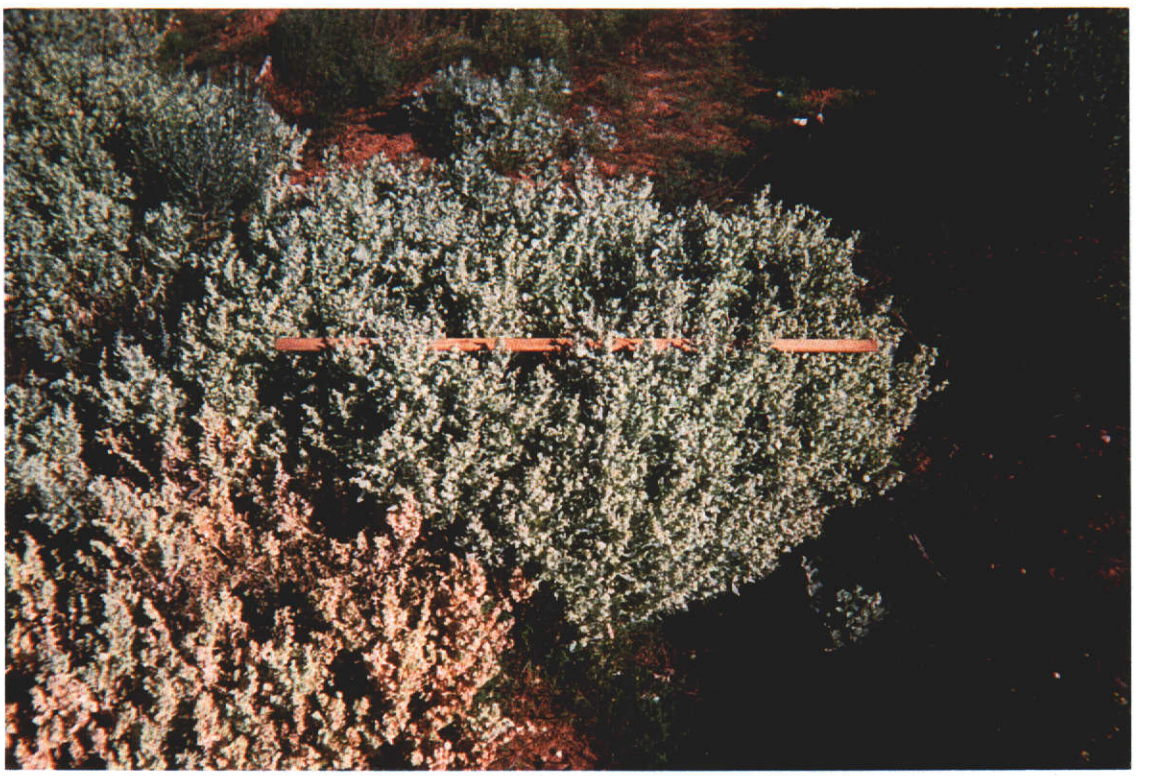


Figure 2.6 *Atriplex codonocarpa* plant growth form.

Maireana georgei (Diels) Paul G. Wilson

Distribution of *M. georgei* populations is shown in Figure 2.7. *Maireana georgei*, commonly known as Golden Bluebush, grows to a height of approximately 50 cm (Fig. 2.8). Branches of *M. georgei* are covered in woolly hair. Leaves are alternate, succulent, and 1 - 1.5 cm long and may be covered by sparse or dense woolly hair. Flowers are small, bisexual and located in the axils of stems and leaves. The seed case is a woody structure, 4 mm in diameter with a surrounding papery golden wing up to 2 cm in diameter (Mitchell and Wilcox 1998).

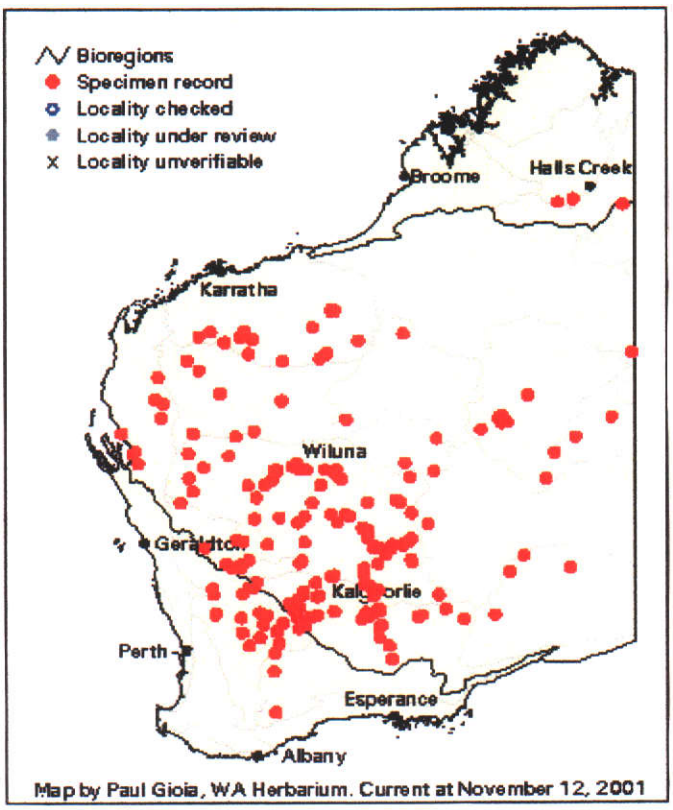


Figure 2.7 Distribution of *M. georgei* populations in Western Australia (reproduced with permission from the authors of Florabase).

Figure 2.8 The above-ground (A) and below-ground (B) form of *M. georgei*.

Maireana brevifolia (R.Br.) Paul G. Wilson

The distribution of *M. brevifolia* populations are shown in Figure 2.9. *Maireana brevifolia*, commonly known as Small Leaf Bluebush or Eastern Cotton Bush, grows to a height of approximately 1 m (Fig. 2.10A). The branches are slender, striate and sparsely woolly. Leaves are fleshy, alternate and obovoid to narrowly fusiform shape. Flowers are bisexual, solitary and glabrous. Fruiting perianths are glabrous with five fan-shaped wings, displaying delicate brown venation when dry. The perianth lobes are thick, fleshy and sharply demarcated from the wings (Mitchell and Wilcox 1998). The root system is tuberous and consists of several laterals along the length of a taproot (Short 1998) (Fig 2.10B).

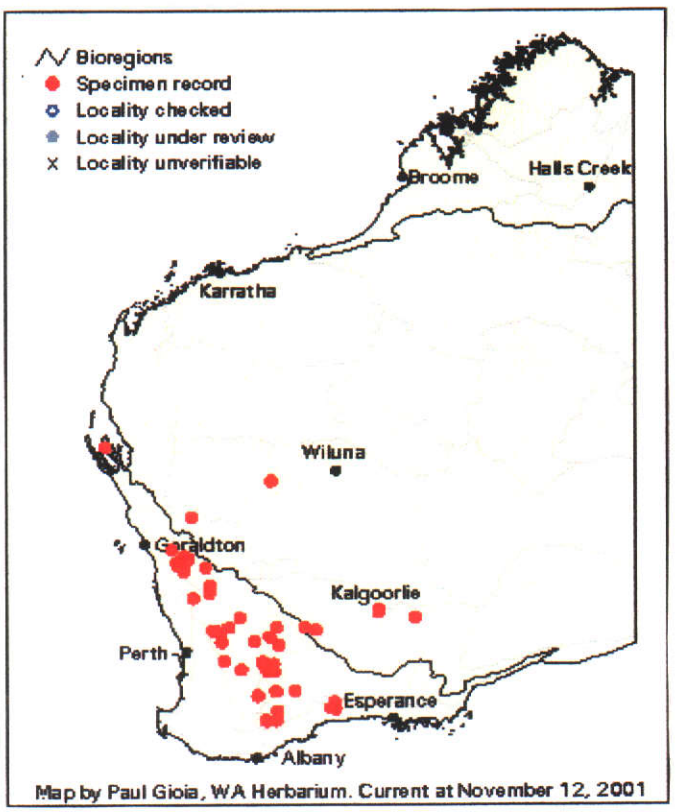


Figure 2.9 Distribution of *M. brevifolia* populations in Western Australia (reproduced with permission from the authors of Florabase).

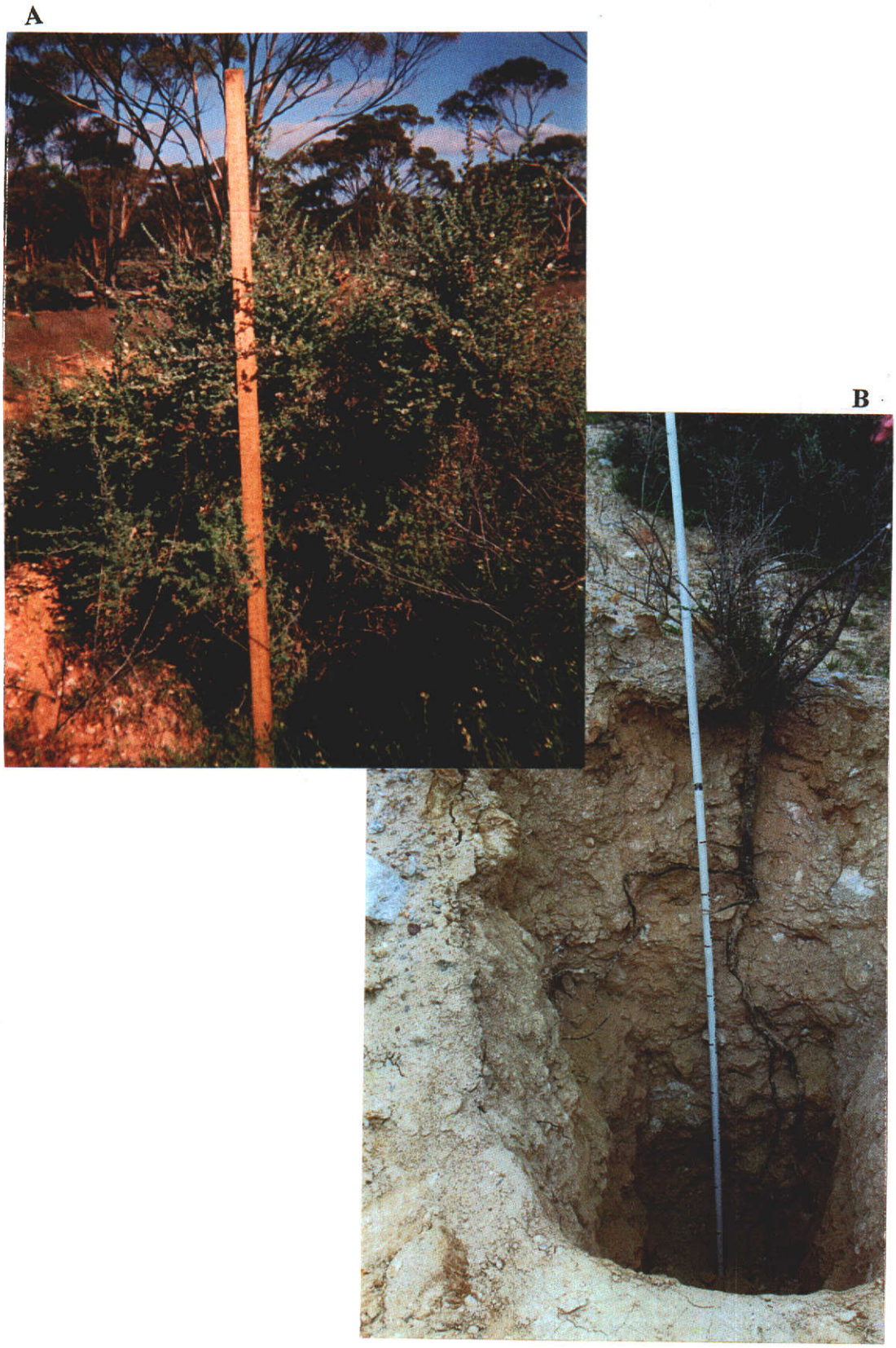


Figure 2.10 The above-ground (A) and below-ground (B) form of *M. brevifolia*.

Enchylaena tomentosa (R. Br)

Distribution of *E. tomentosa* populations is shown in Figure 2.11. *Enchylaena tomentosa*, or Ruby Saltbush, grows to a height of approximately 1 m (Fig. 2.12). The stems are soft, brittle and typically covered by dense woolly hair. Leaves are succulent, usually densely woolly, cylindrical, 1-2 cm long, pointed at the tips, greyish-green and alternate. Flowers are small, solitary and located in the leaf axils. The fruit are succulent, orange-red berries, which turn black when dry (Mitchell and Wilcox 1998).

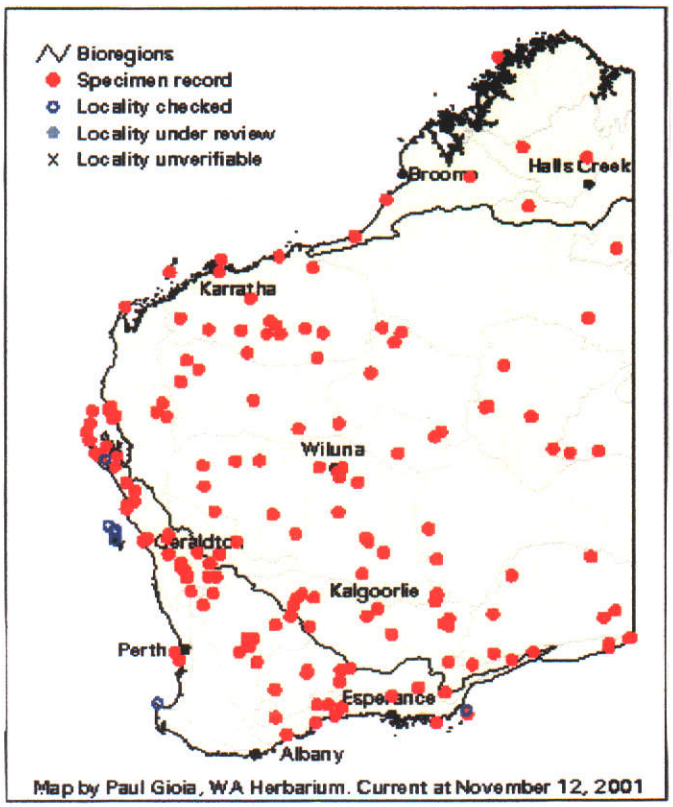


Figure 2.11 Distribution of *E. tomentosa* populations in Western Australia (reproduced with permission from the authors of Florabase).

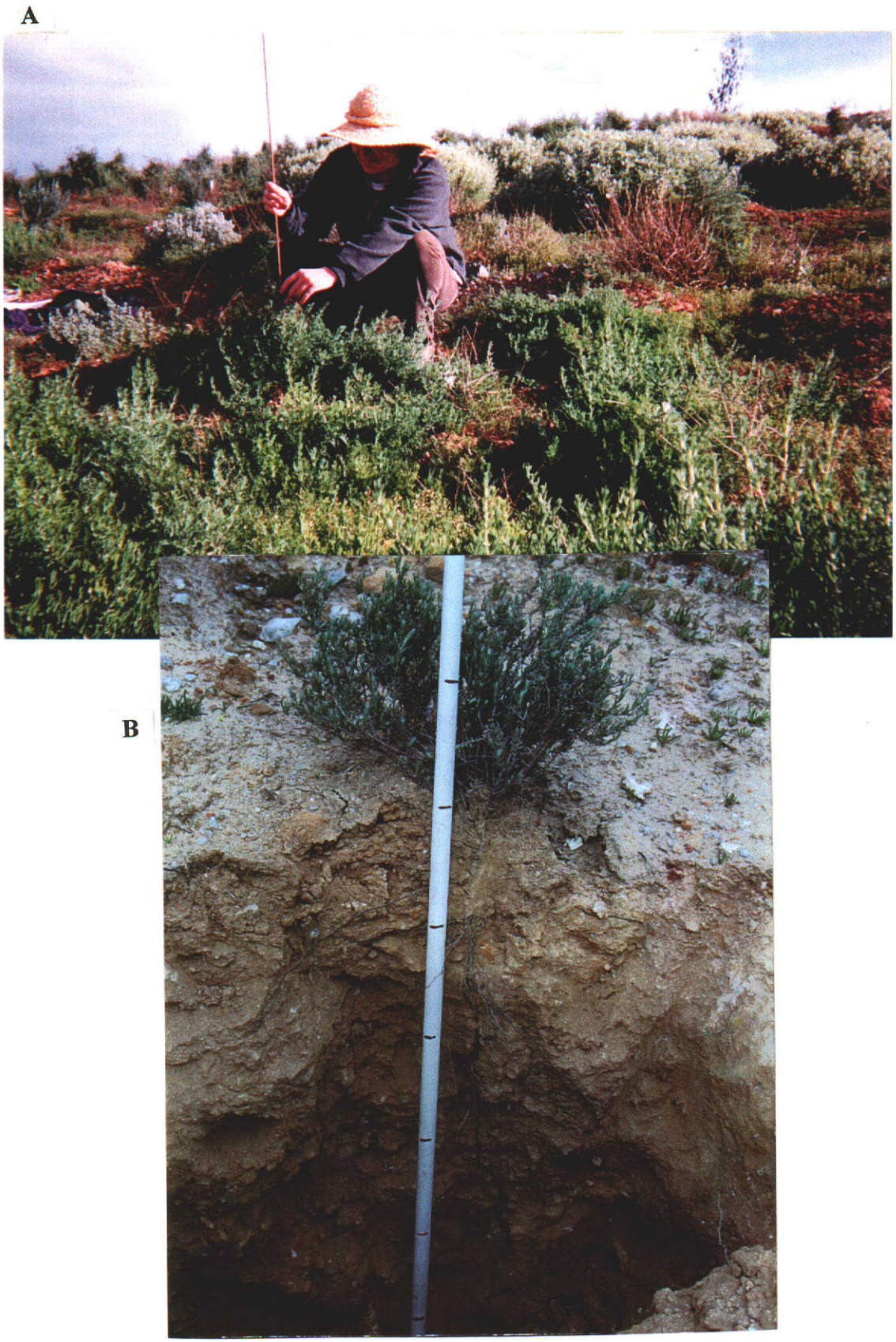


Figure 2.12 The plant growth form of *E. tomentosa.*

These species are preferred for initial revegetation of mine waste and tailings dumps, due to their presence in the local vegetation, their high tolerance of salinity and ability to grow well in harsh arid environments.

MINING PROCEDURES AND REHABILITATION PRACTICES

Gold and nickel mining is currently a major industry in the Goldfields region of Western Australia, which covers an area from 30° to 31° south latitude and 120° to 121° east longitude. Mining for gold and nickel involves removing rock lying above the mineral deposits (overburden) and then processing the rock containing the desired mineral. Processing involves crushing of the mineral-rich rock and treatment with chemicals to extract the gold or nickel. The resulting tailings material is highly saline and consists of very fine soil particles. Tailings are pumped as slurry into a dam. Unprocessed overburden is used to create the walls of the tailings dam.

Rehabilitation of mining disturbances is an essential component of mining operations. Under the Mining Act 1978, it is stated:

> " No developmental or productive mining or construction activity [will be] commenced until the tenement holder has submitted a plan of the proposed operations and measures to safeguard the environment to the State Mining Engineer (SME) for assessment and until his written approval has been obtained" (Department of Minerals and Energy 1998).

The Western Australian Department of Minerals and Energy (DME) (1998) acts on behalf of the Minister for Mines as a regulator of environmental protection and rehabilitation. A notice of intent (NOI) will initially outline the environmental impacts that may arise from mining and how the company will manage these impacts. When the disturbance of land from mining requires rehabilitation, the mining company must submit a bond in the form of a bank guarantee to the DME. The bond is returned to the mining company following mining and rehabilitation is complete to the satisfaction of the DME.

Extensive rehabilitation programmes are expected to be developed during the operational phases of mining (Department of Minerals and Energy 1996). Rehabilitation monitoring schemes and completion criteria should also be developed by the mining company. Completion criteria should be based on the knowledge of the local environment, the constraints of the mining operation and post mining land use objectives.

The rehabilitation of waste rock and tailings material is essential to prevent erosion, to stabilise the soil and to return the environment back to its natural state. The following basic objectives have been provided as guidelines for waste dump design by the Western Australian Department of Minerals and Energy (DME) (1996):

- "Where possible, waste rock should be returned to previously excavated areas,
- The height, area and shape of the waste rock dump should be designed with regard to the area of land available, the general topography of the area and the vegetation in the area,
- Waste materials should be handled only once,
- All completed surfaces of the waste dump should be stable and able to resist long term erosion,
- Topsoil salvaged from the advancing waste dump should be immediately spread on prepared waste dump surfaces,
- Previously stockpiled subsoil and topsoil should be spread on all completed surfaces where practicable and re-vegetated with suitable vegetation,
- Design and construction of the waste dumps should be such that the completed out slopes do not exceed 20^{o} from the horizontal,
- Surface drainage should be constructed to control (and infiltrate) heavy rainfall events. (Provided infiltration will not lead to Acid Rock Drainage or other adverse leachate (saline) in the future)."

Following these procedures, the area is sown with a diverse broadcast seed mix immediately prior to winter rainfall. The seed mix should be representative of the surrounding natural vegetation and tolerant of the low nutrient and often saline conditions

of the waste materials. Monitoring of rehabilitated sites is conducted annually to assess revegetation establishment and development.

EXPERIMENTAL OUTLINE

The following chapter is a field study and was situated on the walls of the decommissioned tailings dam at the Three Mile Hill mine site. The study area was divided into two areas: site A and site B. Chapters 4 - 6 involved the use of pot trials at Curtin University of Technology, Perth. The final chapter was conducted in the laboratory at Curtin University of Technology, Perth.

CHAPTER 3: EFFECTS OF PLANT DENSITY ON INTRA- AND INTER-SPECIFIC COMPETITION: A FIELD TRIAL

INTRODUCTION

Mine rehabilitation sites in the Goldfields region of Western Australia are often seeded with a broadcast mixture containing *Enchylaena tomentosa*, *Atriplex* and *Maireana* species. Successful mine site rehabilitation in the Goldfields region of Western Australia requires the establishment of a diverse range of species that are tolerant of high salinity, provide soil protection, minimise erosion, are adapted to semi-arid conditions and provide a mixture of relatively rapid and slow growing species. Rehabilitated sites are seeded with a variety of species at densities that aim to maximise overall plant diversity and minimise dominance. Broadcast densities of individual species in the seed mixture are selected to reflect the population composition of mature, plant communities (Brearley and Whitten 1996).

The ability of particular species to dominate the composition of vegetation communities reflect differential competition for limited resources. Species better adapted to harsh, arid environments and the soil characteristics of mine waste should have a competitive advantage. Species dominance can vary from site to site with rainfall events and resource limitations (i.e. nutrients and light) likely to account for this variation (Yeaton and Cody 1976, Tilman 1982, Kadmon 1995). Thus, environmental conditions will play an important role in determining plant community structure and the outcome of competitive interactions.

Competition in field studies is typically determined by measuring the spacing patterns of plant species. The distance between individuals, in conjunction with population density, provide variables for measuring spacing distances and patterns (Clark and Evans 1954). Positive regression of distances between neighbouring plants and the sum of their aboveground sizes (e.g. volume, cover, biomass, height) quantify plant competition (Fowler 1986). The angle of the regression slope indicates the intensity of competition,

whereas its coefficient of determination (R^2) measures the importance of competition (Welden *et al.* 1988).

Plant age often affects the outcome of the competition analyses. When neighbouring individuals are young (small) and establishing roots in the same subsurface soil layers, the distance between a plant and its nearest-neighbour may not be significant (Yeaton and Cody 1976). Competition, however, plays an increasingly important role as plants grow (Phillips and MacMahon 1981). Large plants, therefore, tend to be more widely spaced than smaller plants (Yeaton and Cody 1976). Studies of *Atriplex* spp. shrub-steppe communities have shown phase-dependent patterns also to be age-dependent (Malik *et al.* 1976).

In natural environments, however, established plant communities are likely to have a range of plant ages, making the analysis of spacing patterns more complex. Competition may also induce aggregated spatial distributions (Pielou 1960) with many young, small plants growing in vacant gaps amongst large, mature plants. Mining rehabilitation is likely to show age-dependent spatial distribution patterns within the first plant generation that develops after seeding. Natural variation in plant density (due to variable seed production, germination and predation) will be reflected in the spatial distribution and community structure of subsequent plant generations (Pantastico-Caldas and Venable 1993). Natural limiting factors that affect population density, however, will be species specific.

An understanding of the processes of competition will enable land managers to determine whether *Maireana* spp. and *Enchylaena tomentosa* can persist in both intra- and inter-specific competitive environments and contribute to overall community diversity. Such knowledge will allow broadcast seed densities to be adjusted so that plant composition and diversity in rehabilitated areas is comparable to surrounding undisturbed vegetation. The objective of this chapter was to examine the effect of broadcast seed density on plant distribution and community structure on post-mining rehabilitation.

Specifically, the aim of field trials conducted in this study was to determine:

1) Whether competition was dependent on the density and composition of broadcast seed.

2) The extent of competition between plants grown in monoculture and/or 2-species mixtures.

3) Whether competition was species dependent.

MATERIALS AND METHODS

Pre-experimental set-up

Site Preparation

Study sites were located at the Three Mile Hill mine site (Herald Operations Pty. Ltd.), located 2 km north east of Coolgardie, Western Australia (Fig. 3.1). An area of approximately four hectares was selected on the walls of the Greenfields decommissioned tailings dam, which is composed of waste rock. The slope of the wall was no greater than 20°. The waste material was covered with topsoil and deep-ripped across the slope to a depth of 1 m, using a D9 grader. Plots, 10 m x 10 m (100 m^2), were established.

Seed Testing

Seeds of *A. bunburyana*, *A. codonocarpa*, *E. tomentosa*, *M. brevifolia*, and *M. georgei*, supplied by contractors (Nindethana Seed Suppliers), were tested for quality, viability and final germination percentage. Quality testing involved the observation and a count of the number of seeds that were immature (based on size and colour of the seed), insect damaged (holes in the seed) or had a dry and shrivelled appearance. Viability testing involved cutting the seed in half and observing the seed contents (endosperm colour and moisture content). The quality and viability testing each involved three replicates of 50 seeds. Final germination percentage was determined by placing seeds on moist filter paper, in petri dishes at 20 °C and counting the number of germinants after 21 days. There were four replicates of 25 seeds. Dormancy testing involved a comparison of the final

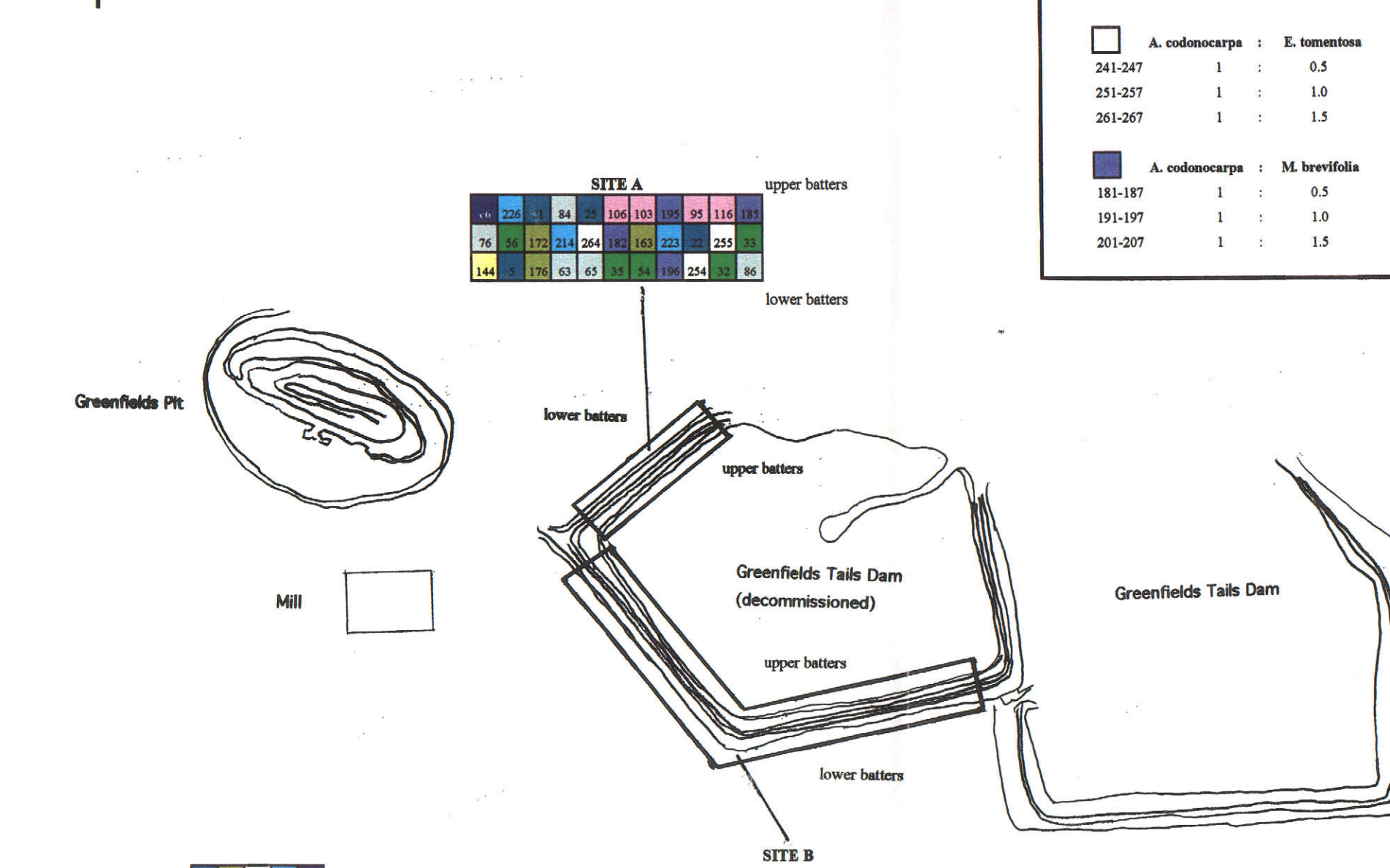


Figure 3.1 The layout of Site A and B showing the contour of the Greenfields dam and plot locations.

Data Collection

Recruit Assessment

Seedlings were assessed in October (spring) 1998, five to six months after seeding. Five quadrats (1 m x 1 m) were randomly placed within each plot, and the number of seedlings of each species recorded. Plots containing the annual, *A. codonocarpa,* were reassessed in January (summer) 1999, nine months after seeding. All other plots were reassessed in June (winter) 1999, 14 months after seeding. Homogeneity of variance was determined using Levenes test. The data were $\log_{10}$ transformed if they were not normally distributed. One-way analysis of variance (ANOVA) was conducted to assess differences between the number of germinants produced by different seed densities. The Kruskal-Wallis non-parametric test was used when normality could not be achieved by $\log_{10}$ transformation of data. Tukey's Compromise (post-hoc test) was employed to determine differences between means (Ott, 1988). Analyses were conducted on both 1998 and 1999 data.

Plant size and spatial distribution measurements were recorded during the second seedling assessment. The total number of plants within each plot was determined. Measurements were recorded for a maximum of 30 pairs of nearest neighbours, chosen at random, per plot. The distance to the nearest intra- or inter-specific neighbour was measured. No plant was used in more than one pairing. Pairs of plants, in which another plant (of any species) grew closer to one of the plants or between the pair of plants, were not sampled. Size measurements, of both plants, included height (cm, H), maximum width (cm, W1) and width 90° to the maximum width (cm, W2). Plant cover and volume estimates were calculated using the following equations:

$$\text{Cover } (cm^2) = W1 \times W2$$

$$\text{Volume } (cm^3) = H \times W1 \times W2$$

A composite soil sample (approx. 100g), representative of three random samples within each plot, was collected. Samples were dried at 40°C for 24 hr, passed through a 2 mm

sieve and diluted to a 1:5 soil to deionised water solution. The slurry was agitated for 1 hour and then left to stand for 24 hours. Samples were then analysed for electrical conductivity ($EC_{1:5}$, Activon Model 301) and pH (Beckman H5) according to Rayment and Higginson (1992).

Those seedlings that did not establish were not replaced. The intended density of the plots was not the same as the existing density. The seven plots also differed from each other within each density regime. The plots for each density regime were, therefore, combined. A simple non-hierarchical cluster analysis (2001, SPSS Inc.) was used to order plots into four groups based on the number of plants per species per plot, salinity and pH.

Where cluster analyses were performed, homogeneity of variance was determined using Levenes test (Ott 1988). The data was $\log_{10}$ transformed if they were not normally distributed. One-way analysis of variance (ANOVA), using species plant density, salinity and pH as covariates, was performed on the plant growth parameters (i.e. height, cover, volume and mean distance between nearest neighbours) to determine differences between the four clusters. The Kruskal-Wallis non-parametric test was used when normality could not be achieved by $\log_{10}$ transformation of data. This test approximates the parametric ANOVA procedure. The nearest-neighbour distances and the sizes of nearest neighbours of each of the four clusters were then analysed using linear regression. The sum of either height, cover or volume of neighbouring plants ($\log_{10}$) was regressed against the nearest-neighbour distances ($\log_{10}$).

RESULTS

Recruit Assessment (1998)

Enchylaena tomentosa

The number of *E. tomentosa* ($F_{2, 87} = 2.54$, $P = 0.085$) and *A. bunburyana* ($F_{2, 87} = 1.50$, $P = 0.232$) recruits did not differ between density treatments when sown together (Fig. 3.3A). There was, however, a significant increase in the number of *E. tomentosa* recruits when sown at higher densities with *A. codonocarpa* ($F_{2, 87} = 3.88$, $P = 0.027$, Fig. 3.3B). In monoculture greater seeding densities also produced greater numbers of recruits ($F_{2, 87} = 6.83$, $P = 0.002$, Fig. 3.3C). The number of *A. codonocarpa* recruits showed no significant difference between treatments ($F_{2, 87} = 1.43$, $P = 0.245$). The number of recruits was low relative to the number of seed applied (12 - 36 m^{-2}).

Maireana brevifolia

The density of *M. brevifolia* across all species and density combinations was also low relative to the density of seed sown (Fig. 3.4). The number of *M. brevifolia* recruits did not differ between the density treatments when sown with either *A. bunburyana* ($F_{2, 87} = 3.05$, $P = 0.054$, Fig 3.4A) or *A. codonocarpa* seeds ($F_{2, 87} = 1.76$, $P = 0.180$, Fig 3.4B). The number of *A. bunburyana* ($F_{2, 87} = 0.41$, $P = 0.665$) and *A. codonocarpa* ($F_{2, 87} = 1.42$, $P = 0.248$) recruits remained constant regardless of the sown density of *M. brevifolia*. There was, however, a significantly greater number of recruits when *M. brevifolia* monocultures were sown at a density of 36 plants per m^2 ($F_{2, 87} = 5.48$, $P = 0.006$, Fig. 3.4C).

Maireana georgei

The number of *M. georgei* recruits was greatest when seeds were sown at a density 1.5 times that of *A. bunburyana* seeds ($F_{2, 87} = 8.79$, $P < 0.001$, Fig 3.5A). There was, however, no significant difference between treatments when *M. georgei* was sown with *A. codonocarpa* plants ($F_{2, 87} = 2.54$, $P = 0.365$, Fig 3.5B) or in monoculture ($\chi^2_2 = 2.57$, $P = 0.277$, Fig 3.5C). The number of *A. bunburyana* ($F_{2,87} = 0.54$, $P = 0.584$) and *A. codonocarpa* ($F_{2, 87} = 0.18$, $P = 0.835$) recruits did not differ when sown with

increasing densities of *M. georgei* seeds. Density of recruits was low relative to the number of seed sown.

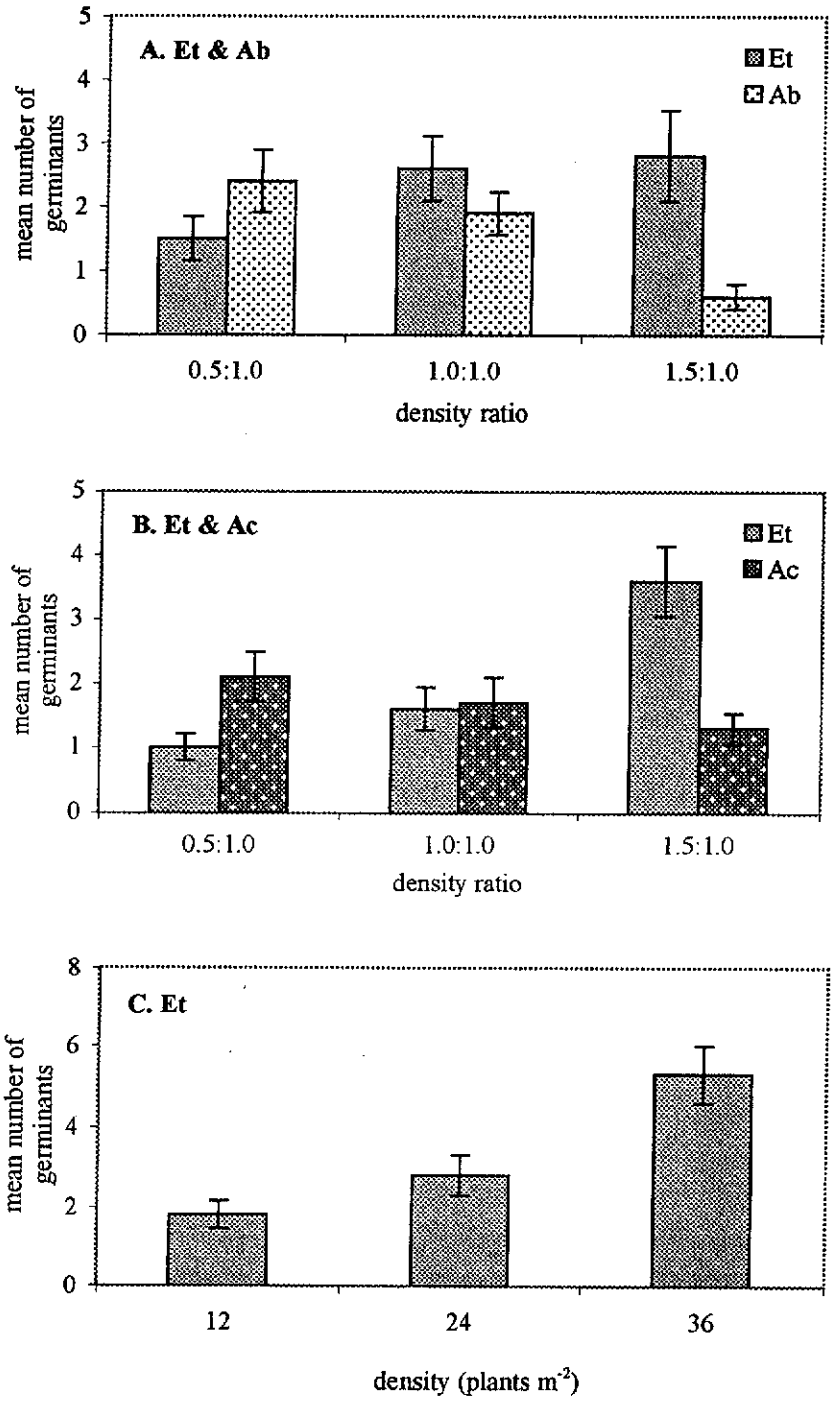


Figure 3.3 The mean number of *E. tomentosa* seedlings when sown with *A. bunburyana* (A), *A. codonocarpa* (B) or in monoculture (C) at three seed density ratios. Bars represent standard error.

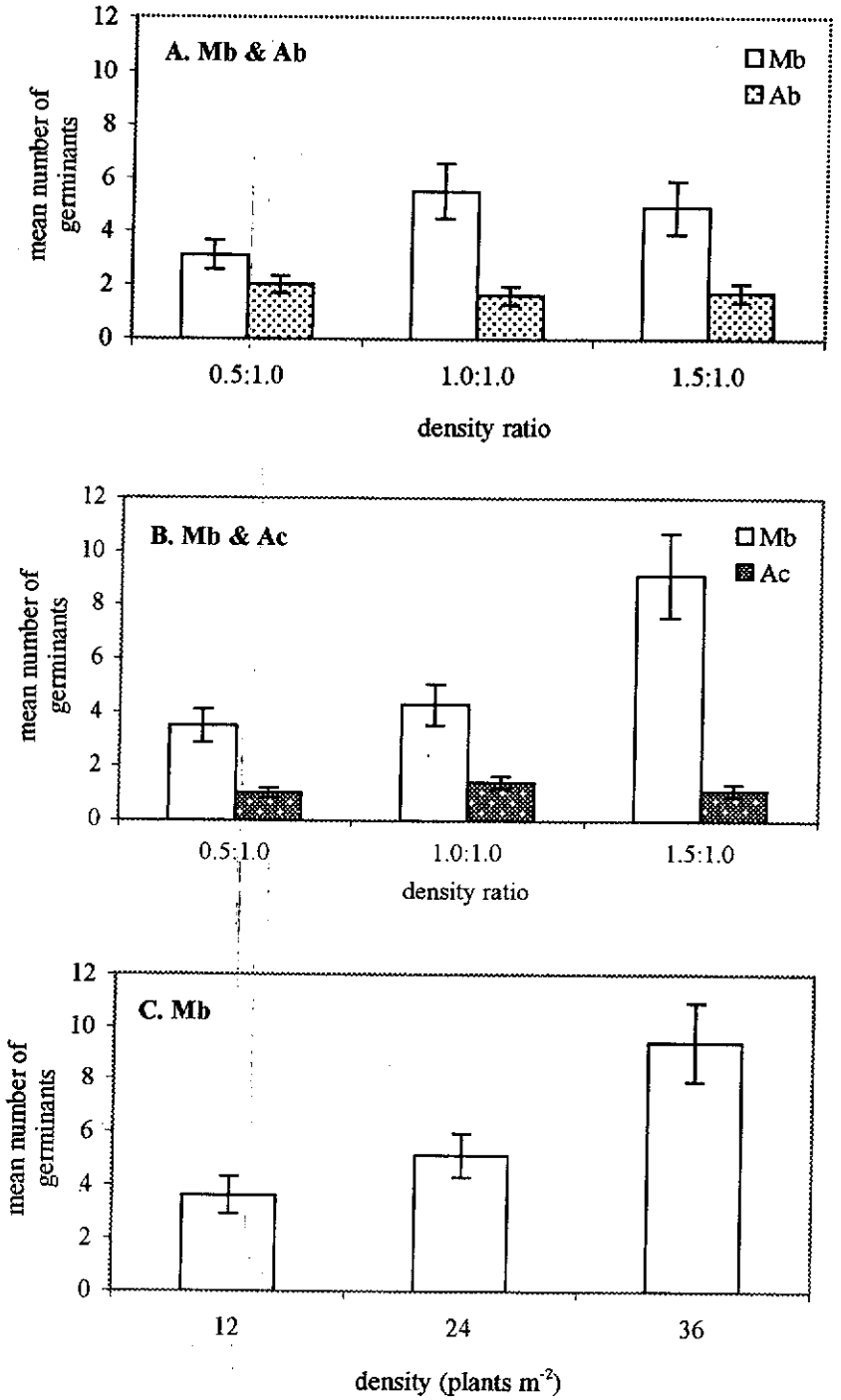


Figure 3.4 The mean number of seedlings of *M. brevifolia* and *A. bunburyana* (A), *A. codonocarpa* (B) when grown together or in monoculture (C) at three sown density ratios. Bars represent standard error.

Observations

Five to six months following seeding there was a dense cover of the annual herb, *Carrichtera annua* (commonly known as wards weed) in rehabilitated areas (Fig. 3.6). At site A, the weed was brown and desiccated, compared to Site B where it was still actively growing. *Maireana brevifolia* was the only chenopod species to have grown taller than the wards weed. *Atriplex codonocarpa* plants grew in dense stands at the western end of site A and the number of wards weeds were also lower in this area. Two forms of *A. codonocarpa,* having different types of leaves were growing in plots that were not sown with *A. codonocarpa* seeds. Grasses and weedy and native annuals were not as prominent on upper wall slopes compared to lower slopes. Better establishment of the seeded species occurred on the upper areas of the slope and at the lowest point of the contours. *Maireana brevifolia* and *A. codonocarpa* were often found growing outside the plots into which their seeds have been broadcast. One possibility, is that strong winds may have been a vector for the movement of these seeds from the plots into which they were broadcast.

Figure 3.6 Site A of the trial area showing wards weed to be prominent vegetation. *Maireana brevifolia* is also shown growing out of the canopy of the Wards weed.

Establishment Assessment (1999)

Enchylaena tomentosa

There were no significant differences in the number of *E. tomentosa* ($F_{2,\ 15}$ = 2.42, P = 0.123) and *A. bunburyana* ($F_{2,\ 15}$ = 0.02, P = 0.980) seedlings in response to broadcast seeding density treatments (Fig 3.7A). There were, however, significant increases in the number of *E. tomentosa* seedlings, which survived when sown at increasing densities with *A. codonocarpa* ($F_{2,\ 18}$ = 18.84, P < 0.001, Fig 3.7B) and in monoculture ($F_{2,\ 13}$ = 12.11, P = 0.001, Fig 3.7C). The number of *A. codonocarpa* ($F_{2,18}$ = 0.20, P = 0.824) seedlings did not differ between treatments.

Maireana brevifolia

Assessment of seedling survival showed there to be no significant difference in the number of *M. brevifolia* seedlings when sown with varying ratios of *A. bunburyana* ($F_{2,\ 16}$ = 0.22, P = 0.808, Fig 3.8A), or when sown at a range of densities in monoculture ($F_{2,\ 15}$ = 2.72, P = 0.098, Fig 3.8C). The number of surviving *M. brevifolia* seedlings increased when sown at increasing seed densities with *A. codonocarpa* ($F_{2,\ 18}$ = 5.39, P = 0.015, Fig 3.8B). The number of surviving seedlings of *A. bunburyana* ($F_{2,\ 16}$ = 2.51, P = 0.113) and *A. codonocarpa* ($F_{2,\ 18}$ = 1.83, P = 0.188) were not affected by the sown density of *M. brevifolia* seeds.

Maireana georgei

The number of surviving *M. georgei* seedlings did not significantly differ when sown at varying densities with either *A. bunburyana* ($F_{2,\ 18}$ = 3.34, P = 0.059, Fig. 3.9A) or *A. codonocarpa* ($F_{2,\ 13}$ = 1.43, P = 0.275, Fig. 3.9B). Even when grown in monoculture, increasing the broadcast seed density did not result in increased numbers of surviving seedlings of *M. georgei* ($F_{2,\ 12}$ = 3.19, P = 0.077, Fig 3.9C). Survival of *A. bunburyana* ($F_{2,\ 18}$ = 1.18, P = 0.329) and *A. codonocarpa* ($F_{2,\ 13}$ = 1.05, P = 0.379) seedlings was unaffected by the density at which *M. georgei* was sown.

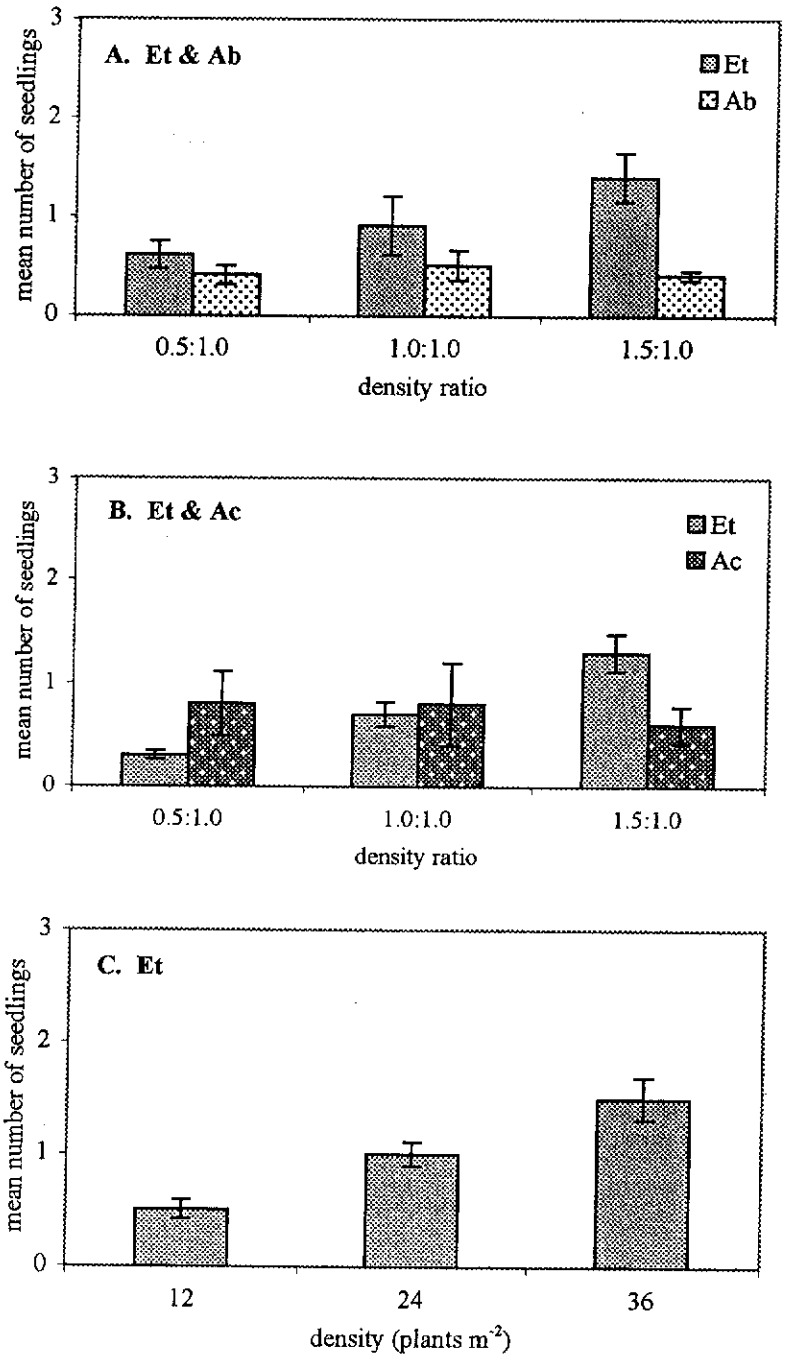


Figure 3.7 The number of seedlings of *E. tomentosa* and *A. bunburyana* (A), *A. codonocarpa* (B) or in monoculture (C) to survive the summer season when sown at three different density ratios. Bars represent standard error.

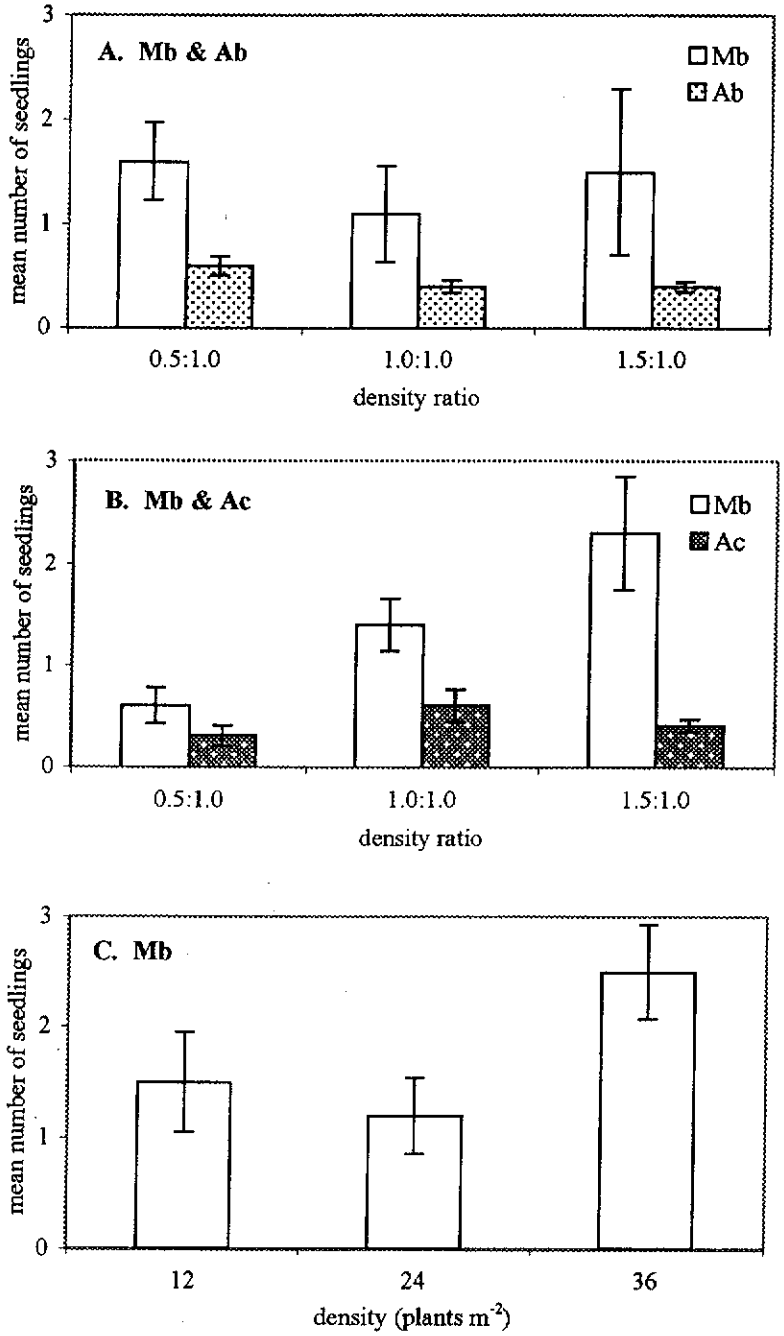


Figure 3.8 The number *M. brevifolia* seedlings when grown with *A. bunburyana* (A), *A. codonocarpa* (B) or in monoculture (C) to survive the summer season. Bars represent standard error.

Observations

Emu footprints and scats were observed on the rehabilitation area (Fig. 3.10A). The observation of *E. tomentosa* seedlings growing out of the scats indicates that emus had eaten the fruits. Seedlings of *E. tomentosa* were found growing under mature plants (Fig. 3.10B). By 14 months adult plants of both *E. tomentosa* and *M. brevifolia* were in the latter stages of fruiting (most fruit dispersed). At the same time, *M. georgei* plants were in the early stages of fruiting (most fruit immature). Those growing under the canopy of *A. bunburyana*, however, were tall, spindly and not fruiting. Individuals of both *A. bunburyana* and *A. codonocarpa* were not fruiting at this second assessment (14 months), however, there were many young seedlings of *A. codonocarpa* germinating. Dense patches of *M. brevifolia* and *E. tomentosa* plants had fallen over since the first assessment. Individual *M. brevifolia* and *E. tomentosa* plants had 'fallen away from the patch centre' and produced lateral branches, which then grew upwards. The wards weeds that were present throughout the rehabilitation area at the first assessment were dead.

Figure 3.10 Emu footprints (A) observed on the field site and *E. tomentosa* seedlings germinating under the foliage of an adult plant (B).

Cluster Analysis

Enchylaena tomentosa

Four clusters resulted from the cluster analysis and were characterised by the density of plant species, soil pH and salinity. This was performed when *E. tomentosa* was grown with either *A. bunburyana* or *A. codonocarpa* or in monoculture. All clusters were significantly different in plant density, soil pH and salinity when grown with each of the *Atriplex* species and in monoculture ($P < 0.001$) (Table 3.1).

Clusters 1 and 2 had the greatest euclidian distance of 1354 separating them, when *E. tomentosa* plants were grown with *A. bunburyana* (Table 3.1A). Cluster 3 was closer to cluster 1 whereas cluster 4 was closer to cluster 2. Cluster 1 had the highest mean soil salinity and mean *E. tomentosa* plant density, in comparison to cluster 2, which had a low mean soil salinity and half the mean density of *E. tomentosa* plants. The lowest mean *E. tomentosa* plant density and soil pH and the highest mean *A. bunburyana* plant density were characteristic of cluster 4.

When *E. tomentosa* was grown in association with *A. codonocarpa* plants, clusters 1 to 4 remained in that order according to the euclidian distance separating each from the other (Table 3.1B). The mean soil salinity and mean plant densities of *E. tomentosa* and *A. codonocarpa* were lowest in cluster 1. Cluster 4 was characterised by the highest mean soil salinity, pH and *E. tomentosa* plant density, whereas cluster 2 had the greatest mean *A. codonocarpa* plant density.

Clusters 1 and 2, of *E. tomentosa* monocultures, had a maximum euclidian distance of 2605 separating them (Table 3.1C). Cluster 4 and more so, cluster 3, were both closer to cluster 2 than they were to cluster 1. Cluster 1 had the highest mean soil salinity while cluster 2 had the lowest mean soil salinity. A more alkaline pH and the lowest mean *E. tomentosa* plant density characterised cluster 3.

Table 3.1 Four clusters of plots containing *E. tomentosa* plants grown with *A. bunburyana* (A), *A. codonocarpa* (B) or in monoculture (C). Distances separating the four clusters from each other are shown. Areas are shaded to prevent repetition of distance data. Mean number of plants per plot of each species, mean salinity (mS cm^{-1}) and pH are given for each cluster. The total number of replicates (n) for each cluster and *F* and *P* values for each characteristic are described.

A.	***Enchylaena tomentosa* and *Atriplex bunburyana***					
distances	**1**	**2**	**3**	**4**	***F***	***P***
cluster 1		1354	599	898		
2			755	460		
3				301		
4						
n	61	230	61	158		
Total Et	241	112	170	35	100.94	**<0.001**
Total Ab	43	33	39	87	13.36	**<0.001**
Salinity	1.43	0.21	1.13	0.74	1.98	**<0.001**
pH	8.39	8.63	8.43	7.9	76.53	**<0.001**

B.	***Enchylaena tomentosa* and *Atriplex codonocarpa***					
distances	**1**	**2**	**3**	**4**	***F***	***P***
cluster 1		272	567	921		
2			338	686		
3				356		
4						
n	126	85	63	60		
Total Et	61	101	76	122	25.81	**<0.001**
Total Ac	39	160	76	67	69.15	**<0.001**
Salinity	0.36	0.60	0.93	1.28	1.50	**<0.001**
pH	8.56	8.63	8.38	8.73	7.58	**<0.001**

C.	***Enchylaena tomentosa* monoculture**					
distances	**1**	**2**	**3**	**4**	***F***	***P***
cluster 1		2605	1967	1528		
2			639	1077		
3				441		
4						
n	30	194	145	110		
Total Et	118	154	94	127	20.54	**<0.001**
Salinity	2.92	0.20	0.77	1.54	6.66	**<0.001**
pH	8.49	8.18	9.18	7.79	49.17	**<0.001**

Enchylaena tomentosa and Atriplex bunburyana

There were significant differences in the height of *E. tomentosa* plants between clusters (Fig. 3.11A, Table 3.2). The covariates, pH and *E. tomentosa* density, influenced plant height. There was, however, no significant difference between clusters in terms of height, cover, and volume of *A. bunburyana*. The cover (Fig. 3.11B) and volume (Fig. 3.11C) of *E. tomentosa* did not significantly differ between clusters. Soil pH had a significant effect on plant height and cover. Species density also influenced the plant cover, whereas only density of *A. bunburyana* influenced plant volume. Mean distances between *E. tomentosa* plants and their nearest neighbour did not significantly differ between clusters (Fig. 3.11D). Soil pH and *A. bunburyana* density influenced the distance between nearest neighbours of *E. tomentosa* and *A. bunburyana*.

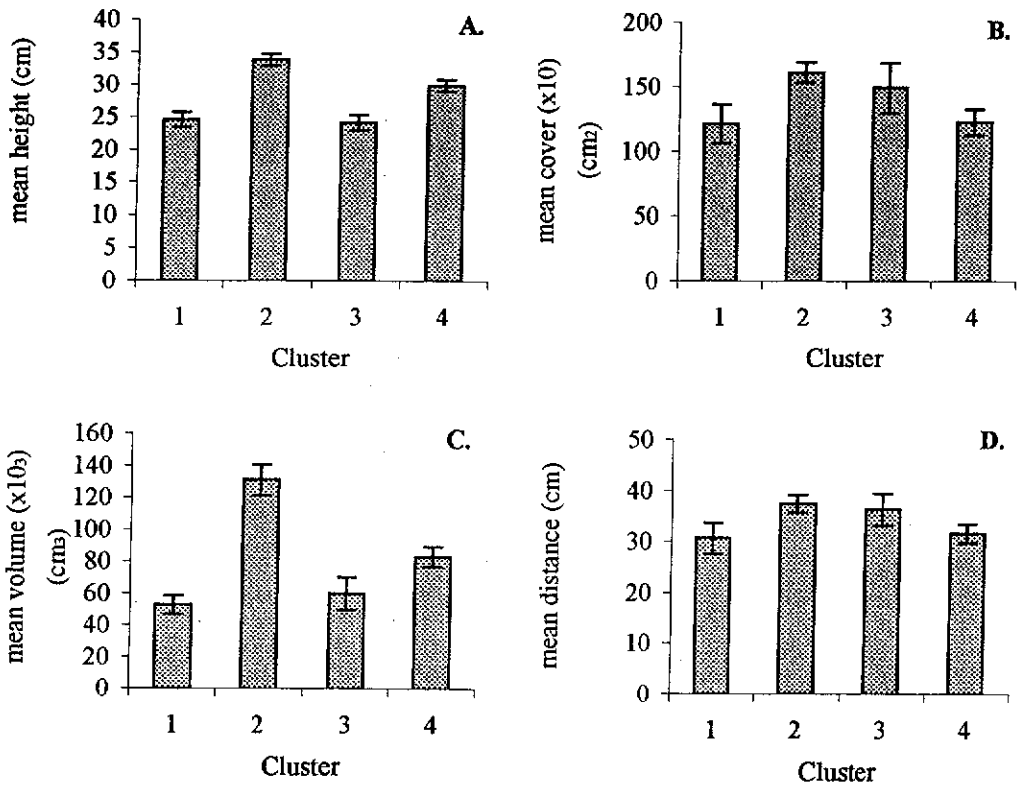


Figure 3.11 The mean height (cm) (A), cover (x10) (cm^2) (B) and volume ($x10^3$) (cm^3) (C) of *E. tomentosa* plants when grown with *A. bunburyana* for each cluster. The mean distance (cm) between *E. tomentosa* plants and their nearest neighbouring *A. bunburyana* plant for each cluster (D). Bars represent standard error.

Table 3.2 One-way ANOVA calculated on the growth parameters (height, cover and volume) and nearest neighbour distance of *E. tomentosa* and *A. bunburyana* from clusters 1-4. Salinity, pH and the total number of *E. tomentosa* (Et) and *A. bunburyana* (Ab) plants per plot were used as covariates. The degrees of freedom (df), *F* and *P* values are shown.

	Enchylaena tomentosa			*Atriplex bunburyana*		
	df	***F***	***P***	***df***	***F***	***P***
Height						
Intercept	1	37.77	**<0.001**	1	38.29	**<0.001**
Salinity	1	2.23	0.136	1	1.10	0.294
pH	1	8.88	**0.003**	1	10.53	**0.001**
Total Et	1	10.27	**0.001**	1	0.44	0.506
Total Ab	1	0.12	0.732	1	3.83	0.051
Cluster	3	2.66	**0.048**	3	0.50	0.680
Error	411			411		
Total	419			419		
Cover						
Intercept	1	0.93	0.336	1	55.97	**<0.001**
Salinity	1	1.54	0.215	1	0.75	0.386
pH	1	0.36	0.548	1	4.19	**0.041**
Total Et	1	0.36	0.546	1	4.82	**0.029**
Total Ab	1	5.66	**0.018**	1	12.39	**<0.001**
Cluster	3	0.886	0.449	3	0.61	0.611
Error	411			411		
Total	419			419		
Volume						
Intercept	1	297.07	**<0.001**	1	289.31	**<0.001**
Salinity	1	6.74	**0.010**	1	1.22	0.271
pH	1	3.74	0.054	1	0.21	0.644
Total Et	1	3.25	0.072	1	2.29	0.131
Total Ab	1	0.06	0.804	1	5.64	**0.018**
Cluster	3	2.43	0.065	3	0.66	0.580
Error	411			411		
Total	419			419		
Distance						
Intercept	1	0.01	0.905			
Salinity	1	3.44	0.065			
pH	1	5.77	**0.017**			
Total Et	1	3.15	0.077			
Total Ab	1	10.01	**0.002**			
Cluster	3	2.07	0.103			
Error	411					
Total	419					

For all clusters, there was no significant relationship between nearest neighbour distance and the sum of the height of *E. tomentosa* individuals and their nearest *A. bunburyana* neighbour (Table 3.3A). Measurements of nearest neighbour distance were significantly positively related to the sum of plant cover for all clusters (Table 3.3B). In addition, all four clusters revealed significantly positive relationships between nearest neighbour distance and the sum of the volumes of nearest neighbouring plants (Table 3.3C). The positive slopes indicated that the combined size of the plant pairs increased when the distance separating them increased.

Table 3.3 Linear analysis of nearest neighbour distance (log_{10}) versus the sum (log_{10}) of the heights (A), covers (B) and volumes (C) of *E. tomentosa* plant's and their nearest *A. bunburyana* (Ab) neighbour. The transformed estimate of slope, the probability level of whether slope and the adjusted coefficient of determination (R^2) are greater than zero are given for each regression. Shaded areas highlight significant *P* values.

	A. height			B. cover			C. volume		
Cluster	**slope**	***P***	**Adj. R^2**	**slope**	***P***	**Adj. R^2**	**slope**	***P***	**Adj. R^2**
1	0.20	0.126	0.02	0.43	<0.001	0.17	0.34	0.003	0.10
2	0.05	0.430	0.00	0.39	<0.001	0.15	0.21	0.003	0.04
3	0.14	0.390	0.00	0.55	<0.001	0.29	0.37	0.001	0.12
4	0.03	0.692	0.01	0.45	<0.001	0.20	0.24	0.003	0.05

Enchylaena tomentosa and Atriplex codonocarpa

The mean height of *E. tomentosa* (Fig. 3.12A) could not be normalised by transformation of data. Kruskal-Wallis analysis, however, showed there to be no significant difference in plant height between clusters (Table 3.4). Plant volume of *E. tomentosa* (Fig. 3.12C) differed significantly between clusters as did height, cover and volume of *A. codonocarpa*. The seeding density of both *E. tomentosa* and *A. codonocarpa* had significant effects on plant height and volume whereas only cover of *E. tomentosa* was affected by seeding density. Soil characteristics (salinity and pH) also produced significant differences in plant height and cover. There were no significant differences between clusters based on the distance between neighbouring plants (Fig. 3.12D).

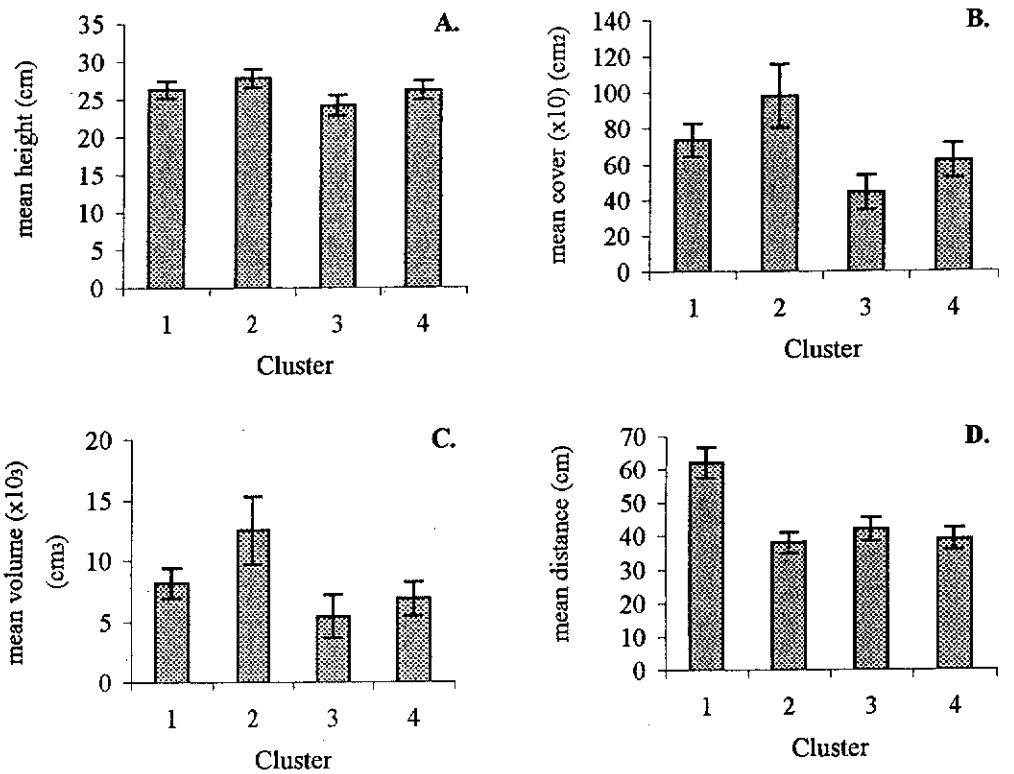


Figure 3.12 The mean height (cm) (A), cover (x10) (cm^2) (B) and volume ($x10^3$) (cm^3) (C) of *E. tomentosa* plants when grown with *A. codonocarpa* plants for each cluster. The mean distance (cm) between *E. tomentosa* plants and their nearest neighbour for each cluster (D). Bars represent standard error.

Table 3.4 One-way ANOVA calculated on growth parameters (height, cover and volume) and nearest neighbour distance of *E. tomentosa* and *A. codonocarpa* from clusters 1-4. Salinity, pH and the total number of *E. tomentosa* (Et) and *A. codonocarpa* (Ab) plants per plot were used as covariates. The degrees of freedom (df), *F* and *P* values are shown. χ^2 values are given when the non-parametric Kruskal Wallis test was used.

	Enchylaena tomentosa			*Atriplex codonocarpa*		
	df	***F***	***P***	***df***	***F***	***P***
Height						
Intercept				1	75.17	**<0.001**
Salinity				1	3.92	**0.049**
pH				1	0.79	0.375
Total Et				1	11.08	**0.001**
Total Ac		χ^2		1	4.92	**0.027**
Cluster	3	4.94	0.177	3	7.86	**<0.001**
Error				326		
Total				334		
Cover						
Intercept	1	3.19	0.075	1	24.59	**<0.001**
Salinity	1	1.56	0.213	1	0.00	0.958
pH	1	3.41	0.066	1	4.04	**0.045**
Total Et	1	1.39	0.240	1	20.89	**<0.001**
Total Ac	1	1.61	0.206	1	1.12	0.292
Cluster	3	2.33	0.074	3	4.67	**0.003**
Error	326			326		
Total	334			334		
Volume						
Intercept	1	8.77	**0.003**	1	79.39	**<0.001**
Salinity	1	1.52	0.219	1	1.82	0.179
pH	1	1.47	0.226	1	0.05	0.822
Total Et	1	2.00	0.158	1	17.76	**<0.001**
Total Ac	1	2.30	0.130	1	3.91	**0.049**
Cluster	3	2.70	**0.046**	3	7.18	**<0.001**
Error	326			326		
Total	334			334		
Distance						
Intercept	1	19.99	**<0.001**			
Salinity	1	0.01	0.931			
pH	1	0.01	0.935			
Total Et	1	0.04	0.839			
Total Ac	1	1.22	0.270			
Cluster	3	1.72	0.162			
Error	326					
Total	334					

There was a positive relationship between nearest neighbour distance and plant height of *E. tomentosa* within Cluster 4 (Table 3.5). All clusters displayed positive relationships between nearest neighbour distance and the sum of *E. tomentosa* and *A. codonocarpa* cover and volume. The larger plants were growing farther apart in comparison to the smaller plants, which indicated that inter-specific competition was occurring between *E. tomentosa* and *A. codonocarpa*. Low R^2 and slope values indicate that competition lacks in importance and strength, respectively.

Table 3.5 Linear analysis of nearest neighbour distance (log_{10}) versus the sum (log_{10}) of the heights (A), covers (B) and volumes (C) of *E. tomentosa* (Et) plants and their nearest *A. codonocarpa* (Ac) neighbour. The transformed estimate of slope, the probability level of whether slope and the adjusted coefficient of determination (R^2) are greater than zero are given for each regression. Shaded areas highlight significant *F* values.

	A. height			B. cover			C. volume		
Cluster	**slope**	***P***	**Adj. R^2**	**slope**	***P***	**Adj. R^2**	**slope**	***P***	**Adj. R^2**
1	0.13	0.141	0.01	0.23	0.009	0.05	0.19	0.008	0.05
2	0.15	0.181	0.01	0.37	<0.001	0.13	0.23	0.004	0.09
3	0.17	0.198	0.01	0.38	0.002	0.13	0.25	0.009	0.09
4	0.30	0.019	0.08	0.43	0.001	0.17	0.32	0.001	0.17

Enchylaena tomentosa monoculture

There were significant differences for all of the growth parameters (i.e. height, cover and volume) in *E. tomentosa* monoculture clusters (Table 3.6, Fig. 3.13A, B, C, respectively). Plant density significantly influenced differences between clusters, and soil pH also significantly affected plant cover and volume. Mean distances between neighbouring *E. tomentosa* individuals differed significantly between clusters and was influenced by soil characteristics and plant density (Fig. 3.13D).

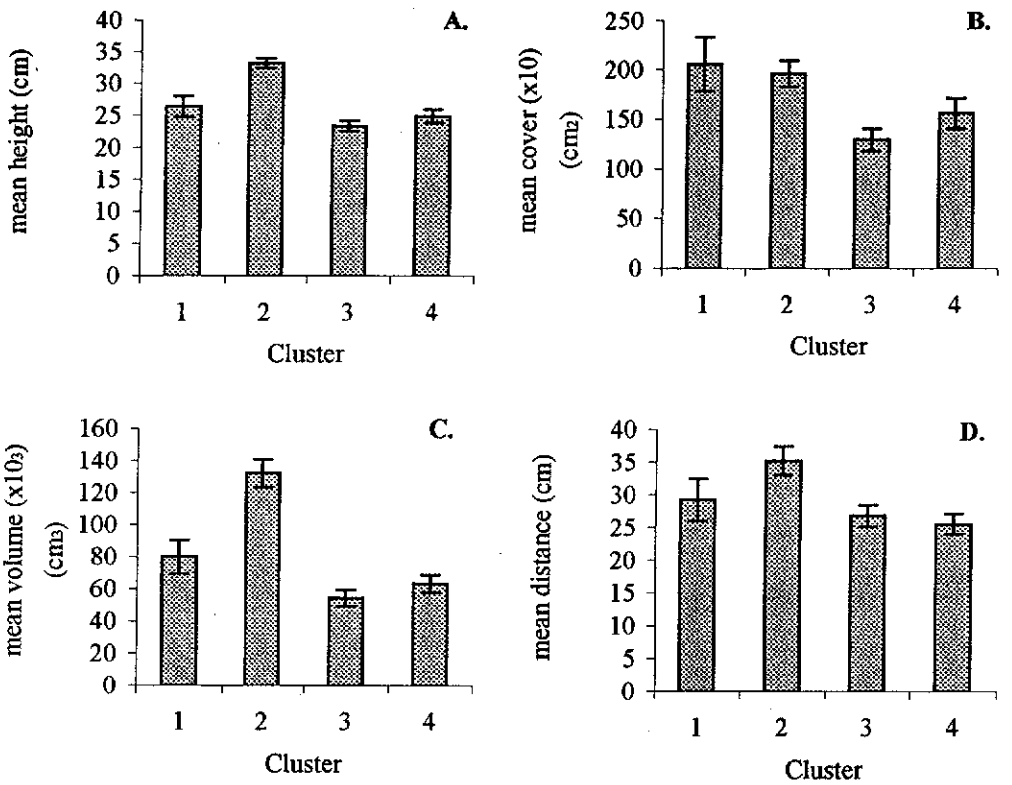


Figure 3.13 The mean height (cm) (A), cover (x10) (cm^2) (B) and volume ($x10^3$) (cm^3) (C) of *E. tomentosa* and mean distance (cm) between *E. tomentosa* plants and their nearest neighbour (D) for each cluster. Bars represent standard error.

Table 3.6 One-way ANOVA calculated on growth parameters (height, cover and volume) and nearest neighbour distance of *E. tomentosa* from clusters 1-4. Salinity, pH and the total number of *E. tomentosa* (Et) plants per plot were used as covariates. The degrees of freedom (df), *F* and *P* values are shown.

	***Enchylaena tomentosa* monoculture**		
	df	***F***	***P***
Height			
Intercept	1	141.87	**<0.001**
Salinity	1	0.93	0.335
pH	1	3.48	0.063
Total Et	1	28.19	**<0.001**
Cluster	3	13.70	**<0.001**
Error	442		
Total	449		
Cover			
Intercept	1	12.46	**<0.001**
Salinity	1	2.23	0.136
pH	1	5.53	**0.019**
Total Et	1	11.45	**0.001**
Cluster	3	2.63	**0.050**
Error	442		
Total	449		
Volume			
Intercept	1	214.77	**<0.001**
Salinity	1	0.04	0.845
pH	1	8.23	**0.004**
Total Et	1	24.41	**<0.001**
Cluster	3	10.48	**<0.001**
Error	442		
Total	449		
Distance			
Intercept	1	70.01	**<0.001**
Salinity	1	8.32	**0.004**
pH	1	11.31	**0.001**
Total Et	1	7.58	**0.006**
Cluster	3	4.25	**0.006**
Error	442		
Total	449		

Intra-specific competition was occurring between plants in most clusters. Clusters 2 - 4 displayed positive relationships between nearest neighbour distance and the sum of nearest neighbour plant height and volume (Table 3.7). Furthermore, all clusters showed positive relationships between nearest neighbour distance and the sum of the nearest neighbours plant cover. This showed that small plants grew close together, whereas, larger plants grew further apart. This nearest neighbour distance versus plant size relationship, however, was weak (i.e. low R^2 values).

Table 3.7 Linear analysis of nearest neighbour distance (log_{10}) versus the sum (log_{10}) of the heights (A), covers (B) and volumes (C) of *E. tomentosa* (Et) plants and their nearest neighbour. The transformed estimate of slope, the probability level of whether slope and the adjusted coefficient of determination (R^2) are greater than zero are given for each regression. Shaded areas highlight significant *P* values.

	A. height			B. cover			C. volume		
Cluster	**slope**	***P***	**Adj. R^2**	**slope**	***P***	**Adj. R^2**	**slope**	***P***	**Adj. R^2**
1	-0.06	0.743	0.00	0.39	0.034	0.12	0.15	0.521	0.00
2	0.38	<0.001	0.14	0.60	<0.001	0.36	0.50	<0.001	0.28
3	0.25	0.002	0.06	0.55	<0.001	0.30	0.40	<0.001	0.19
4	0.20	0.042	0.03	0.49	<0.001	0.24	0.39	<0.001	0.13

Maireana brevifolia

Four clusters resulted from the cluster analysis and were characterised by density of plant species and soil pH and salinity. All clusters were significantly different in these characteristics (Table 3.8). This was performed for *M. brevifolia* when grown in association with either *Atriplex* species or in monoculture.

Clusters 2 and 3 had a maximal euclidian distance of 1093 separating them when *M. brevifolia* was grown in association with *A. bunburyana* plants (Table 3.8A). The euclidian distances showed that cluster 1 was closer to cluster 2, while cluster 4 was closer to cluster 3. The highest mean plant densities of both *M. brevifolia* and *A. bunburyana* were characteristic of cluster 2, whereas the highest mean soil salinity and lowest mean pH were characteristic of cluster 3.

When *M. brevifolia* was grown with *A. codonocarpa* plants, the euclidian distances separating the clusters placed them in the order of 4, 2, 1 and 3 (Table 3.8B). Cluster 3 had the lowest mean soil salinity, whereas cluster 4 had the highest mean soil salinity and the highest mean *A. codonocarpa* plant density. The highest mean *M. brevifolia* plant density was a characteristic of cluster 2. In contrast, cluster 1 had the lowest mean *M. brevifolia* plant density and the highest soil pH.

In monoculture, clusters 1, 2 and 4 were situated close together, whereas cluster 3 was situated at euclidian distances greater than 1000 from the other clusters (Table 3.8C). Cluster 3 had a high mean soil salinity of 2.04 in comparison to 0.35, 0.45 and 0.74 of clusters 2, 1 and 4, respectively. Cluster 1 had the highest whereas cluster 2 had the lowest mean *M. brevifolia* plant density. The mean soil pH was lowest in cluster 4 and highest in cluster 3.

Table 3.8 Four clusters of plots containing *M. brevifolia* plants grown with *A. bunburyana* (A), *A. codonocarpa* (B) or in monoculture (C). Distances separating the four clusters from each other. Areas are shaded to prevent repetition of distance data. Mean number of plants per plot of each species, mean salinity (mS/cm) and pH are listed. The total number of replicates (n) for each cluster and *F* and *P* values for each characteristic are described.

A.	***Maireana brevifolia* and *Atriplex bunburyana***					
distances	**1**	**2**	**3**	**4**	***F***	***P***
cluster 1		340	927	552		
2			1093	782		
3				396		
4						
n	312	90	85	32		
Total Mb	28	540	51	27	559.13	**<0.001**
Total Ab	35	66	38	57	105.67	**<0.001**
Salinity	0.42	0.33	1.31	0.96	2.86	**<0.001**
pH	9.21	8.79	8.7	8.75	96.76	**<0.001**

B.	***Maireana brevifolia* and *Atriplex codonocarpa***					
distances	**1**	**2**	**3**	**4**	***F***	***P***
cluster 1		296	296	709		
2			461	642		
3				1000		
4						
n	73	61	120	58		
Total Mb	85	360	134	128	239.96	**<0.001**
Total Ac	43	48	43	89	48.57	**<0.001**
Salinity	0.62	0.73	0.32	1.32	0.84	**<0.001**
pH	9.01	8.8	8.64	8.38	47.00	**<0.001**

C.	***Maireana brevifolia* monoculture**					
distances	**1**	**2**	**3**	**4**	***F***	***P***
cluster 1		240	1560	438		
2			1691	531		
3				1160		
4						
n	121	290	62	121		
Total Mb	343	121	158	147	357.57	**<0.001**
Salinity	0.45	0.35	2.04	0.74	4.05	**<0.001**
pH	8.67	8.56	8.71	8.5	2.93	**0.033**

Maireana brevifolia and Atriplex bunburyana

There were significant differences in the height of *M. brevifolia* plants between clusters (Fig. 3.14A), which was significantly influenced by both soil salinity and pH (Table 3.9). The cover (Fig. 3.14B), volume (Fig. 3.14C) and nearest neighbour distance (Fig. 3.14D) did not significantly differ between clusters. The density of *A. bunburyana,* soil salinity and pH had an overall effect on plant cover and volume of *M. brevifolia*. Normality of *A. codonocarpa* plant height, cover and volume could not be obtained by transformation of the data. Kruskal-Wallis analyses showed that significant differences existed between clusters for all measured growth parameters (height, cover and volume) (Table 3.9).

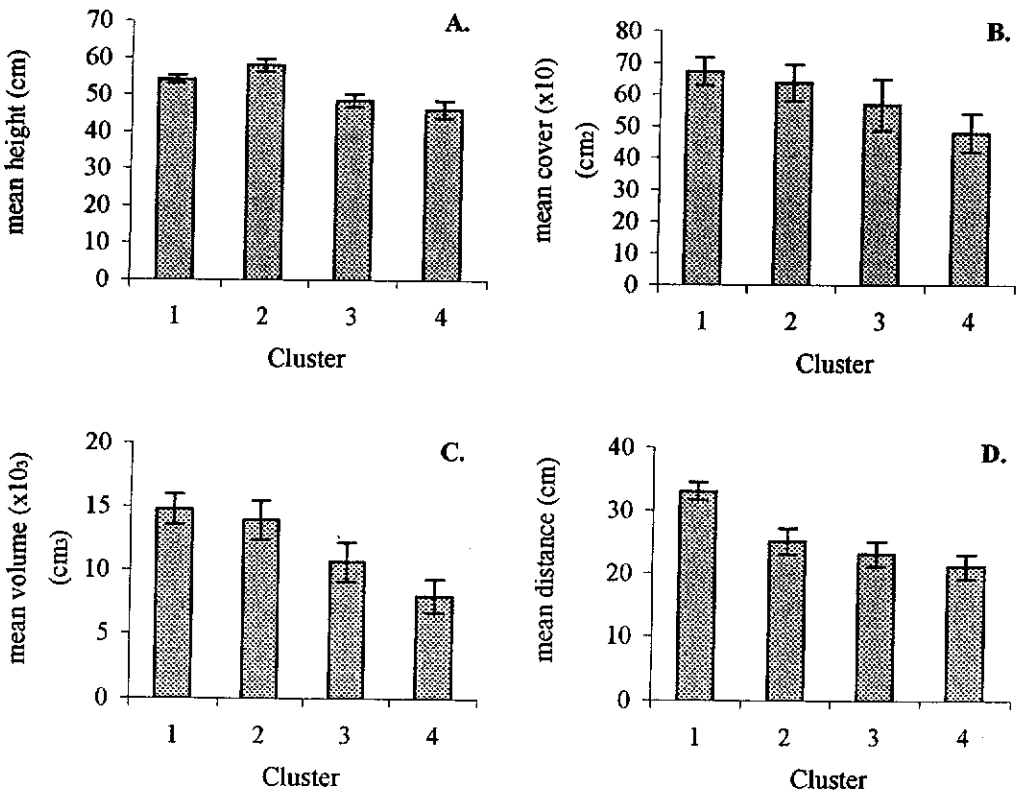


Figure 3.14 The mean height (cm) (A), cover (x10) (cm^2) (B) and volume ($x10^3$) (cm^3) (C) of *M. brevifolia* plants when grown with *A. bunburyana* for each cluster. The mean distance (cm) between *M. brevifolia* plants and their nearest neighbour for each cluster (D). Bars represent standard error.

Table 3.9 One-way ANOVA calculated on growth parameters (height, cover and volume) and nearest neighbour distance of *M. brevifolia* and *A. bunburyana* from clusters 1-4. Salinity, pH and the total number of *M. brevifolia* (Mb) and *A. bunburyana* (Ab) plants per plot were used as covariates. The degrees of freedom (df), *F* and *P* values are shown. χ^2 values are given when the non-parametric Kruskal Wallis test was used.

	Maireana brevifolia			*Atriplex bunburyana*		
	df	***F***	***P***	***df***	***F***	***P***
Height						
Intercept	1	25.47	**<0.001**			
Salinity	1	13.87	**0.024**			
pH	1	5.12	**<0.001**			
Total Mb	1	1.15	0.283			
Total Ab	1	0.73	0.393		χ^2	
Cluster	3	2.86	**0.036**	3	18.00	**<0.001**
Error	478					
Total	486					
Cover						
Intercept	1	4.52	0.034			
Salinity	1	2.27	0.132			
pH	1	0.86	0.354			
Total Mb	1	3.17	0.076			
Total Ab	1	13.96	**<0.001**		χ^2	
Cluster	3	1.41	0.238	3	46.20	**<0.001**
Error	478					
Total	486					
Volume						
Intercept	1	123.61	**<0.001**			
Salinity	1	7.18	**0.008**			
pH	1	5.17	**0.023**			
Total Mb	1	2.10	0.148			
Total Ab	1	5.73	**0.017**		χ^2	
Cluster	3	2.27	0.079	3	33.72	**<0.001**
Error	478					
Total	486					
Distance						
Intercept	1	30.28	**<0.001**			
Salinity	1	0.18	0.669			
pH	1	2.41	0.121			
Total Mb	1	1.86	0.174			
Total Ab	1	1.20	0.273			
Cluster	3	0.84	0.475			
Error	478					
Total	486					

For clusters 1 to 3, there were significant positive relationships between nearest neighbour distance and the sum of plant height, cover and volume of *M. brevifolia* and the nearest neighbouring *A. bunburyana* individual (Table 3.10). The consistent positive values are a clear indication that inter-specific competition is occurring between plants in these clusters. Cluster 4 showed no significant relationship existed between the combined plant sizes and the distance separating nearest neighbours.

Table 3.10 Linear analysis of nearest neighbour distance (log_{10}) versus the sum (log_{10}) of the heights (A), covers (B) and volumes (C) of *M. brevifolia* (Et) plants and their nearest *A. bunburyana* (Ab) plant. The transformed estimate of slope, the probability level of whether slope and the adjusted coefficient of determination (R^2) are greater than zero are given for each regression. Shaded areas highlight significant *P* values.

	A. height			B. cover			C. volume		
Cluster	**slope**	***P***	**Adj. R^2**	**slope**	***P***	**Adj. R^2**	**slope**	***P***	**Adj. R^2**
1	0.18	0.001	0.03	0.45	<0.001	0.20	0.43	<0.001	0.14
2	0.28	0.009	0.07	0.55	<0.001	0.30	0.66	<0.001	0.22
3	0.31	0.005	0.09	0.56	<0.001	0.30	0.72	<0.001	0.26
4	0.00	0.725	0.00	0.11	0.541	0.00	0.00	0.911	0.00

Maireana brevifolia and Atriplex codonocarpa

Mean height of *M. brevifolia* did not differ between clusters when grown with *A. codonocarpa* at varying densities (Fig. 3.15A, Table 3.11). However, it was influenced by salinity. Cover (Fig. 3.15B) and volume (Fig. 3.15C) of *M. brevifolia* differed significantly between clusters. Plant cover was significantly affected by soil salinity and pH, and plant density while plant volume was only affected by soil salinity. There were no significant differences in mean neighbouring plant distances between clusters (Fig. 3.15D). Distances between neighbouring plants, however, were influenced by the density of *M. brevifolia* plants.

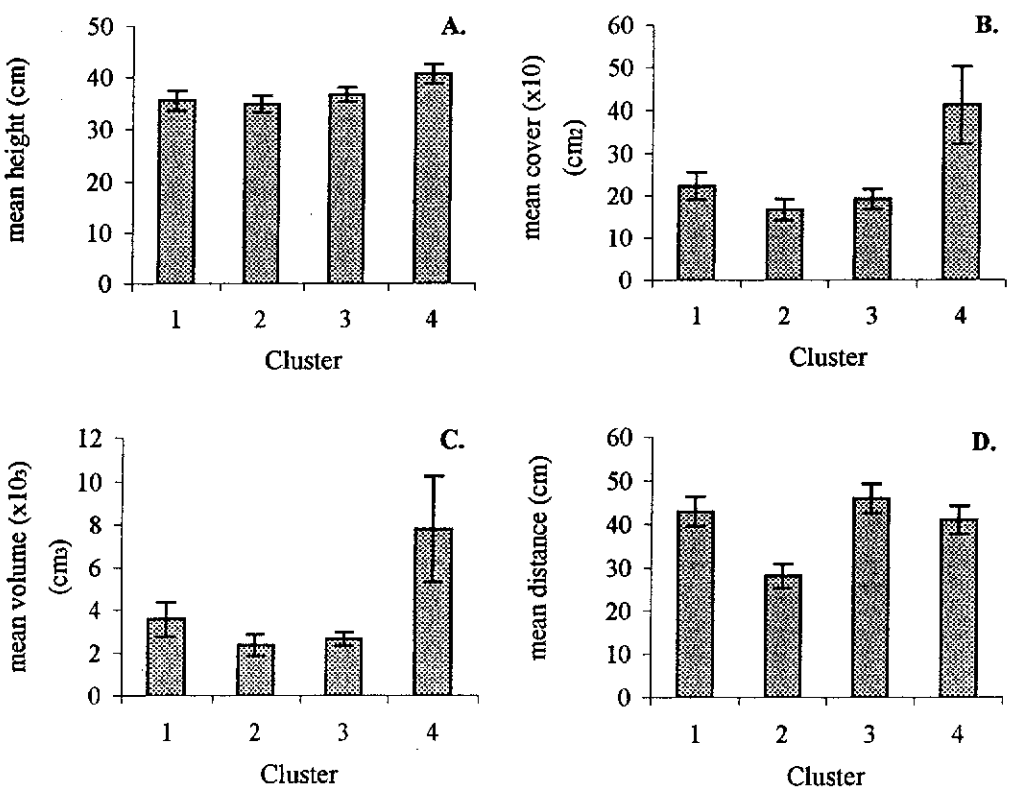


Figure 3.15 Mean height (cm) (A), cover (x10) (cm^2) (B) and volume ($x10^3$) (cm^3) (C) of *M. brevifolia* plants when grown with *A. codonocarpa* for each cluster. The mean distance (cm) between *M. brevifolia* plants and their nearest neighbour for each cluster (D). Bars represent standard error.

Table 3.11 One-way ANOVA calculated on growth parameters (height, cover and volume) of *M. brevifolia* and *A. codonocarpa* from clusters 1-4. Salinity, pH and the total number of *M. brevifolia* (Mb) and *A. codonocarpa* (Ac) plants per plot were used as covariates. The degrees of freedom (df), *F* and *P* values are shown. χ^2 values are given when the non-parametric Kruskal-Wallis test was used.

	Maireana brevifolia			*Atriplex codonocarpa*		
	df	***F***	***P***	***df***	***F***	***P***
Height						
Intercept	1	1.73	0.190			
Salinity	1	3.96	**0.048**			
pH	1	0.44	0.507			
Total Mb	1	0.34	0.561			
Total Ac	1	3.72	0.055		χ^2	
Cluster	3	1.25	0.293	3	8.02	**0.046**
Error	304					
Total	312					
Cover						
Intercept	1	5.18	**0.024**	1	0.187	0.666
Salinity	1	8.61	**0.028**	1	12.86	**<0.001**
pH	1	0.86	**0.003**	1	0.08	0.780
Total Mb	1	0.77	**0.003**	1	1.19	0.276
Total Ac	1	10.03	**0.032**	1	1.54	0.216
Cluster	3	2.16	**0.021**	3	3.75	**0.011**
Error	304			304		
Total	312			312		
Volume						
Intercept	1	7.63	**0.006**			
Salinity	1	7.83	**0.005**			
pH	1	0.95	0.330			
Total Mb	1	0.39	0.532			
Total Ac	1	9.78	**0.002**		χ^2	
Cluster	3	1.95	0.122	3	3.69	0.297
Error	304					
Total	312					
Distance						
Intercept	1	6.99	**0.009**			
Salinity	1	0.20	0.656			
pH	1	0.00	0.986			
Total Mb	1	13.83	**<0.001**			
Total Ac	1	0.34	0.560			
Cluster	3	0.59	0.624			
Error	304					
Total	312					

Clusters 2 and 4 displayed positive relationships between the sums of plant volume and cover of *M. brevifolia* and their nearest neighbouring *A. codonocarpa* individual, and the distance separating the pair of plants (Table 3.12). A lack of significance in the relationship between nearest neighbour distance and the sum of their sizes (i.e. height, cover and volume) occurred for the remaining clusters. The lack of consistency and low R^2 values suggests that inter-specific competition is less likely to occur between individuals of *M. brevifolia* and *A. codonocarpa*.

Table 3.12 Linear analysis of nearest neighbour distance (log_{10}) versus the sum (log_{10}) of the heights (A), covers (B) and volumes (C) of *M. brevifolia* (Mb) plants and their nearest *A. codonocarpa* (Ac) plant. The transformed estimate of slope, the probability level of whether slope and the adjusted coefficient of determination (R^2) are greater than zero are given for each regression. Shaded areas highlight significant *P* values.

	A. height			B. cover			C. volume		
Cluster	**slope**	***P***	**Adj. R^2**	**slope**	***P***	**Adj. R^2**	**slope**	***P***	**Adj. R^2**
1	0.21	0.079	0.03	0.11	0.348	0.00	0.15	0.072	0.03
2	0.20	0.130	0.02	0.50	<0.001	0.24	0.59	<0.001	0.20
3	0.10	0.273	0.00	0.12	0.197	0.01	0.11	0.127	0.01
4	0.13	0.320	0.00	0.39	0.002	0.14	0.24	0.014	0.09

Maireana brevifolia monoculture

For all four clusters there were significant differences in plant height, cover, volume and distances between nearest neighbouring plants (Fig. 3.16, Table 3.13). Plant height was significantly influenced by soil salinity and pH and the plant density. In contrast, plant cover was only influenced by soil pH. Plant volume and nearest neighbour distances were analysed using the non-parametric Kruskal-Wallis test and, thus, covariates were not incorporated into the analysis.

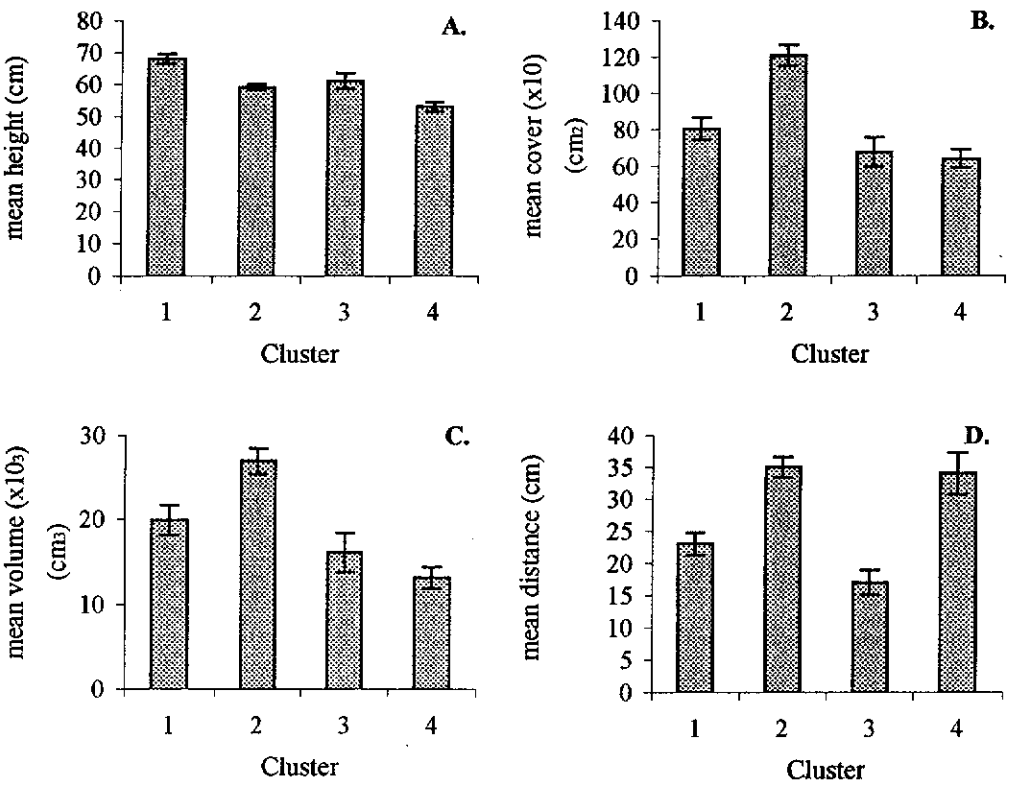


Figure 3.16 The mean height (cm) (A), cover (x10) (cm^2) (B) and volume ($x10^3$) (cm^3) (C) of *M. brevifolia* and mean distance (cm) between *M. brevifolia* plants and their nearest neighbour (D) for each cluster. Bars represent standard error.

Table 3.13 One-way ANOVA calculated on growth parameters (height, cover and volume) and nearest neighbour distance of *M. brevifolia* from clusters 1-4. Salinity, pH and the total number of *M. brevifolia* (Mb) plants per plot were used as covariates. The degrees of freedom (df), *F* and *P* values are shown. χ^2 values are given when the non-parametric Kruskal-Wallis test was used.

	Maireana brevifolia		
	df	***F***	***P***
Height			
Intercept	1	27.45	**0.045**
Salinity	1	1.71	**0.003**
pH	1	2.81	**0.005**
Total Mb	1	0.52	**0.001**
Cluster	3	6.97	**0.034**
Error	587		
Total	594		
Cover			
Intercept	1	191.26	**<0.001**
Salinity	1	0.07	0.786
pH	1	6.10	**0.014**
Total Mb	1	0.65	0.419
Cluster	3	10.01	**<0.001**
Error	587		
Total	594		
Volume			
Intercept			
Salinity			
pH			
Total Mb		χ^2	
Cluster	3	49.05	**<0.001**
Error			
Total			
Distance			
Intercept			
Salinity			
pH			
Total Mb		χ^2	
Cluster	3	49.38	**<0.001**
Error			
Total			

Clusters 3 - 4 showed positive relationships between the sum of the heights of nearest neighbouring *M. brevifolia* plants and the distance separating them (Table 3.14). Significant, positive relationships between nearest neighbour distance and the sum of covers and volumes of nearest neighbouring *M. brevifolia* plants were displayed for all clusters. Intra-specific competition is clearly occurring between plants of the four clusters. Low R^2 values, however, indicate that competition plays a small role in determining plant size.

Table 3.14 Linear analysis of nearest neighbour distance (log_{10}) versus the sum (log_{10}) of the heights (A), covers (B) and volumes (C) of *M. brevifolia* (Mb) plants and their nearest neighbour. The transformed estimate of slope, the probability level of whether slope and the adjusted coefficient of determination (R^2) are greater than zero are given for each regression. Shaded areas highlight significant *P* values.

	A. height			B. cover			C. volume		
Cluster	**slope**	***P***	**Adj. R^2**	**slope**	***P***	**Adj. R^2**	**slope**	***P***	**Adj. R^2**
1	0.12	0.192	0.01	0.51	<0.001	0.25	0.43	<0.001	0.20
2	0.09	0.134	0.01	0.36	<0.001	0.13	0.27	<0.001	0.09
3	0.37	0.003	0.12	0.46	<0.001	0.20	0.30	<0.001	0.19
4	0.36	<0.001	0.12	0.62	<0.001	0.38	0.61	<0.001	0.33

Maireana georgei

The four clusters produced by simple cluster analysis were characterised by species density and soil salinity and pH, when *M. georgei* was grown in association with *A. bunburyana* or in monoculture (Table 3.15). All characteristics showed significant differences between clusters regardless of species combinations. The low numbers of *M. georgei* individuals per plot when grown with *A. codonocarpa* prevented further nearest neighbour analyses occurring.

Cluster 1 and 2 had a maximal euclidian distance of 770 separating them when *M. georgei* was grown with *A. bunburyana* plants (Table 3.15A). Clusters 3 and 4 were situated between clusters 1 and 2. Cluster 2 was characterised by the highest mean soil salinity, whereas cluster 1 had the lowest mean soil salinity and *M. georgei* plant density and the highest mean soil pH. Cluster 3, in contrast, had the highest mean *M. georgei* plant density. All clusters had similar mean *A. bunburyana* plant densities ranging from 42 to 49.

The clusters of *M. georgei* monocultures were all situated close together in comparison to the clusters of other species combinations (Table 3.15B). A maximum euclidian distance of 394 separated clusters 1 and 2. Cluster 1 was characterised by the highest mean *M. georgei* plant density, lowest mean soil salinity and pH. Cluster 2 had the highest mean soil salinity and a low mean *M. georgei* plant density, similar to cluster 3. Clusters 2 and 4 had the highest mean soil pH of 9.28 and 9.30, respectively.

Table 3.15 Four clusters of plots containing *M. georgei* plants grown with *A. bunburyana* (A) or in monoculture (B). Distances separating the four clusters from each other. Shading prevented repetition of distance data. Mean number of plants per plot of each respective species, mean salinity (mS cm^{-1}) and pH are described. The total number of replicates (n) for each cluster and *F* and *P* values for each characteristic are described.

A.	***Maireana georgei* and *Atriplex bunburyana***					
distances	**1**	**2**	**3**	**4**	***F***	***P***
cluster 1		770	259	440		
2			575	341		
3				308		
4						
n	204	129	60	226		
Total Mg	133	271	316	146	338.82	**<0.001**
Total Ab	47	49	42	43	4.33	**<0.001**
Salinity	0.37	1.13	0.55	0.81	1.69	**<0.001**
pH	8.85	8.51	8.39	8.58	53.55	**<0.001**

B.	***Maireana georgei* monoculture**					
distances	**1**	**2**	**3**	**4**	***F***	***P***
cluster 1		394	122	318		
2			282	86		
3				214		
4						
n	76	10	29	67		
Total Mg	73	20	18	66	55.71	**<0.001**
Salinity	0.27	0.66	0.37	0.58	1.37	**<0.001**
pH	8.89	9.28	9.15	9.3	16.17	**<0.001**

Maireana georgei and Atriplex bunburyana

There were significant differences in plant height, cover and volume of *M. georgei* between each of the four clusters (Fig. 3.17A, B, C, Table 3.16) influenced by soil salinity or pH or both. There were no differences in *A. bunburyana* plant height between clusters, however, there were significant differences in plant cover and volume. Soil salinity significantly affected both plant cover and volume of *A. bunburyana*. In addition, *M. georgei* plant density significantly affected *A. bunburyana* plant volume. The mean distance between the nearest *M. georgei* and *A. bunburyana* plants differed significantly between clusters (Fig. 3.17D). The nearest neighbour distance was significantly influenced by soil salinity and *A. bunburyana* plant density.

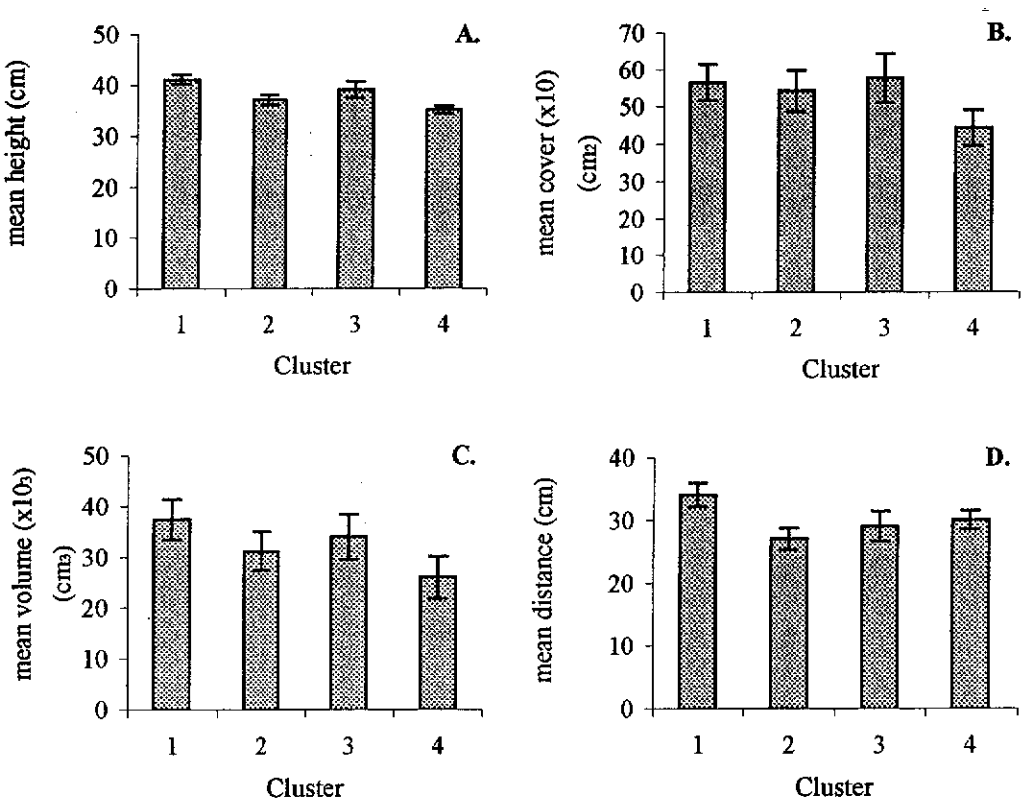


Figure 3.17 The mean height (cm) (A), cover (x10) (cm^2) (B) and volume ($x10^3$) (cm^3) (C) of *M. georgei* plants when grown with *A. bunburyana* plants in each cluster. The mean distance (cm) between *M. georgei* plants and their nearest neighbour for each cluster (D). Bars represent standard error.

Table 3.16 One-way ANOVA calculated on growth parameters (height, cover and volume) and nearest neighbour distance of *M. georgei* and *A. bunburyana* from clusters 1-4. Salinity, pH and the total number of *M. georgei* (Mg) and *A. bunburyana* (Ab) plants per plot were used as covariates. The degrees of freedom (df), *F* and *P* values are shown. χ^2 values are given when the non-parametric Kruskal-Wallis test was used.

	Maireana georgei			*Atriplex bunburyana*		
	df	***F***	***P***	***df***	***F***	***P***
Height						
Intercept	1	1.36	0.243			
Salinity	1	6.32	**0.012**			
pH	1	0.16	0.686			
Total Mg	1	0.03	0.870			
Total Ab	1	0.38	0.539		χ^2	
Cluster	3	9.80	**<0.001**	3	6.83	0.078
Error	595					
Total	603					
Cover						
Intercept	1	5.93	0.015	1	33.64	**<0.001**
Salinity	1	14.46	**<0.001**	1	20.47	**<0.001**
pH	1	5.91	**0.015**	1	0.004	0.947
Total Mg	1	0.24	0.622	1	3.41	0.065
Total Ab	1	0.00	0.986	1	1.62	0.203
Cluster	3	6.01	**<0.001**	3	19.82	**<0.001**
Error	595			595		
Total	603			603		
Volume						
Intercept	1	4.96	0.026	1	145.95	**<0.001**
Salinity	1	13.57	**<0.001**	1	18.40	**<0.001**
pH	1	4.19	**0.041**	1	0.05	0.816
Total Mg	1	0.23	0.634	1	5.12	**0.024**
Total Ab	1	0.04	0.843	1	2.26	0.134
Cluster	3	6.06	**<0.001**	3	16.84	**<0.001**
Error	595			595		
Total	603			603		
Distance						
Intercept	1	10.71	**0.001**			
Salinity	1	6.68	**0.010**			
pH	1	0.08	0.775			
Total Mg	1	0.64	0.426			
Total Ab	1	4.03	**0.045**			
Cluster	3	4.20	**0.006**			
Error	595					
Total	603					

There were significant relationships between the mean distance separating nearest *M. georgei* and *A. bunburyana* neighbours and the sum of their heights for clusters one and four (Table 3.17). All clusters showed positive relationships between the distances separating neighbouring *M. georgei* and *A. bunburyana* individuals and the sums of their cover and volume. This clearly shows that the combined sizes of the plants decrease the closer the nearest neighbouring plants grow together, indicating inter-specific competition.

Table 3.17 Linear analysis of nearest neighbour distance (log_{10}) versus the sum (log_{10}) of the heights (A), covers (B) and volumes (C) of *M. georgei* (Mg) plants and their nearest *A. bunburyana* (Ab) plant. The transformed estimate of slope, the probability level of whether slope and the adjusted coefficient of determination (R^2) are greater than zero are given for each regression. Shaded areas highlight significant *P* values.

	A. height			B. cover			C. volume		
Cluster	**slope**	***P***	**Adj. R^2**	**slope**	***P***	**Adj. R^2**	**slope**	***P***	**Adj. R^2**
1	0.38	<0.001	0.14	0.61	<0.001	0.38	0.59	<0.001	0.35
2	0.08	0.427	0.00	0.38	<0.001	0.14	0.29	<0.001	0.09
3	0.13	0.314	0.00	0.30	0.022	0.07	0.29	0.034	0.06
4	0.32	<0.001	0.10	0.50	<0.001	0.25	0.52	<0.001	0.25

Maireana georgei monoculture

M. georgei plant height (Fig. 3.18A) and cover (Fig. 3.18B) and distance between nearest *M. georgei* individuals (Fig. 3.18D) did not significantly differ between clusters. Both plant height and nearest neighbour plant distance were influenced by plant density (Table 3.18). *Maireana georgei* plant volume differed between clusters (Fig. 3.18C) and was significantly influenced by plant density.

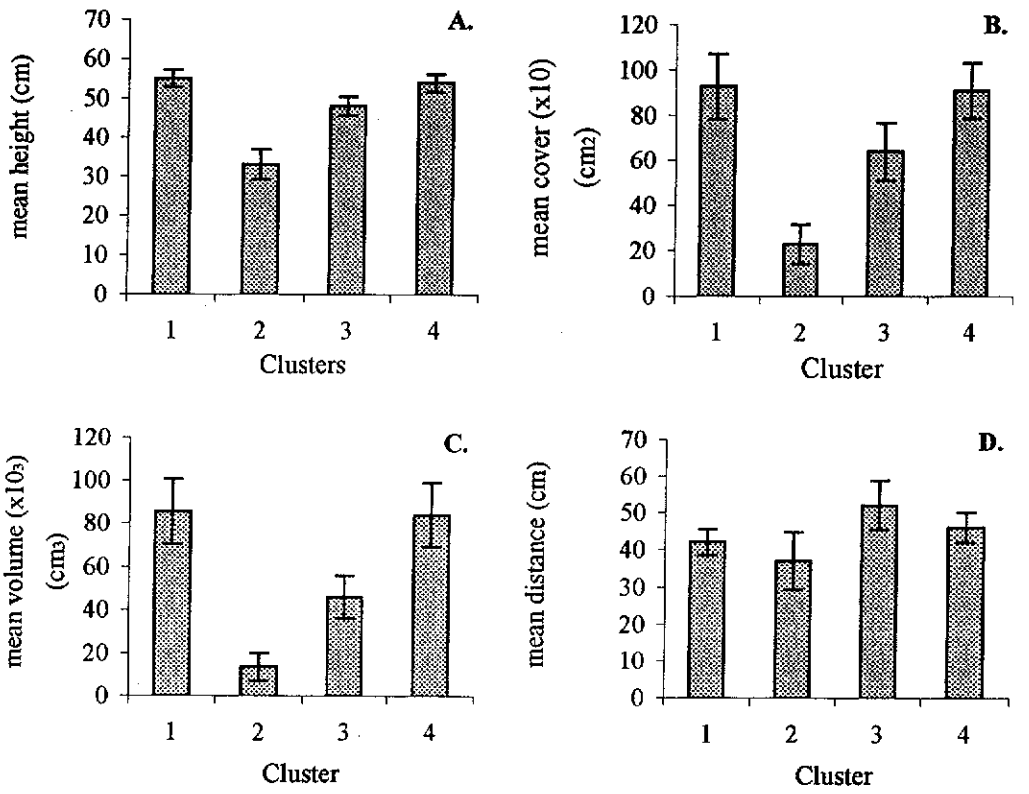


Figure 3.18 The mean height (cm) (A), cover (x10) (cm^2) (B) and volume ($x10^3$) (cm^3) (C) of *M. georgei* and mean distance (cm) between *M. georgei* plants and their nearest neighbour (D) for each cluster. Bars represent standard error.

Table 3.18 One-way ANOVA calculated on growth parameters (height, cover and volume) and nearest neighbour distance of *M. georgei* from clusters 1-4. Salinity, pH and the total number of *M. georgei* (Mg) plants per plot were used as covariates. The degrees of freedom (df), *F* and *P* values are shown.

	Maireana georgei		
	df	***F***	***P***
Height			
Intercept	1	1.02	0.315
Salinity	1	0.72	0.396
pH	1	0.04	0.845
Total Mg	1	6.52	**0.012**
Cluster	3	1.77	0.154
Error	175		
Total	182		
Cover			
Intercept	1	2.90	0.090
Salinity	1	0.88	0.349
pH	1	2.59	0.109
Total Mg	1	2.28	0.133
Cluster	3	0.90	0.443
Error	175		
Total	182		
Volume			
Intercept	1	9.18	**0.003**
Salinity	1	0.81	0.370
pH	1	0.00	0.958
Total Mg	1	4.34	**0.039**
Cluster	3	2.82	**0.040**
Error	175		
Total	182		
Distance			
Intercept	1	0.76	0.386
Salinity	1	0.17	0.682
pH	1	2.22	0.138
Total Mg	1	4.00	**0.047**
Cluster	3	1.02	0.386
Error	175		
Total	182		

Clusters 1 and 3 revealed significant positive relationships between the distance separating nearest neighbouring *M. georgei* plants and the sums of their cover or volume (Table 3.19). The combined height of the *M. georgei* plant pairs showed no relationship with the distance separating them.

Table 3.19 Linear analysis of nearest neighbour distance (log_{10}) versus the sum (log_{10}) of the heights (A), covers (B) and volumes (C) of *M. georgei* (Mg) plants and their nearest neighbour. The transformed estimate of slope, the probability level of whether slope and the adjusted coefficient of determination (R^2) are greater than zero are given for each regression. Shaded areas highlight significant *P* values.

	A. height			B. cover			C. volume		
Cluster	**slope**	***P***	**Adj. R^2**	**slope**	***P***	**Adj. R^2**	**slope**	***P***	**Adj. R^2**
1	0.20	0.079	0.03	0.30	0.008	0.10	0.28	0.014	0.07
2	0.05	0.898	0.00	0.02	0.953	0.01	0.04	0.911	0.00
3	0.00	0.719	0.00	0.61	<0.001	0.31	0.53	0.003	0.26
4	0.00	0.292	0.00	0.11	0.358	0.00	0.05	0.680	0.00

DISCUSSION

The growth and establishment of target native species on the waste materials produced by mining operators involves complex interactions between numerous biological and edaphic factors (Finucane 1995, Barrett 2000). The factors identified and examined in this study were plant density, plant species, soil characteristics (i.e. salinity and pH) and intra- and inter-specific competition. There were no clear trends where one specific factor influenced growth of individual species. Rather plant growth and establishment were affected by several factors in combination.

Germination and seedling establishment

The number of recruits of *E. tomentosa*, *M. brevifolia* and *M. georgei* at the time of the first assessment was substantially lower than the sown seed density. Seed dormancy, which is characteristic of *M. georgei* (Osborne *et al.* 1993) and *A. codonocarpa* seeds (as suggested by the characteristic light and dark coloured seeds – Anderson 1982), is likely to account for the low numbers of recruits of these species. In addition, poor seedling recruitment is consistent with the results of other studies (Fenner 1987, Morgan 1995, Curtis 1996, Booth *et al.* 1999). In field situations, it is difficult to precisely determine the reasons for large numbers of seedling deaths because constant monitoring is not feasible (Fenner 1987). Seedling death may be attributed to many factors (e.g. competition, low soil moisture, predation, failure to form mycorrhizae and allelopathy).

One possibility for low seedling survival in field trials may be that survival is dependent on the number of suitable microsites (Jennings *et al.* 1993, Morgan 1995). In this thesis, there was largely no difference in the number of surviving germinants, regardless of the broadcast seed density. If the lowest broadcast seed density used the maximum number of suitable microsites, then the number of surviving seedlings would be the same even for greater broadcast seed application rates. Seedling recruitment is potentially on-going, provided that suitable microsites are available (Morgan 1995). The characteristics of microsites that can make them suitable for seedling establishment include protection from predators and climatic extremes, provision of adequate nutrients and moisture and

absence of allelopathic substances (Morgan 1995). If the number of seedlings to survive reflects the number of suitable microsites, it would seem that there was large variation of suitable microsites available on the waste material examined in this study. The soil characteristics of salinity and pH, for example, may have contributed to microsite variability. Jennings *et al.* (1993) found that the size and abundance of rock fragments on the soil surface influenced the number of suitable microsites. Although the characteristics of rock fragments on the soil surface were not measured in this study, they may have contributed to the variation in seedling recruitment.

Wards weed, a native of the Mediterranean, is abundant in the Goldfields and Nullabor shrublands of Western Australia (Hussey *et al.* 1997). Wards weed was also abundant throughout the study area and may have adversely affected seedling number. Reduced light, nutrients, soil temperatures and moisture levels may all be limiting resources due to uptake by annual species (Reichenberger and Pyke 1990, Caldwell *et al.* 1995, Morgan 1995, Booth *et al.* 1999). Aggressive competition, between the annuals and surrounding seedlings, for these resources may have resulted in mortality during various stages of early development. If some seedlings do survive, root growth is likely to be stunted in the first year. Reichenberger and Pyke (1990) emphasised the importance of below-ground gaps for root establishment to ensure survival of perennial seedlings in arid and semi-arid ecosystems. Although it was beyond the scope of my study, the impact of weeds on the survival and establishment of seedlings of native species in areas rehabilitated following mining requires further research.

The number of successful recruits was species-specific, and indicated that species characteristics may play a strong role in determining competitive ability. At the first assessment, there were large numbers of *M. brevifolia* seedlings, relative to the other species examined. Seedling recruitment, however, varies temporally (from season to season) and spatially (from place to place) (Fenner 1987, Pons 1991, Booth *et al.* 1999). Variation in environmental conditions within and between years will ensure a high degree of genetic diversity within populations as well as a high degree of phenotypic plasticity in

seedlings (Fenner 1987). Under different sets of environmental conditions in previous or future years, other species may well have shown evidence of higher seedling recruitment.

After 14 months, *M. brevifolia* seedling survival remained greater than the other chenopod species. This may indicate a greater ability to compete with introduced and native annual species as well as a greater tolerance to low moisture availability during the summer months. Barker (1975) noted that, although *M. brevifolia* was a perennial and had a suckering rootstock, it showed poor drought tolerance, often being completely defoliated after dry periods. Therefore it would seem that aggressive competitiveness in the presence of weeds rather than drought tolerance was facilitating establishment.

Competition

There was a high degree of variability in the density of chenopod plants germinating independent of the broadcast seed density. Simple cluster analysis was used to regroup the data and produce four significant groups for each species combination. Summary tables (Tables 3.20 - 3.22) have been included in this discussion to assist with the interpretation of the results. Both *E. tomentosa* and *M. brevifolia* monocultures showed significant growth differences (i.e. height, cover, volume) between clusters whereas only one parameter differed between clusters grown with *A. bunburyana* and *A. codonocarpa* (Tables 3.20, 3.21). *Enchylaena tomentosa* plant growth parameters were clearly influenced by plant density when grown in monoculture and may be an indication that intra-specific competition is the main mode of competition occurring for this species.

The occurrence of *E. tomentosa* and *M. brevifolia* intra-specific competition was clearly supported by significant linear regressions of nearest neighbour distance versus the sum of the heights, covers or volumes of the plant pairs (Tables 3.7 and 3.14, respectively). Interestingly, *E. tomentosa* cluster 1 showed no significant linear regression analysis. A high mean soil salinity, characteristic of this cluster may have affected the plant density at which competition occurs (Table 3.20). Limiting factors, such as salinity, can influence the plant density at which competition will occur.

There were also significant differences in plant height between clusters when *E. tomentosa* or *M. brevifolia* plants were grown with *A. bunburyana*. This may suggest that competition for light was occurring. A negative slope of the regression of nearest neighbour distance versus the sum of their heights would have indicated asymmetric competition for light (Welden *et al.* 1988, Wagner and Radosevich 1998). The significant positive slopes, however, of those clusters showing significant regressions indicated either light competition did not occur or increasing distances from the *A. bunburyana* canopy had sufficiently weakened the R^2 value when height was measured.

Competition for soil resources was reflected by the positive regressions of nearest neighbour distance versus their combined cover or volumes. Others have also concluded that competition for resources was reflected by the positive regressions of plant volume or cover versus nearest neighbour distance (Welden *et al.* 1988, Wagner and Radosevich 1998). Below-ground competition is more likely to occur when soil moisture or nutrients are limiting (Phillips and MacMahon 1981, Wilson and Tilman 1993). Low moisture and nutrient availability is characteristic of semi-arid and arid environments (Phillips and MacMahon 1981). Below-ground competition is, therefore, likely to be the dominant mode of inter- and intra-specific competition of *E. tomentosa* or *M. brevifolia* in monoculture or when grown in association with *A. bunburyana*.

When *M. brevifolia* and *E. tomentosa* were grown with *A. codonocarpa*, competition was limited to positive regressions of only a few clusters. Inter-specific competition, in the presence of *A. codonocarpa*, may not be an important factor determining *M. brevifolia* and *E. tomentosa* abundance and contribution to community structure. Inter-specific competition may be more important and intense at the early seedling stage during the winter months, when growth of grasses and annuals is fast and aggressive in comparison to perennials or other woody species (Florentine 1999).

Table 3.20 Parameters of species density, salinity and pH for each cluster are characterised as high (H), medium (M) and low (L) for *E. tomentosa* (Et) when grown with either *Atriplex* species or in monoculture. *E. tomentosa* mean density (plants $plot^{-1}$) of 0 - 80 = 'L', 81 - 160 = 'M' and 160 - 240 = 'H', *A. bunburyana* (Ab) and *A. codonocarpa* (Ac) mean density (plants $plot^{-1}$) of 0 - 55 = 'L', 56 - 110 = 'M' and 111 - 165 = 'H', salinity (mS cm^{-1}) of 0.00 - 1.00 = 'L', 1.01 - 2.00 = 'M' and 2.01 - 3.00 = 'H' and pH of 7.8 - 8.2 = 'L', 8.3 - 8.7 = 'M' and 8.8 - 9.2 = 'H'. Significance ($P < 0.05$) from one-way ANOVA of cluster differences and covariates (plant density, salinity and pH) using plant growth parameters (i.e. height, cover and volume) and nearest neighbour distances are indicated by '*'.

Et & Ab					**height**	**cover**	**volume**	**distance**
cluster	**1**	**2**	**3**	**4**	*			
Et density	H	M	H	L	*			
Ab density	L	L	L	M		*		*
Salinity	M	L	M	L			*	
pH	M	M	M	L	*			*

Et & Ac					**height**	**cover**	**volume**	**distance**
cluster	**1**	**2**	**3**	**4**			*	
Et density	L	M	L	M				
Ac density	L	H	M	M				
Salinity	L	L	L	M				
pH	M	M	M	M				

Et monoculture					**height**	**cover**	**volume**	**distance**
cluster	**1**	**2**	**3**	**4**	*	*	*	*
Et density	M	M	M	M	*	*	*	*
Salinity	H	L	L	M				*
pH	M	L	H	L		*	*	*

Table 3.21 Parameters of species density, salinity and pH for each cluster are characterised as high (H), medium (M) and low (L) for *M. brevifolia* (Mb) when grown with either *Atriplex* species or in monoculture. *M. brevifolia* mean density (plants plot^{-1}) of 0 - 150 = 'L', 150 - 300 = 'M' and 300 - 450 = 'H', *A. bunburyana* (Ab) and *A. codonocarpa* (Ac) mean density (plants plot^{-1}) of 0 - 55 = 'L', 56 - 110 = 'M' and 111 - 165 = 'H', salinity (mS cm^{-1}) of 0.00 - 1.00 = 'L', 1.01 - 2.00 = 'M' and 2.01 - 3.00 = 'H' and pH of 7.8 - 8.2 = 'L', 8.3 - 8.7 = 'M' and 8.8 - 9.2 = 'H'. Significance ($P < 0.05$) from one-way ANOVA of cluster differences and covariates (plant density, salinity and pH) using plant growth parameters (i.e. height, cover and volume) and nearest neighbour distances are indicated by '*'.

Mb & Ab					**height**	**cover**	**volume**	**distance**
cluster	**1**	**2**	**3**	**4**	*			
Mb density	L	H	L	L				
Ab density	L	M	L	M		*	*	
Salinity	L	L	M	L	*		*	
pH	H	H	M	H	*		*	

Mb & Ac					**height**	**cover**	**volume**	**distance**
cluster	**1**	**2**	**3**	**4**		*		
Mb density	L	H	L	L		*		*
Ac density	L	L	L	M		*	*	
Salinity	L	L	L	M	*	*	*	
pH	H	H	M	M		*		

Mb monoculture					**height**	**cover**	**volume**	**distance**
cluster	**1**	**2**	**3**	**4**	*	*	*	*
Mb density	H	L	M	L	*			
Salinity	L	L	H	L	*			
pH	M	M	M	M	*	*		

Maireana georgei showed a reverse effect in comparison to *E. tomentosa* and *M. brevifolia* when comparing where significant differences between clusters occurred (Table 3.22). All measured plant growth parameters showed significant differences between clusters when *M. georgei* was grown with *A. bunburyana* compared to when grown in monoculture. Competition also occurred between plants of all clusters when *M. georgei* was grown with *A. bunburyana* compared to the monoculture clusters. The density of *M. georgei* plants in monoculture, however, was low compared to medium and high densities when grown with *A. bunburyana*. Inter-specific competition is likely to regulate the abundance of *M. georgei* plants on revegetation areas in the presence of *A. bunburyana*. Inter-specific competition may play a more important role, in comparison to intra-specific competition, in determining the abundance of *M. georgei* within revegetation communities.

Table 3.22 Parameters of species density, salinity and pH for each cluster are characterised as high (H), medium (M) and low (L) for *M. georgei* (Mg) when grown with either *Atriplex bunburyana* (Ab) or in monoculture. *Maireana georgei* mean density (plants $plot^{-1}$) of 0 - 125 = 'L', 126 - 250 = 'M' and 251 - 375 = 'H', *A. bunburyana* mean density (plants $plot^{-1}$) of 0 - 55 = 'L', 56 - 110 = 'M' and 111 - 165 = 'H', salinity of 0.00 - 1.00 = 'L', 1.01 - 2.00 = 'M' and 2.01 - 3.00 = 'H' and pH of 7.8 - 8.2 = 'L', 8.3 - 8.7 = 'M' and 8.8 - 9.2 = 'H'. Significance ($P < 0.05$) from one-way ANOVA of cluster differences and covariates (plant density, salinity and pH) using plant growth parameters (i.e. height, cover and volume) and nearest neighbour distances are indicated by '*'.

Mg & Ab					**height**	**cover**	**volume**	**distance**
cluster	**1**	**2**	**3**	**4**	*	*	*	*
Mg density	M	H	H	M				
Ab density	L	L	L	L				*
Salinity	L	M	L	L		*	*	*
pH	H	M	M	M	*	*	*	

Mg monoculture					**height**	**cover**	**volume**	**distance**
cluster	**1**	**2**	**3**	**4**			*	
Mg density	L	L	L	L	*		*	*
Salinity	L	L	L	L				
pH	H	H	H	H				

Regression analysis of nearest neighbour distance versus the sum of heights, covers or volumes of nearest neighbours revealed that competition was occurring in some clusters for every species combination. The coefficient of determination (R^2) values did not increase with increasing plant density. This was also found in a study of intra-specific competition of *Xanthium strumarium* (Asteraceae) at different plant densities, which concluded that those plants did not suffer competition from neighbouring plants unless they were extremely close (Weiner *et al.* 2000). This may also be the case for the target species used in this study, given that their root system consist primarily of a tap root with few laterals. The lateral roots and their respective density, however, may play an important role in competition for below-ground resources (Bouma *et al.* 2001). *Atriplex bunburyana* has more lateral roots in the upper 15 cm of soil compared to *M. brevifolia* whose laterals are spaced along the length of the taproot (Short 1998). *Atriplex bunburyana* may have the advantage of obtaining moisture during infrequent summer storms.

Low R^2 values indicate that the importance of competition to survival and establishment of species in this study is very weak. Low R^2 values were also obtained in similar studies (Welden *et al.* 1988, Kubota and Hara 1995, Peterson and Squiers 1995). Kubota and Hara (1995) attributed low R^2 values (although regression models were significant) to greater effects of factors other than competition. One-way ANOVA, comparing mean plant height, cover or volume between clusters, showed variable results as did the use of plant density and soil characteristics as covariates. In most chenopod combinations, growth of target species was influenced by one or more of these factors. Higher R^2 values may have been obtained in the absence of limiting factors contributing to variation in plant performance but this is unrealistic in the natural environment (Silander and Pacala 1985, Wagner and Radosevich 1998). The young age of the 14 month old plants may also have contributed to low values.

The slope of the regressions, which indicate competition intensity (Welden *et al.* 1988), were also positive. Neither the importance of competition nor competition intensity was positively correlated with soil salinity or pH values obtained in this study. There was also no evidence of density dependence of the population dynamics of *E. tomentosa* and both *Maireana* species. The results obtained from the current study are consistent with those reflecting competition in other low productivity environments such as tundra (Summul *et al.* 2000), high alpine (Olofsson *et al.* 1999) and semi-arid desert (Yeaton and Cody 1976, Welden *et al.* 1988).

CONCLUSION

The establishment of target native species in mine site revegetation involves complex interactions between many factors, some of which, were demonstrated in this study (i.e. density, species, soil characteristics and competition). It was evident that intra- and inter-specific competition did occur between species of *Enchylaena* and *Maireana*. Intra-specific competition of *E. tomentosa* and *M. brevifolia* was evident within the environmental conditions of this study. Inter-specific competition also occurred when *E. tomentosa, M. brevifolia* and *M. georgei* were grown with *A. bunburyana*.

Competition, however, was highly unlikely when these species are grown with *A. codonocarpa*.

Although the importance and intensity of competition was low for all species combinations, it can be expected that they will change with time as the plants mature and attain greater size. Nearest neighbour measurements at three and five years since sowing may provide additional information about competition processes within chenopod communities.

Competition was, however, not dependent on broadcast seed density. Broadcasting of seeds at higher densities did not result in increased numbers of surviving seedlings, suggesting that the number of microsites available for germinant establishment may be limiting. In addition, these sites may have been completely occupied at the lowest seed density used in my study. Climatic conditions, the number of suitable microsites and weed competition will most likely influence the number of chenopod seedlings that survive. This in turn determines seedling densities and the age that they become large enough to interact and thus compete with each other for limiting resources.

Management Implications

The results of this chapter have highlighted the complexity of processes involved in plant community development on revegetation areas. The evidence resulting from this chapter should be used by managers during the development of restoration protocols and completion criteria. Some practical considerations should include:

- Broadcasting of seed at high densities will not necessarily result in an increased abundance of seedlings. Seedling recruitment may be improved by increasing the number of suitable microsites for survival and establishment (e.g. improved site preparation techniques) and minimising weed competition (e.g. development of weed eradication programs).

- Plant community structure following seedling establishment is dependent on limiting and regulatory processes, such as, annual climatic conditions, soil characteristics and intra- and inter-specific competition. Due to these processes the diversity and abundance of species within these plant communities, several years after sowing, can not necessarily be pre-determined by the components of the broadcast seed mixture. Therefore, it is necessary to set flexible completion criteria for the revegetation of waste and tailings materials.

CHAPTER 4: THE IMPLICATIONS OF VARYING PLANT DENSITY ON THE GROWTH OF THE FIVE CHENOPOD SPECIES

INTRODUCTION

The density of organisms within a community often determines whether or not significant intra- and inter-specific competition occurs (Callaway and Walker 1997, Dietz *et al.* 1998). Plant size also affects competition, particularly when plants grow in high densities. In order for competition to occur, plants must be large enough to interact (Weiner 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, especially when the density of plants increases (Hall 1978).

Studies to establish the degree of intra- and inter-specific plant competition often involve growing species of interest at different densities in pots in glasshouse conditions. Pot trials allow for better control of important environmental conditions such as nutrient, temperature and water regimes. Currently, there are three experimental designs routinely used to assess the effects of plant density on competitive processes. These are the replacement series (or substitutive), simple pair-wise and additive designs (Coussens and O'Neill 1993, Gibson *et al.* 1999).

The replacement series design compares the growth of two species when grown together in varying proportions to the growth of each species in monoculture. This design has been used to study competitive aggressiveness of *Pinus radiata*, *Eucalyptus regnans* and *Acacia melanoxylon* (Bi and Turvey 1994). The design is, however, limited to one region of the mixed density plane. That is, the results are only indicative of the effects of varying species proportions for one total plant density (Firbank and Watkinson 1985). This may result in incorrect inferences being made from species' relative performances and interactions (Connolly *et al.* 1990, Coussens and O'Neill 1993, Connolly 1997). The design is also biased, with a previous study indicating that in the first two years of

growth, there was a bias towards larger plants, which declined in the third year (Grace *et al.* 1992).

The simple pair-wise design, usually maintains a 1:1 ratio of the two competitors and is particularly useful in altering the environmental conditions under which the plants are grown. It is commonly used when comparing the effects of variable resource regimes on intra- and inter-specific competitive interactions between plants (Vargos-Mendoza and Fowler 1998, Hartley and Amos 1999). This design, however, does not allow conclusions to be drawn on the effects of altering ratios of each of the competing species.

The additive design ensures that the density of one species is constant while the density of the other species is varied. This design has been effectively used in a study of seven perennial and annual herbs that compared competitive effect with competitive response (Goldberg and Landa 1991). This design has also been used to determine optimal sowing patterns in mixed cropping systems (Firbank and Watkinson 1985). This design has been criticised because, as density increases of one species, so too does the proportion of the total number of plants, thus the effects of density and frequency can be confounded (Rew *et al.* 1995).

The main aim of the experiments reported in this chapter was to complement the field trial in chapter 3 and determine whether or not increasing densities of the target species in the seed mixture will affect survival and establishment rates on mine site revegetation areas. With current methods, *M. georgei* and *E. tomentosa* do not usually establish successfully in rehabilitated areas. *Maireana brevifolia* is a successful coloniser and it was, therefore, chosen to provide a contrast. All three target species were compared with *A. bunburyana* and *A. codonocarpa,* which often dominate areas rehabilitated following mining. It is expected that competition from *Atriplex* species could be detrimental to growth of *M. brevifolia*, *M. georgei* and *E. tomentosa.*

This chapter had three specific aims:

1) To determine whether intra-specific competition occurred in *M. brevifolia*, *M. georgei* and *E. tomentosa* when they were grown at different densities in monoculture.

2) To determine the responses (i.e. height and biomass) of *M. brevifolia*, *M. georgei* and *E. tomentosa* when grown with either *A. bunburyana* or *A. codonocarpa* as compared to monocultures (at a density of two plants per pot).

3) To determine the response of *A. bunburyana* and *A. codonocarpa* when grown with increasing densities of *M. brevifolia*, *M. georgei* and *E. tomentosa*. This will permit an assessment of whether or not increasing densities of these chenopods will restrict growth of individual *A. bunburyana* and *A.codonocarpa* plants, thereby providing the chenopods of interest with a competitive advantage.

MATERIALS AND METHODS

Topsoil, representative of that of the natural environment of chenopod species, was collected from areas surrounding the Westonia open-pit gold mine. The topsoil consisted of a dense clay containing 0.74 % organic carbon, 3.5 mg kg^{-1} nitrate, 1.0 mg kg^{-1} ammonium, 6.9 mg kg^{-1} phosphorous, 179.8 mg kg^{-1} potassium, 5.3 mg kg^{-1} sulphur, 344.6 mg kg^{-1} iron, an $EC_{1:5}$ of 0.1 mS cm^{-1} conductivity and a pH of 8.0 (Wesfarmer CSBP Laboratory). Although the topsoil was representative of the nutrients available to plants in the upper soil horizon, it was not representative of the soil profile through which the roots would grow. The compaction of the clay soil type in the pots would significantly reduce drainage. Therefore the topsoil was mixed with sand at a 1:1 ratio.

Seeds of *M. georgei*, *M. brevifolia*, *E. tomentosa*, *A. bunburyana* and *A. codonocarpa* were obtained from the semi-arid region of Kalgoorlie in Western Australia in 1997 (Nindethana Seed Services). *Maireana georgei* seeds were extracted from the fruiting body to overcome dormancy (Osborne *et al.* 1993). Seeds of the other four species were not extracted from their fruiting bodies. In August 1998 (winter), seeds were sown in free draining plastic pots (26.5 cm diameter and 25 cm high) at densities greater than required to ensure appropriate seedling germination and establishment rates.

Excess seedlings were removed after germination to manipulate the required densities. In the first experiment, *M. georgei*, *M. brevifolia* and *E. tomentosa* were grown in

monoculture at densities of one, two, four or ten plants per pot. In the second experiment, one plant of either *A. bunburyana* or *A. codonocarpa* was grown with either one plant of *M. georgei*, *M. brevifolia* or *E. tomentosa*. In the third experiment, *M. georgei*, *M. brevifolia* and *E. tomentosa* were grown at densities of one, two or four plants with one plant of either *A. bunburyana* or *A. codonocarpa*.

All pots were kept outdoors in a field trial area at Perth, Western Australia. Plants were watered once daily for 15 minutes during summer by an automatic watering system and weeded as required. Plants were not watered by an automatic watering system during winter because there was adequate rainfall for plant survival (Fig. 4.1). Fertilizer was not added to the pots. Mean temperatures ranged from 17 to 32 °C during summer and 8 to 19 °C in winter (Western Australian Bureau of Meteorology). There was high seedling death after a severe storm in September 1998, which caused the loss of some replicates in the first (Table 4.1A) and third experiments (Table 4.1B and 4.1C). Treatments containing four plants of *M. georgei* grown with one plant of *A. bunburyana,* or in monoculture, could not be considered because there were null repetitions. The number of replicate pots for the second experiment was 20 with half harvested at six months and the remainder at twelve months.

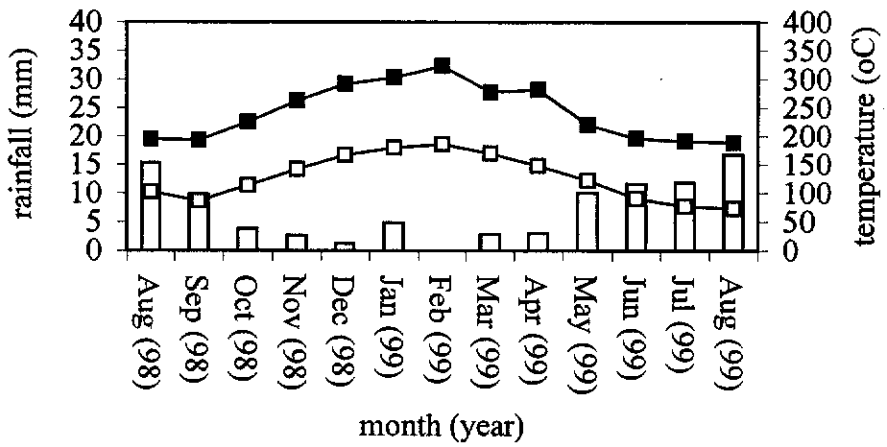


Figure 4.1 Mean monthly rainfall, minimum and maximum temperatures occurring in the Perth region during the period of the trial (Bureau of Meteorology, Western Australia).

Table 4.1 The number of replicate pots for the chenopod species (T), *Enchylaena tomentosa* (Et), *Maireana brevifolia* (Mb) and *Maireana georgei* (Mg) when grown in monoculture (A), and when grown with *Atriplex codonocarpa* (B) or *Atriplex bunburyana* (C). The different plant densities and harvest times are also shown.

A	6 months				12 months			
	plants per pot				plants per pot			
	1	2	4	10	1	2	4	10
Et	10	10	10	10	10	10	10	3
Mb	10	10	10	10	10	10	10	10
Mg	10	10	6	10	10	7	0	9

B	6 months				**C**	12 months		
	plants per pot					plants per pot		
	1Ac	1Ac+1T	1Ac+2T	1Ac+4T	1Ab	1Ab+1T	1Ab+2T	1Ab+4T
Et	10	10	10	10	10	10	10	9
Mb	10	10	10	10	10	10	10	7
Mg	10	10	10	10	10	10	10	0

Plant height of approximately half of the pots of each of the target species was measured six months after seedling emergence and then seedlings were harvested. The roots were washed clean of soil and each plant was divided into shoot and root components; that is, each plant was treated individually. Shoots and roots were dried in an oven at 60 °C for three days and the two components were then weighed. Root to shoot ratios were calculated for each replicate for each species. The same procedure was repeated for the twelve month harvest. The annual, *Atriplex codonocarpa* was harvested at six months and the perennial, *A. bunburyana*, was harvested at 12 months.

The homogeneity of variances was tested using Levene's test (Ott 1988). Where required, data were $\log_{10}$ transformed to produce normal distribution. Plant height and shoot and root weights at the different density treatments were analysed by one way analysis of variance (ANOVA) using SPSS 10.0 for Macintosh (1989-2000, SPSS Inc.) software. The means were compared using the Tukey's Compromise post-hoc test. Where homogeneity of variances could not be corrected by $\log_{10}$ transformation of data, the non-parametric Kruskal-Wallis test was used. This test approximates the parametric ANOVA procedure.

RESULTS

Experiment 1: Chenopod growth in monoculture

Enchylaena tomentosa

The height of six month old *E. tomentosa* plants significantly decreased when densities exceeded two plants per pot ($F_{3, 166} = 34.18$, $P < 0.001$). The height of twelve month old *E. tomentosa* plants, however, did not significantly differ between density treatments ($F_{3, 108} = 1.88$, $P = 0.138$, Fig. 4.2A). The root and shoot dry weight of individual plants decreased with increasing planting density for both six month ($F_{3, 166} = 67.89$, $P < 0.001$ and $F_{3, 166} = 59.08$, $P < 0.001$, respectively) and 12 month ($F_{3, 108} = 4.49$, $P = 0.006$ and $F_{3, 108} = 8.77$, $P < 0.001$, respectively) old plants (*F*ig. 4.2B, 4.2C). The root to shoot ratios were highest at densities of ten plants per pot at the six ($F_{3, 166} = 3.78$, $P = 0.012$) and twelve ($\chi^2_{3, 0.05} = 20.12$, $P < 0.001$) month harvest (Fig. 4.2D). All six month old plants at all densities had greater shoot than root biomass. At 12 months old, however, plants at higher density (4 - 10 plants per pot) had more root than shoot biomass.

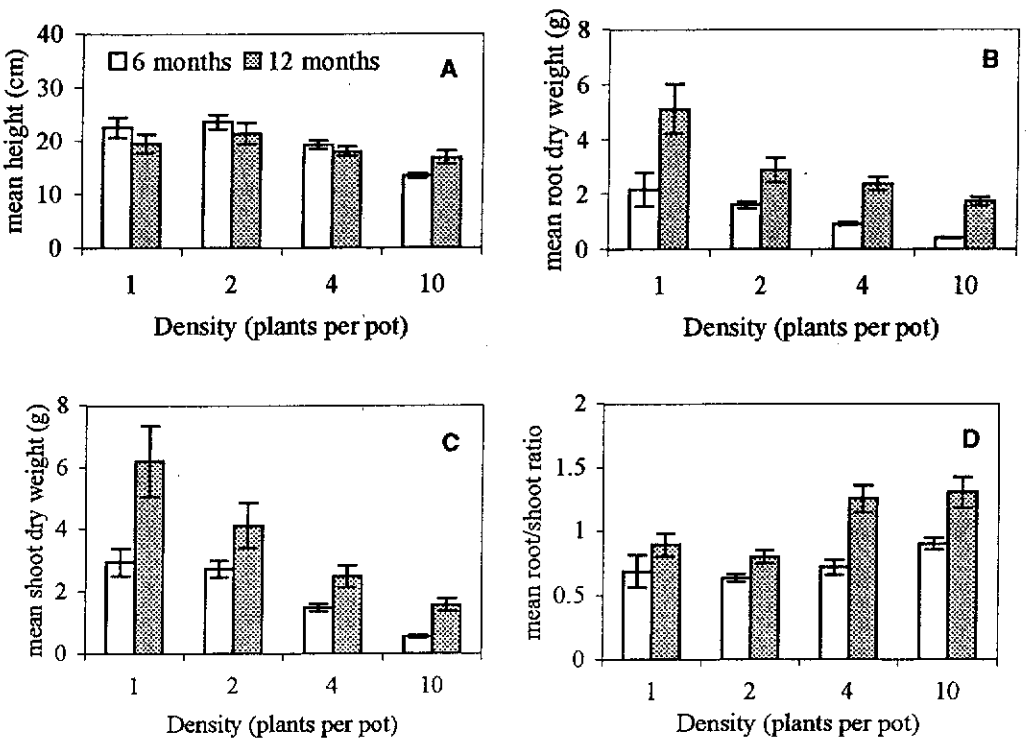


Figure 4.2 *Enchylaena tomentosa* mean height (A), root dry weight (B), shoot dry weight (C) and root/shoot ratio (D) when grown in monoculture at differing plant densities. Bars indicate standard errors.

Maireana brevifolia

There was a clear correlation between the height of *M. brevifolia* and plant density. Six month old *M. brevifolia* plants were shorter in height as plant density increased ($F_{3, 165}$ = 51.67, $P < 0.001$, Fig. 4.3A). By 12 months there were no differences in height between planting densities of 1 - 4 plants per pot, however, plants at densities of ten per pot were significantly shorter ($F_{3, 140}$ = 13.05, $P < 0.001$). The root and shoot dry weight decreased as plant density increased in six ($F_{3, 165}$ = 110.32, $P < 0.001$ and $F_{3, 165}$ = 101.07, $P <$ 0.001, respectively) and 12 ($F_{3, 140}$ = 28.34, $P = 0.000$ and $F_{3,140}$ = 21.41, $P < 0.001$, respectively) month old plants (Fig. 4.3B, 4.3C). The root to shoot ratio increased as planting density increased in six month old *M. brevifolia* plants (χ^2_3 = 38.82, $P < 0.001$), but there was no significant difference in this ratio at 12 months ($F_{3, 147}$ = 1.35, $P = 0.259$, Fig. 4.3D). Individuals had equal root and shoot biomass when grown at densities of 1 - 4 plants per pot but had greater root than shoot biomass when grown at a density of ten plants per pot for both six and 12 month old *M. brevifolia* plants.

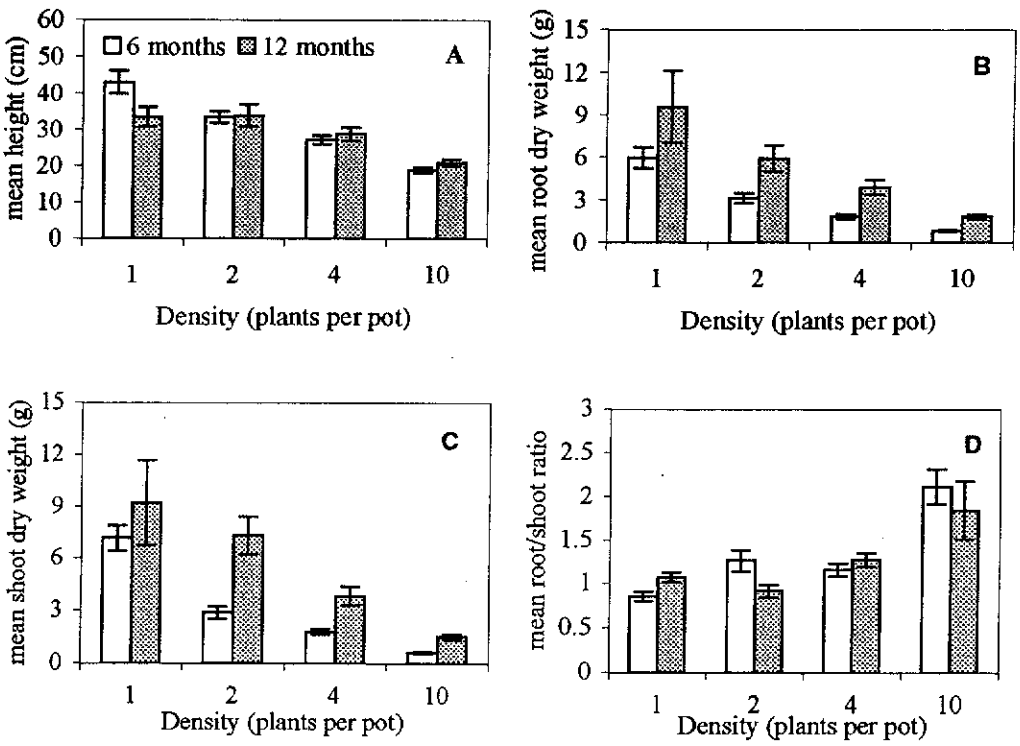


Figure 4.3 The mean height (A), root dry weight (B), shoot dry weight (C) and root/shoot ratio (D) of *Maireana brevifolia* when grown in monoculture at differing densities. Bars indicate standard errors.

Maireana georgei

The height of *M. georgei* plants was unaffected by planting density at both six ($\chi^2_3 = 8.49$, $P = 0.037$) and 12 ($F_{2,107} = 0.72$, $P = 0.489$) months of age (Fig 4.4A). The root and shoot dry weights of six month old ($\chi^2_3 = 42.58$, $P < 0.001$ and $\chi^2_3 = 34.32$, $P < 0.001$, respectively) (Fig 4.4B) and 12 month old ($F_{2,107} = 23.66$, $P = 0.000$ and $\chi^2_3 = 53.73$, $P < 0.001$, respectively) (Fig 4.4C) plants decreased as plant density increased. Root to shoot ratios did not significantly differ with increasing density of six month old *M. georgei* plants ($F_{3, 150} = 1.38$, $P = 0.252$). In contrast, at 12 months, plants had significantly higher ratios at a density of ten plants per pot compared to densities of one and two plants per pot ($F_{2, 104} = 26.37$, $P < 0.001$). Generally, plants had greater shoot than root biomass, regardless of plant density, for both the six and 12 month old *M. georgei* plants.

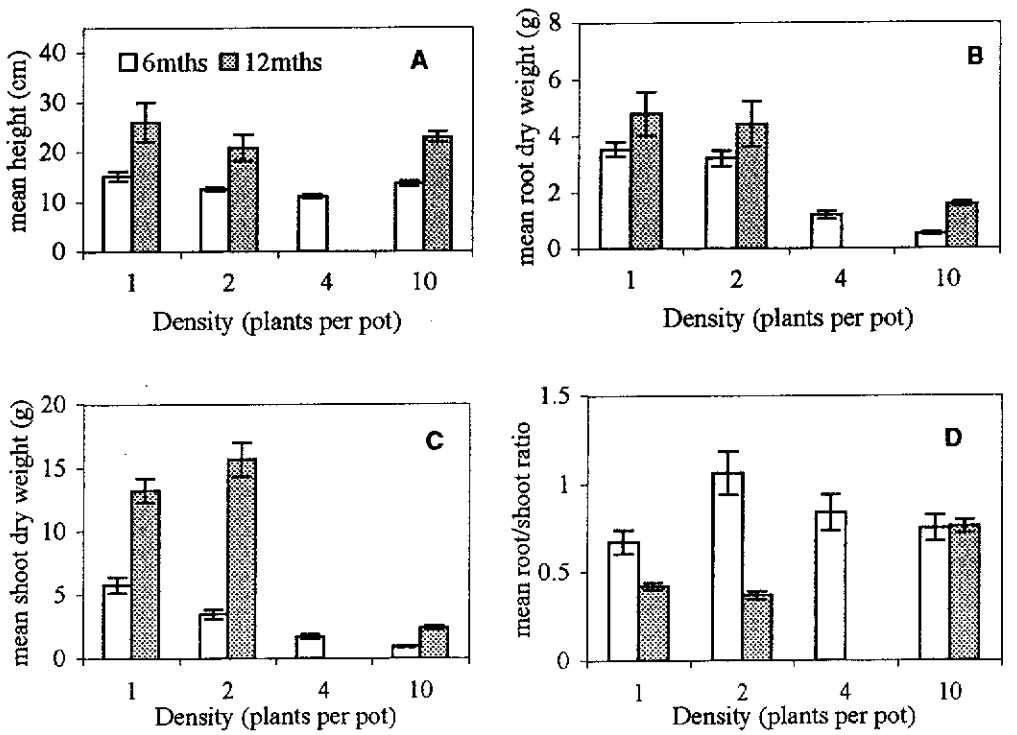


Figure 4.4 *Maireana georgei* mean height (A), root dry weight (B) and shoot dry weight (C) and root/shoot ratio (D) when grown in monoculture at differing densities. Bars indicate standard errors.

Mortality

For *E. tomentosa*, *M. brevifolia* and *M. georgei* there was little or no mortality observed at six months of age across all planting densities. However, there were some plant deaths during the 6 - 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 ten plants per pot. *M. georgei* had 35% and 16% mortality, at a density of two and ten plants per pot, respectively, by the 12 month harvest.

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 to plants grown in two-species mixtures (with *A. bunburyana* or *A. codonocarpa*) at a density of two plants per pot (Tables 4.2 - 4.4). No mortality was recorded when these plants were grown in association with *A. bunburyana* and *A. codonocarpa.*

Enchylaena tomentosa

There was no significant difference between the height of six month old *E. tomentosa* plants grown in monoculture or with *Atriplex* species (Table 4.2). Shoot dry weight of *E. tomentosa* was significantly greater when grown in association with *A. codonocarpa* compared to *A. bunburyana.* There was no significant difference, however, between six month old *E. tomentosa* grown in monoculture or with *Atriplex* species. The root dry weight of six month *E. tomentosa* plants was significantly greater when grown with *A. codonocarpa*, compared to plants grown in monoculture or with *A. bunburyana.* At 12 months, plant height and shoot and root dry weight of *E. tomentosa* was significantly greater when grown with *A. codonocarpa* compared to when grown with *A. bunburyana* or in monoculture.

Table 4.2 Growth parameters (means and the standard errors in brackets) of plants aged 6 and 12 months. One-way ANOVA summaries compare *E. tomentosa* (Et) (at a density of two plants per pot) grown in monoculture with those grown in 2 species mixtures (one plant of *E. tomentosa* and one plant of *A. bunburyana* (Ab) or *A. codonocarpa* (Ac)) ($P < 0.05$). Similar letters indicate means, which are not significantly different, based on Tukeys Compromise test ($P < 0.05$).

6mths					
	Et	**Et (Ab)**	**Et (Ac)**	***F***	***P***
Height (cm)	23.45^{a} (1.30)	18.79^{a} (2.43)	23.84^{a} (3.04)	$F_{2,37} = 1.60$	0.216
Shoot Dry Weight (g)	2.70^{ab} (0.26)	1.61^{b} (0.41)	3.59^{a} (0.57)	$F_{2,37} = 5.13$	**0.011**
Root Dry Weight (g)	1.59^{b} (0.13)	0.98^{b} (0.31)	1.94^{a} (0.32)	$F_{2,37} = 4.77$	**0.014**
12mths					
	Et	**Et (Ab)**	**Et (Ac)**	***F***	***P***
Height (cm)	21.25^{b} (1.97)	21.67^{b} (1.11)	33.47^{a} (3.64)	$F_{2,35} = 5.27$	**0.010**
Shoot Dry Weight (g)	4.09^{b} (0.74)	2.82^{b} (0.56)	6.75^{a} (0.90)	$F_{2,35} = 4.11$	**0.025**
Root Dry Weight (g)	2.86^{b} (0.45)	2.67^{b} (0.70)	5.19^{a} (0.61)	$F_{2,35} = 5.35$	**0.009**

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 4.3). Root dry weight of *M. brevifolia* were, however, reduced grown alongside *A. bunburyana* plants. At 12 months of age, plant height and shoot and root dry weights of *M. brevifolia* did not differ when grown in association with *Atriplex* species or in monoculture.

Table 4.3 Growth parameters (means and the standard errors in brackets) of plants aged 6 and 12 months. One-way ANOVA summaries compare *M. brevifolia* (Mb) (at a density of two plants per pot) grown in monoculture with those grown in 2 species mixtures (one plant of *M. brevifolia* and one plant of *A. bunburyana* (Ab) or *A. codonocarpa* (Ac)) ($P < 0.05$). Similar letters indicate means, which are not significantly different, based on Tukeys Compromise test ($P < 0.05$).

6mths					
	Mb	**Mb(Ab)**	**Mb(Ac)**	***F***	***P***
Height (cm)	33.32[a] (1.61)	33.25[a] (2.88)	27.62[a] (1.85)	$F_{2,37} = 2.20$	0.126
Shoot Dry Weight (g)	2.84[a] (0.35)	2.38[a] (0.42)	2.81[a] (0.28)	$F_{2,37} = 0.40$	0.675
Root Dry Weight (g)	3.10[a] (0.30)	1.6[b] (0.30)	2.79[a] (0.29)	$F_{2,37} = 5.62$	**0.007**
12mths					
	Mb	**Mb(Ab)**	**Mb(Ac)**	***F***	***P***
Height (cm)	33.71[a] (3.02)	28.05[a] (2.70)	31.15[a] (2.74)	$F_{2,37} = 0.83$	0.442
Shoot Dry Weight (g)	7.29[a] (1.10)	3.30[a] (0.75)	4.26[a] (0.63)	$F_{2,37} = 2.68$	0.082
Root Dry Weight (g)	5.88[a] (0.92)	3.47[a] (0.72)	4.62[a] (0.64)	$F_{2,37} = 1.86$	0.171

Maireana georgei

The height of six month old *M. georgei* plants grown with *A. bunburyana* was significantly greater than that of plants grown in monoculture or with *A. codonocarpa* (Table 4.4). Twelve month old *M. georgei* plants also exhibited increased plant height when grown with *A. bunburyana*. Shoot dry weights of six month old *M. georgei* plants were significantly greater when grown with *A. codonocarpa* compared to when grown with *A. bunburyana* or in monoculture. At 12 months, however, *M. georgei* shoot dry weight was greatest when grown in monoculture. Root dry weight of six month old *M. georgei* plants was significantly lower when grown with *A. bunburyana* compared to plants grown in monoculture. At 12 months, there was no significant difference in root dry weight between *M. georgei* grown in monoculture or with *Atriplex* species.

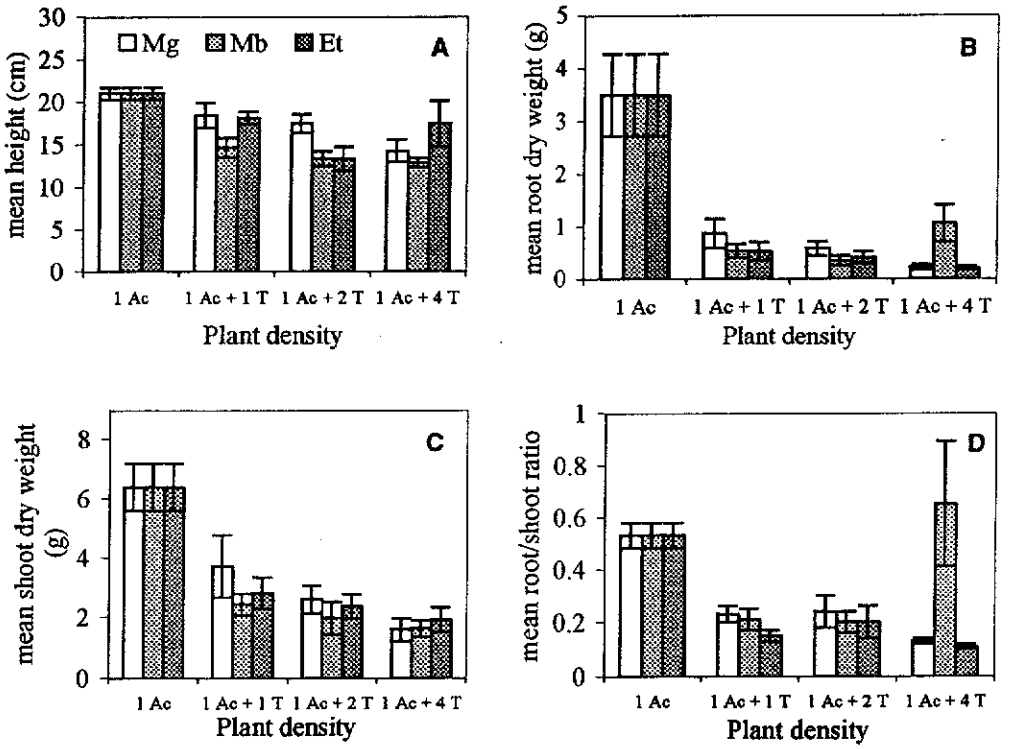
Table 4.4 Growth parameters (means and the standard errors in brackets) of plants aged 6 and 12 months. One-way ANOVA summaries compare *M. georgei* (Mg) (at a density of two plants per pot) grown in monoculture with those grown in 2 species mixtures (one plant of *M. georgei* and one plant of *A. bunburyana* (Ab) or *A. codonocarpa* (Ac)) ($P < 0.05$). Similar letters indicate means, which are not significantly different, based on Tukeys Compromise test ($P < 0.05$). χ^2 values are given when the Kruskal-Wallis non-parametric test was used.

6mths					
	Mg	**Mg(Ab)**	**Mg(Ac)**	***F***	***P***
Height (cm)	12.51^{c} (0.34)	24.73^{a} (1.52)	15.20^{b} (1.02)	$F_{2,37} = 55.36$	**<0.001**
Shoot Dry Weight (g)	3.41^{b} (0.36)	3.04^{b} (0.60)	5.40^{a} (0.54)	$F_{2,37} = 5.96$	**0.006**
Root Dry Weight (g)	3.19^{a} (0.28)	1.69^{b} (0.36)	2.34^{ab} (0.34)	$F_{2,37} = 5.67$	**0.007**
12mths					
	Mg	**Mg(Ab)**	**Mg(Ac)**	***F***	***P***
Height (cm)	20.81^{b} (2.69)	39.20^{a} (2.71)	21.32^{b} (1.50)	$F_{2,31} = 16.61$	**<0.001**
Shoot Dry Weight (g)	15.61^{a} (1.35)	6.83^{b} (0.63)	10.21^{b} (0.97)	$F_{2,31} = 16.69$	**<0.001**
Root Dry Weight (g)	4.39^{a} (0.8)	2.97^{a} (0.37)	4.79^{a} (0.33)	$\chi^2_2 = 5.806$	0.055

Experiment 3: Growth of *Atriplex codonocarpa* and *A. bunburyana* when grown with the three chenopod species of interest

Atriplex codonocarpa

Plant height, root and shoot dry weight of six month old *A. codonocarpa* plants decreased as the density of the target plants increased (Fig 4.5). The root/shoot ratio of six month old *A. codonocarpa* plants was 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.

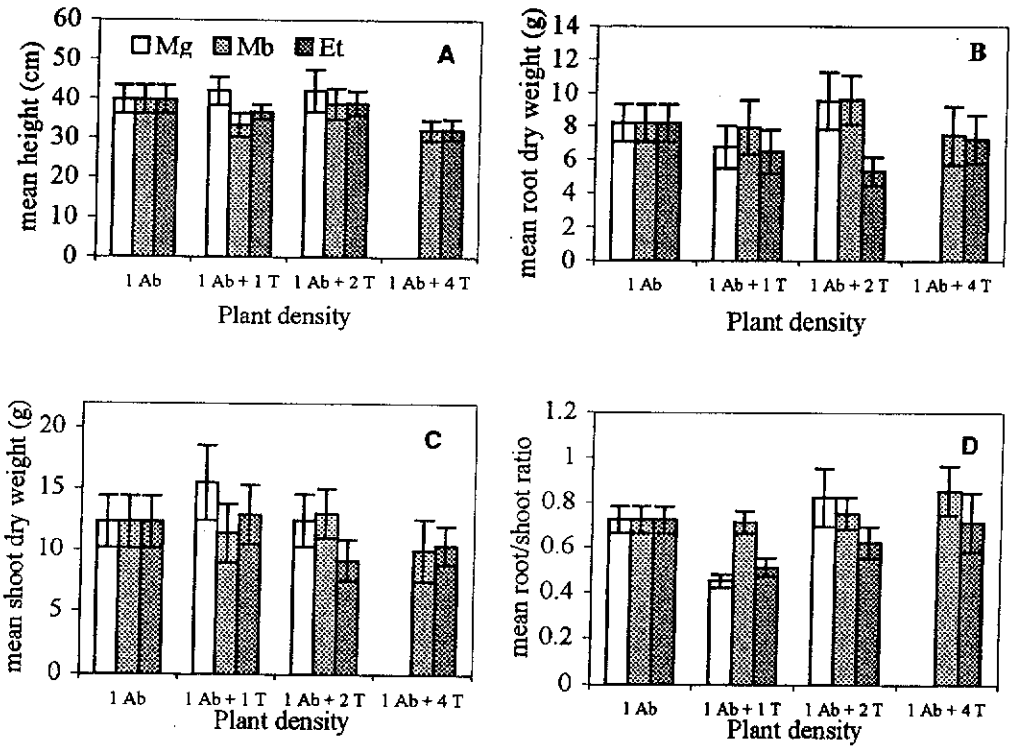


	Height (cm)		Root DW (g)		Shoot DW (g)		Root/shoot ratio	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Et	$F_{3,36} = 3.93$	0.159	$F_{3,36} = 39.03$	**<0.001**	$F_{3,36} = 13.21$	**<0.001**	$F_{3,36} = 22.19$	**<0.001**
Mb	$F_{3,36} = 20.11$	**<0.001**	$\chi^2_3 = 18.53$	**<0.001**	$F_{3,36} = 17.13$	**<0.001**	$\chi^2_3 = 12.25$	**0.007**
Mg	$\chi^2_3 = 12.85$	**0.005**	$F_{3,36} = 28.79$	**<0.001**	$F_{3,36} = 8.04$	**<0.001**	$F_{3,36} = 18.57$	**<0.001**

Figure 4.5 Mean *A. codonocarpa* (Ac) plant height (A), root dry weight (B), shoot dry weight (C) and root/shoot ratio (D) when grown with increasing numbers of the three chenopod species (T) ; *M. brevifolia* (Mb), *E. tomentosa* (Et) or *M. georgei* (Mg). Bars indicate mean ± SE. The control consisted of one plant of *A. codonocarpa* or *A. bunburyana* per pot. The table is a summary of the *F* and *P* values from one-way ANOVAs performed on each of the measured *A. codonocarpa* growth parameters.

Atriplex bunburyana

There were no significant differences in plant height, root or shoot dry weight of *A. bunburyana* plants grown with different plant densities of the three competing chenopod species (Fig. 4.6). Root/shoot ratios of *A. bunburyana* did not differ when the plant density of either *E. tomentosa* or *M. brevifolia* was increased. *Atriplex bunburyana* root/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.



	Height (cm)		Root DW (g)		Shoot DW (g)		Root/shoot ratio	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Et	$F_{3,35} = 1.20$	0.326	$F_{3,35} = 1.06$	0.376	$F_{3,35} = 0.75$	0.528	$F_{3,35} = 1.53$	0.224
Mb	$F_{2,33} = 1.18$	0.333	$F_{3,33} = 0.38$	0.771	$F_{3,33} = 0.29$	0.829	$F_{3,33} = 0.71$	0.553
Mg	$F_{2,27} = 0.08$	0.922	$F_{2,27} = 0.99$	0.380	$F_{2,27} = 0.52$	0.599	$F_{2,27} = 5.16$	**0.013**

Figure 4.6 *Atriplex bunburyana* (Ab) plant height (A), root dry weight (B), shoot dry weight (C) and root/shoot ratio (D) when grown with increasing numbers of the target plants (T); *M. brevifolia* (Mb), *E. tomentosa* (Et) or *M. georgei* (Mg). The control consisted of one plant of *A. codonocarpa* or *A. bunburyana* per pot. Bars indicate mean ± SE. The table displays the *F* and *P* values from one-way ANOVAs performed on each of the measured *A. bunburyana* growth parameters.

DISCUSSION

Competition plays an important role in determining the botanical composition of plant communities (Wilson 1988a). Interactions between plants growing at different densities in the same location are dependent on species characteristics and the conditions under which they grow (Wilson 1988a). Conditions that may influence the outcome of plant interactions include available soil volume (pot size) (McConnaughay and Bazzaz 1991), time (age of plants) (Wilson 1988b) and resource availability (Bi and Turvey 1994). Different species may also exhibit different sensitivities to these conditions (Pantastico-Caldas and Venable 1993). Although the environmental conditions experienced by the pot trial were different to those in the field at Coolgardie, they provide valuable insight into the mechanisms of competitive interaction of chenopods (Gibson *et al.* 1999).

Root competition is the main mode of competition determining plant community structure in arid and semi-arid environments. Nutrients and space were the likely cause of intra- and inter-specific competition in the current study. In the natural environment, however, moisture availability is also a limiting resource and likely to be a cause of competition. The growth form and correlated traits determine the competitive ability of plants (Dietz *et al.* 1998). Both *A. bunburyana* and *M. brevifolia* have a greater overall height and biomass, in comparison to the other species. These traits give these species a competitive advantage over smaller species. Size differences will likely cause asymmetric competition, where larger plants obtain more of the available resources (Weiner *et al.* 1997). Sufficient evidence shows that asymmetric competition regulates growth of plants in semi-arid and arid environments (Cable 1969, Yeaton and Cody 1976, Goldberg and Novoplansky 1997, Vargas-Mendoza and Fowler 1998, Pugnaire and Luque 2001).

Is intra-specific competition occurring between plants of the three chenopod species of interest?

The negative impact expressed in the growth attributes of the three chenopod species with increasing plant density is indicative of competition (Weiner 1997, Vargas-Mendoza and Fowler 1998). This was particularly evident when the chenopod species was grown in monoculture and it occurred independent of plant age. A change in allocation of resources between roots and shoots indicates the type of competition that is 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 below-ground competition. Restrictions imposed by available soil volume (pot size) and soil nutrients may have increased with time and became 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 to the other species. Allocation of resources into the roots may make a species superior when competing for nitrogen (Gleeson and Tilman 1990, Witkouski 1991, Dietz *et al.* 1998). Larger root systems are beneficial when competing for nutrients, particularly in the nutrient-poor soil of many semi-arid environments (Aerts 1999). The onset of nutrient deficiencies can trigger the development of higher root/shoot ratios (see review of Clarkson and Hanson 1980). This may provide an explanation for the better establishment success of *M. brevifolia* compared to that of *E. tomentosa* and *M. georgei*, especially on mine site revegetation areas.

Is inter-specific competition occurring when the selected chenopod species 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 to 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 above-ground 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 to the available space when grown in monoculture or in the presence of an *A. bunburyana* plant.

Inter-specific competition when grown in the presence of *A. 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*. Competition for light is a key causal factor of the observed effects of increases in plant height (Newman 1973). 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 "snowballs" over time until shorter plants are totally suppressed (Newman 1973, Rhodes and 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. Aggressiveness of *Acacia melanoxylon* was reflected by its relatively unchanged shoot/root ratio in response to inter-specific competition (Bi and Turvey 1994). *Atriplex bunburyana* showed a similar response when grown with *E. tomentosa* and *M. brevifolia.* The growth of the annual, *A.codonocarpa,* in contrast, decreased when the density of the three chenopod species was increased. As indicated by increased shoot biomass, *A. codonocarpa* increased its allocation of resources to its shoot when grown with *M. georgei* or *E. tomentosa.* The effects of competition were expressed by increased growth of the above-ground plant tissues (Dietz *et al.* 1998), and in this instance, may have resulted from the relatively short life-cycle of *A. codonocarpa* and its need to reproduce within a short space of time.

CONCLUSION

Interactions between plants are induced by the necessity to share limited resources (Lemaire and Millard 1999). Nutrients and space were limiting factors during the pot trials, and became more limiting as plants grew. Those species that have a faster growth rate may have a competitive advantage particularly in nutrient poor environments (Aerts 1999, Cahill Jr. 1999). *Atriplex bunburyana* demonstrated more aggressiveness as a competitor relative to the other species examined. *Maireana brevifolia* also showed an ability to be competitive in comparison to *M. georgei* and *E. tomentosa.* Intra- and inter-specific competition occurred between both these species and the species of *Atriplex. Atriplex codonocarpa* was a weak competitor under the conditions of the pot trial but this may be a consequence of the limited space and nutrient availability of the pots in comparison to the natural environment in which they would normally occur.

Management Implications

The results outlined in this chapter provide an indication that intra- and inter-specific competition does occur between the five chenopods studied. Revegetation programs should take into account the competitive aggressiveness of *A. bunburyana*. The ability of this species to out compete both *Maireana* species and *E. tomentosa* provides evidence of its ability to dominate revegetation areas several years after sowing. When determining the components, and their 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.

CHAPTER 5: SALINITY AND MOISTURE RELATIONS OF *A. BUNBURYANA*, *A. CODONOCARPA*, *M. BREVIFOLIA*, *M. GEORGEI* AND *E. TOMENTOSA*

INTRODUCTION

Mine waste, in particular tailings materials, is often highly saline. The utilization of chenopod species in the revegetation of mine site areas in the goldfields region of Western Australia is due, in part, to their ability to tolerate highly saline soils (Mitchell and Wilcox 1998). Although the members of the Chenopodiaceae family are halophytes they do, however, show variation in optimal growth at differing concentrations of salt (Black 1960, Aslam *et al.* 1988, Malcom *et al.* 1988, Groom *et al.* 1993).

The accumulation of high NaCl levels within chenopod plants aids in their tolerance to saline soils (Black 1955, Dodd and Donovan 1999, Glenn *et al.* 1999). Chenopod species are able to tolerate highly saline environments by storing NaCl in their shoot tissues (Black 1955, 1958, 1960, Gale and Poljakoff-Maber 1970, Short and Colmer 1999). The storage of NaCl in their leaves has the advantage of reflecting light and minimising heat load and water loss during summer (Sharma 1982).

Water conservation is essential to plant survival in semi arid and arid environments and chenopods display a variety of morphological and physiological traits that allow them to tolerate drought. Some chenopod species have deep and extensive root systems, while others have shallow fibrous root systems (Carrodus and Specht 1965, Jones and Hodgkinson 1970). Plants with deep root systems are thought to be better adapted to drought conditions than those with shallow root systems (Sharma 1982, Ishikawa *et al.* 1996). Plants with shallow root systems, however, often have other physiological attributes that allow them to tolerate drought conditions (Carrodus and Specht 1965, Jones and Hodgkinson 1970). *Atriplex vesicaria*, a shallow rooted species, for example, was able to extract a significantly greater percentage of moisture from the soil compared to the deep-rooted species, *Maireana sedifolia* (Carrodus and Specht 1965). In addition to the size of the root system, fast root growth

rates provide the added advantage of greater access to soil moisture during periods of low moisture availability (Jones and Hodgkinson 1970).

Some chenopod species have the ability to extract soil water at exceedingly low water potentials, whereas others have greater control over their rate of water use (Sharma 1976). During dry summer periods, photosynthesis and transpiration slows, with water uptake maintaining plant survival rather than growth. Transpiration rates of *Atriplex* and *Maireana* species are generally very low (Kaplan and Gale 1972, Sharma 1976, 1982). Reduced hydraulic conductivity of the root system, in response to salinity, may contribute to such low transpiration rates (Kaplan and Gale 1972). The positive effects of salinity on plant water relations can be of substantial ecological value to species in semi-arid and arid environments (Gates 1972, Groome *et al.* 1993).

Chenopods may share acquired water with their neighbours. During periods of low moisture availability, shallow-rooted plants may have access to the water obtained by their deep-rooted neighbours. The mechanism explaining the movement of water through the roots from deep moist soils to shallow dry soils is referred to as 'hydraulic lift' (HL) (Caldwell *et al.* 1989). Facelli and Temby (2002) recently found that trenching decreased the number of annual seedlings growing under the canopy of *Atriplex vesicaria* plants. During the trenching process HL had been prevented by the severing of *A.vesicaria* roots. Prior to trenching, a large fraction of daily transpiration was lifted at night. This source of water was used to rehydrate some of the soil in the upper layers making moisture available to the annual seedlings.

In contrast, water is known to be a limiting resource over which plants in semi-arid and arid environments may compete (Cable 1969, Eissenstat and Caldwell 1988, Kadmon 1995, Goldberg and Novoplansky 1997, Hartvigsen 2000). Traits that enable plants to be superior competitors for moisture in semi-arid and arid environments include:

- rapid water extraction rates during times of adequate water availability (Carrodus and Specht 1965, Eissenstat and Caldwell 1988),
- fast root growth rates (Cable 1969, Jones and Hodgkinson 1970, Hartvigsen 2000),
- extended growth periods into the summer season (Cable 1969),

- ability to store water (e.g. succulence and tuberous roots, Ishikawa *et al.* 1996, Pyankov *et al.* 2000), and
- deep root systems (Fowler 1986, Pyankov *et al.* 2000).

Such plant traits may be inter-related or independent. Succulents, such as cacti, typically have shallow root systems (Fowler 1986). In contrast, a combination of succulence with a deep root system provides *Haloxylon ammodendron* with a competitive advantage (Pyankov *et al.* 2000). Competition and variety of plant growth form creates a diverse range of niches allowing different resource use by species and coexistence (Fowler 1986). Species with similar mechanisms of water acquisition and use are, however, likely to be in direct competition.

Most studies in semi-arid and arid environments have focussed on the ability of plant species to compete for moisture while some studies have examined salinity and moisture availability to account for plant community distribution patterns (Dodd and Donovan 1999, Egan and Ungar 2000, Pyankov *et al.* 2000). There is, however, little research incorporating the interaction of NaCl and moisture in terms of plant species competition. Pulsing regimes (i.e. watering at different time intervals) were incorporated into the design of the experiments in this chapter because they have a greater impact on the ability of plants to compete in semi-arid environments in comparison to total water availability (Goldberg and Novoplansky 1997, Novoplansky and Goldberg 2001).

The aim of this chapter was to compare the competitive ability of five chenopod species and their respective mechanisms of tolerating salinity under short-term drought conditions. The outcomes of these trials were then used to assess the competitive abilities of the five chenopod species studied, particularly with respect to their ability to tolerate the environmental conditions where these plants naturally occur.

Specifically, the aims of this chapter are to investigate:

1) each species' ability to tolerate salinity under short term drought conditions,

2) attributes that contribute to competitive ability under high salinity and drought conditions, and

3) each species' ability to utilise NaCl under short-term drought conditions.

MATERIALS AND METHODS

Pre-experimental set-up

Pots used in this trial had a diameter of 17.5 cm and height of 16.0 cm. They were lined with plastic bags to control drainage and to inhibit leaching of added NaCl. The soil mixture was composed of 50% Westonia topsoil and 50% sand as in previous pot trials (Chapter 4).

Seeds of *A. bunburyana, A. codonocarpa, M. brevifolia, M. georgei* and *E. tomentosa* were germinated in trays of sand in a glasshouse under ambient conditions. When four weeks old they were transplanted, one plant per pot, and were kept well watered for four weeks. Pots were placed under a covered polytunnel to prevent rainfall disrupting the watering regimes. Mean temperatures during the period of the trial (summer 1999/2000) are shown in Figure 5.1.

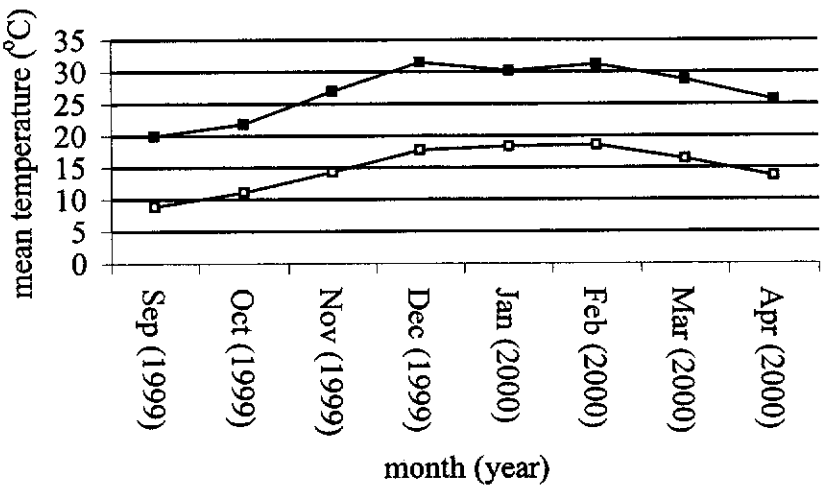


Figure 5.1 Mean monthly temperatures of the Perth Region from December 1999 to April 2000 (Bureau of Meteorology, Western Australia).

Treatment Design

Three soil moisture and three salinity treatments were applied in a randomised block design to all five species with ten replicates per treatment. Sodium chloride, dissolved in deionised water, was used to achieve electrical conductivity measurements of 2.5 and 5.0 mS cm^{-1} in a 1:5 soil: deionised water solution ($EC_{1:5}$). The soil salinity treatments were similar to the soil salinity of waste materials on the Herald Resources mine site (Chapter 3). Although no NaCl was added to the 0.0 mS cm^{-1} ($EC_{1:5}$) treatment, a minimal concentration of 0.1 mS cm^{-1} ($EC_{1:5}$) existed in the soil.

The total NaCl needed to be added to the soil to achieve 2.5 and 5.0 mS cm^{-1} was determined prior to experimentation. This was achieved by adding five different amounts of NaCl to five lots of the soil mixture, mixing and then measuring the salinity of three soil sub-samples, each 20g. The resulting mean salinities were then plotted on a graph to determine how much salt needed to be added to the pots to achieve 2.5 or 5.0 mS cm^{-1} treatments. Salt solutions were made up in 20L containers and plants were then watered with 100ml samples (approx. 2% of field capacity). NaCl solutions were added dayly over a period of four weeks until the desired concentrations were reached. At the end of the four weeks, moisture treatments then commenced for a period of two months. Moisture treatments involved the addition of 100 ml of rainwater per pot at two, four or eight day intervals. NaCl and water solutions were applied to the soil surface and a perforated down tube to prevent local concentration of NaCl and water at the soil surface.

Data Collection

Maximum and minimum air temperature was recorded at two day intervals within the polytunnel. The number of branches, plant height (H), maximum width (W1) and the width 90° to the maximum width (W2) were recorded. Four assessments were made: 1) before NaCl application (8 weeks old), 2) after NaCl application (12 weeks old), 3) after 4 weeks of moisture treatment (16 weeks old), and 4) prior to harvest after 8 weeks of moisture treatment (20 weeks old).

Further measurements were recorded prior to plant harvest including leaf thickness and leaf area of ten mature leaves taken at random from six plants for each treatment. Measurements of leaf thickness were excluded from plants growing under the four day watering regime. Leaf thickness was measured with Vernier callipers and leaf areas were determined using a digital image analyser (DIAS, Delta-T Devices, Cambridge, UK). Three seedlings from each salinity treatment were also selected from the two and eight day watering regimes to measure xylem water potentials. Predawn and midday xylem pressures, before and after watering, of three replicate plants from each salinity treatment and grown under a two or eight day watering regime were measured using a pressure chamber (Soil Moisture Equipment Corporation Model 3005). At harvest, leaf, stem and root weights (wet and dry) were recorded. Plant mortality was also recorded at harvest.

Data Calculations

Succulence and leafiness were calculated according to Gale and Poljakoff-Mayber (1970) using the following equations:

$$\text{Succulence} = \frac{\text{total fresh weight}}{\text{total dry weight}}$$

$$\text{Leafiness} = \frac{\text{total leaf fresh weight}}{\text{total stem fresh weight}}$$

Above-ground volume of each species was estimated as:

$$\text{Volume (cm}^3\text{)} = H \times W1 \times W2$$

Plant relative growth rate (RGR) was calculated as:

$$\text{RGR (day}^{-1}\text{)} = \frac{[\ln (v_2 / v_1)]}{t_2 - t_1}$$

where:

v_1 = plant volume at first assessment,

v_2 = plant volume at second assessment, and

$t_2 - t_1$ = time difference (days) between first and second assessments.

Homogeneity of variances was tested using Levenes test and $\log_{10}$ transformation occurred when data was not normally distributed. A two way ANOVA was performed to compare soil salinity and water frequency treatments and a one way ANOVA was performed to compare salinity treatments under specific watering frequencies for the following plant measurements;

- root and shoot weights,
- number of branches produced and plant height,
- leafiness, succulence and leaf thickness,
- predawn and midday water potentials, and
- RGR.

RESULTS

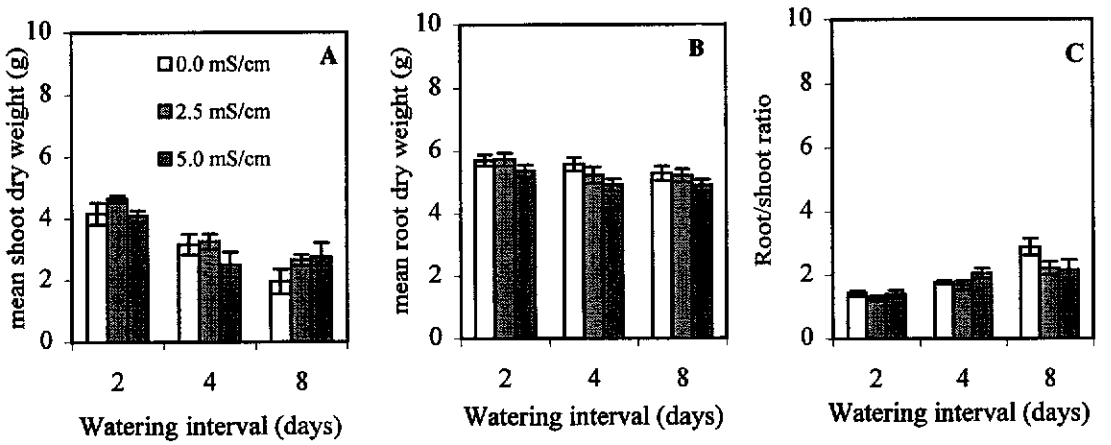
Mortality

All plants survived the salinity treatments and the watering regimes, except those growing in non-saline soil (0.0 mS cm^{-1} $EC_{1:5}$) and watered every eight days. Chenopod species growing under this regime had variable mortality rates: 20% for *M. georgei*, 30% for *A. bunburyana*, 40% for *E. tomentosa*, and 50% for both *M. brevifolia* and *A. codonocarpa* plants.

Shoot and Root Dry Weights and Biomass Allocation Pattern

The shoot dry weight of *M. georgei* decreased in response to the less frequent watering regimes (Fig. 5.2A). The root dry weight also significantly decreased in response to less frequent watering regimes (Fig. 5.2B). When plants were watered at four day intervals, root dry weights decreased with increasing NaCl ($F_{2,27}$ = 4.52, P = 0.020). Shoot dry weights, however, only showed significant decreases between 2.5 and 5.0 mS cm^{-1} NaCl treatments when plants were watered at four day intervals ($F_{2,27}$ = 3.77, P = 0.036). Salinity had no effect on shoot or root dry weight, however, when plants were watered at

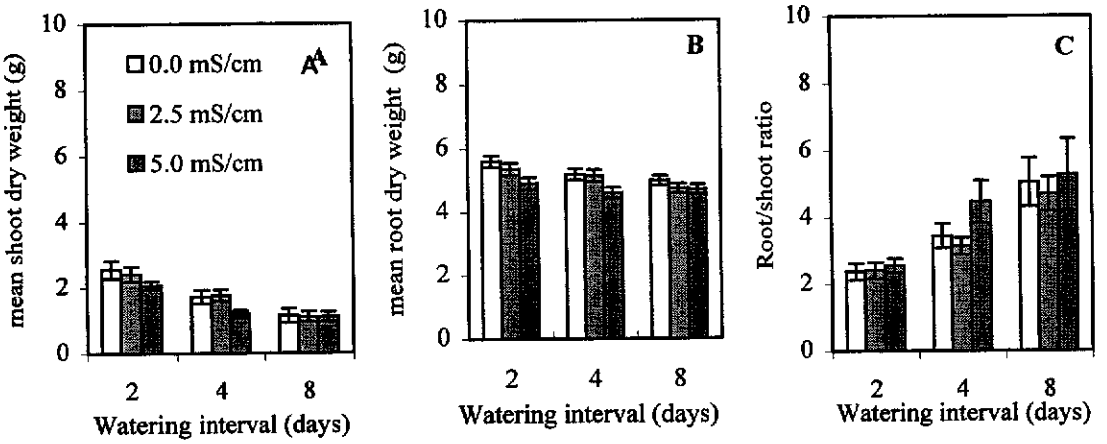
two ($F_{2,27}$ = 1.08, P = 0.355 and $F_{2,27}$ = 2.92, P = 0.072, respectively) or eight day intervals ($F_{2,24}$ = 0.72, P = 0.496 and $F_{2,24}$ = 2.17, P = 0.134, respectively). The root/shoot ratio increased in response to less frequent watering regimes (Fig. 5.2C).



	Shoot DW (g)		Root DW (g)		Root/shoot ratio	
FACTOR	$F_{8,76}$	P	$F_{8,76}$	P	$F_{8,76}$	P
salt	1.84	0.166	15.79	**<0.001**	1.10	0.299
water	26.18	**<0.001**	15.99	**<0.001**	20.49	**0.001**
salt x water	1.33	0.267	0.03	0.859	0.06	0.802

Figure 5.2 Mean shoot (A) and root (B) dry weights and root/shoot ratio (C) of *M.georgei* plants grown in soil salinities of 0.0, 2.5 or 5.0 mS cm^{-1} and watered every 2,4 or 8 days. Bars indicate standard errors. F and P values from a two-way analysis of variance for shoot and root dry weight are shown.

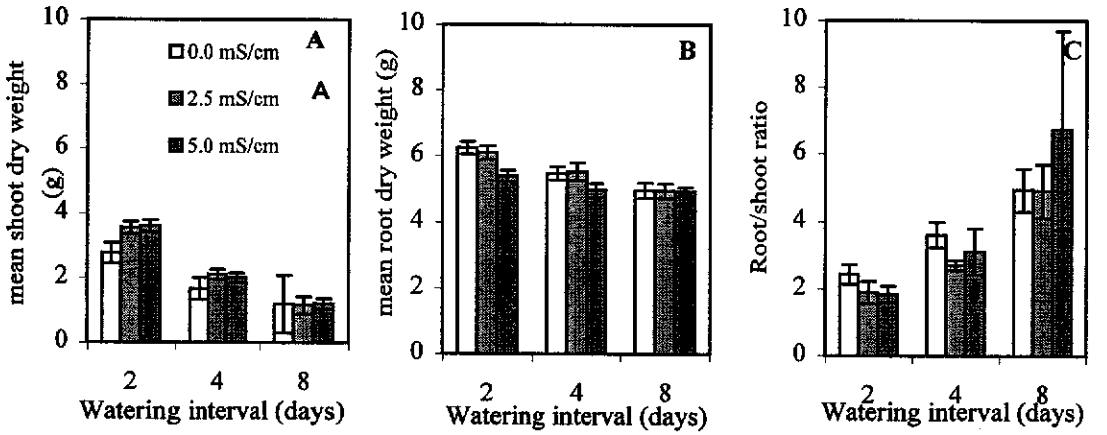
The root and shoot dry weight of *E. tomentosa* plants correlated positively with watering frequency (Fig. 5.3A, B). Specifically, the root dry weight decreased significantly in response to NaCl treatments of 5.0 mS/cm when grown under a two day ($F_{2,27} = 14.75$, $P < 0.001$) and four day ($F_{2,27} = 9.01$, $P = 0.001$) watering regime. The shoot dry weight did not, overall, respond to the NaCl treatments although a significant decrease occurred when plants were grown under a four day watering regime in response to salinity ($F_{2,27} = 3.51$, $P = 0.044$). *Enchylaena tomentosa* allocated more biomass to the roots when watered less frequently (Fig. 5.2C).



	Shoot DW (g)		Root DW (g)		Root/shoot ratio	
FACTOR	$F_{8,72}$	P	$F_{8,72}$	P	$F_{8,72}$	P
salt	2.77	0.069	0.25	0.618	0.11	0.742
water	30.17	**<0.001**	17.55	**<0.001**	5.41	**0.023**
salt x water	0.71	0.586	4.43	0.038	0.02	0.884

Figure 5.3 Mean shoot (A) and root (B) dry weights and root/shoot ratio (C) of *E. tomentosa* plants grown in soil salinities of 0.0, 2.5 or 5.0 mS cm^{-1} and watered every 2, 4 or 8 days (see Fig. 5.1 for legend). Bars indicate standard errors. *F* and *P* values from a two-way ANOVA for shoot and root dry weight are shown.

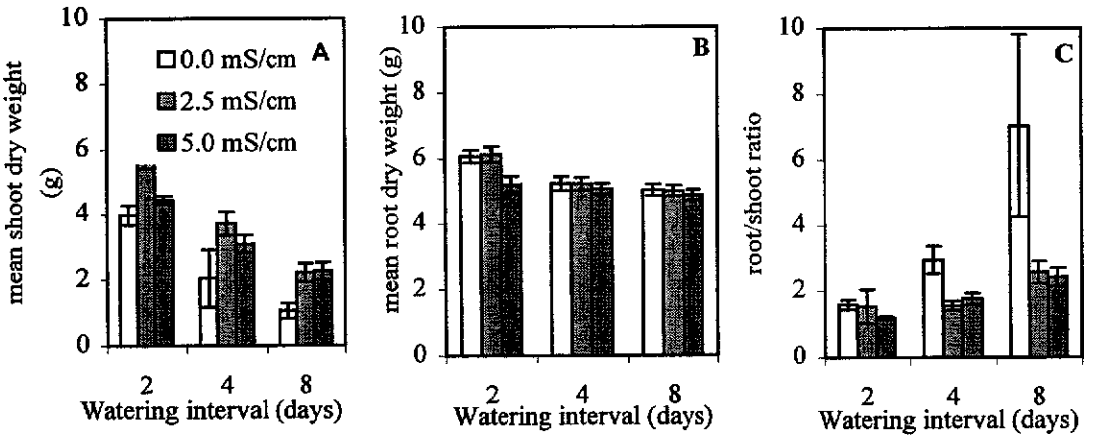
The shoot and root dry weight of *M. brevifolia* plants decreased significantly in response to decreased moisture availability (Fig. 5.4A, B). The root dry weight, however, decreased in response to NaCl treatments, specifically, when plants were grown in soil of 5.0 mS cm^{-1} and watered every two ($F_{2,25} = 12.12$, $P < 0.001$) and four ($F_{2,25} = 3.91$, $P = 0.033$) days. An interaction effect showed that salinity had no effect on root dry weight when water availability decreased (i.e. eight day watering interval) (Fig. 5.4B). The root/shoot ratio decreased in response to less frequent watering regimes (Fig. 5.4C).



	Shoot DW (g)		Root DW (g)		Root/shoot ratio	
FACTOR	$F_{8,70}$	P	$F_{8,70}$	P	$F_{8,70}$	P
salt	1.16	0.319	1.62	0.206	2.62	0.110
water	23.50	**<0.001**	39.89	**<0.001**	10.30	**0.002**
salt x water	0.41	0.802	9.71	**0.003**	0.772	0.383

Figure 5.4 Mean shoot (A) and root (B) dry weights and root/shoot ratio (C) of *M. brevifolia* plants grown in soil salinities of 0.0, 2.5 or 5.0 mS cm^{-1} and watered every 2,4 or 8 days (see Fig. 5.1 for legend). Bars indicate standard errors. *F* and *P* values from a two-way ANOVA for shoot and root dry weight are shown.

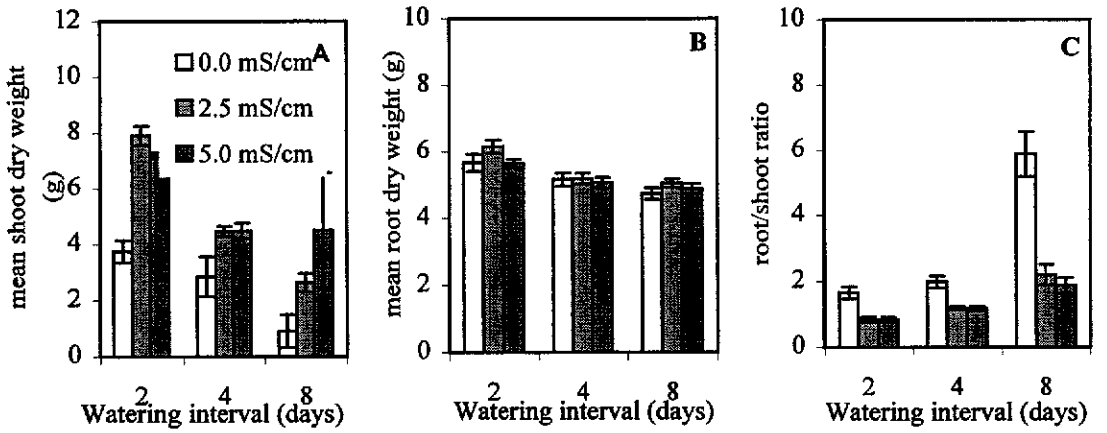
The shoot dry weight of *A. bunburyana* plants increased significantly when grown under increasing moisture availability and increasing NaCl treatments (Fig. 5.5A). The shoot dry weight showed significant increases when plants were grown under NaCl treatments compared to the 'no salt added' treatments and watered every four ($F_{2,25}$ = 6.99, P = 0.004) and eight ($F_{2,25}$ = 8.76, P = 0.001) days. The root dry weight, however, decreased in response to decreased water availability (Fig. 5.5B). The root dry weight significantly decreased in response to a NaCl treatment of 5.0 mS cm^{-1} when plants were grown under a two day watering regime ($F_{2,24}$ = 20.07, P < 0.001). An interaction effect showed that salinity had no effect on root dry weight when water availability decreased (i.e. four and eight day watering interval) (Fig. 5.5B). The root/shoot ratio increased in response to less frequent watering regimes (Fig. 5.5C). An interaction effect showed that the root/shoot ratio decreased in response to NaCl treatments at watering intervals of 4 and 8 days.



	Shoot DW (g)		Root DW (g)		Root/shoot ratio	
FACTOR	$F_{8,70}$	P	$F_{8,70}$	P	$F_{8,70}$	P
salt	12.53	**<0.001**	0.97	0.327	16.303	**<0.001**
water	45.07	**<0.001**	24.62	**<0.001**	23.089	**<0.001**
salt x water	0.762	0.553	6.00	**0.017**	6.058	**0.016**

Figure 5.5 Mean shoot (A) and root (B) dry weights and root/shoot ratio (C) of *A. bunburyana* plants grown in soil salinities of 0.0, 2.5 or 5.0 mS cm^{-1} and watered every 2, 4 or 8 days. Bars indicate standard errors. F and P values from a two-way ANOVA for shoot and root dry weight are shown.

The shoot dry weight of *A. codonocarpa* plants increased in response to increased water availability and increased salinity treatments (Fig. 5.6A), whereas the root dry weight increased in response to increased water availability only (Fig 5.6B). The shoot dry weight of plants increased when grown in saline soil of 2.5 and 5.0 mS cm^{-1}, and under the two and four day watering regimes ($F_{2,25}$ = 14.84, P < 0.001 and $F_{2,25}$ = 10.28, P = 0.001, respectively). The plants allocated more biomass to the roots compared to the shoots when watered less frequently (Fig 5.6C). An interaction effect showed that salt decreased the root/shoot ratio under less frequent watering regimes.



	Shoot DW (g)		Root DW (g)		Root/shoot ratio	
FACTOR	$F_{8,73}$	P	$F_{8,73}$	P	$F_{8,73}$	P
salt	11.68	**<0.001**	0.45	0.506	0.14	0.714
water	16.22	**<0.001**	15.82	**<0.001**	3.49	0.065
salt x water	1.39	0.247	0.49	0.486	29.82	**<0.001**

Figure 5.6 Mean shoot (A) and root (B) dry weights and root/shoot ratio (C) of *A. codonocarpa* plants grown in soil salinities of 0.0, 2.5 or 5.0 mS cm^{-1} and watered every 2, 4 or 8 days. Bars indicate standard errors. Significance values from a two way ANOVA for shoot and root dry weight are shown.

Plant height and number of branches

Height of *M. georgei* plants decreased significantly in response to decreased water availability ($F_{8,77} = 6.24$, $P < 0.001$, Fig. 5.7). *Maireana georgei* plants showed greatest height at salinities of 2.5 mS cm^{-1}, and lowest heights when grown at salinities of 5.0 mS cm^{-1} ($F_{8,77} = 3.11$, $P < 0.050$). This was most pronounced at the eight day watering regime. The number of branches on *M. georgei* plants decreased in response to increasing NaCl and decreasing moisture availability (Table 5.2).

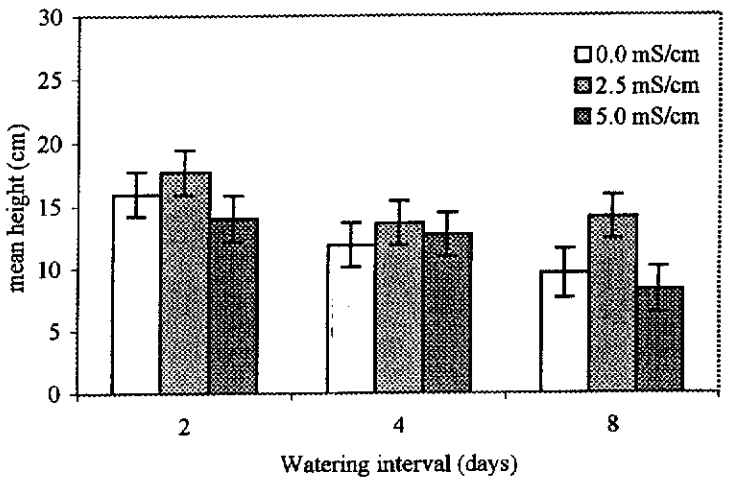


Figure 5.7 Mean height of *M. georgei* plants grown in soil salinities of 0.0, 2.5 or 5.0 mS cm^{-1} and watered under three different regimes at 2, 4 or 8 day intervals. Bars indicate standard errors.

Table 5.2 Mean number of branches and standard errors (*se*) of chenopod species grown in soil salinities of 0.0, 2.5 or 5.0 mS cm^{-1} and watered at 2, 4 or 8 day intervals. The *F* and *P* values from a two-way ANOVA, are shown for water, salt and water x salt interaction.

Species	Watering interval (days)	Salinity (mS/cm) 0.0		2.5		5.0	
		mean	*se*	mean	*se*	mean	*se*
M. georgei							
	2	16	*1.1*	18	*1.5*	14	*0.8*
	4	17	*0.8*	15	*1.1*	13	*0.9*
	8	15	*0.8*	15	*0.6*	12	*0.8*
		F	***P***				
	salt	$F_{2,76}$=9.18	**<0.001**				
	water	$F_{2,76}$=4.21	**0.019**				
	salt x water	$F_{4,76}$=0.77	0.547				
E. tomentosa							
	2	36	*3.4*	33	*3.0*	32	*2.3*
	4	33	*1.8*	32	*2.8*	23	*3.6*
	8	30	*3.8*	26	*2.6*	27	*4.0*
		F	***P***				
	salt	$F_{2,70}$=2.19	0.120				
	water	$F_{2,70}$=3.10	0.051				
	salt x water	$F_{4,70}$=0.76	0.556				
M. brevifolia							
	2	58	*6.8*	53	*4.5*	49	*5.6*
	4	44	*3.2*	49	*3.3*	49	*3.2*
	8	20	*7.8*	43	*3.3*	39	*2.3*
		F	***P***				
	salt	$F_{2,66}$=1.76	0.180				
	water	$F_{2,66}$=12.45	**<0.001**				
	salt x water	$F_{4,66}$=2.61	**0.043**				
A.bunburyana							
	2	26	*2.3*	33	*2.6*	28	*2.2*
	4	23	*1.9*	26	*1.8*	24	*1.8*
	8	20	*1.9*	20	*2.9*	25	*2.4*
		F	***P***				
	salt	$F_{2,68}$=1.79	0.174				
	water	$F_{2,68}$=7.01	**0.002**				
	salt x water	$F_{4,68}$=1.28	0.278				
A. codonocarpa							
	2	12	*1.2*	18	*1.1*	18	*0.8*
	4	11	*0.9*	17	*1.0*	16	*0.9*
	8	6	*1.5*	13	*1.2*	12	*0.7*
		F	***P***				
	salt	$F_{2,74}$=26.94	**<0.001**				
	water	$F_{2,74}$=21.76	**<0.001**				
	salt x water	$F_{4,74}$ = 0.41	0.799				

The height of *E. tomentosa* decreased in response to greater concentrations of NaCl ($F_{8,74} = 5.91$, $P = 0.004$) and decreased water availability ($F_{8,74} = 3.59$, $P = 0.032$, Fig. 5.8). There was no significant difference in the number of branches produced in response to the NaCl or water regimes (Table 5.2).

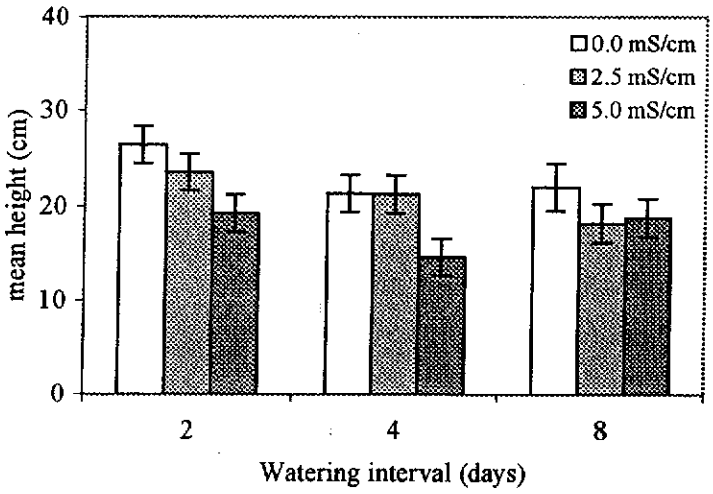


Figure 5.8 Mean height of *E. tomentosa* plants grown in soil salinities of 0.0, 2.5 or 5.0 mS cm^{-1} and watered every 2, 4 or 8 days. Bars indicate standard errors.

The height of *M. brevifolia* plants increased in response to increased water availability ($F_{8,68}$ = 8.27, P = 0.001) but did not respond significantly to the NaCl treatments ($F_{8,68}$ = 1.00, P = 0.372, Fig. 5.9). The number of branches increased in response to increased water availability but showed no response to the NaCl treatments (Table 5.2). The number of branches was, however, greater when plants were grown in soil of 2.5 and 5.0 mS cm^{-1} salinity and placed under the eight day watering regime. An interaction effect showed that the number of branches increased in response to NaCl at a watering interval of eight days. However the number of branches did not change in response to salinity when the plants were watered at intervals of two and four days.

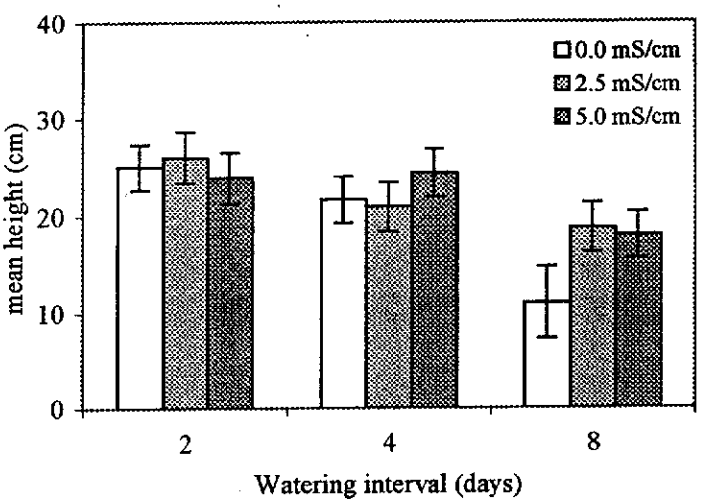


Figure 5.9 Mean height of *M. brevifolia* plants grown in soil salinities of 0.0, 2.5 or 5.0 mS cm^{-1} and watered every 2, 4 or 8 day intervals. Bars indicate standard errors.

The *A. bunburyana* plants increased in height ($F_{8,70}$ = 7.50, P = 0.001, Fig. 5.10) and number of branches (Table 5.2) in response to increased water availability. They did not, however, respond to the presence of NaCl ($F_{8,70}$ = 1.78, P = 0.176).

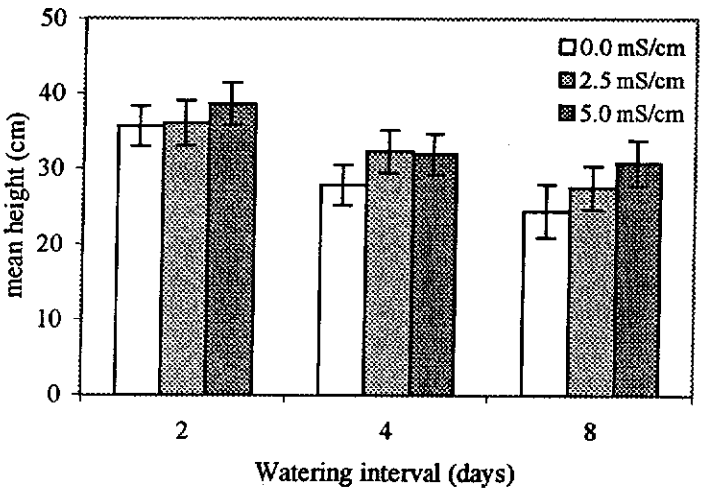


Figure 5.10 Mean height of *A. bunburyana* plants grown in soil salinities of 0.0, 2.5 or 5.0 mS cm^{-1} and watered every 2, 4 or 8 day intervals. Bars indicate standard errors.

The height of *A. codonocarpa* plants increased in response to increased water availability ($F_{8,75}$ = 20.49, P < 0.001) but showed no response to the presence of NaCl ($F_{8,75}$ = 2.67, P = 0.076, Fig. 5.11). The number of branches increased in response to increased water availability and the presence of NaCl (Table 5.2).

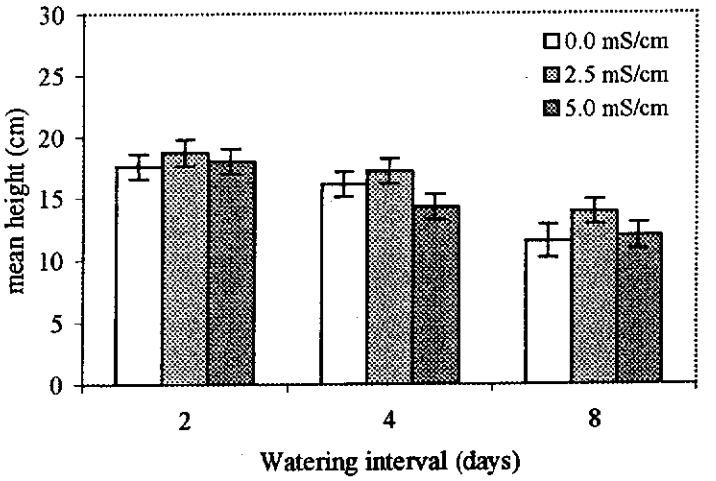


Figure 5.11 Mean height of *A. codonocarpa* plants grown in soil salinities of 0.0, 2.5 or 5.0 mS cm^{-1} and watered at 2, 4 or 8 day intervals. Bars indicate standard errors.

Leaf Characteristics: Leafiness, succulence and thickness

The leafiness of *M. georgei* plants increased ($F_{2,76}$ = 3.13, P = 0.050, Fig. 5.12A), succulence decreased ($F_{2,76}$ = 25.09, P < 0.001, Fig 5.12B) and leaf thickness decreased ($F_{1,354}$ = 514.05, P < 0.001, Fig. 5.12C) in response to decreasing water availability. Increasing salinity caused leafiness ($F_{2,76}$ = 8.81, P < 0.001), succulence ($F_{2,76}$ = 8.60, P < 0.001) and leaf thickness ($F_{1,354}$ = 109.80, P < 0.001) of *M. georgei* plants to increase.

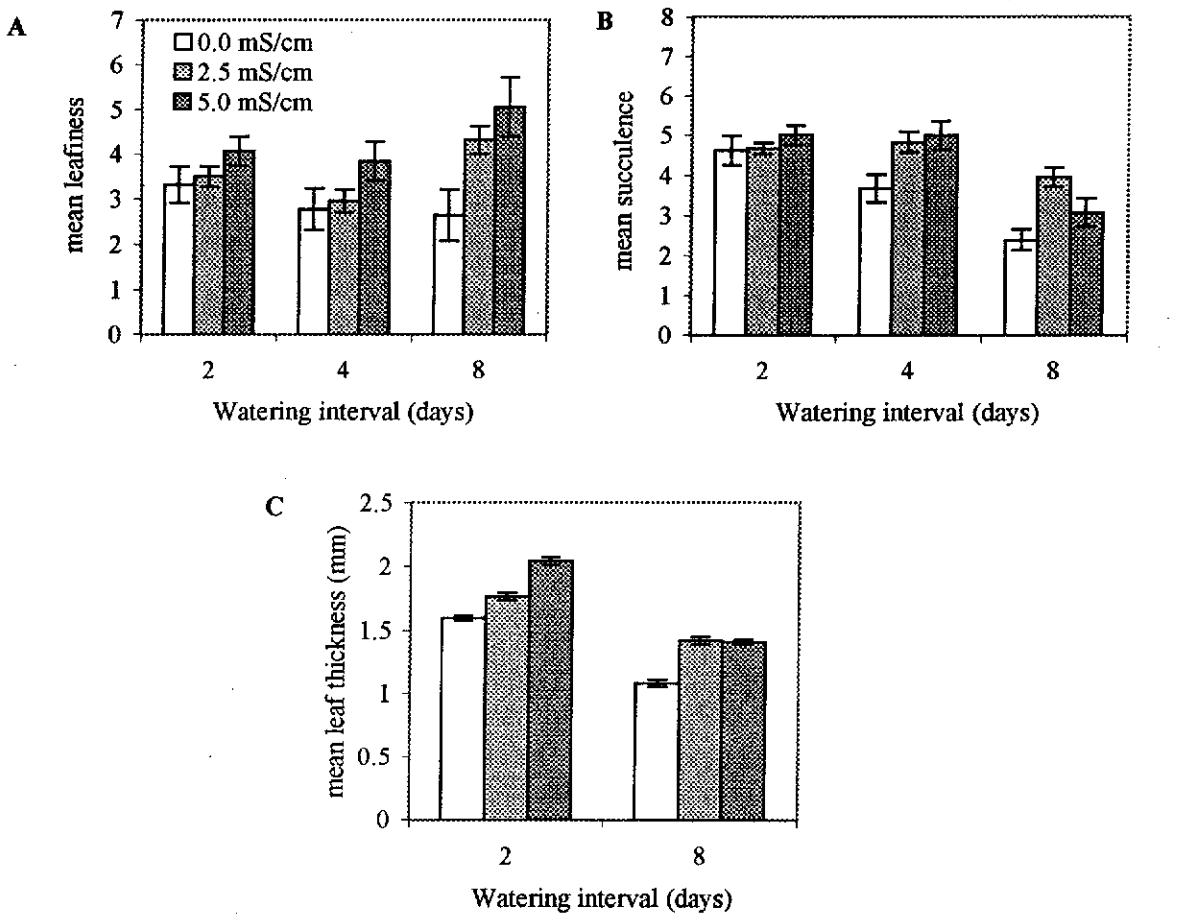


Figure 5.12 Mean leafiness (A), succulence (B) and leaf thickness (C) of *M.georgei* plants grown in soil salinities of 0.0, 2.5 or 5.0 mS cm^{-1} and watered every 2, 4 or 8 days. Bars indicate standard errors.

The leafiness ($F_{2,72}$ = 5.22, P = 0.008, Fig. 5.13A), succulence ($F_{2,72}$ = 17.57, P < 0.001, Fig 5.13B) and leaf thickness ($F_{1,344}$ = 151.21, P < 0.001, Fig 5.13C) of *E. tomentosa* plants decreased in response to decreased water availability. An interaction effect showed that leafiness and leaf thickness increased as water availability increased and salinity increased ($F_{8,72}$ = 3.12, P = 0.020 and $F_{2,344}$ = 5.24, P = 0.006, respectively). The leaf succulence also increased in response to increasing salinity ($F_{2,72}$ = 16.23, P < 0.001), but no relationship existed between salinity and watering regime ($F_{4,72}$ = 1.06, P = 0.385).

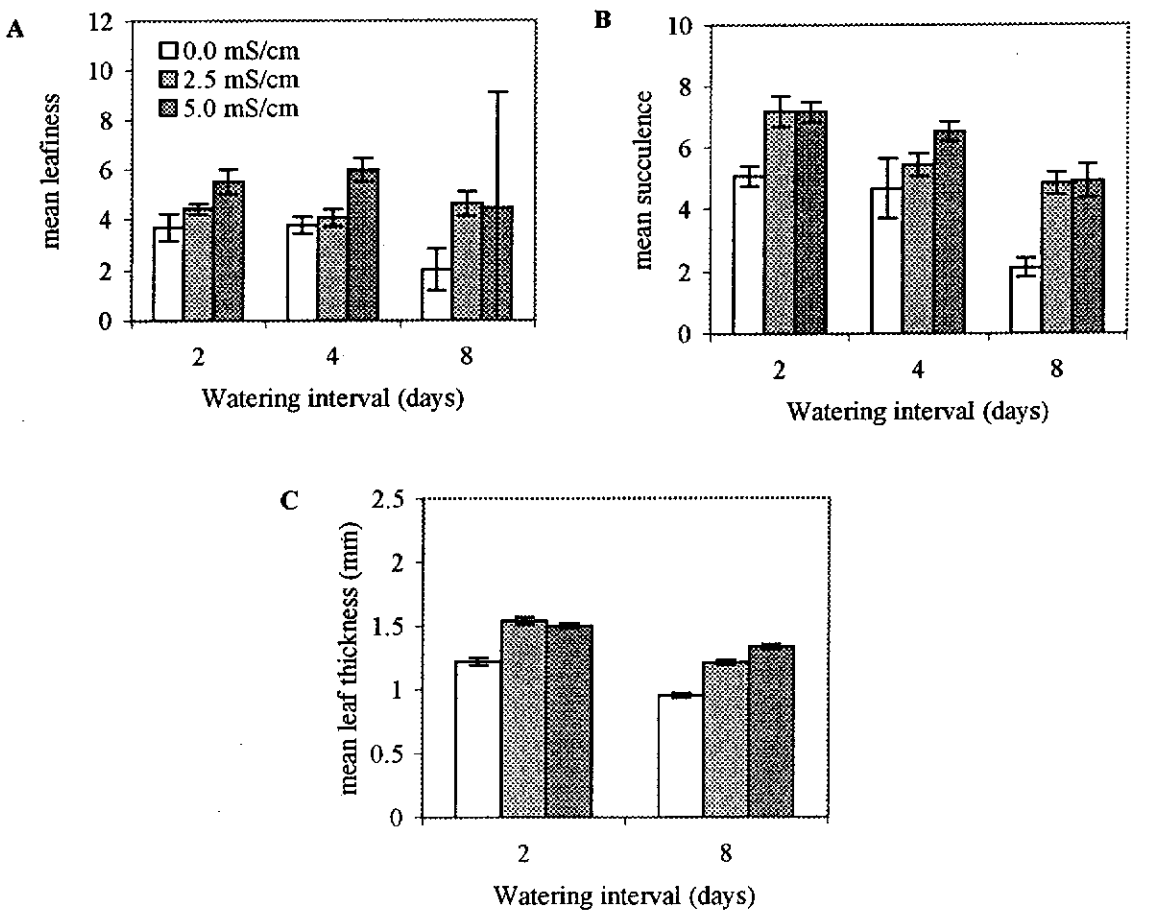


Figure 5.13 Mean leafiness (A), succulence (B) and leaf thickness (C) of *E. tomentosa* plants grown in soil salinities of 0.0, 2.5 or 5.0 mS cm^{-1} and watered every 2, 4 or 8 days. Bars indicate standard errors.

An interaction effect showed that leafiness of *M. brevifolia* plants increased as water availability decreased and salinity increased ($F_{8,70}$ = 3.71, P = 0.009, Fig. 5.14A). Leaf succulence did not differ between water ($F_{2,70}$ = 0.286, P = 0.752) or NaCl regimes ($F_{2,70}$ = 1.47, P = 0.237, Fig. 5.14B). The leaf thickness did, however, increase as water availability increased and salinity increased ($F_{2,344}$ = 3.69, P = 0.026, Fig. 5.14C).

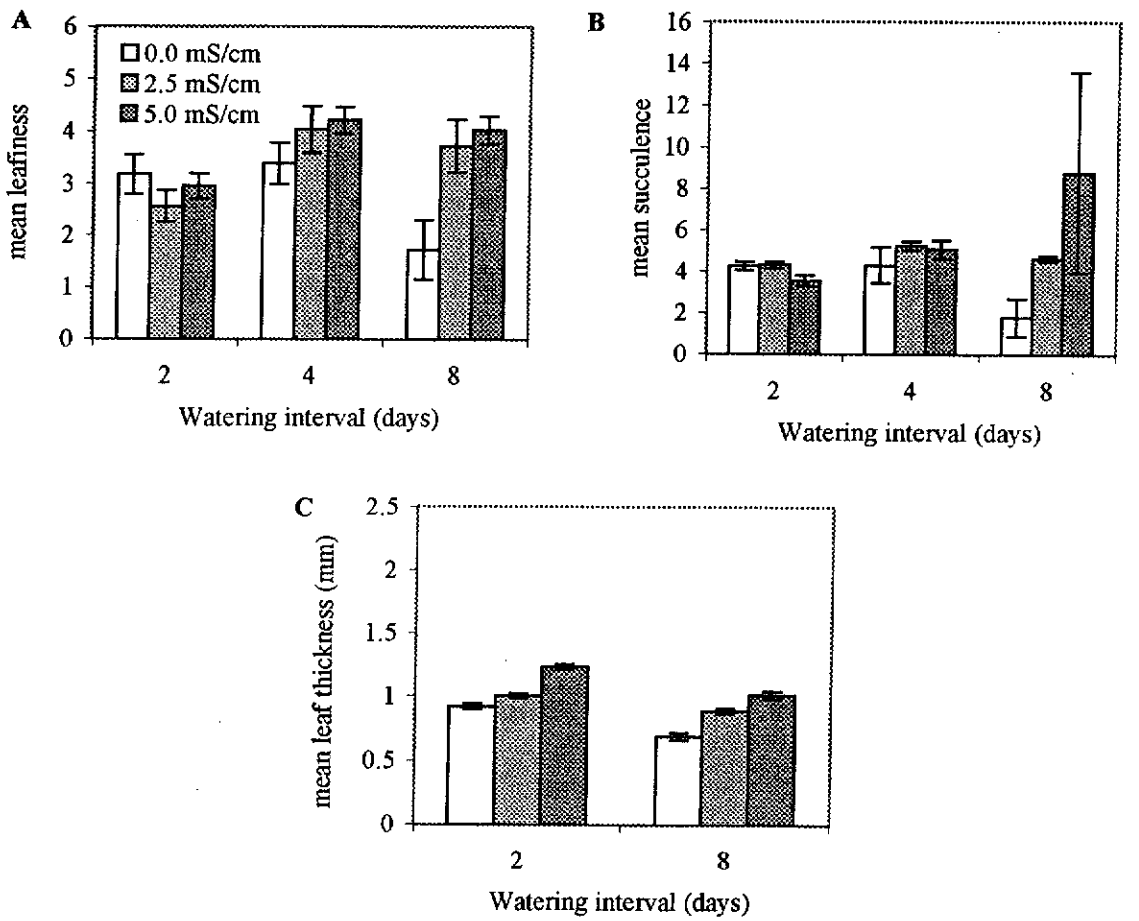


Figure 5.14 Mean leafiness (A), succulence (B) and leaf thickness (C) of *M. brevifolia* plants grown in soil salinities of 0.0, 2.5 or 5.0 mS cm^{-1} and watered every 2, 4 or 8 days. Bars indicate standard errors.

The leafiness of *A. bunburyana* plants increased in response to increased moisture availability ($F_{2,70}$ = 5.62, P = 0.005), but showed no response to NaCl treatments ($F_{2,70}$ = 0.51, P = 0.605, Fig. 5.15A). The succulence showed no overall response to moisture ($F_{2,70}$ = 1.74, P = 0.183) or NaCl treatments ($F_{2,70}$ = 1.08, P = 0.344, Fig. 5.15B), however, there was a specific and significant increase in succulence in response to NaCl when plants were watered every two days ($F_{2,23}$ = 5.64, P = 0.010). Leaf thickness decreased in response to increased water availability ($F_{1,344}$ = 24.50, P < 0.001) but increased when grown in saline soil of 2.5 and 5.0 mS cm^{-1} ($F_{2,344}$ = 13.18, P < 0.001, Fig. 5.15C).

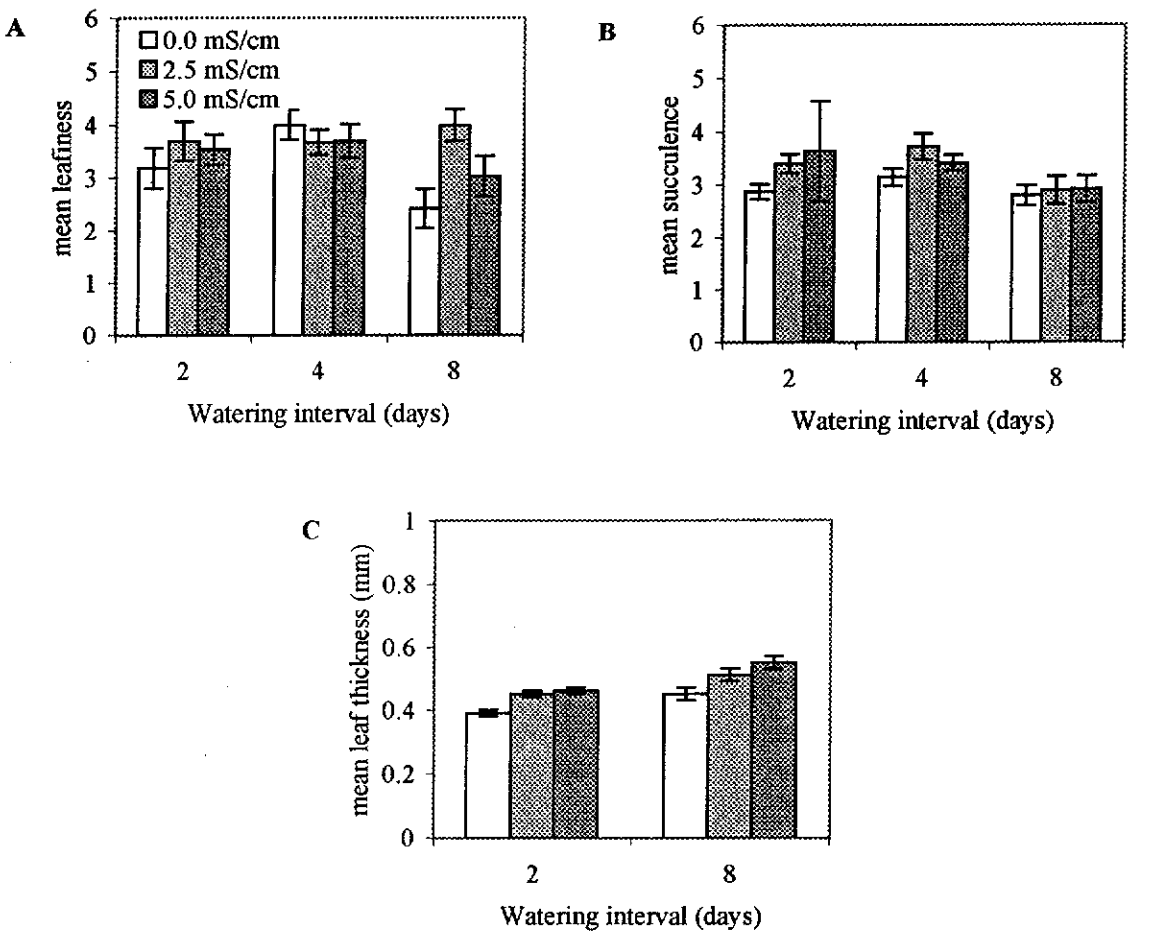


Figure 5.15 Mean leafiness (A), succulence (B) and leaf thickness (C) of *A. bunburyana* plants grown in soil salinities of 0.0, 2.5 or 5.0 mS cm^{-1} and watered every 2, 4 or 8 days. Bars indicate standard errors.

Plants of *A. codonocarpa* exhibited decreased leafiness ($F_{2,73}$ = 5.20, P = 0.008, Fig. 5.16A) and increased succulence ($F_{2,73}$ = 12.98, P < 0.001, Fig. 5.16B) in response to more frequent water availability. Plant succulence also increased in response to increasing soil salinity ($F_{2,73}$ = 11.94, P < 0.001). The leaf thickness also increased as watering frequency and salinity increased ($F_{2,334}$ = 3.57, P < 0.029, Fig. 5.16C).

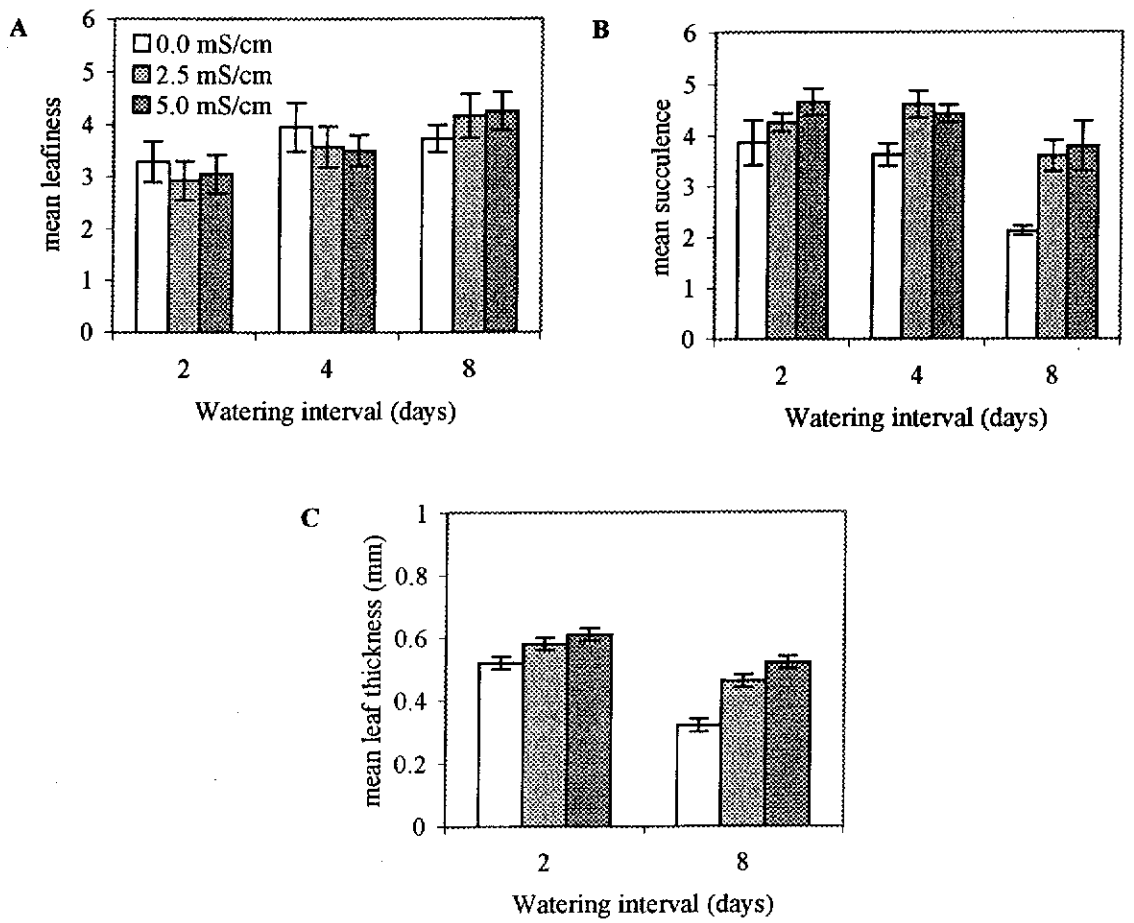


Figure 5.16 Mean leafiness (A), succulence (B) and leaf thickness (C) of *A. codonocarpa* plants grown in soil salinities of 0.0, 2.5 or 5.0 mS cm^{-1} and watered every 2, 4 or 8 days. Bars indicate standard errors.

Water Potentials

Predawn and midday water potentials measured prior to water addition was significantly different between the two and eight day watering intervals for all five chenopod species (Table 5.3, Fig. 5.17 - 5.21). *Maireana georgei* plants, grown in soil of 5.0 mS cm^{-1} salinity and under a two day watering regime, had a significantly lower predawn water potential after water addition (Fig. 5.17A, Table 5.3) and a lower midday water potential prior to water addition (Fig. 5.17B). When *M. georgei* plants were grown under an eight day watering regime the presence of NaCl had no effect on the predawn or midday water potentials prior or after water addition (Fig. 5.17C, D).

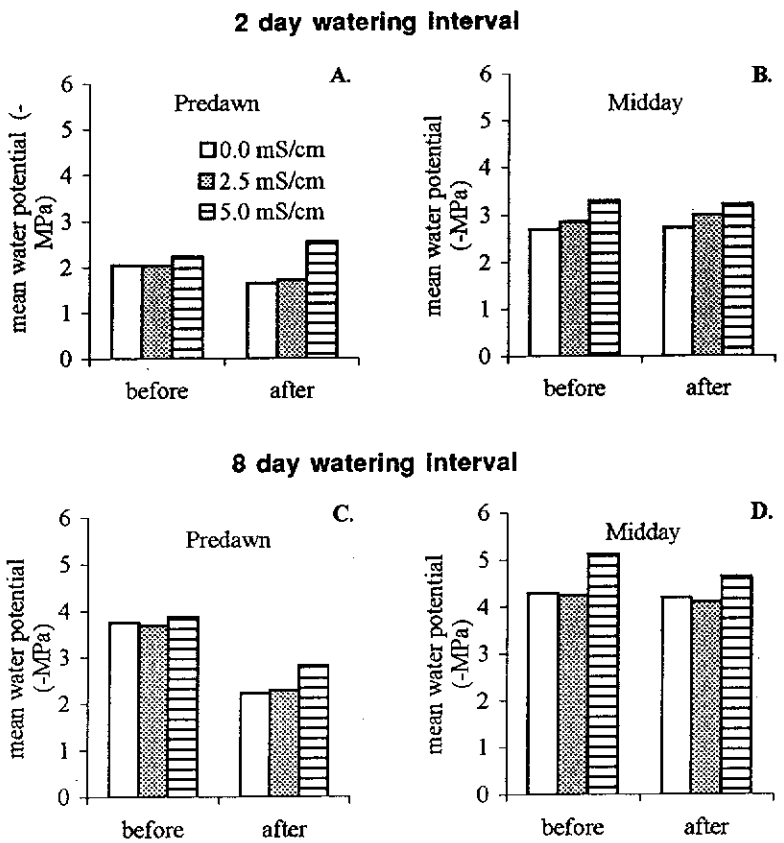


Figure 5.17 Mean water potentials of *M. georgei* plants grown in soil salinities of 0.0, 2.5 or 5.0 mS cm^{-1} under two day (A, B) or eight day (C, D) watering intervals. Water potentials were measured: predawn (A, C) on the day of watering (before) and on the day after watering (after), and midday (B, D) the day before watering (before) and on the day of watering (after). Note: Due to the small sample size, the standard errors are so large that they have been omitted for the sake of clarity.

Table 5.3 The levels of significance for all species from one-way and two-way ANOVA's for water potentials taken at midday, before and after water addition and at predawn, before and after water addition. The water potentials were measured in plants that were growing in soil salinities of 0.0, 2.5 or 5.0 mS cm^{-1} and under a two or eight day watering regime.

Species	Midday				Pre-dawn			
	before water		*after water*		*before water*		*after water*	
M. georgei	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**
one way								
salt (2 day watering regime)	5.18	**0.024**	1.15	0.351	0.73	0.501	14.67	**0.001**
salt (8 day watering regime)	3.70	0.059	0.79	0.477	0.07	0.931	0.08	0.920
two way								
salt	7.96	**0.002**	1.51	0.242	0.18	0.833	5.08	**0.015**
water	101.95	**<0.001**	33.65	**<0.001**	36.35	**<0.001**	4.86	**0.038**
salt x water	0.61	0.554	0.24	0.787	0.01	0.993	0.22	0.804
E. tomentosa								
one way								
salt (2 day watering regime)	6.55	**0.012**	**6.3**	**0.013**	**7.44**	**0.008**	**4.59**	**0.033**
salt (8 day watering regime)	2.92	0.092	1.1	0.363	0.28	0.760	0.860	0.448
two way								
salt	6.06	**0.008**	0.44	0.651	1.49	0.246	0.11	0.899
water	16.78	**<0.001**	36.27	**<0.001**	50.27	**<0.001**	28.59	**<0.001**
salt x water	0.57	0.571	3.82	**0.037**	0.11	0.897	2.67	0.091
M. brevifolia								
one way								
salt (2 day watering regime)	2.00	0.178	0.99	0.400	2.80	0.101	1.56	0.249
salt (8 day watering regime)	3.75	0.057	1.07	0.381	0.35	0.712	5.76	**0.022**
two way								
salt	3.21	0.061	1.76	0.196	0.16	0.852	5.33	**0.013**
water	31.95	**<0.001**	26.75	**<0.001**	44.77	**<0.001**	39.38	**<0.001**
salt x water	1.76	0.196	1.10	0.351	1.02	0.378	0.43	0.659
A.bunburyana								
one way								
salt (2 day watering regime)	6.14	**0.015**	4.98	**0.027**	8.25	**0.006**	1.88	0.195
salt (8 day watering regime)	5.54	**0.022**	11.60	**0.002**	0.29	0.754	1.41	0.281
two way								
salt	10.63	**0.001**	16.75	**<0.001**	1.50	0.244	2.27	0.126
water	78.27	**<0.001**	59.94	**<0.001**	33.33	**<0.001**	26.46	**<0.001**
salt x water	1.31	0.289	1.87	0.177	0.31	0.740	0.29	0.755
A. codonocarpa								
one way								
salt (2 day watering regime)	8.38	**0.005**	9.70	**0.003**	2.71	0.107	8.37	**0.005**
salt (8 day watering regime)	3.12	0.089	1.42	0.286	0.84	0.457	1.67	0.242
two way								
salt	7.54	**0.004**	6.39	**0.007**	0.21	0.816	3.04	0.070
water	38.97	**<0.001**	46.09	**<0.001**	11.55	**0.003**	1.34	0.261
salt x water	1.00	0.386	0.08	0.923	0.68	0.517	2.71	0.091

The *E. tomentosa* plants grown under a two day watering regime showed a significant decrease in predawn and midday water potential, before and after water addition, when NaCl was present (Fig. 5.18A, B, Table 5.3). When *Enchylaena tomentosa* plants were grown under an eight day watering regime there was no significant difference between salinity treatments regardless of time of measurement (Fig. 5.18C, D).

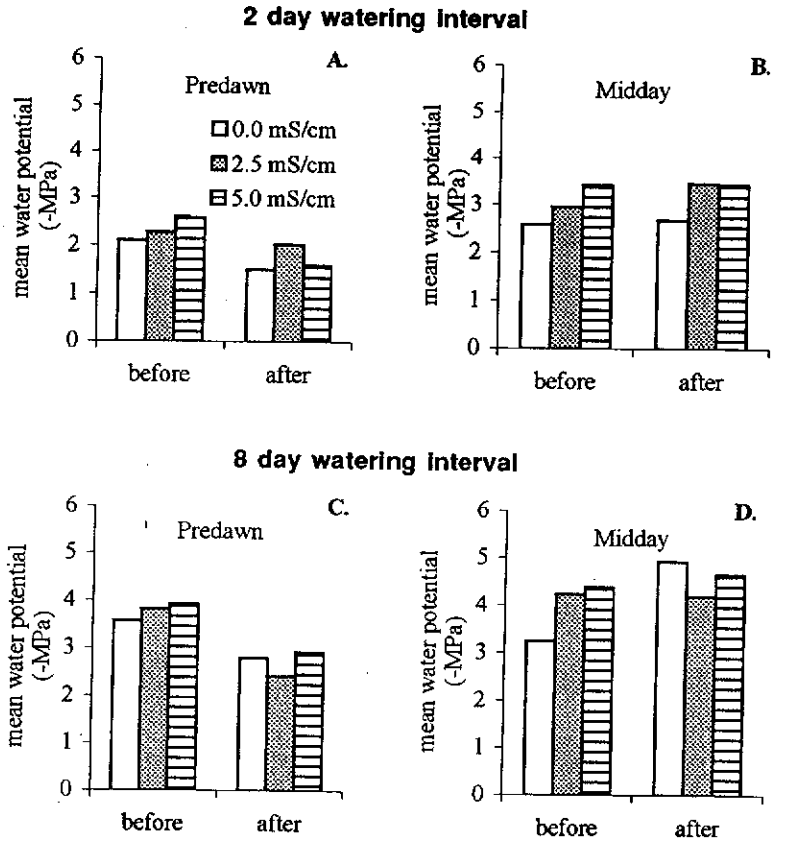


Figure 5.18 Mean water potentials of *E. tomentosa* plants grown in soil salinities of 0.0, 2.5 or 5.0 mS cm^{-1} under two day (A, B) or eight day (C, D) watering intervals. Water potentials were measured: predawn (A, C) on the day of watering (before) and on the day after watering (after), and midday (B, D) the day before watering (before) and on the day of watering (after). Note: Due to the small sample size, the standard errors are so large that they have been omitted for the sake of clarity.

When *M. brevifolia* plants were grown under a two day watering regime the predawn water potential showed no significant difference between NaCl treatments (Fig. 5.19A, Table 5.3). The midday water potentials showed no significant differences between NaCl treatments regardless of watering regime (Fig. 5.19B, D). The predawn water potential of *M. brevifolia,* when growing under the eight day watering interval, was significantly lower when the plant was grown in 5.0 mS cm^{-1} of NaCl (Fig. 5.19C).

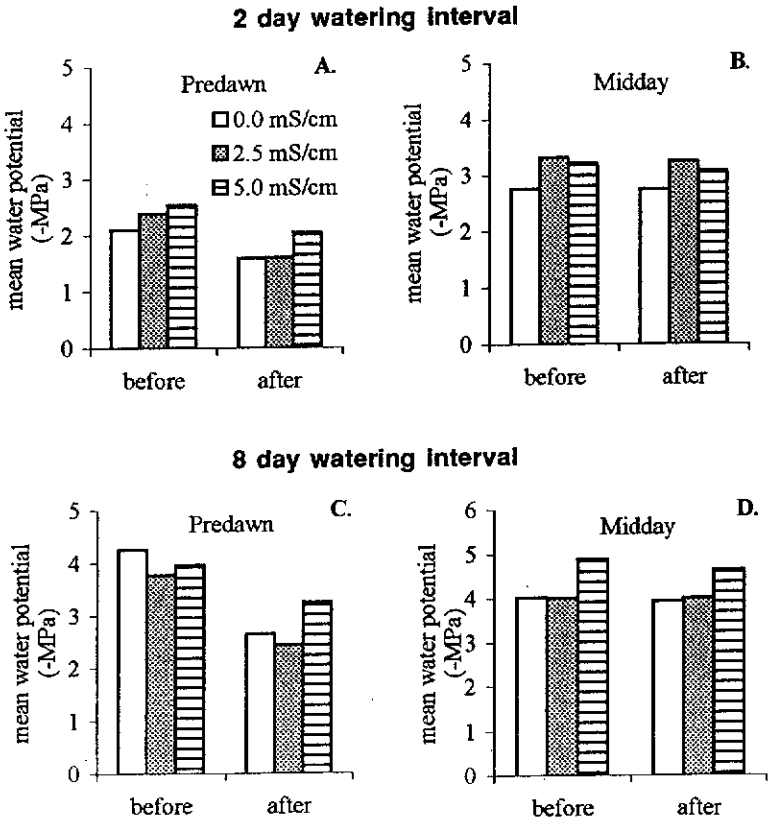


Figure 5.19 Mean water potentials of *M. brevifolia* plants grown in soil salinities of 0.0, 2.5 or 5.0 mS cm^{-1} under two day (A, B) or eight day (C, D) watering intervals. Water potentials were measured: predawn (A, C) on the day of watering (before) and on the day after watering (after), and midday (B, D) the day before watering (before) and on the day of watering (after). Note: Due to the small sample size, the standard errors are so large that they have been omitted for the sake of clarity.

When *A. bunburyana* plants were grown under a two day watering regime, the predawn water potentials measured prior to water addition were significantly lower in response to salt (Fig. 5.20A, Table 5.3). The water potential measurements, taken immediately after watering, however, showed no significant differences between NaCl treatments, regardless of watering frequency (Fig. 5.20A, C). The midday water potentials showed significant differences between NaCl treatments regardless of measurement time and watering regime (Fig 5.20B, D).

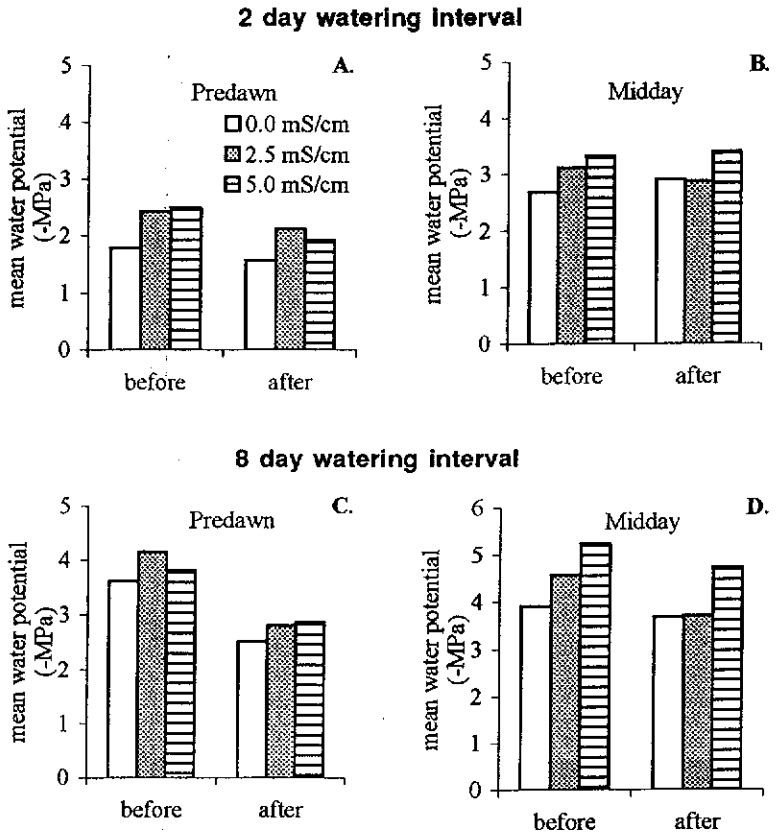


Figure 5.20 Mean water potentials of *A. bunburyana* plants grown in soil salinities of 0.0, 2.5 or 5.0 mS cm^{-1} under two day (A, B) or eight day (C, D) watering intervals. Water potentials were measured: predawn (A, C) on the day of watering (before) and on the day after watering (after), and midday (B, D) the day before watering (before) and on the day of watering (after). Note: Due to the small sample size, the standard errors are so large that they have been omitted for the sake of clarity.

Predawn water potentials, recorded after water addition, of *A. codonocarpa* plants, grown under the two day watering regime, were significantly lower in response to increasing salinity treatments (Fig. 5.21A, Table 5.3). When *A. codonocarpa* plants were grown under a two day watering regime the presence of NaCl also lowered midday water potentials (recorded prior to and after water addition) (Fig. 5.21B). The plants growing under the eight day watering regime showed no significant differences in predawn or midday water potentials in response to the salinity treatments (Fig. 5.21C, D).

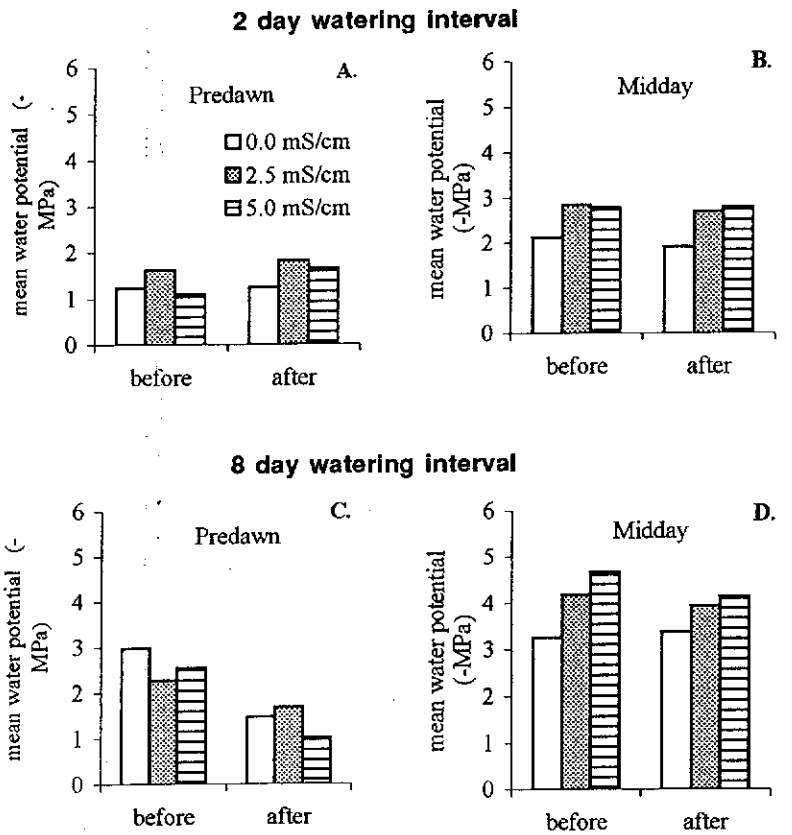


Figure 5.21 Mean water potentials of *A. codonocarpa* plants grown in soil salinities of 0.0, 2.5 or 5.0 mS cm^{-1} under two day (A, B) or eight day (C, D) watering intervals. Water potentials were measured: predawn (A, C) on the day of watering (before) and on the day after watering (after), and midday (B, D) the day before watering (before) and on the day of watering (after). Note: Due to the small sample size, the standard errors are so large that they have been omitted for the sake of clarity.

Relative Growth Rate

The relative growth rates (RGR) of *M. georgei* plants showed no response to NaCl treatments during each of the three periods; 8 - 12 weeks old (NaCl application) ($F_{2,76}$ = 1.15, P = 0.324), 12 - 16 weeks old (watering regime) ($F_{2,76}$ = 1.56, P = 0.218), and 16 - 20 weeks (watering regime) ($F_{2,76}$ = 0.25, P = 0.782, Fig. 5.22). During the watering regime at 12 - 16 and 16 - 20 weeks old, RGR decreased in response to decreasing water availability ($F_{2,76}$ = 6.61, P = 0.002 and $F_{2,76}$ = 3.25, P = 0.044, respectively). Negative growth rates may be a result of leaf loss and branch death.

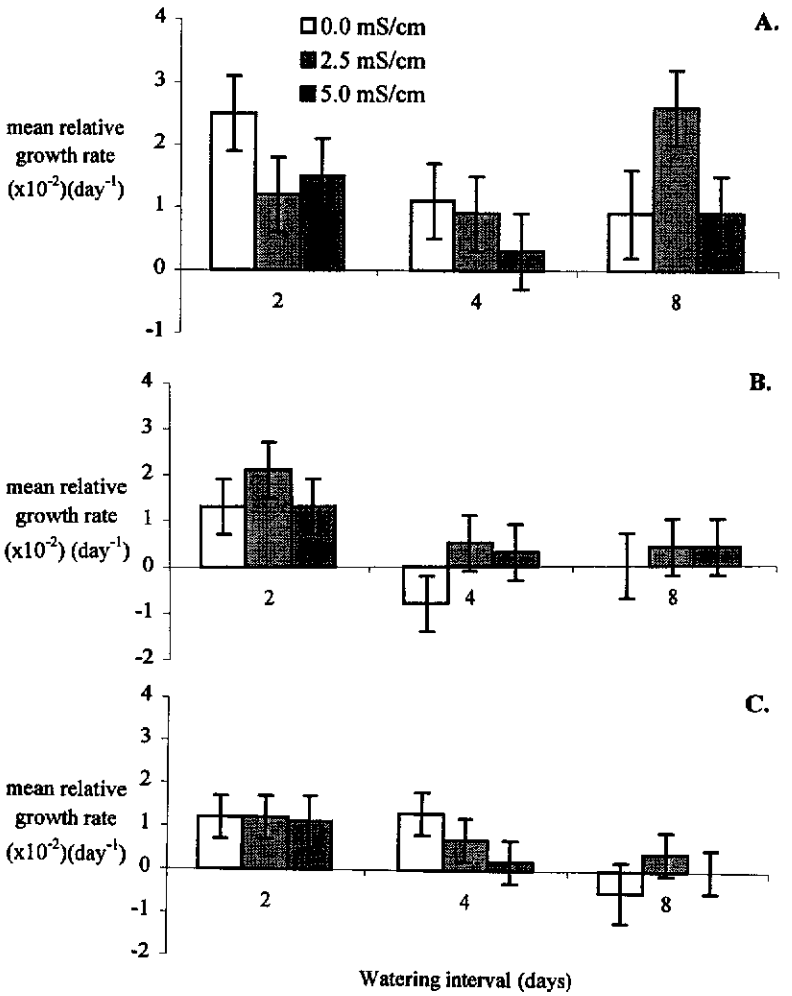


Figure 5.22 Mean relative growth rate (day^{-1}) of *M. georgei* plants during the time of NaCl application (8 - 12 weeks of age) (A), the introduction of the watering regime (12 - 16 weeks of age) (B) and the continuation of the watering regime (16 - 20 weeks of age) (C). Plants were growing in soil salinities of 0.0, 2.5 or 5.0 mS cm^{-1} and under a 2, 4 or 8 day watering interval. Bars indicate standard errors.

NaCl application had no effect on RGR of *E. tomentosa* plants during each of the three measured age periods: 8 - 12 weeks old ($F_{2,72}$ = 1.29, P = 0.283), 12 - 16 weeks old ($F_{2,72}$ = 1.28, P = 0.285) or 16 - 20 weeks old ($F_{2,72}$ = 0.99, P = 0.378, Fig. 5.23). RGR of *E. tomentosa* decreased significantly in response to decreased water availability during the 12 - 16 weeks old period ($F_{2,72}$ = 4.54, P = 0.014), but there was no significant difference attributable to watering regime during the 16 - 20 weeks old period ($F_{2,72}$ = 1.54, P = 0.221).

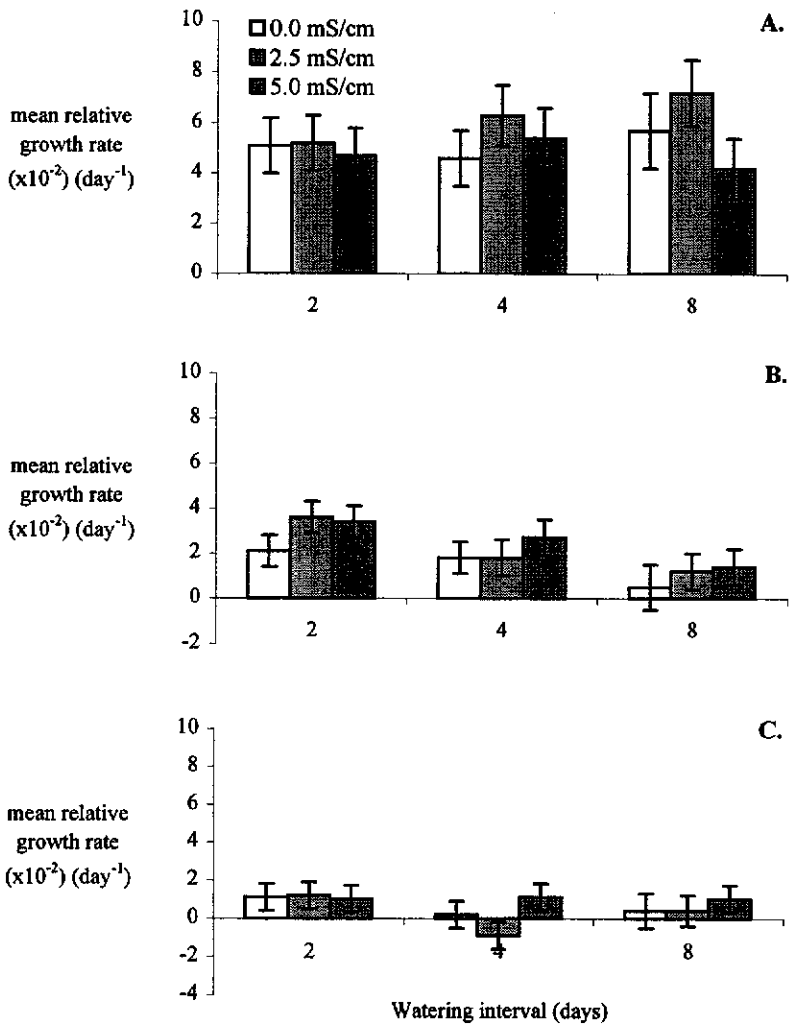


Figure 5.23 Mean relative growth rate (day^{-1}) of *E. tomentosa* plants during the time of NaCl application (8 - 12 weeks old) (A), the introduction of the watering regime (12 - 16 weeks old) (B) and the continuation of the watering regime (16 - 20 weeks old) (C). Bars indicate standard errors. Plants were grown in soil salinities of 0.0, 2.5 or 5.0 mS cm^{-1} and under a 2, 4 or 8 day watering regime.

The RGR of *M. brevifolia* plants did not change in response to water or NaCl regimes, for each of the measured time periods; 8 - 12 weeks old ($F_{2,66}$ = 2.72, P = 0.073 and $F_{2,66}$ = 3.10, P = 0.052, respectively), 12 - 16 weeks old ($F_{2,66}$ = 1.85, P = 0.165 and $F_{2,66}$ = 2.03, P = 0.140, respectively) and 16 - 20 weeks old ($F_{2,66}$ = 1.12, P = 0.331 and $F_{2,66}$ = 0.76, P = 0.472, respectively) (Fig. 5.24). There was, however, an interaction effect during the 16 - 20 week old time period, which showed that decreasing water contributed to decreased RGR when NaCl was not available, but increased when NaCl was present ($F_{4,66}$ = 2.72, P = 0.037).

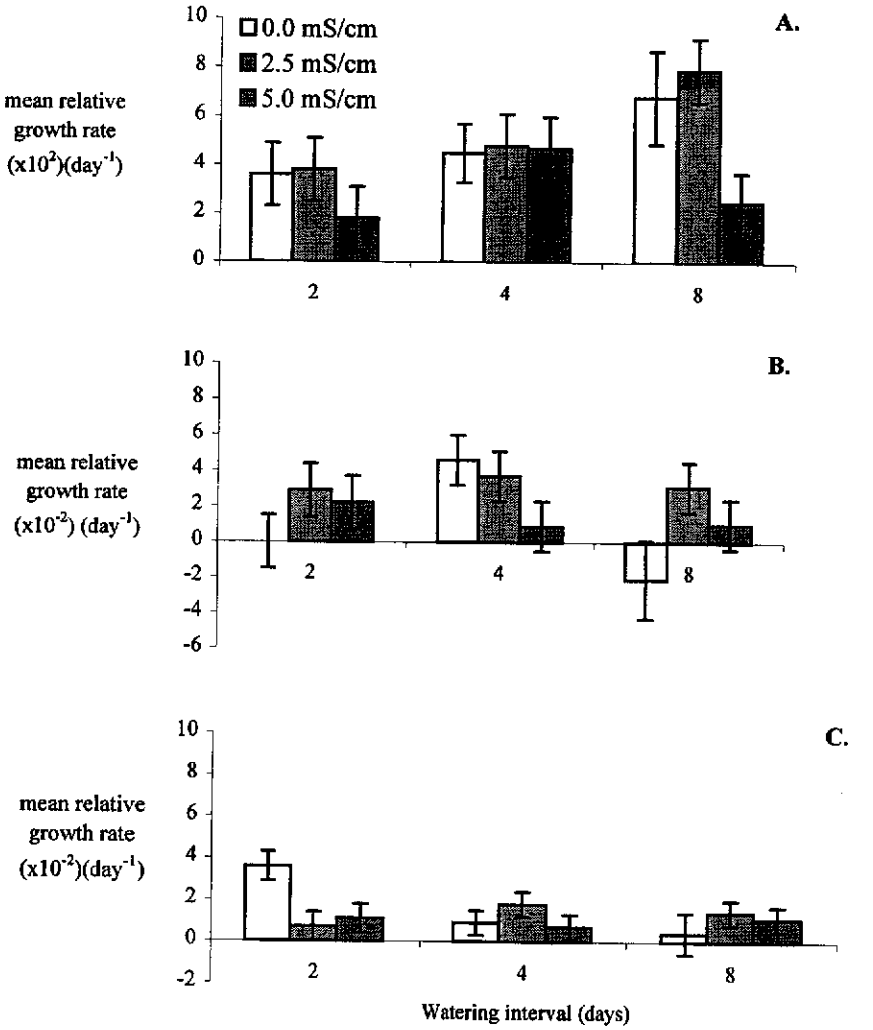


Figure 5.24 Mean relative growth rate (day^{-1}) of *M. brevifolia* plants during the time of NaCl application (8 - 12 weeks old) (A), the introduction of the watering regime (12 - 16 weeks old) (B) and the continuation of the watering regime (16 - 20 weeks old) (C). Plants were growing in soil salinities of 0.0, 2.5 or 5.0 mS cm^{-1} and under a 2, 4 or 8 day watering regime. Bars indicate standard errors.

Atriplex bunburyana plants exhibited no change in RGR in response to either NaCl or watering regimes during the 8 - 12 week old period (Fig. 5.25). The RGR decreased significantly in response to decreased water availability during the 12 - 16 week old period ($F_{2,68}$ = 12.12, P < 0.001). The NaCl and water regimes had an effect on RGR during the 16 - 20 week old period, with decreases in response to decreased water availability ($F_{2,68}$ = 4.30, P = 0.017), and increases in response to increased soil salinity ($F_{2,68}$ = 5.21, P = 0.008).

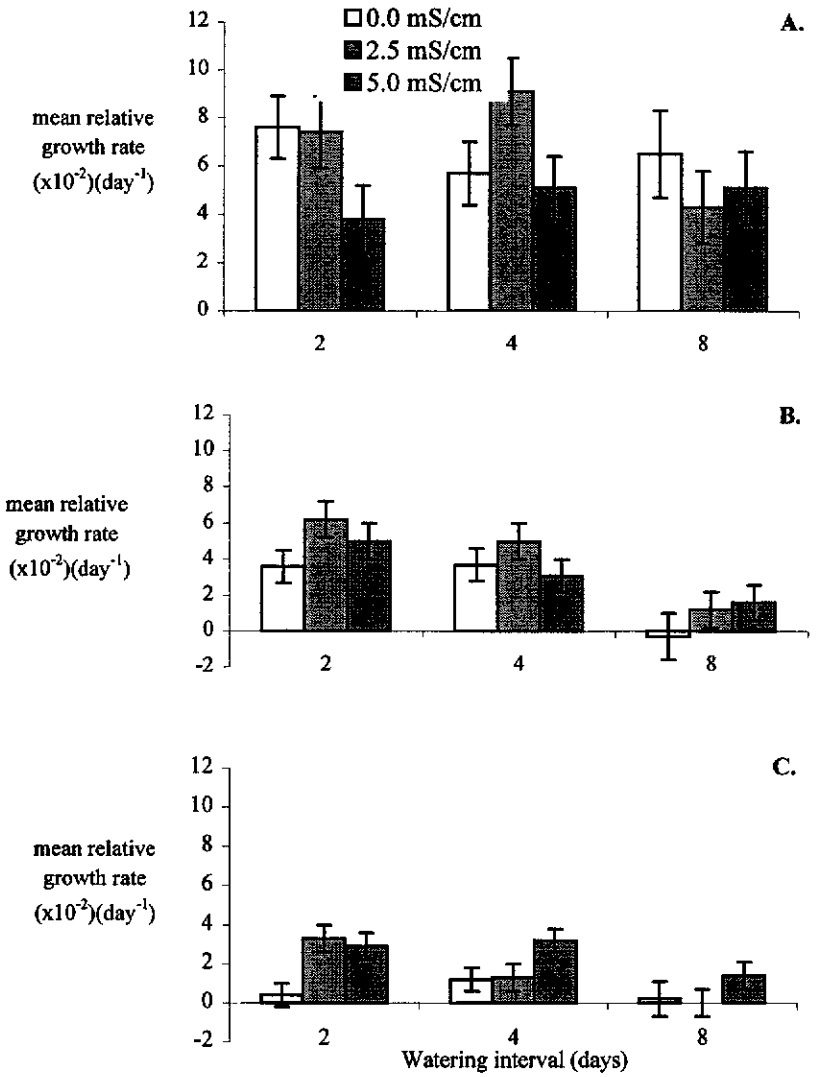


Figure 5.25 Mean relative growth rate (day^{-1}) of *A. bunburyana* plants during the time of NaCl application (8 - 12 weeks old) (A), the introduction of the watering regime (12 - 16 weeks old) (B) and the continuation of the watering regime (16 - 20 weeks old) (C). Bars indicate standard errors. Plants were growing in soil salinities of 0.0, 2.5 or 5.0 mS cm^{-1} and under a 2, 4 or 8 day watering regime.

The RGR of *A. codonocarpa* plants decreased significantly in response to lower water availability (Fig. 5.26). This was evident for the first the two plant age periods (12 - 16 and 16 - 20 weeks old), when the three water regimes had been introduced ($F_{2,73}$ = 13.21, $P < 0.001$ and $F_{2,73}$ = 4.45, P = 0.015, respectively). During the 12 - 16 week old period, increased salinity caused a higher RGR when water was available every two days, but resulted in decreased RGR when water was only available every one day in eight ($F_{4,73}$ = 4.24, P = 0.004).

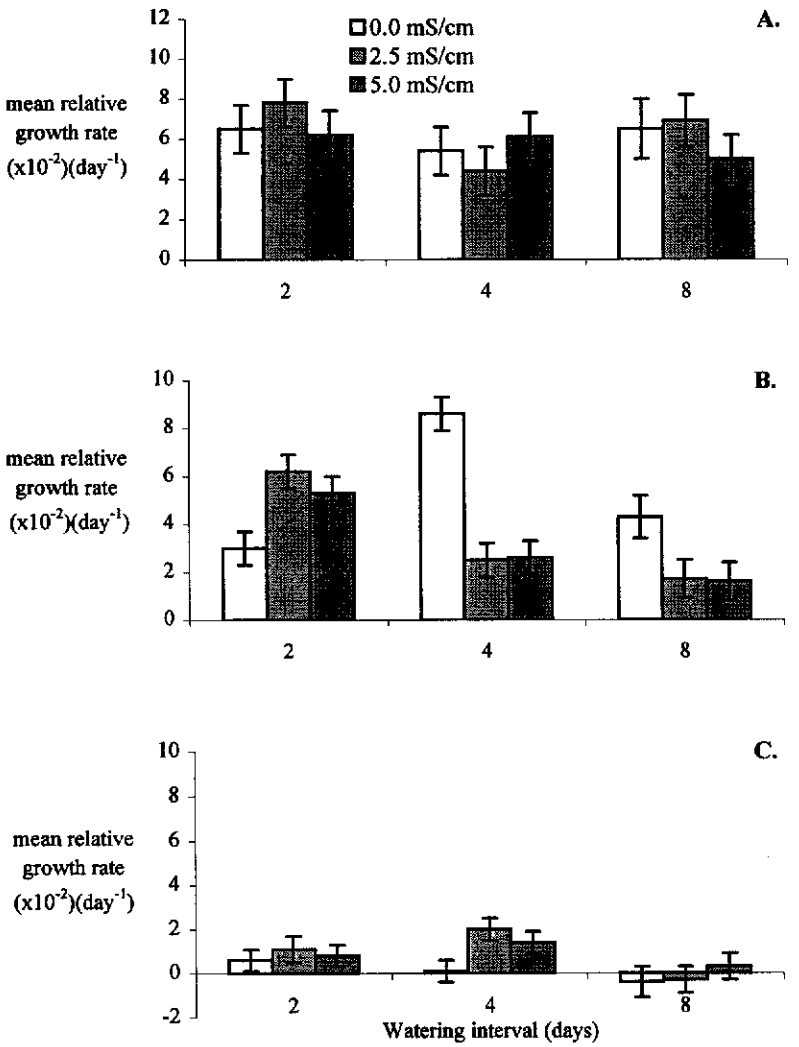


Figure 5.26 Mean relative growth rate (day^{-1}) of *A. codonocarpa* plants during the time of NaCl application (8 - 12 weeks old) (A), the introduction of the watering regime (12 - 16 weeks old) (B) and the continuation of the watering regime (16 - 20 weeks old) (C). Bars indicate standard errors. Plants were growing in soil salinities of 0.0, 2.5 or 5.0 mS cm^{-1} and under a 2, 4 or 8 day watering regime.

DISCUSSION

Plant performance is affected by limiting factors, such as water availability and soil salinity, common in semi-arid and arid environments. These factors influence distribution and performance of chenopods in the harsh environments of Australia (Malik *et al.* 1976). Moisture and salinity often operate in a discontinuous, and at times, in a stochastic manner. Competition intensity is likely to fluctuate, depending on the changing moisture and salinity conditions (Kadmon 1995).

Chenopods display a wide array of genetic diversity and adaptations to stress conditions (Kelley *et al.* 1982). High growth rates and a maximisation of resource capture under high stress is characteristic of good competitors (Nernberg and Dale 1997). The characterisation of the five chenopods based on their tolerance of short-term drought and saline conditions may contribute to their competitive ability under these conditions. The better growth of *M. brevifolia* and both *Atriplex* species, reflected by increases in shoot dry weight in response to salt in at least one watering regime, may show a superior competitive ability compared to *M. georgei* and *E. tomentosa*.

Seedling Mortality

All five chenopod species examined in the current study displayed a tolerance to soil salinity up to 5.0 mS cm^{-1}. Indeed, seedling mortality only occurred in the "no salt" treatments, exposed to the greatest water stress. The mortality rates for each species differed, with *M. georgei* having the lowest (20%), and *M. brevifolia* and *A. codonocarpa* (50%) the highest. Such variation in plant response may reflect differences in drought tolerance when NaCl is absent from the soil. This response highlights an almost obligate requirement for at least some level of NaCl in the soil during drought periods (also see Sharma 1982) by all five chenopod species.

Under highly saline conditions, mortality is likely to be density-independent (Jefferies *et al.* 1981, Wilkon-Michalska 1985). Although no mortality occurred at the highest soil salinity treatment in the current study, the combination of no salinity and short-term drought showed density-independent mortality, with *A. codonocarpa* and *M.*

brevifolia having the highest mortality. Density dependent mortality of *A. triangularis* occurred under moderate salinity conditions as a result of intra-specific competition (Drake and Ungar 1989). Although density under increasing saline conditions was not addressed in this study, both density-independent drought and salinity stress and density-dependent factors are likely to determine chenopod community structure on mine waste materials in the goldfields region of Western Australia.

Plant Growth

The current study has shown that plant growth (decreases in root and shoot dry weights of all five chenopods) was adversely affected by increased water deficits. Soil type also plays an important role in determining a plant's ability to tolerate drought (Fox *et al.* 1990, Fletcher 1992, Williams *et al.* 1998) and salinity (Barson *et al.* 1994). The topsoil used in my trials was obtained from the natural environment in which these species grow. Other environmental factors also determine the water availability and plant uptake (e.g. sporadic rainfall, soil water holding capacity, evaporation rates) and will influence a species' ability to grow and persist (Sharma 1976). These factors may also impact on the ability of the five chenopod species to grow and establish on mine site revegetation areas.

Overall, NaCl treatments increased growth of the *Atriplex* spp. and *M. brevifolia* plants, especially when watered less frequently. However, when plants were grown under more frequent watering regimes, high soil salinity (5.0 mS cm^{-1}) was often shown to be inhibitory to all of the chenopod species. The root dry weight of the *Atriplex* spp. increased when grown in soil of 2.5 mS cm^{-1} salinity but was inhibited at the highest salinity regime of 5 mS cm^{-1}. Similar findings have resulted for other chenopods (Sharma 1982, Kelley *et al.* 1982, Groom *et al.* 1993, Short and Colmer 1999). At high concentrations, NaCl inhibits plant growth by depressing the net photosynthetic rate, chlorophyll content and dark respiration (Shaybany and Kashirad 1978, Kolchevskii *et al.* 1995). At lower concentrations, NaCl has been shown to stimulate photosynthesis in *Eucalyptus camaldulensis* (Rawat and Banerjee 1998).

Atriplex bunburyana was the only species for which relative growth rate (RGR) was positively correlated with salinity. The ability of *A. bunburyana* seedlings to tolerate

higher levels of NaCl may enable them to extend their growing season into the summer period. This may give them a competitive advantage mainly because larger plants with deeper roots can better exploit soil resources such as soil moisture (Harris and Wilson 1970, Gordon and Rice 2000). The increase in RGR and root dry weight of *A. bunburyana* may reflect an ability for increased survival when grown under soil salinity conditions which appear to be detrimental to many other chenopods (e.g. *M. georgei* and *E. tomentosa*).

Leaf Characteristics

High salinity improved water status of all species as reflected by increases in leaf thickness and succulence. This has been demonstrated by *Atriplex nummularia* in a similar study of soil salinity regimes and water stress (Gates 1972). This mechanism enables the plants to tolerate NaCl uptake by diluting cell salinity levels: increasing water content and increasing the size of mesophyll cells (Black 1958, Short and Colmer 1999). The leafiness of *M. georgei* and *E. tomentosa* plants increased when grown in the presence of NaCl, as did the leafiness of *M. brevifolia,* but only when watering frequency decreased. An increase in leafiness is due to a breakdown of hormone-induced apical dominance causing sprouting of lateral leaf buds. This is a characteristic of salinity damage (Gale and Poljakoff-Mayber 1970).

Water Relations

Minimal information can be drawn, from the measured predawn and midday water potentials, about the physiology of the five chenopod species water relations. A small sample size due to the number of species and treatments, the lack of measures of turgor pressure and osmotic potentials make it impossible to draw comparisons between the physiologies of each of the five chenopods. All species withstood exceedingly low water potentials. Increased NaCl caused the five chenopod species to be under greater water stress as reflected by the midday water potentials. Soil water potential, as reflected by pre-dawn water potentials, decreased in response to decreased watering frequency. The soil water potential of *A. codonocarpa* was higher in comparison to the other species. Water uptake of *A. codonocarpa* may have been lower in comparison to the other species. Other studies have shown that NaCl is beneficial to the water relations of chenopod species

(Sharma 1982). For example, NaCl improved water relations of *Atriplex halimus* by lowering the transpiration rate (Kaplan and Gale 1972). When soil water potentials are extremely low, chenopods are also able to extract water by maintaining lower leaf water potential compared to that of the soil. This is achieved by accumulating solutes in the leaves (Black 1955, 1958, Sharma 1976, 1982).

CONCLUSION

It has been possible, from the results described in this chapter, to elucidate some of the processes involved in the survival and successful establishment of the chenopod species in the arid and semi-arid environments. Under conditions of low soil salinity combined with drought conditions, the *E.tomentosa* and *M. georgei* plants are less likely to suffer density-independent mortality in comparison to *A. codonocarpa* and *M. brevifolia*.

All five species utilised NaCl as a mechanism for tolerating water stress. However, the minimal impact that salt seems to have on their growth, may contribute to the competitive ability of each species. It is postulated that as the intensity of dry conditions increases, and thus water availability decreases, the less adapted species, *E. tomentosa* and *M. georgei,* were not able to compete for limited water resources as effectively as the species of *Atriplex* and *M. brevifolia* when growing in soil with salinities 2.5 - 5.0 mS cm^{-1}. The greater ability of the species of *Atriplex* and *M. brevifolia* to grow better in relatively high levels of soil salinity (i.e. higher relative growth rates and increased shoot dry weights) may give them a competitive 'edge' over *E. tomentosa* and *M. georgei*.

Management Implications

The ability of the five chenopod species to tolerate reasonably high salinities under drought conditions was species-specific. Their ability to survive and establish, under high salinity and drought conditions, will also determine their competitive ability. The chenopods' relative abilities to compete for limiting resources, such as moisture and nutrients, may ultimately impact on the diversity and species abundance of plant communities. An understanding of species-specific tolerances to soil conditions of the

restoration areas (e.g. soil moisture and salinity) is necessary when determining the components of the seed mixture to be broadcast.

CHAPTER 6: EFFECTS OF SHADE ON THE GROWTH OF CHENOPODS THAT ARE ADAPTED TO HIGH LIGHT IRRADIATION

INTRODUCTION

Light is essential to a plant's growth and survival through its conversion of light energy into chemical energy by the process of photosynthesis. Many plants are able to sense the direction, intensity and wavelength of light, all of which play a regulatory role in the seasonal and daily timing of plant growth (Ehleringer and Forseth 1990), reproduction, and germination (Gutterman 1993). Plants are able to utilize a broad spectrum of light intensities ranging from full sunlight to less than 1% (Levitt 1972, Mansfield and Jones 1976).

Some plant adaptations to low light intensity have resulted in morphologies that maximize light capture, such as large leaves, abundant chloroplasts, and greater allocation of resources to above-ground plant biomass (Levitt 1972, Valladares and Pearcy 1998). In contrast, plants in high light intensity environments may exhibit adaptations, which allow them to survive in such environments. These include the ability to incline their leaves (Anderson 1982, Ehleringer and Forseth 1990, Valladares and Pugnaire 1999), increased leaf reflectance through secretion of salt (Anderson 1982), the production of smaller leaves, and defoliation during summer (Barker 1975, Russell *et al.* 1990). In semi-arid and arid environments, where light intensity is generally high, other factors such as limited water availability and high leaf temperatures are indirectly related to the effects of light intensity (Ehleringer and Forseth 1990, Pugnaire *et al.* 1996c)

Plant canopies can restrict the quantity and quality of light reaching plants that grow below (Rhodes and Stern 1978, Gilbert *et al.* 2001), and may affect both the growth rate and habit of under-storey plants (Fitter and Hay 1989, Gilbert *et al.* 2001), particularly plants adapted to high irradiation levels (Rhodes and Stern 1978, Stoneman 1992). In such plants, branching, root growth and leaf production may be suppressed when light intensity is below the optimal levels required. Interestingly, leaf area and plant height appear to increase during the episodes of low light intensity (Rhodes and Stern 1978).

Some plants will expend considerable resources in these situations, attaining a greater height than their immediate competitors (Cahill Jr. 1999), which may have a large impact on the outcome of competitive processes (Newman 1973).

When two plants are in close proximity, not only will they compete for light, but they may also be competing for the available soil nutrients and moisture (Fitter and Hay 1989, Ruthven 2001). A complex relationship, therefore, may exist between above- and below-ground competition between the two plants. Root competition may cause a reduction in the nutrient supply to shoots, thus lowering shoot efficiency. In turn, this may reduce the plant's ability to compete for light, thereby ultimately slowing the flow of assimilates to the roots. This may result in the impairment of root function (Cahill Jr. 1999, Fitter and Hay 1989).

Surprisingly, there may also be benefits to a smaller plant growing under the canopy of another plant (often referred to as the 'nurse' plant). These may include: lower ambient temperatures, higher soil moisture levels in the microhabitat, decreased salinity levels in the immediate area (Callaway 1994), increased oxygen in the soil, protection from wind and herbivores (Carlsson and Callaghan 1991) and greater nutrient availability (Garcia-Moya and McKell 1969; Callaway 1995; Pugnaire *et al.* 1996c). Such benefits have been documented in many arid and semi-arid plant communities (Yeaton 1978, Silverton and Wilson 1994, Pugnaire *et al.* 1996a, Pugnaire *et al.* 1996b). In most cases, however, there is a trade-off between the ability of a plant to tolerate lower light radiation and the benefits accrued from greater levels of shade (i.e. lower light intensity) (Carlsson and Callaghan 1991, Callaway 1995).

Competition for light is usually thought to occur mostly in fertile environments (Aerts 1999). The availability of light in semi-arid and arid regions is usually a plentiful resource and competition for this resource is often overlooked as an important factor in intra- and inter-specific competition between plants. Plants that occur in semi-arid and arid regions are usually adapted to cope with high levels of solar irradiation. Therefore, when two plants are growing together there is almost always some competition for available resources, including light. The characteristics of the canopy, the growth rate,

and size of plants at maturity will determine whether or not light becomes a limiting factor (Gilbert *et al.* 2001).

Preliminary observations of one year old vegetation at the field site (Herald Resources mine site, Chapter 3) indicate that *M. georgei* plants growing under the canopy of *A. bunburyana* plants were adversely affected compared to those *M. georgei* plants growing in full sun. These shaded plants were spindly, small and did not produce fruit, reflecting either competition for light and/or competition for below-ground resources such as nutrients and/or water. In contrast, *E. tomentosa* exhibited increased biomass when grown with *A. codonocarpa* plants (Chapter 4). The aim of the pot trial experiments described in this chapter was to determine whether shade influenced the growth of the chenopod species, *E. tomentosa*, *M. brevifolia* and *M. georgei*.

MATERIALS AND METHODS

Four week old seedlings of *M. brevifolia, M. georgei and E. tomentosa* were planted singly in pots (17.5 cm in diameter and 16.0 cm height) in a soil mixture of 1:1 topsoil (obtained from Westonia, Western Australia) and sand (as previously described in Chapter 4). The plants were grown outdoors at the Field Trial Area, Curtin University of Technology, Perth, Western Australia. Ten plants of each species were grown under one of three light regimes: 1) full sunlight, 2) shade cloth of 70 % inhibition rating (providing a light intensity of approximately 40 000 lux at midday), and 3) shade cloth of 90% inhibition rating (providing a light intensity of approximately 10, 500 lux at midday). All plants were watered daily for 15 minutes with an automatic overhead watering system.

The height and number of branches of each plant was measured prior to being placed under the different light treatments. At fortnightly intervals for six weeks, the height (h) of all plants was remeasured as well as the maximum plant width (w1), 90° to the maximum width (w2) and the number of branches per plant was also recorded. Plant volume and cover were estimated using the following equations:

$$\text{Volume} = h \times w1 \times w2,$$

$$\text{Cover} = w1 \times w2.$$

At the time of final harvest, 15 mature leaves were randomly collected from three plants of each species and relative leaf area (RLA) measurements were taken using an image analyser (DIAS II, Delta-T Devices, Cambridge, England). The dry weight of these leaves (LFWT) was measured after they had been dried at 60 °C for four days. The plants were harvested at three months. The shoot dry weight, total leaf dry weight (TOTLFWT), and root dry weight was measured after the plant material was dried at 60°C for four days. Total photosynthetic surface area (PSA) was calculated using the following equation:

$$PSA = (TOTLFWT / LFWT) \times RLA$$

Homogeneity of variances was tested using Levenes test and data were $\log_{10}$ transformed when the data were not normally distributed. Plant height, and root or shoot weights for the different light intensity treatments were analysed using a one way analysis of variance (ANOVA) using SPSS 10.0 for Macintosh software (1989-2000, SPSS Inc.) and the means compared using Tukey's Compromise post hoc test. When variances were not homogenous after $\log_{10}$ transformation of data, the non-parametric Kruskal-Wallis test was used (Ott 1988).

RESULTS

Effects on plant biomass

The root dry weight of *Enchylaena tomentosa* plants did not differ significantly between treatments ($F_{2,29}$ = 1.55, P = 0.231), but shoot dry weight of this species did ($F_{2,29}$ = 30.49, P < 0.001, Fig. 6.1). The total plant biomass showed a positive response to the shade treatments ($F_{2,29}$ = 14.27, P < 0.001).

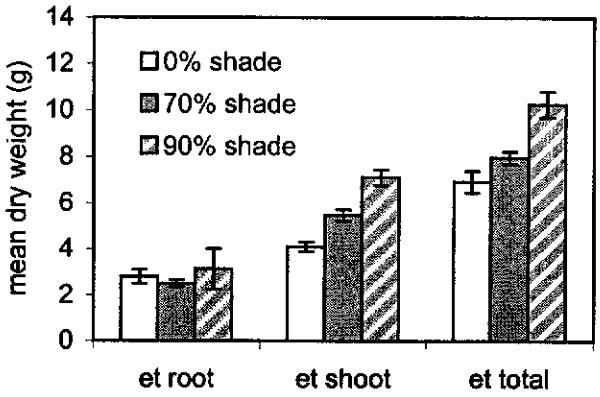


Figure 6.1 Mean root, shoot and total dry weight of three month old *E. tomentosa* (et) plants grown under three shade regimes (0% shade, 70% shade and 90% shade). Significant differences between treatments are indicated by different letters (P<0.05). Bars indicate standard errors.

Maireana brevifolia root and total dry weight did not differ significantly between light intensity treatments ($F_{2,29}$ = 1.16, P = 0.331 and $F_{2,29}$ = 0.66, P = 0.524, respectively), but shoot dry weight, however, increased in response to shade ($F_{2,29}$ = 7.25, P = 0.003, Fig. 6.2).

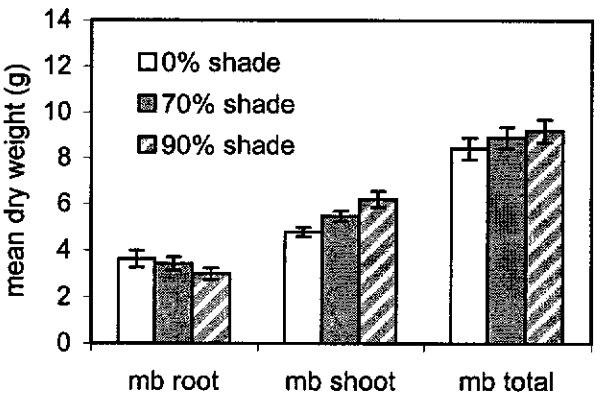


Figure 6.2 Mean *M. brevifolia* (mb) root, shoot and total dry weight at three months of age grown under three shade regimes (0% shade, 70% shade and 90% shade). Significant differences between treatments are indicated by different letters (P<0.05). Bars indicate standard errors.

The root dry weight of *M. georgei* plants decreased when grown under 90% shade ($F_{2,29} = 6.44$, $P = 0.006$). However, shoot and total dry weight did not significantly differ between shade treatments ($F_{2,29} = 0.08$, $P = 0.923$ and $F_{2,29} = 0.81$, $P = 0.456$, respectively, Fig. 6.3).

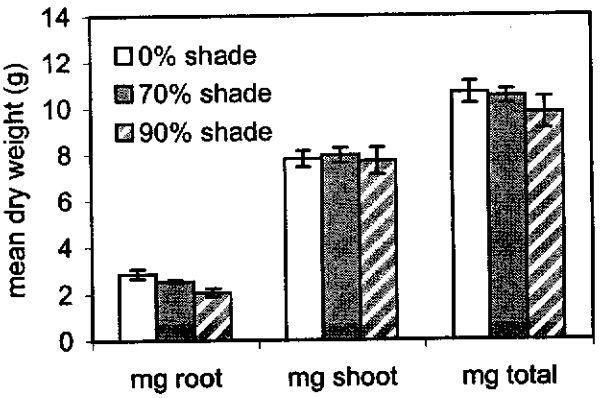


Figure 6.3 Mean root, shoot and total dry weight of three month old *M. georgei* (mg) plants grown under one of three shade regimes (0% shade, 70% shade and 90% shade). Significant differences between treatments are indicated by differing letters (P<0.05). Bars indicate standard errors.

Volume and Plant Structure

The plant volume of each species was calculated at six, eight and ten weeks of age (Fig. 6.4, Table 6.1). *Enchylaena tomentosa* (Fig. 6.4A) and *M. brevifolia* (Fig. 6.4C) plant volumes were significantly greater when grown under shade at eight and ten weeks of age. *Maireana georgei* plant volume was significantly greater, at eight and ten weeks of age, when grown under 70% shade (Fig. 6.4E).

Maireana brevifolia and *E. tomentosa* plants "collapsed" and their lateral branches grew upwards when grown in shade. When this occurred, there were significant increases in plant cover (Fig. 6.4B, 6.4D). *Maireana georgei* maintained its structure throughout the experiments, regardless of the shade treatment, with no significant differences in plant cover between treatments (Fig. 6.4F).

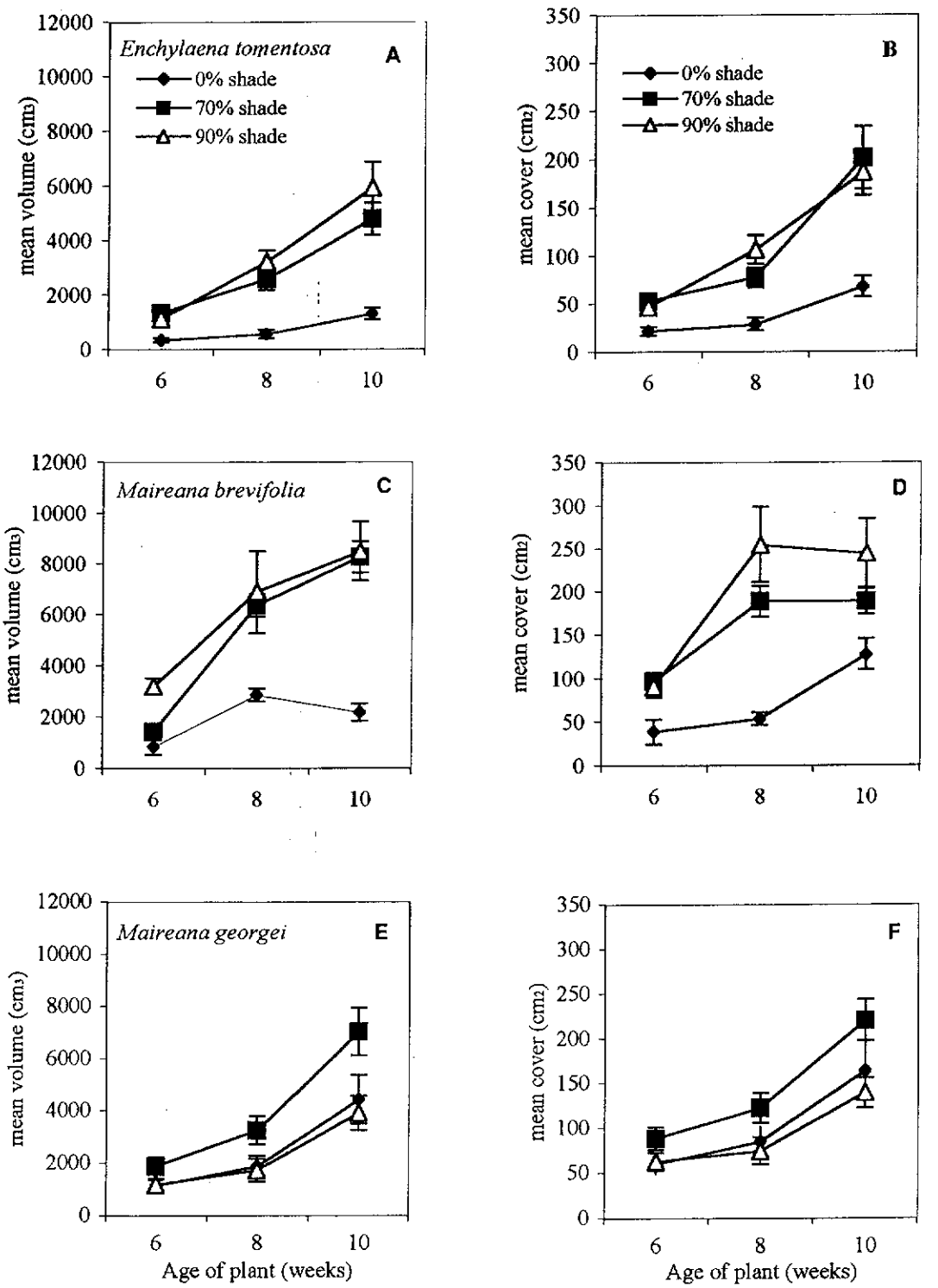


Figure 6.4 Mean volume (cm^3) (A, C, E) and cover (cm^2) (B, D, F) during the growing season of *E. tomentosa*, *M. brevifolia* and *M. georgei* plants grown under one of three shade regimes (0% shade, 70% shade and 90% shade). Bars indicate standard errors.

Table 6.1 *F* and *P* values from one-way ANOVA of plant volume and cover of the chenopod species grown under the different light treatments (0% shade, 70% shade and 90% shade).

		Volume		Cover	
Species	Plant Age (weeks)	$F_{2, 29}$	*P*	$F_{2, 29}$	*P*
E. tomentosa					
	6	11.87	**< 0.001**	9.51	**0.001**
	8	14.07	**< 0.001**	11.78	**< 0.001**
	10	9.91	**0.001**	9.09	**0.001**
M. brevifolia					
	6	11.58	**< 0.001**	6.16	**0.006**
	8	10.75	**< 0.001**	11.04	**<0.001**
	10	9.49	**0.001**	4.07	**0.029**
M. georgei					
	6	3.12	0.060	2.01	0.154
	8	3.43	**0.047**	2.40	0.110
	10	3.97	**0.031**	2.40	0.111

Total leaf biomass, relative leaf area and total photosynthetic surface area (PSA)

Maireana georgei leaf dry weight did not change significantly in response to the different shade treatments ($F_{2, 29}$ = 2.37, P = 0.115). Leaf dry weight of *E. tomentosa* plants increased when grown in 90% shade ($F_{2, 29}$ = 16.26, P < 0.001). In contrast, *M. brevifolia* leaf dry weight decreased in response to shade ($F_{2, 29}$ = 7.27, P = 0.003, Fig. 6.5).

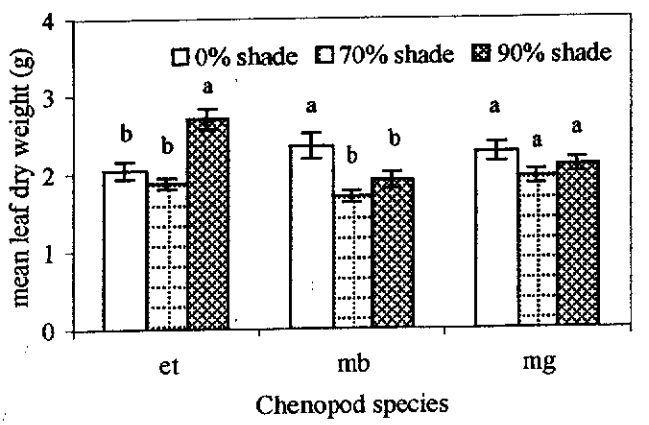


Figure 6.5 Mean leaf dry weight of the target species, *E. tomentosa* (et), *M. brevifolia* (mb) and *M. georgei* (mg), at three months of age, grown under three light regimes (0% shade, 70% shade and 90% shade). Similar letters indicate no significant differences between means using Tukey's Compromise (p<0.05). Bars indicate standard errors.

The relative leaf area of *E. tomentosa* plants increased in response to 70% shade, but relative leaf area showed no difference between 0% and 90% shade ($F_{2,\ 44} = 8.56$, $P = 0.001$). Relative leaf area of *Maireana georgei* plants increased in response to both shade regimes ($F_{2,\ 44} = 7.13$, $P = 0.002$). Relative leaf area of *Maireana brevifolia*, however, was unaffected by light intensity ($F_{2,\ 44} = 2.08$, $P = 0.132$, Fig. 6.6).

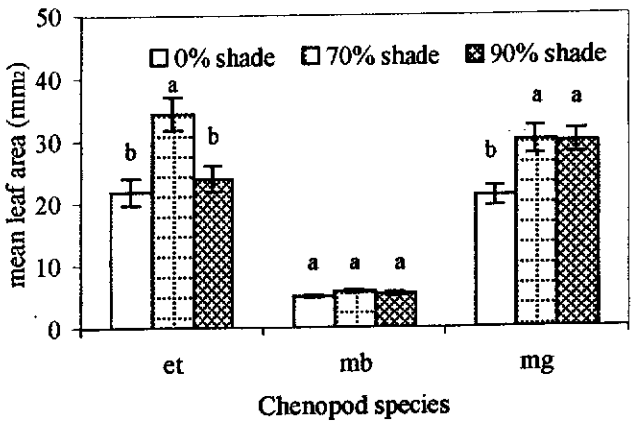


Figure 6.6 Mean relative leaf area of the target species, *E. tomentosa* (et), *M. brevifolia* (mb) and *M. georgei* (mg), at three months of age, when grown under three light regimes (0% shade, 70% shade and 90% shade). Similar letters indicate that there are no significant differences between means using Tukey's Compromise ($p<0.05$). Bars indicate standard errors.

The total photosynthetic surface area (PSA) of *E. tomentosa* ($F_{2,\ 29} = 39.45$, $P < 0.001$) and *M. brevifolia* ($F_{2,\ 29} = 7.58$, $P = 0.003$) plants decreased significantly when grown under 70% shade. Total PSA remained unchanged in response to 90% shade compared to full sunlight. Total plant PSA of *M. georgei* showed no change in response to either shade treatment ($F_{2,\ 29} = 0.99$, $P = 0.386$, Fig. 6.7).

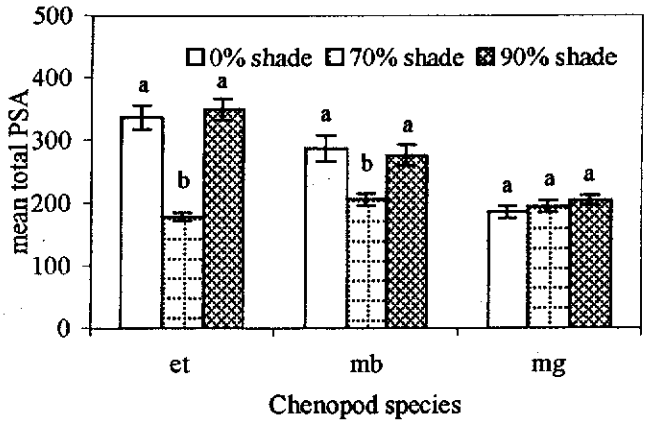


Figure 6.7 Mean total PSA of the target species, *E. tomentosa* (et), *M. brevifolia* (mb) and *M. georgei* (mg), at three months of age, grown under three light regimes (0% shade, 70% shade and 90% shade). Similar letters indicate that there are no significant differences between means using Tukey's Compromise ($p<0.05$). Bars indicate standard errors.

Root to Shoot Ratio, Branching and Plant Height

At harvest, all species had increased their shoot biomass in response to both shade treatments as reflected by the decrease in the root: shoot ratios of *E. tomentosa* ($F_{2,29} = 10.28$, $P = 0.001$), *M. brevifolia* ($F_{2,29} = 7.43$, $P = 0.003$) and *M. georgei* ($F_{2,29} = 3.43$, $P = 0.049$, Fig. 6.8).

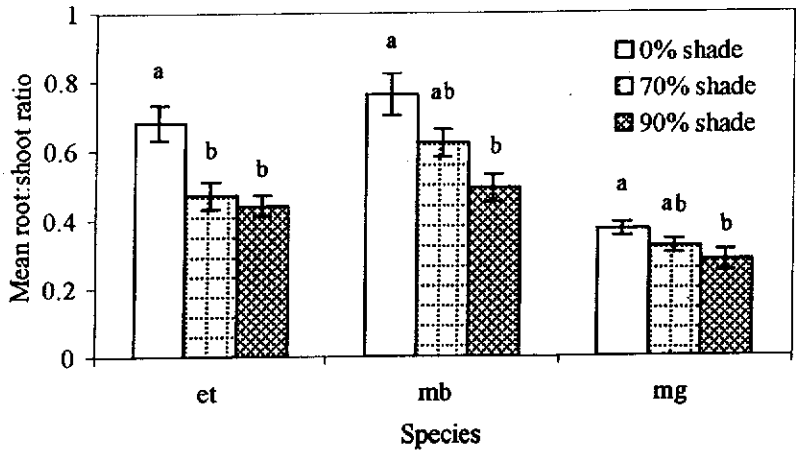


Figure 6.8 Mean root: shoot ratio of the plant species grown under each of three light regimes (0% shade, 70% shade and 90% shade). Significant differences between treatments are indicated by differing letters ($P<0.05$). Bars indicate standard errors.

Prior to placing the plants at 4 weeks of age into the shade treatments, height and the number of branches were measured (Fig. 6.9, Table 6.2). *Enchylaena tomentosa* plants placed in the 0% shade regime were significantly shorter than those plants placed in the other shade regimes. *Maireana brevifolia* plants placed in the 70% shade regime were significantly taller than those plants placed in 0% and 90% shade regimes. *Maireana georgei* plants placed in the 0% shade regime had significantly more branches than those plants placed in 70% and 90% shade regimes.

The two weekly assessments between four and eight weeks showed that at eight weeks *M. georgei* plants produced less branches when grown under both shade treatments and had a significantly lower mean plant height when grown in 90% shade compared to full sunlight (Fig. 6.9, Table 6.2). Assessments of the number of branches at ten weeks and plant height at six and ten weeks showed no significant differences between treatments. *Maireana brevifolia* produced less branches when in shade at six and eight weeks, but increased in height in response to shade at six, eight and ten weeks (Fig. 6.9, Table 6.2). *Enchylaena tomentosa* responded to shade by growing taller, which was apparent at each

assessment period (Fig. 6.9, Table 6.2). This species also produced significantly more branches at the eight and ten week assessments.

Table 6.2 *F* and *P* values from one-way ANOVA of branches and plant height of the chenopod species grown under the different light treatments (0% shade, 70% shade and 90% shade).

		Branches		Height	
Species	Plant Age (weeks)	$F_{2,29}$	*P*	$F_{2,29}$	*P*
E. tomentosa					
	4	0.04	0.960	7.67	**0.002**
	6	1.71	0.200	14.92	**0.000**
	8	5.89	**0.007**	16.36	**0.000**
	10	4.71	**0.017**	3.87	**0.033**
M. brevifolia					
	4	1.61	0.218	5.28	**0.012**
	6	6.33	**0.006**	11.81	**0.000**
	8	5.47	**0.010**	7.09	**0.003**
	10	1.48	0.246	3.78	**0.036**
M. georgei					
	4	7.59	**0.002**	0.94	0.403
	6	5.06	**0.014**	2.55	0.097
	8	4.88	**0.016**	3.78	**0.036**
	10	1.93	0.164	2.95	0.069

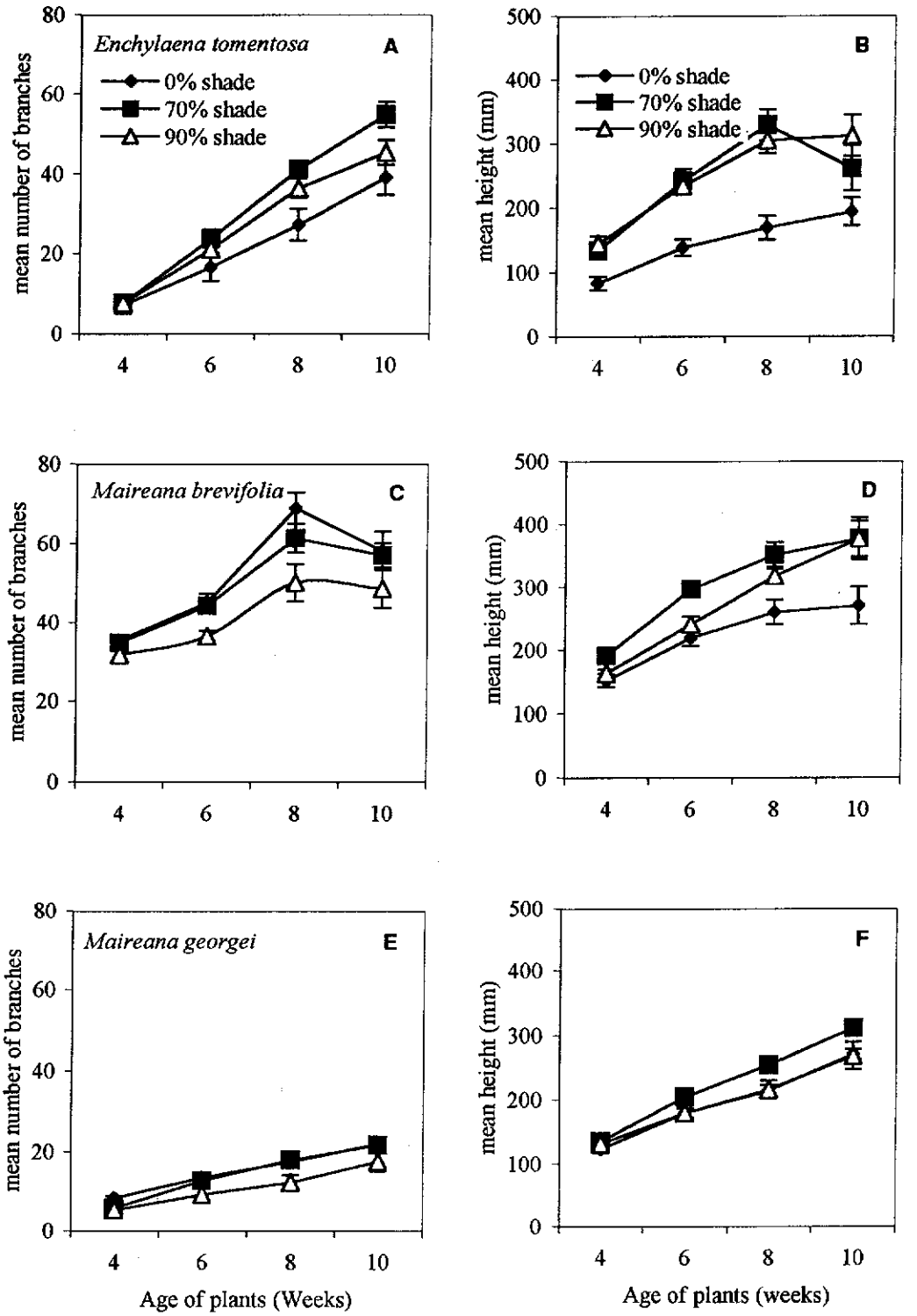


Figure 6.9 Mean total branches (A, C, E) and height (B, D, F) of plants during the growing season of the chenopod species grown under the different light treatments (0% shade, 70% shade and 90% shade). Bars indicate standard errors.

DISCUSSION

The structure of the plant influences the micro-environment immediately below it, with temperature, relative humidity, radiated heat, soil temperature and soil heat flow influenced by the cover provided by the canopy. Processes such as photosynthesis, transpiration, cell enlargement and photomorphogenesis are, therefore, likely to be affected by plant canopies (Campbell and Norman 1990). This in turn can influence the outcomes of competition between species. The shade experiments mimicked the effects of plant canopy by limiting the amount of available light. The shade cloth used, however, provided a consistent light intensity, which is not usually the case in the natural environment. Other factors also need to be considered, such as, direct or diffuse sunlight, the density of the foliage canopy and the extent to which gaps in the foliage or the effects of wind allow sunlight to penetrate different areas of the canopy (Rhodes and Stern 1978, Gilbert *et al.* 2001). Not withstanding this, it seems likely that the responses of the species of chenopods grown under the shade conditions in my study indicated their likely responses when they grow under the canopy of another plant.

Positive and negative interactions often occur in harsh environments (Olofsson *et al.* 1999). Facilitation in harsh environments occurs when the amelioration of harsh conditions by one plant favour growth of another to the extent that it outweighs the negative effects exerted by that same plant (Olofsson *et al.* 1999). The attributes of *E. tomentosa* plants, in response to shade, suggest a greater competitive ability to obtain an adequate level of resources under the canopy of larger plants. This could provide *E. tomentosa* with a competitive advantage. *Enchylaena tomentosa* seedlings may have a greater chance of survival and hence establishment under the canopy of another plant. The germination and establishment of seedlings under a 'nurse' plant may also provide other benefits such as lower summer temperatures, higher levels of organic matter, improved retention of soil water and protection from herbivores (Fowler 1986, Callaway 1995, Pugnaire *et al.* 1996c, Pugnaire and Haase 1996, Holmgren *et al.* 1997). The benefits that this plant species gains from lower irradiation levels, especially when growing under larger shrub canopies may not be a coincidence. The fleshy seeds of *E. tomentosa* plants are likely to be an attractive food source to birds. Larger shrub branches are commonly used as perches where faeces are deposited (Yeaton 1978). Bird faeces

would also contribute to the nutrient accumulation below the canopy of the 'nurse' shrub (Silverton and Wilson 1994).

Plant height, crown spread patterns and branching characteristics are very important in determining a plant's ability to compete for space and to adequately spread its photosynthetic organs, the leaves (Wilson 1988b, Fitter and Hay 1989, Tremmel and Bazzaz 1995, Sumida and Komiyama 1997). The flexibility in plant structure exhibited by *E. tomentosa* and *M. brevifolia* in response to shading suggests an ability of these species to compete successfully for light. These species responded to shade by "falling on their sides". Their lateral branches then grew upwards and thus cover increased. This change in structure increased the resource-gathering ability of these plants by increasing the surface area of foliage exposed to light. It also reduced leaf self-shading by increasing the number of leaves directly exposed to light.

Interestingly, *M. brevifolia* demonstrated increased shoot biomass, plant volume, plant cover and plant height in response to shade. The increase in above-ground biomass indicates that this species requires high light intensities. The decrease in root/shoot ratio in response to shade indicated that increased resources were allocated to the shoots in response to shade. The allocation of resources to the shoots in response to shade is also characteristic of other species (Damgaard 1999). The change in resource allocation into above-ground biomass reflects the competitive ability of *M. brevifolia*. The structural and physiological plasticity exhibited by individual species will determine their ability to cope with shaded environments (Valladares and Pearcy 1998).

The root/shoot ratio of *M. georgei* also decreased in response to shade. The number of branches also decreased, but plant height increased in response to shade treatments. The mechanism of resource allocation in *M. georgei* appeared to be different to that in *E. tomentosa* and *M. brevifolia*. *Maireana georgei* had a lower root biomass, whereas *E. tomentosa* and *M. brevifolia* increased their shoot biomass in response to shade. A lower root biomass is a disadvantage to plants competing for soil nutrients and/or water, which are usually limiting resources in arid and semi-arid areas (Rhodes and Stern 1978, Cahill

Jr. 1999). This may result in a compounding effect that would disadvantage *M. georgei* plants, especially when growing under the canopy of another plant.

Plant structure, cover and volume, of *M. georgei* did not change when the plants were grown under shade. The decreased root biomass, decreased plant height and a reduction in the number of branches all indicated that *M. georgei* was less tolerant of low levels of irradiation. This suggests that *M. georgei* is unlikely to be able to compete well for and tolerate low levels of light in the presence of other plants. This was supported by observations at the field trial study (Herald Resources, Coolgardie) (Chapter 3), where *M. georgei* plants were small and spindly when growing under the canopy of *A. bunburyana*. In addition a previous study has shown that photosynthesis of ten species of the *Chenopodiaceae* family was severely depressed when plants were grown in highly saline soils (Kolchevskii *et al.* 1995). This suggests that the effects of shade may be compounded when *M. georgei* plants are grown in saline soils, as their photosynthetic capacity is likely to be reduced.

One-sided asymmetric above-ground competition, where larger plants have a suppressive effect on the growth of smaller plants by shading, is likely to play a significant regulatory role in chenopod communities. The diversity of chenopod growth forms is likely to contribute to the process. Species-specific growth forms correspond to successional status of each species in other plant communities (Kubota and Hara 1995). The lack of shade tolerance exhibited by *M. georgei* suggests successive generations of *M. georgei* seedlings, or delayed germinants due to seed dormancy factors, are unlikely to establish and survive under the canopy of larger plants, such as *A. bunburyana*. In densely populated sites of other species, an above-ground competitive effect has been found to be more intense (Kubota and Hara 1996).

CONCLUSION

The shading effect that one plant can exert on a smaller plant, either of the same or of a different species, can play a significant role in arid zone ecology. The three chenopod species used in this study showed different growth responses in comparison to each other when grown under shade. The shade in this pot trial was consistent, which is not likely to

be the case in the field where the changing position of the sun may cause less consistency. The pot trial, however indicated that *M. georgei* was intolerant to shading by larger neighbours. The success of any species is dependent on the size structure of the competing populations (Goldberg 1990). The fast growth rate and larger size at maturity of aggressive competitors, such as *A. bunburyana*, is likely to result in *M. georgei* plants being out competed with respect to light when these plants grow in close proximity. *Maireana brevifolia* will be more competitive for available light when in close proximity to another plant, such as *A. bunburyana*. *Enchylaena tomentosa* has attributes, which allow its growth to be facilitated by the canopy of other plants. Its establishment success, when growing under the canopy of another plant, would therefore be dependent on the intensity of below-ground competition, which is likely to occur, for space, nutrients and water.

Management Implications

The characteristics of the life form of each species are an important consideration for species components and their respective density within a seed mixture. The results of this chapter have highlighted that plant canopy may have a negative impact on smaller neighbours of some species. It is suggested that species with tall, spreading life forms, such as *A. bunburyana* or *M. brevifolia*, should form a smaller component of the seed mixture in comparison to small, compact life forms, such as *M. georgei*. The density components in the seed mixture, should be adjusted to take into account the life form of each species and will, therefore, ensure a diverse range of life forms is achieved during the revegetation process of mine site areas.

CHAPTER 7: EFFECTS OF ALLELOPATHIC SUBSTANCES ON SEED GERMINATION

INTRODUCTION

Several classes of secondary metabolites, such as monoterpenes and phenols, are produced by plants, including those growing in semi-arid deserts, for the purposes of allelopathy (Mann 1987, Nilsson *et al.* 2000). Allelopathic compounds are substances that inhibit the growth and development of other plants, and are predominantly produced in leaves. Plant material that falls to the ground during "high stress" episodes (e.g. drought) decomposes releasing allelopathic exudates into the surrounding soil. Rains may help with the leaching of exudates through the soil. Once these exudates have infiltrated the soil, they can affect the germination and growth of other plants (Rice 1974, Mann 1987, Saxena *et al.* 1996).

Germination of *Helianthemum squamatum* is, for example, strongly inhibited in soils directly beneath the canopy of *Artemisia herba-alba* (Escudero *et al.* 2000). Both the roots and shoots were found to produce allelopathic substances. Compounds often associated with allelopathy generally inhibit specific biochemical processes that take place during germination. One class of compounds that inhibit germination are phenols (Nilsson *et al.* 2000). Interestingly, activated carbon has been shown to reverse the inhibitory effects of phenols by absorbing such compounds and removing them from the system. In addition, bushfires, a natural occurrence in desert regions, may also play a major role in destroying allelopathic substances by denaturing such compounds (Rice 1974, Mann 1987).

The concentration of allelopathic substances and the sensitivity of species that are affected are important in determining the effectiveness of allelopathic chemicals on the

inhibition of seed germination and seedling growth. In some cases, the same chemical, but at lower concentrations, may have the opposite effect and actually promote growth (Saxena *et al.* 1996). The density of the 'dominant' plants also plays a role in determining the concentration and effectiveness of allelopathic compounds. A number of studies have shown that the effects of phytotoxic substances attenuate when the density of plants increases. This may be due to a dilution effect caused by the uptake by greater numbers of plants (Weidenhamer *et al.* 1989) or, alternatively, as a result of soil detoxification by neighbouring plants (Thijs *et al.* 1994).

This chapter focuses on the effect of different concentrations of aqueous leaf extracts of *A. bunburyana*, *A. codonocarpa*, *M. brevifolia*, *M. georgei* and *E. tomentosa* on seed germination of intra- and inter-specific combinations. A pilot study was initially conducted to indicate whether or not allelopathic compounds existed in the foliage of the five chenopod species and their effects on germination of *M. brevifolia*, *M. georgei* and *E. tomentosa*. The allelopathic effects of these extracts were then tested on *Lactuca sativa* L. (lettuce) seeds, which were chosen for their low genetic variability, high rate of germination and high final germination percentage. Leaf extracts of *A. bunburyana* and *A. codonocarpa* were then tested on the germination of *M. georgei, M. brevifolia* and *E. tomentosa*, as well as their own seed. Finally, extracts of *M. georgei, M. brevifolia* and *E. tomentosa* were tested on the seed of *A. bunburyana* and *A. codonocarpa* as well as on their own seed. This chapter reports the results of these investigations.

MATERIALS AND METHODS

Extraction of allelopathic compounds

The leaves of all five chenopod species were collected from 12 month old plants that had been germinated and grown under the conditions of the pot trials described in Chapter 4. The leaves of each species were dried in an oven at 40 °C for 48 hours and then ground to

a fine powder using a vegetative grinder (Dietz-Motoren KG). Leaf powder (6.0 g) was successively extracted with hexane (200ml) and then filtered using Whatman filter paper. The resulting residue was then extracted with dichloromethane (200ml), followed by methanol (200ml) and then deionised water (200ml) to generate three additional fractions. All extractions were performed overnight. Hexane and dichloromethane were used to extract fat-soluble compounds, while methanol and water removed water-soluble compounds. This method is a commonly used procedure for isolating bioactive compounds (pers. comm. M. Pennacchio). The dry weight of the extract was determined and percentage dry weight (%DW) was determined (Table 7.1):

$$\%DW = \frac{\text{extract dry weight (g)}}{\text{original leaf powder dry weight (g)}} \times 100$$

Table 7.1 Dry weight (wt) and percentage dry weight (% DW) of extracts from each of chenopod species after isolation from leaf powder using successive solvents (hexane, dichloromethane, methanol and water).

	hexane		dichloromethane		methanol		distilled water	
Species	wt (g)	% DW	wt (g)	% DW	wt (g)	% DW	wt (g)	% DW
A. codonocarpa	0.06	1.0	0.81	13.5	0.56	9.3	0.03	0.5
A. bunburyana	0.07	1.2	0.07	1.2	1.35	22.5	0.03	0.5
E. tomentosa	0.09	1.5	0.04	0.7	1.06	17.7	0.04	0.7
M. brevifolia	0.06	1.0	0.04	0.7	0.96	16.0	0.05	0.8
M. georgei	0.06	1.0	0.03	0.5	0.50	8.3	0.04	0.7

Pilot study with chenopod species

The dichloromethane, methanol and aqueous extracts of the chenopod foliage were used to determine the effect on germination of *M. georgei*, *E. tomentosa* and *M. brevifolia*. Seeds were surface sterilised with a 1.5% bleach solution for one minute followed by three washes with sterile water. Seeds were then dried at room temperature and evenly arranged on filter paper (7.0 cm diameter) in petri dishes. Four replicate plates of 25 seeds of each chenopod species were treated with 1 ml of extract solution. This solution had

been made to a concentration of 24 g extract L^{-1} deionised water. Controls for each species consisted of germinating seeds with deionised water only. No statistical analyses were conducted on the data produced because the pilot study was used only as an indicator for allelopathy.

Bioassay of lettuce seed

Germination trials with lettuce seeds were conducted using a range of aqueous dilutions of the various extracts, which were extracted using methanol and deionised water only. Sterile deionised water was used to dissolve dry methanol extracts to concentrations of 25, 12.5, 6.25, 2.5, 0.25, 0.025 g L^{-1}. Water extracts were prepared to concentrations of 6.25, 3.12, 1.55, 0.63, 0.06, 0.006 g L^{-1}. Seeds were surface sterilised with 1.5 % bleach for one minute followed by three washes with sterile water. The seeds were then dried and arranged on filter paper (7.0 cm diameter) in petri dishes. One millilitre of extract was added to each petri dish. This volume was sufficient for these petri dishes. The controls consisted of sterilised deionised water only. Four replicate petri dishes, each containing 25 seeds, were allocated to each treatment. The petri dishes were sealed with plastic wrap (Gladwrap®), to prevent moisture loss and contamination by micro-organisms, and were stored in the dark at a constant 25 °C for seven days. Seeds were considered to have germinated when the radicle protruded at least 1 mm beyond the seed coat.

Bioassays for the germination of chenopod seeds

Each of the aqueous extracts was tested in a concentration-dependent manner on the germination of four of the chenopod species. Seeds of *M. brevifolia* were not viable at the time of these trials and were, therefore, excluded from this study. The controls consisted of sterilised deionised water only. Four replicate plates with 25 seeds of *M. georgei* or *E. tomentosa* were treated with 1 ml of aqueous extract solutions from either *A. bunburyana*,

A. codonocarpa or themselves. Four concentrations of extract were tested on the seeds of each species: 6.25, 3.12, 1.55 and 0.006 g L^{-1}. The extract of *A. codonocarpa* was tested at a concentration of 6.25 g L^{-1} only, due to its limited availability.

Aqueous extracts isolated from the leaves of *M. georgei* and *E. tomentosa* (6.25 g L^{-1}) were tested on germination of *A. codonocarpa* and *A. bunburyana* seeds. Aqueous extracts of *A. bunburyana* and *A. codonocarpa* were also tested intra-specifically using the 6.25 g L^{-1} concentration.

Data Analysis

Germinant numbers for the lettuce seed bioassay were recorded every two days for a total of eight days because the controls achieved complete germination within this time period. The number of germinants were recorded every two days until 14 days had elapsed, which was the time taken for chenopod controls to complete their germination. Final germination percentage was calculated for the lettuce seed bioassay to determine concentrations that produced the greatest inhibition. To gain an understanding of the mechanisms of inhibition, more extensive measures of germination parameters were necessary for *E. tomentosa*, *M. georgei*, *A. bunburyana* and *A. codonocarpa*. The following formulae were used (Saxena *et al.* 1996):

1) Final Germination (FG) %: The maximum average percentage of seeds that had germinated during the experimental period.

2) Mean Period of Final Germination (MPFG) = $\sum N_i D_i / FG$

3) Rate of Germination (RG) = $\sum N_i / D_i$

4) Percentage Inhibition or Stimulation

= 100 - (FG in aqueous extracts (%) / FG in distilled water (%) * 100)

where,

N is the daily increase in seedling number, and

D is the number of days from seed placement (Saxena *et al.* 1996).

Homogeneity of variances was tested using Levenes test. All data were $\log_{10}$ transformed when not normally distributed. One-way ANOVA's were performed on germination parameters for each species tested when subject to different extract concentrations. Differences between means were determined using Tukey's Compromise (Ott 1988).

RESULTS

Pilot Study

Final germination percentages of *M. brevifolia* and *E. tomentosa* decreased when treated with extracts from both *Atriplex* species, as well as from their own species (Table 7.2). Germination of *M. georgei* decreased when seeds were subjected to aqueous leaf extracts that had been isolated using dichloromethane and methanol solvents, but showed little or no decrease when extracts from *A. bunburyana* and *A. codonocarpa* leaves were applied. The final germination percentages of the three chenopod species tested indicated that aqueous leaf extracts isolated using water and methanol had the greatest inhibitory effect. The final germination percentage of all three species decreased in response to the aqueous extracts (Table 7.2).

Table 7.2 Mean final germination percentage of seeds for the three chenopod species treated with leaf extracts isolated using dichloromethane, methanol and water. The concentration was 24 g L^{-1}. The dash (-) indicates tests' that were not performed. Abbreviations; Ab - *Atriplex bunburyana*, Ac - *Atriplex codonocarpa*, Mg - *Maireana georgei*, Et - *Enchylaena tomentosa*, Mb - *Maireana brevifolia*.

	Seed Species		
Extract	**Mg**	**Et**	**Mb**
Dichloromethane			
Ab	88	0	4
Ac	72	24	4
Mg	56	-	-
Et	-	0	-
Mb	-	-	4
Control	88	32	16
Methanol			
Ab	64	4	0
Ac	100	4	0
Mg	0	-	-
Et	-	0	-
Mb	-	-	0
Control	88	36	32
Water			
Ab	0	0	0
Ac	0	0	4
Mg	0	-	-
Et	-	0	-
Mb	-	-	4
Control	100	24	16

Lettuce Seed Germination

Aqueous leaf extracts, that had been isolated using methanol, of *A. codonocarpa* ($F_{6,27} = 108.80$, $P < 0.001$), *A. bunburyana* ($F_{6,27} = 5.59$, $P = 0.001$), *M. brevifolia* ($F_{6,27} = 31.92$, $P < 0.001$), and *M. georgei* ($F_{6,27} = 397.83$, $P < 0.001$), significantly inhibited germination of lettuce seed (Table 7.3). Those extracts isolated with methanol from *E. tomentosa* had no effect on lettuce seed germination ($F_{6,27} = 1.07$, $P = 0.412$), however, stunted root and shoot growth were observed at the higher concentrations.

Table 7.3 Mean number of germinants, standard error (SE), final germination percentage (FG%) and observations of root and shoot growth of 25 lettuce seed tested with concentrations of leaf extracts isolated from each of the five chenopod species. The methanol extract was dried and then redissolved using deionised water. Abbreviations as per table 7.2.

Extract	Conc. (g L^{-1})	Mean	SE	FG%	Observations
Ac	**25**	10.25	2.462	41	root growth stunted
	12.5	0.00	0.000	0	
	6.25	25.00	0.000	100	increased shoot growth, stunted root growth
	2.5	24.75	0.250	99	
	0.25	24.50	0.289	98	
	0.025	24.25	0.479	97	
Ab	**25**	22.50	0.289	90	root and shoot growth stunted
	12.5	23.75	0.479	95	root and shoot growth stunted
	6.25	23.00	1.080	92	root growth stunted
	2.5	25.00	0.000	100	
	0.25	25.00	0.000	100	
	0.025	25.00	0.000	100	
Et	**25**	23.00	1.225	92	root growth stunted
	12.5	22.00	0.913	88	root growth stunted
	6.25	23.50	0.645	94	root growth stunted
	2.5	24.75	0.250	99	
	0.25	24.75	0.250	99	
	0.025	21.50	3.175	86	
Mb	**25**	2.50	0.650	10	root growth stunted
	12.5	0.50	0.290	2	root and shoot growth stunted
	6.25	10.25	1.110	41	
	2.5	18.25	4.820	73	
	0.25	25.00	0.000	100	
	0.025	24.50	0.500	98	
Mg	**25**	0.00	0.000	0	
	12.5	0.00	0.000	0	
	6.25	20.00	1.354	80	root and shoot growth stunted
	2.5	24.75	0.250	99	
	0.25	25.00	0.000	100	
	0.025	23.75	0.750	95	delayed germination rate
Control		25.00	0.000	100	

The aqueous extracts of *A. bunburyana* ($F_{6,27}$ = 454.56, P< 0.001), *M. georgei* ($F_{6,27}$ = 923.26, P < 0.001) and *M. brevifolia* ($F_{6,27}$ = 176.53, P< 0.001) leaves, significantly inhibited germination of lettuce seeds at a concentration of 6.25 g L^{-1} (Table 7.4). Root and shoot growth was inhibited at concentrations as low as 1.55 g L^{-1}. Aqueous leaf extracts of *A. codonocarpa* significantly inhibited lettuce seed germination ($F_{6,27}$ = 443.42, P < 0.001) at concentrations of 6.25 and 3.12 g L^{-1}, and root and shoot growth was stunted at concentrations as low as 1.55 g L^{-1}. The aqueous extracts of *E. tomentosa* did not inhibit the lettuce seed germination ($F_{6,27}$ = 0.612, P = 0.718), but did appear to stunt root and shoot growth as observed at 6.25 and 3.12 g L^{-1}.

Table 7.4 Mean number of germinants, standard error (SE), final germination percentage (FG%) and observations of root and shoot growth of 25 lettuce seed tested with concentrations of leaf extracts isolated from each of the five chenopod species. The aqueous extract was dried and then redissolved using deionised water. Abbreviations as for Table 7.2.

Extract	Conc. (g/L)	Mean	SE	FG%	Observations
Ac	**6.25**	0.00	0.000	0	
	3.12	0.00	0.000	0	
	1.55	20.50	1.320	82	root and shoot growth stunted
	0.63	24.00	0.410	96	
	0.06	25.00	0.000	100	
	0.006	24.50	0.500	98	
Ab	**6.25**	0.00	0.000	0	
	3.12	24.50	0.500	98	root and shoot growth stunted
	1.55	22.50	1.040	90	root and shoot growth stunted
	0.63	25.00	0.000	100	
	0.06	25.00	0.000	100	
	0.006	25.00	0.000	100	
Et	**6.25**	23.80	0.950	95	root and shoot growth stunted
	3.12	24.50	0.290	98	root and shoot growth stunted
	1.55	24.50	0.500	98	
	0.63	24.30	0.480	97	
	0.06	24.50	0.500	98	
	0.006	24.80	0.250	99	
Mb	**6.25**	0.00	0.000	0	
	3.12	24.00	0.410	74	root and shoot growth stunted
	1.55	24.00	0.410	96	root growth stunted
	0.63	18.50	1.710	96	
	0.06	24.50	0.290	98	
	0.006	25.00	0.000	100	
Mg	**6.25**	0.00	0.000	0	
	3.12	24.30	0.250	97	root and shoot growth stunted
	1.55	21.00	0.710	84	root growth stunted
	0.63	25.00	0.000	100	
	0.06	24.50	0.290	98	
	0.006	25.00	0.000	100	
Control		25.00	0.000	100	

Chenopod Seed Germination

Germination of *M. georgei* seeds was inhibited when treated with aqueous leaf extracts of *M. georgei*, *A. bunburyana* and *A. codonocarpa* (Table 7.5). The final germination percentage (FG%) and the rate of germination (RG) decreased, but the mean period of final germination (MPFG) increased in response to increasing concentrations of the extracts.

Table 7.5 Final germination percentage (FG%), rate of germination (RG) (day^{-1}), mean period of final germination (MPFG) (days) and the percentage of inhibition or stimulation of *M. georgei* germination when subject to differing concentrations of extracts isolated from the leaves of *M. georgei* (Mg), *A. bunburyana* (Ab) or *A. codonocarpa* (Ac) is shown. The levels of significance are also shown. Different letters indicates significant differences between concentrations for each of the measure parameters, using Tukey's Compromise.

Seed Species		***Maireana georgei***			
Extract	**Conc. (g/l)**	**FG %**	**RG**	**MPFG**	**Inhib/Stim%**
Mg	6.25	15^{d}	0.5^{c}	9.3^{b}	-83
	3.12	42^{c}	2.8^{b}	4.9^{a}	-52
	1.55	63^{b}	4.2^{ab}	5.0^{a}	-28
	0.006	77^{ab}	5.0^{a}	4.9^{a}	-11
	$F_{4,19}$	**31.81**	**24.11**	**23.30**	
	P	***<0.001***	***<0.001***	***<0.001***	
Ab	6.25	5^{d}	0.2^{c}	7.6^{b}	-94
	3.12	31^{c}	2.0^{bc}	4.6^{a}	-64
	1.55	56^{b}	3.8^{ab}	4.3^{a}	-36
	0.006	71^{ab}	5.2^{a}	4.2^{a}	-18
	$F_{4,19}$	**42.66**	**22.51**	**8.25**	
	P	***<0.001***	***<0.001***	***0.001***	
Ac	6.25	4^{c}	0.1^{c}	10.5^{b}	-95
	1.55	38^{b}	3.1^{b}	3.7^{a}	-56
	$F_{2,11}$	**109.57**	**63.02**	**6.98**	
	P	***<0.001***	***<0.001***	***0.015***	
Control		87^{a}	6^{a}	4.7^{a}	

The final germination percentage of *E. tomentosa* seeds was stimulated and RG increased when treated with low extract concentrations (0.006 g L^{-1}). There was no significant difference, however, when tested at concentrations of 1.55, 3.12 and 6.25 g L^{-1} (Table 7.6). The extracts obtained from *A. bunburyana* leaves inhibited *E. tomentosa* FG and decreased the RG at a concentration of 6.25 g L^{-1}. *Enchylaena tomentosa* seeds showed no germination within 14 days when treated with the aqueous extract of *A. codonocarpa* at a concentration of 6.25 g L^{-1}.

Table 7.6 Different concentrations of aqueous extracts isolated from leaves of *E. tomentosa* (Et), *A. bunburyana* (Ab) or *A. codonocarpa* (Ac) tested on germination of *E. tomentosa* seeds. The germination parameters are the same as those shown in Table 7.5. The levels of significance are also shown. Significant difference between concentrations for each of the measure parameters, using Tukey's Compromise, are indicated by different letters.

Seed Species		***Enchylaena tomentosa***			
Extract	**Conc. (g L^{-1})**	**FG%**	**RG**	**MPFG**	**Inhib/Stim%**
Et	6.25	51^{a}	4.8^{a}	3.3^{a}	-14
	3.12	57^{a}	5.9^{a}	2.9^{a}	-3
	1.55	58^{a}	5.5^{a}	3.2^{a}	-2
	0.006	75^{b}	7.8^{b}	2.9^{a}	27
	$F_{4,19}$	**3.19**	**4.12**	**0.24**	
	P	***0.044***	***0.019***	***0.913***	
Ab	6.25	18^{b}	1.3^{c}	4.9^{b}	-69
	3.12	44^{a}	4.0^{b}	3.8^{a}	-25
	1.55	62^{a}	6.3^{a}	2.8^{a}	5
	0.006	59^{a}	5.3^{a}	3.3^{a}	0
	$F_{4,19}$	**18.25**	**48.51**	$\times_4^2 = 6.14$	
	P	***<0.001***	***<0.001***	***0.189***	
Ac	6.25	0^{b}	0^{b}	0^{b}	100
Control		59^{a}	5.9^{a}	2.9^{a}	

In contrast, *A. codonocarpa* seeds showed no inter-specific response to the application of aqueous extracts from the leaves of *E. tomentosa* and *Maireana* species (Table 7.7). A negative response, however, was recorded when treated with leaf extracts from its own species. The final germination percentage decreased, as did the RG, while MPFG increased when treated with this aqueous extract (6.25 g L^{-1}).

Table 7.7 The effects on germination of *A. codonocarpa* to the aqueous extracts at a concentration of 6 g L^{-1}. These extracts were isolated from the leaves of *A. codonocarpa* (Ac) and each of the target species: *E. tomentosa* (Et), *M. brevifolia* (Mb) and *M. georgei* (Mg). The germination parameters are the same as those shown in Table 7.5. The levels of significance are also shown. Different letters indicates significant differences between extract concentrations for each of the measured parameters.

Seed Species		***Atriplex codonocarpa***			
Extract	**Conc. (g L^{-1})**	**FG %**	**RG**	**MPFG**	**Inhib/Stim%**
Ac	6.25	10^{b}	0.3^{b}	9.8^{b}	-88
Et	6.25	85^{a}	6.7^{a}	3.6^{a}	-1
Mb	6.25	79^{a}	6.7^{a}	3.4^{a}	-8
Mg	6.25	82^{a}	6.8^{a}	3.7^{a}	-5
Control		86^{a}	6.5^{a}	3.8^{a}	
	$F_{4,19}$	**43.51**	**64.86**	**143.11**	
	P	***<0.001***	***<0.001***	***<0.001***	

Atriplex bunburyana germination was inhibited when treated with aqueous leaf extracts of *E. tomentosa* and *M. georgei*, although the greatest inhibition occurred when treated with aqueous leaf extracts of its own species (Table 7.8). MPFG did not significantly differ between treatments.

Table 7.8 The germination parameters of *A. bunburyana,* treated with aqueous extracts at a concentration of 6 g L^{-1}, are shown. The extracts were isolated from the leaves of *A. bunburyana* (Ab) and each of the target species: *E. tomentosa* (Et), *M. brevifolia* (Mb) and *M. georgei* (Mg). The germination parameters are the same as those shown in Table 7.5. The levels of significance are also shown. The letters indicates significant differences between extract concentrations, using Tukey's Compromise.

Seed Species		***Atriplex bunburyana***			
Extract	**Conc. (g L^{-1})**	**FG %**	**RG**	**MPFG**	**Inhib/Stim%**
Ab	6.25	8^{c}	0.4^{d}	6.0^{a}	-88
Et	6.25	43^{b}	3.6^{b}	4.0^{a}	-36
Mb	6.25	42^{b}	3.1^{b}	5.1^{a}	-37
Mg	6.25	27^{b}	1.7^{c}	5.5^{a}	-60
Control		67^{a}	5.9^{a}	5.1^{a}	
	$F_{4,19}$	**29.98**	**31.29**	**0.72**	
	P	***<0.001***	***<0.001***	***0.591***	

DISCUSSION

This chapter specifically involved a study of the effects of allelopathic extracts on intra- and inter-specific chenopod seed germination. It was, however, beyond the scope of this thesis to isolate and identify the active constituents. The overall purpose of this work was to determine whether allelopathy may play a role in plant competition and ultimately, chenopod community structure.

The lettuce seed bioassay, which is routinely used as a front-line, high through-put screen for allelopathic substances (Ghisalberti 1993), indicated that allelopathic substances were in fact present in the leaves of the chenopod species tested. Leaf extracts had a detrimental effect on seed germination, and also stunted the growth of roots and shoots of lettuce and some chenopod seedlings. Seed germination was inhibited, the rate of germination was slower and the mean period of final germination was greater following the application of some leaf extracts. The extent of inhibition was dependent on the species of chenopod from which the extract was isolated, the species of seed on which the extract was acting and the final concentration of the extract used. Similar findings have been reported previously (Friedman *et al.* 1977). The germination of lettuce seed was only inhibited at high concentrations. All four of the chenopod species extracts, however, stunted the growth of lettuce seedling roots and shoots at concentrations specific to each chenopod species. The extracts isolated using deionised water were more potent than those isolated using the methanol solvent. Inhibition of germination and growth of lettuce seeds by allelopathic extracts is consistent with other studies demonstrating the effects of allelopathy on germination (Chiapusio *et al.* 1997, Macias *et al.* 1999, Macias *et al.* 2000, Escudero *et al.* 2000).

Interestingly, germination of *A. bunburyana* and *A. codonocarpa* was not affected by leaf extracts of *M. georgei* and *E. tomentosa*. This provides some evidence of at least one

causal factor for the dominance of *Atriplex* species over these two species. *Maireana georgei* and *E. tomentosa* were, however, inhibited by extracts obtained from their own species. The highest concentration of leachate is likely to occur directly under the canopy of the adult plant where leaf drop is greatest. The inhibition of germination beneath the canopy of the adult plants (Escudero *et al.* 2000) may be a mechanism that restricts resource competition and reduces the likelihood of self-pollination (i.e. ensure hybrid vigour). Allelochemicals released by mature plants have been shown to limit these processes (Werner 1979, Eldridge and Westoby 1991).

Delayed germination of *M. georgei* and *E. tomentosa* seeds when leaf extracts were applied, as shown by a decreased RG and an increase in MPFG, occurred when increasing concentrations of *A. bunburyana* and *A. codonocarpa* extracts were applied. *Maireana georgei* extracts had the same intra-specific effect on its own seeds. Delayed germination (Ross and Harper 1972) and retardation of seedling growth (Witkouski 1991) may be detrimental to seedling survival in semi-arid environments, where soil moisture and nutrients are limiting (Grice and Westoby 1987). Plants that germinate at slower rates are often smaller than those that germinated without delay. This is a disadvantage when competing with neighbouring plants for resources (Ross and Harper 1972, Fowler 1986, Weiner *et al.* 1997).

Extracts isolated from *E. tomentosa* leaves illicite a stimulatory effect on germination of *E. tomentosa* seeds, especially at concentrations of 6 mg L^{-1}. The concentration of the allelopathic leachate in the soil solution may determine its subsequent effect on seed germination. Intra-specific stimulation of germination by water-soluble compounds often occurs at low concentrations in some species (Saxena *et al.* 1996). In contrast to the results of *E. tomentosa* seed germination in the current study, Saxena *et al.* (1996) reported intra-specific inhibition of seed germination at high concentrations as well as

stimulation of germination at low concentrations. This may suggest that two or more compounds are working in tandem in the species tested by this researcher. That may not be the case where the chenopod species in my study are concerned.

The effectiveness of leaf extracts (i.e. allelochemicals) under natural conditions, particularly those experienced in arid and semi-arid environments, were not tested in the current study. The annual, *A. codonocarpa*, however, is likely to release such chemicals each season, particularly when the adult plants die. In contrast, the perennial, *A. bunburyana*, is likely to release allelochemicals when its leaves senesce in response to low water availability during summer or drought. The concentration of allelochemicals in the soil is largely determined by leaf density, rates of decomposition, and the distance between mature plants and seedlings (Mann 1987, Saxena *et al.* 1996, Escudero *et al.* 2000, Nilsson *et al.* 2000).

Rainfall is also an important regulator of this process, especially through its effects on the ultimate concentration of allelopathic chemicals in the soil. Equally as important, are the rate of decomposition on leaf structure, ambient temperature, rainfall, time and the effect of micro-organisms (Friedman *et al.* 1977, Newman and Miller 1977, Ito *et al.* 1998). When the concentration of allelochemicals is such that they can inhibit germination, other factors, including pH, soil type and seed species should also be considered when determining the effectiveness of these chemicals (Saxena *et al.* 1996).

CONCLUSION

This study has shown that all five chenopods appear to produce allelopathic substances, which can be found within their leaves. It has also highlighted that inhibition resulting from these chemicals can be species-specific and may occur only at certain concentrations. At low concentration, *E. tomentosa* leaf extracts actually had a

stimulatory intra-specific effect on plant establishment. These allelochemicals are, therefore, likely to play a dynamic role in the interactions occurring between the species of chenopods on mine site revegetation areas. Further studies are required, however, to determine the conditions under which allelochemicals are produced and what factors regulate the effects of these chemicals in their natural environment.

Management Implications

More practical research of the existence and implications of allelochemicals are required before recommendations for the management of revegetation can be provided. It is important to recognise their existence and possible role in influencing plant succession and the development of sustainable plant communities during the revegetation process. Restoration land managers should take into account the possible existence and role of allelochemicals when establishing protocols for completion criteria.

CHAPTER 8: SYNTHESIS

The concept of competition is central to this thesis. Competition was presented as a possible explanation for the dominance of some species over others on mine site revegetation areas of the goldfields region of Western Australia. The species selected for this study were from the family Chenopodiaceae, which are well known for their ability to tolerate the harsh environmental conditions of areas, often with high levels of soil salinity, such as those seen in the Eastern Goldfields region of Western Australia (Mitchell and Wilcox 1998).

MORPHOLOGICAL CHARACTERISTICS

Life form is thought to contribute to the outcome of competition. Grime and Hodgson (1987) listed the characteristics of those species with high competitive ability as: 1) a robust perennial life form with a strong capacity to ramify vegetatively, 2) the rapid commitment of captured resources to the construction of new leaves and roots, 3) high morphological plasticity during the differentiation of leaves and roots particularly during periods of abiotic stress, and 4) short life cycles of individual leaves and roots (Wetzel and van der Valk 1998). Gaudet and Keddy (1988) found that tall shoots, leaf shape (length: width ratio) and a large canopy diameter significantly correlated with increased competitive ability in wetland plants (Wetzel and van der Valk 1998). For example, the morphological characteristics of *P. arundinacea*, including its rapid growth rate, tall leafy shoots and extensive lateral spread of the canopy and ramets, enabled it to maximise the capture of light and nutrient resources even under low nutrient or soil moisture conditions (Wetzel and van der Valk 1998).

The chenopods investigated in my study had different morphological characteristics. In comparison to the other species of the study, *A. bunburyana* and *M. brevifolia* both have tall canopies with extensive lateral spread in comparison to *A. codonocarpa, E. tomentosa* and *M. georgei*. These attributes alone may provide an explanation for the ability of *A. bunburyana* to generally out compete other species and for *M. brevifolia* to establish successfully regardless of the presence of other similarly related species. The

morphological characteristics of *M. georgei* (a small robust life form) may provide a possible explanation for its inability to compete.

The outcomes of this project have, however, shown that morphological characteristics alone do not provide a total explanation of the outcome of competitive processes active in a given ecosystem. For example, *A. codonocarpa*, a small annual that grows to 30 cm high and *E. tomentosa*, also a small shrub with a spreading habit, both shown to establish successfully on mine site areas and yet the morphological characteristics of both species do not support the characteristics outlined above for highly competitive plants (e.g. Grime and Hodgson 1987, Gaudet and Keddy 1988, Wetzel and van der Valk 1998). Nevertheless, both these species are able to persist in the presence of other chenopods, which exhibit more of the 'traditional' plant characteristics required to be a 'good competitor'.

EFFECT OF PLANT DENSITY

The first objective of this study was to determine whether or not competition was occurring. This was approached by using variations in plant density for each species. These trials were undertaken in the field at mine site revegetation areas (Chapter 3) as well as with pot trials (Chapter 4). The density of plants is often used to determine whether inter- and/or intra-specific competition are occurring and, if so, the intensity of this competition (Coussens and O'Neil 1993, Callaway and Walker 1997, Dietz *et al.* 1998, Gibson *et al.* 1999). Field trials (Chapter 3) showed that the performance and growth of the chenopods following their first year after sowing was influenced by environmental conditions as well as inter- and/or intra-specific competition. The overall size of the field site and heterogeneity of soil characteristics associated with this site may have influenced the outcome of the plant trials. Nevertheless these trials did, however, highlight the complexity of interactions occurring between environmental factors, the plant communities and the effects of inter- and intra-specific competition.

The pot trial (Chapter 4), which examined the effects of plant density for the different species sown in monoculture or in two-species mixtures, had a somewhat contrasting

result to the field trial. All plant species, except *A. bunburyana,* reacted negatively to the presence of a neighbouring plant. These plants were, however, grown in a smaller quantity of soil and were closer together due to the size of the pot. It is likely that below-ground space (McConnaughlay and Bazzaz 1991) and nutrients (Bi and Turvey 1994) are more limiting in pots than when plants are grown under natural conditions. The threshold point at which nutrients and space were limiting may have been reached at a later stage in the field in comparison to the pots. Thus the resulting competition in the field may be reduced in these arid environments because abiotic factors (e.g. rainfall) are limiting population growth and plants rarely have sufficient sustained resources to obtain a level of biomass where competitive processes become more evident.

RESOURCE REQUIREMENTS

The second objective of the thesis was to determine how resource limitations could influence the outcome of competition. This was approached by attempting to measure the performance of the five chenopod species when grown under different conditions of soil moisture, salinity and light intensity. Species with lower resource requirements than their conspecifics should have a competitive advantage (Florence 1996, Damgaard 1999), and this was illustrated by *A. bunburyana* (Chapter 4). Those plants, which can tolerate, or have the ability to take up lower levels of resources, will also have a competitive edge. Nutrients and water are often limiting, whereas, light intensity and salinity levels are very high in the semi-arid and arid regions of Western Australia. The five chenopod species were adapted to grow under these harsh conditions, although the extent of salt tolerance, drought tolerance and light intensity requirements may vary between species. Nutrients, temperature and soil characteristics are other environmental conditions that may be significant for the performance of these chenopod species, but it was beyond the scope of this project to investigate these.

Decreasing moisture availability had a negative effect on all species studied. The presence of salt, however, under varying moisture availability regimes revealed a broad spectrum of responses by these chenopods. The annual, *A. codonocarpa* and perennial, *M. brevifolia* exhibited a preference for saline conditions and both had a superior ability to

tolerate limiting water availability in the presence of relatively high salinity levels compared to the other species. *Enchylaena tomentosa* responded negatively while *M. georgei* and *A. bunburyana* responded in the middle of the spectrum. Interestingly, *M. brevifolia* increased in height (Chapter 5). Height provides plants with a competitive advantage when competing for light (Newman 1973, Rhodes and Stern 1978).

Plant species growing in semi-arid/ arid regions are usually adapted to grow under high light intensity and this is usually associated with high temperatures. Chenopods display a variety of life forms to help overcome the potential harmful effects of these conditions (Mitchell and Wilcox 1998). *Atriplex bunburyana* is a large spreading shrub in comparison to *E. tomentosa* and *M. georgei*. *Maireana georgei* had a small, "straggly" life form and produced no fruit when growing under the canopy of *A. bunburyana* in comparison to plants growing outside of the canopy (Chapter 4). Low levels of light have a negative effect on the rate of biomass accumulation of *M. georgei* but had no such effect on *M. brevifolia* and *E. tomentosa*. Thus these chenopods seem to occupy different micro-niches, which enable these species to coexist in much of the arid zone. However, depending upon local conditions some species will often out compete the others. Decreased root dry weight may also be a disadvantage when competing for water and nutrients, which, in turn, may have a compounding negative effect on the successful establishment of the plant.

ALLELOPATHY

Finally, allelopathy was studied to provide some insight as a possible mechanism of competition, which is apparent between some species of the chenopods studied. Allelopathy may play a role in influencing the ultimate density obtained by each species, particularly with respect to future generations, and the composition of individual plant communities. Allelopathy is an important process occurring between plants that are competing for limiting resources. Allelopathic substances were present in the leaf extracts of all five chenopod species. Other studies from elsewhere have also found plants growing in desert regions produce such substances (Mann 1987, Nilsson *et al.* 2000). Differences in germination response existed between species due to species-specific

effects of extract concentration and origin. Both *Atriplex* species germinated, and thus were not negatively affected, when exposed to the maximum concentrations of allelopathic substances isolated from the leaves of *M. georgei*, *E. tomentosa* and *M. brevifolia*. The concentration of the allelochemicals may determine their effectiveness when inhibiting germination (Friedman *et al.* 1977). The seed of *M. georgei*, *E. tomentosa* and *M. brevifolia* were inhibited at lower concentrations of leaf extracts isolated from both *Atriplex* species.

Enhancement of germination can also occur when seeds are treated with low concentrations of some of these allelochemicals (Saxena *et al.* 1996). For example, germination of *E. tomentosa* seeds was facilitated by the addition of low concentrations of the aqueous extract obtained from the leaves of *E. tomentosa* plants. Interestingly, in all other species, germination was inhibited by leaf extracts from their own respective species. This mechanism may ensure that the mature plant does not compete with its offspring for limiting resources. The mature plant is likely to have a better chance of survival under the harsh conditions of arid and semi-arid regions (Werner 1979, Eldridge and Westoby 1991). This mechanism of self-preservation may have adaptative significance.

CONCLUSION

What attributes allow *A. bunburyana* and *A. codonocarpa* to be dominant species?

The growth of *A. bunburyana* was not impaired by the presence of other plants, regardless of the species or their numbers and shows a tolerance of inter-specific competitors such as *E. tomentosa* and *Maireana* species used in this study. The seeds of *A. bunburyana* plants could tolerate high concentrations of the leaf extracts of *Enchylaena tomentosa* and *Maireana* species but not that of its own species. These leaf extracts are likely to have contained allelopathic substances. Future generations would be able to establish but may not out compete the mature established plants of their own species. The tall, spreading life form of this species also contributes to its competitive ability by restricting the availability of light to smaller plants growing under its canopy.

The annual, *A. codonocarpa* appears more susceptible to competition for nutrients and space when grown with *E. tomentosa* and both species of *Maireana*. It did, however, show superior mechanisms for tolerating relatively high salinities in a low moisture environment. This species also produces seeds, which range in colour from light brown to black. Black seeds exhibit dormancy whereas light brown seeds will germinate almost immediately after imbibition (Anderson 1982). Therefore the time of germination in this species is staggered and summer rainfall is unlikely to cause all the seeds to germinate at the same time. *Atriplex codonocarpa* plants also release and tolerate allelopathic substances in much the same way as *A. bunburyana*.

Why do *E. tomentosa* and *M. georgei* plants become subordinant species?

Growth of *E. tomentosa* and *M. georgei* plants were adversely affected when grown with both species of *Atriplex* as well as when grown intra-specifically. This suggests a lack of ability to compete for nutrients, water or space. *Enchylaena tomentosa* reacted negatively to high concentrations of NaCl with a decrease in overall plant biomass but excelled in shade. *Maireana georgei* tolerated high concentrations of salt but plant biomass decreased during the shade treatments. This may offer an explanation for its "straggly", non-fruiting life form observed when growing under the canopy of *A. bunburyana* plants in the field. The reduced ability of *M. georgei* plants to compete for nutrients or water would compound the effects of shade and possibly cause a 'snow-ball' effect. The germination and growth of both *M. georgei* and *E. tomentosa* was inhibited by the addition of leaf extracts, isolated from the *Atriplex* species as well as that of their own respective species. This again suggests that allelochemicals were likely to be present in these extracts and were important regulators of plant biomass.

Why was *M. brevifolia* the most competitive member of the *Maireana* genus?

The growth of *M. brevifolia* was inhibited by both species of *Atriplex* as well as when grown in monoculture (i.e. intra-specific competition was evident). However, this species showed superior mechanisms for tolerating relatively high salinity levels under drought conditions. It was also tolerant of the effects of shade at least at the levels examined in this study. The tall life form exhibited plasticity when subject to shade and salt regimes as

plants grown under these conditions fell on their side and several lateral branches with an upward growth were produced. This change in plant structure is likely to result in an increase of photosynthetic surface area and leafiness in response to shady and saline conditions. Unfortunately, the effects of allelopathic substances on germination could not be determined as the available seed proved not to be viable.

Management Implications

This thesis has focussed on factors affecting plant community structure on revegetation areas of mine sites in the eastern goldfields region of Western Australia. Only five species of chenopods were studied. Twenty to thirty species of chenopods are routinely selected as components of broadcast seed mixtures on waste and tailings materials. It is difficult, therefore, to provide specific suggestions of sowing regimes and site preparation techniques for restoration managers without specific experimentation to illustrate their effectiveness. Two areas have been highlighted in Chapter 3 that will greatly improve the abundance of plants on revegetation areas. The first, is to increase, through the development of site preparation techniques, the number of suitable microsites for seedling survival and establishment. The second, is to develop weed eradication programs.

This research has also shown some specific areas of consideration when choosing species components and their respective densities within a seed mixture. Species characteristics that should be considered are;

- competitiveness (Chapters 3 and 4)
- resource tolerance limits (Chapter 5)
- resource requirements (Chapters 5 and 6)
- life form (Chapter 6)

A comparison of species characteristics will ensure that a seed mixture, comprising a selection of species and their respective densities, will be balanced. In addition, it will be reflected by a primary succession plant community that is diverse and abundant. The further development of current seeding regimes incorporating these suggestions may greatly improve the likelihood of achieving sustainable plant communities within relatively short periods of time.

Future Research

This thesis has identified some of the processes, which are likely to be important when assessing the likely competition between the main chenopod species of the eastern goldfields region of Western Australia, particularly with respect to the revegetation of disturbed lands. Nearest-neighbour measurements should again be repeated when the plants are five years old and obtained their maximum size and when their resource requirements are likely to be greatest. This would help determine any long-term effects of differing plant densities. It may also provide a more realistic time-scale for assessing competitive processes. The importance and intensity of competition between chenopod species when growing together in the natural environment may provide further insight into the outcomes of plant community succession on revegetation areas. A study of secondary succession is also required to understand the effects of competition on plant community structure and sustainability of these communities on mine site revegetation areas.

REFERENCES

Aerts, R. (1999). Interspecific competition in natural plant communities: mechanisms, trade-offs and plant-soil feedbacks. *Journal of Experimental Botany* **50**, 29-37.

Aerts, R., Boot, R. G. A., and van der Aart, P. J. M. (1991). The relation between above- and belowground biomass allocation patterns and competitive ability. *Oecologia* **87**, 551-559.

Aguiar, M. R., and Sala, O. E. (1994). Competition, facilitation, seed distribution and the origin of patches in a Patagonian steppe. *Oikos* **70**, 26-34.

Amaranthus, M. P., and Perry, D. A. (1994). The functioning of ectomycorrhizal fungi in the field: linkages in space and time. *Plant and Soil* **159**, 133-140.

Anderson, D. J. (1967). Studies on structure in plant communities V. Pattern in *Atriplex vesicaria* communities in South-Eastern Australia. *Australian Journal of Botany* **15**, 451-458.

Anderson, D. J. (1982). Environmental adaptive traits in arid zone plants. *In* "Evolution of the flora and fauna of arid Australia" (W. R. Barker and P. J. M. Greenslade, eds.), pp. 133-139. Peacock Publications, Prewville, South Australia.

Aslam, Z., Barrett-Lennard, E. G., and Greenway, H. (1988). Effects of external concentration of potassium plus sodium and postium-sodium on the growth and ion relations of *Atriplex amnicola*. *Journal of Plant Physiology* **133**, 228-234.

Barker, S. (1975). Shrub population dynamics under grazing - within paddock studies. *In* "Studies of the Australian arid zone IV. Chenopod shrublands" (R. D. Graetz and K. M. W. Howes, eds.), pp. 83-106. Commonwealth Scientific and Industrial Research Organization, Deniliquin.

Barrett, G. J. (2000). Revegetation of salt-affected land after mining: Germination and establishment of halophytes. Ph.D. Thesis, Curtin University of Technology, Perth.

Barson, M. M., Abraham, B., and Malcom, C. V. (1994). Improving the productivity of saline discharge areas: An assessment of the potential use of saltbush in the Murray-Darling basin. *Australian Journal of Experimental Agriculture* **34**, 1143-1154.

Battaglia, M. (1996). Effects of seed dormancy and emergence time on the survival and early growth of *Eucalyptus delegatensis* and *E. amygdalina*. *Australian Journal of Botany* **44**, 123-137.

Beard, J. S. (1978). The vegetation of the Kalgoorlie area, Western Australia. Vegmap Publications, Perth.

Bell, D. T., Plummer, J. A., and Taylor, S. K. (1993). Seed germination ecology in Southwestern Western Australia. *The Botanical Review* **59**, 24-57.

Bell, D. T., Rokich, D. P., McChesney, C. J., and Plummer, J. A. (1995). Effects of temperature, light and gibberellic acid on the germination of seeds of 43 species native to Western Australia. *Journal of Vegetation Science* **6**, 797-806.

Bell, D. T., Vlahos, S., and Bellairs, S. M. (1990). Seed ecology in relation to reclamation: lessons from mined lands in Western Australia. *Proceedings of the Ecological Society of Australia* **16**, 531-535.

Berkowitz, A. R., Canham, C. D., and Kelly, V. R. (1995). Competition vs facilitation of tree seedling growth and survival in early successional communities. *Ecology* **76**, 1156-1168.

Bi, H., and Turvey, N. D. (1994). Inter-specific competition between seedlings of *Pinus radiata*, *Eucalyptus regnans* and *Acacia melanoxylon*. *Australian Journal of Botany* **42**, 61-70.

Black, R. F. (1955). Effect of sodium chloride on leaf succulence and area of *Atriplex hastata* L. *Australian Journal of Biological Sciences* **6**, 305-321.

Black, R. F. (1958). Effect of NaCl in water culture on the ion uptake and growth of *Atriplex hastata* L. *Australian Journal of Biological Sciences* **9**, 67-81.

Black, R. F. (1960). Effects of NaCl on the ion uptake and growth of *Atriplex vesicaria* Heward. *Australian Journal of Biological Sciences* **13**, 247-267.

Boot, R. G. A., and Mensink, M. (1990). Size and morphology of root systems of perrenial grasses from contrasting habitats as affected by nitrogen supply. *Plant and Soil* **129**, 291-299.

Booth, D. T., Gores, J. K., Schuman, G. E., and Olson, R. A. (1999). Shrub densities on pre-1995 reclaimed mine lands in Wyoming. *Restoration Ecology* **7**, 24-32.

Bouma, T. J., Nielsen, K. L., Hal, J. V., and Koutstaal, B. (2001). Root system topology and diameter distribution of species from habitats differing in inundation frequency. *Functional Ecology* **15**, 360-369.

Brearley, D. R., and Osborne, J. M. (1997a). "Ecosystem development of revegetation on tailings: Westonia - April 1997 summary." Curtin University of Technology, Perth.

Brearley, D. R., and Osborne, J. M. (1997b). "Placer (Granny Smith) waste dumps 1996 revegetation assessment: 1994, 1995 and 1996 seedings and shrubland - rehabilitation comparison." Curtin University of Technology, Perth.

Brearley, D. R., and Whitten, V. (1996). "Goldfan Rehabilitation: 1996 Summary." Curtin University of Technology, Perth.

Brown, J. H., and Kodric-Brown, A. (1979). Convergence, competition and mimicry in a temperate community of hummingbird-pollinated flowers. *Ecology* **60**, 1022-1035.

Bruelisauer, A. R., Bradfield, G. E., and Maze, J. (1996). A thermodynamic interpretation of succession. *Coensus* **11**, 73-76.

Cable, D. R. (1969). Competiion in the semidesert grass-shrub type as influenced by root systems, growth habits, and soil moisture extraction. *Ecology* **50**, 27-38.

Cahill Jr., J. F. (1999). Fertilization effects on interactions between above- and belowground competition in an old field. *Ecology* **80**, 466-480.

Caldwell, M. M. (1974). Physiology of desert halophytes. *In* "Ecology of halophytes" (R. J. Reimold and W. H. Queen, eds.), pp. 355-378. Academic Press, Inc., New York.

Caldwell, M. M., Dawson, T. and Richards, J. 1998. Hydraulic lift: consequences of water efflux from the roots of plants. *Oecologia* **113**, 151-161.

Callaway, R. M. (1994). Facilitative and interfering effects of *Arthrocnemum subterminale* on winter annuals. *Ecology* **75**, 681-686.

Callaway, R. M. (1995). Positive Interactions among plants. *The Botanical Review* **61**, 306-349.

Callaway, R. M., and Walker, L. R. (1997). Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology* **78**, 1958-1965.

Campbell, G. S., and Norman, J. M. (1990). The description and measure of plant canopy structure. *In* "Plant canopies: their growth, form and function" (G. Russell, B. Marshall and P. G. Jarvis, eds.), pp. 178. Cambridge University Press, Cambridge.

Carlsson, B. A., and Callaghan, T. V. (1991). Positive plant interactions in tundra vegetation and the importance of shelter. *Journal of Ecology* **79**, 973-983.

Carrodus, B. B., and Specht, R. L. (1965). Factors affecting the relative distribution of *Atriplex vesicaria* and *Kochia sedifolia* (Chenopodiaceae) in the arid zone of South Australia. *Australian Journal of Botany* **13**, 419-433.

Chiapusio, G., Sanchez, A. M., Reigosa, M. J., Gonzalez, L., and Pellissier, F. (1997). Do germination indices adequately reflect allelochemical effects on the germination process? *Journal of Chemical Ecology* **23**, 2445-2453.

Chiarello, N., Hickman, J. C., and Mooney, H. A. (1982). Endomycorrhizal role for interspecific transfer of phosphorus in a community of annual plants. *Science* **217**, 941-943.

Christie, P., Newman, E. I., and Campbell, R. (1974). Grassland species can influence the abundance of microbes on each other's roots. *Nature* **250**, 570-571.

Clark, P. J., and Evans, F. C. (1954). Distance to nearest neighbour as a measure of spatial relationships in populations. *Ecology* **35**, 445-453.

Collins, R. P., and Rhodes, I. (1993). Influence of root competition on compatibility between white clover and perennial ryegrass populations during seedling establishment. *Grass and Forage Science* **49**, 506-509.

Connolly, J. (1997). Substitutive experiments and evidence for competitive hierarchies in plant communities. *Oikos* **80**, 179-182.

Connolly, J., Wayne, P., and Murray, R. (1990). Time course of plant-plant interactions in experimental mixtures of annuals: density, frequency and nutrient effects. *Oecologia* **82**, 513-526.

Cousens, R., and O'Neill, M. (1993). Density dependence of replacement series experiments. *Oikos* **66**, 347-352.

Cowling, S. W. (1969). A study of vegetation activity patterns in a semi-arid environment. Ph.D. Thesis, University of New England.

Curtis, N. P. (1996). Germination and Seedling Survival Studies of *Xanthorrhoea australis* in the Warby Range State Park, North-eastern Victoria, Australia. *Australian Journal of Botany* **44**, 635-647.

Dale, M. (1985). Graph theoretical methods for comparing phytosociological structures. *Vegetatio* **63**, 79-88.

Damgaard, C. (1999). A test of asymmetric competition in plant monocultures using the maximum likelihood function of a simple growth model. *Ecological Modelling* **116**, 285-292.

Darwin, C. (1998). "The origin of species by means of natural selection," Senate, Twickenham.

Day, T. A., and Wright, R. G. (1989). Positive plant spatial association with *Eriogonum ovalifolium* in primary succession on cinder cones: Seed-trapping nurse plants. *Vegetatio* **70**, 37-45.

Department of Minerals and Energy. (1996). Guidelines for Mining in Arid Environments. June 1996. Mining Operations Division, Departments of Minerals and Energy, Western Australia, Perth.

Department of Minerals and Energy. (1998). Guidelines to help you get Environmental Approval for Mining Projects in Western Australia. March 1998. Mining Operations Division, Departments of Minerals and Energy, Western Australia, Perth.

Dietz, H., Steinlein, T., and Ullmann, I. (1998). The role of growth form and correlated traits in competitive ranking of six perennial ruderal plant species grown in unbalanced mixtures. *Acta Oecologica* **19**, 25-36.

Dixon, K. W., and Meney, K. A. (1994). Seed quality for minesite rehabilitation. *In* "National Workshop on Native Seed Biology for Revegetation".

Dodd, G. L., and Donovan, L. A. (1999). Water potential and ionic effects on germination and seedling growth of two cold desert shrubs. *American Journal of Botany* **86**, 1146-1153.

Drake, D. R., and Ungar, I. A. (1989). Effects of salinity, nitrogen and population density on the survival, growth and reproduction of *Atriplex triangularis* (Chenopodiaceae). *American Journal of Botany* **76**, 1125 - 1133.

Egan, T. P., and Ungar, I. A. (2000). Similarity between seed banks and above-ground vegetation along a salinity gradient. *Journal of Vegetation Science* **11**, 189-194.

Ehleringer, J. R., and Forseth, I. N. (1990). Diurnal leaf movements and productivity in canopies. *In* "Plant canopies: their growth, form and function" (G. Russell, B. Marshall and P. G. Jarvis, eds.), pp. 178. Cambridge University Press, Cambridge.

Eissenstat, D. M., and Caldwell, M. M. (1988). Competitive ability is linked to rates of water extraction. *Oecologia* **75**, 1-7.

Eldridge, D. J., and Westoby, M. (1991). Recruitment and survival in *Atriplex vesicaria* populations in semi-arid western New South Wales, 1977-1987. *Australian Journal of Ecology* **16**, 309-314.

Escudero, A., Albert, M. J., Pita, J. M., and Perez-Garcia, F. (2000). Inhibitory effects of *Artemisia herba-alba* on the germination of the gypsophyte *Helianthemum squamatum*. *Plant Ecology* **148**, 71-80.

Facelli, J. M. and Temby, A.M. 2002. Multiple effects of shrubs on annual plant communities in arid lands of South Australia. *Austral Ecology* **27**, 422-432.

Fahey, T., Battles, J. J., and Wilson, G. F. (1998). Responses of early successional northern hardwood forests to changes in nutrient availability. *Ecological Monographs* **68**, 183-212.

Fenner, M. (1987). Seedlings. *The New Phytologist* **106**, 35-47.

Finucane, S. (1995). Applying the concept of provenance to seed collection. *In* "20th Annual Environmental Workshop", pp. 300-330. Minerals Council of Australia, Darwin.

Firbank, L. G., and Watkinson, A. R. (1985). On the analysis of competition within two species mixtures of plants. *Journal of Applied Ecology* **22**, 503-517.

Fitter, A. H., and Hay, R. K. M. (1989). "Environmental physiology of plants," 2/Ed. Academic Press Ltd, London.

Fletcher, D. L. (1992). Factors affecting woody perrenial establishment on a saline mullock dump in semi-arid Western Australia. Masters Thesis, Curtin University of Technology, Perth.

Florence, R. G. (1996). "Ecology and silviculture of Eucalypt forests," CSIRO Publishing, Collingwood.

Florentine, S. K. (1999). Ecology of *Eucalyptus vitrix* in grassland in the floodplain of the Fortescue River. Ph.D. Thesis, Curtin University of Western Australia, Perth.

Fowler, N. (1986). The role of competition in plant communities in arid and semiarid regions. *Annual Review of Ecological Systemics* **17**, 89-110.

Fox, J. E. D., Neilsen, J. R., and Osborne, J. M. (1990). Eucalyptus seedling growth and salt tolerance from the north-eastern goldfields of Western Australia. *Journal of Arid Environments* **19**, 45-53.

Friedman, J., Orshan, G., and Ziger-cfir, Y. (1977). Suppression of annuals by *Artemisia herba-alba* in the Negev desert of Israel. *Journal of Ecology* **65**, 413-426.

Gale, J., and Poljakoff-Mayber, A. (1970). Interrelations between growth and photosynthesis of salt bush (*Atriplex halimus* L.) grown in saline media. *Australian Journal of Biological Sciences* **23**, 937-945.

Garcia-Moya, E., and McKell, C. M. (1969). Contribution of shrubs to the nitrogen economy of a desert-wash plant community. *Ecology* **51**, 81-88.

Gates, C. T. (1972). Ecological response of the Australian native species *Acacia harpophylla* and *Atriplex nummularia* to soil salinity: effects of water content, leaf area and transpiration rate. *Australian Journal of Botany* **20**, 261-272.

Gaudet, C. L., and Keddy, P. A. (1988). A comparative approach to predicting competitive ability from plant traits. *Nature* **334**, 242-243.

Ghisalberti, E. l. (1993). Detection and isolation of bioactive natural products. *In* "Bioactive natural products. Detection, isolation and structural determination." (S. M. Colegate and R. J. Molyreux, eds.), pp. 528. CRC Press, Boca Raton.

Gibson, D. J., Connolly, J., Hartnett, D. C., and Weidenhamer, J. D. (1999). Designs for greenhouse studies of interactions between plants. *Journal of Ecology* **87**, 1-16.

Gilbert, I. R., Jarvis, P. J., and Smith, H. (2001). Proximity signal and shade avoidance differences between early and late successional trees. *Nature* **411**, 792-795.

Gilbert, M. A., and Robinson, A. D. (1984). Studies on competition for sulfer between subterranean clover and annual ryegrass. II* Interrelation of nitrogen supply and soil temperature. *Australian Journal of Agriculture Resources* **35**, 65-73.

Gioia, P. (2001). Florabase Map. Vol. 2001. http://www.calm.wa.gov.au . Western Australian Herbarium, Department of Conservation and Land Management.

Gleeson, S. K., and Tilman, D. (1990). Allocation and the transient dynamics of succession on poor soils. *Ecology* **71**, 1144-1155.

Glenn, E. P., Brown, J. J., and Blumwald, E. (1999). Salt tolerance and crop potential of halophytes. *Critical Reviews in Plant Sciences* **18**, 227-255.

Goldberg, D., and Novoplansky, A. (1997). On the relative importance of competition in unproductive environments. *Ecology* **85**, 409-418.

Goldberg, D. E. (1990). Components of resource competition in plant communities. *In* "Perspectives on Plant Competition" (J. B. Grace and D. Tilman, eds.), pp. 27-50. Academic Press, San Diego.

Goldberg, D. E., and Landa, K. (1991). Competitive effect and response: Hierachies and correlated traits in the early stages of competition. *Journal of Ecology* **79**, 1013-1030.

Goldberg, D. E., Turkington, R., Olsvig-Whittaker, L., and Dyer, A. R. (2001). Density dependence in an annual plant community: Variation among life history stages. *Ecological Monographs* **71**, 423-446.

Goodall, D. W. (1975). The chenopod shrublands of Australia - an integrated view. *In* "Studies of the Australian arid zone IV. Chenopod shrublands" (R. D. Graetz and K. M. W. Howes, eds.), pp. 189-196. Commonwealth Scientific and Industrial Research Organization, Deniliquin.

Gordon, D. R., and Rice, K. J. (2000). Competitive suppression of *Quercus douglasii* (Fagaceae) seedling emergence and growth. *American Journal of Botany* **87**, 986-994.

Grace, J. B., Keough, J., and Guntenspergen, G. R. (1992). Size bias in traditional analyses of substitutive competition experiments. *Oecologia* **90**, 429-434.

Grice, A. C., and Westoby, M. (1987). Aspects of the dynamics of the seed-banks and seedling populations of *Acacia victoriae* and *Cassia* spp. in arid Western New South Wales. *Australian Journal of Ecology* **12**, 209-215.

Grime, J. P., and Hodgson, J. G. (1987). Botanical contributions to contemporary ecological theory. *New Phytologist* **106**, 283-296.

Grist, E. P. M. (1999). The significance of spatio-temporal neighbourhood on plant competition for light and space. *Ecological Modelling* **121**, 63-78.

Groom, P. K., Fox, J. E. D., and Dunlop, J. N. (1993). Salt tolerance in *Rhagodia eremaea*. *Mulga Research Journal* **11**, 35-42.

Gutterman, Y. (1993). "Seed germination in desert plants," Springer-Verlag, New York.

Hall, R. L. (1978). The analysis and significance of competitive and non-competitive interference between species. *In* "Plant Relations in Pastures" (J. R. Wilson, ed.). Commonwealth Scientific and Industrial Research Organisation, Melbourne.

Harris, G. A., and Wilson, A. M. (1970). Competition for moisture among seedlings of annual and perennial grasses as influenced by root elongation at low temperature. *Ecology* **51**, 530-534.

Hartley, S. E., and Armos, L. (1999). Competitive interactions between *Nardus stricta* L. and *Calluna vulgaris* (L.) Hull: the effect of fertilizer and defoliation on above- and below-ground performance. *Journal of Ecology* **87**, 330-340.

Hartvigsen, G. (2000). Competition between co-dominant plants of the Serengeti plains depends on competitor identity, water, and urine. *Plant Ecology* **148**, 31-41.

Holmgren, M., Scheffer, M., and Huston, M. A. (1997). The interplay of facilitation and competition in plant communities. *Ecology* **78**, 1966-1975.

Hussey, B. M. J., Keighery, G. J., Cousens, R. D., Dodd, J., and Lloyd, S. G. (1997). "Western Weeds: A guide to the weeds of Western Australia.," The Plant Protection Society of Western Australia (Inc.), Victoria Park.

Ishikawa, S. I., Furukawa, A., and Oikawa, T. (1996). Photosynthetic responses to drought conditions in three coastal dune plants in relation to their zonal distribution. *Australian Journal of Botany* **44**, 381-391.

Ito, I., Kobayashi, K., and Yoneyama, T. (1998). Fate of Dehydromatricaria Ester added to soil and its implications for the allelopathic effect of *Solidago altissima* L. *Annals of Botany* **82**, 625-630.

Jefferies, R. L., Davy, A. J., and Rudmick, J. (1981). Population biology of the salt-marsh annual *Salicornia europaea* agg. *Journal of Ecology* **69**, 17-21.

Jones, R., and Hodgkinson, K. C. (1970). Root growth of Rangeland chenopods: Morphology and production of *Atriplex nummularia* and *Atriplex vesicaria*. *In* "Studies of the Australian arid zone: The biology of Atriplex" (R. Jones, ed.), pp. 77-86. Commonwealth Scientific and Industrial Research Organisation, Deniliquin.

Kadmon, R. (1995). Plant competition along soil moisture gradients: a field experiment with the desert annual *Stipa capensis*. *Journal of Ecology* **83**, 253-262.

Kaplan, A., and Gale, J. (1972). Effect of sodium chloride on the water balance of *Atriplex halimus*. *Australian Journal of Biological Sciences* **25**, 895-903.

Keddy, P. A. (1989). "Competition," Chapman and Hall, London.

Kelley, D. B., Goodin, J. R., and Miller, D. R. (1982). Biology of Atriplex. *In* "Contributions to the ecology of halophytes" (D. N. Sen and K. S. Rajpurchit, eds.). W. Junk Publishers, The Hague.

Kolchevskii, K. G., Kocharyan, N. I., and Koroleva, O. Y. (1995). Effect of salinity on photosynthetic characteristics and ion accumulation in C3 and C4 plants of Ararat plain. *Photosynthetica* **31**, 277-282.

Kramer, P. J. (1980). Drought, stress and origin of adaptations. *In* "Adaptation of plants to water and high temperature stress" (N. C. Turner and P. J. Kramer, eds.), pp. 7-20. John Wiley and Sons, New York.

Kubota, Y., and Hara, T. (1995). Tree competition and species coexistence in a sub-boreal forest, Northern Japan. *Annals of Botany* **76**, 503-512.

Kubota, Y., and Hara, T. (1996a). Allometry and competition between saplings of *Picea jezoensis* and *Abies sachalinensis* in a Sub-boreal Coniferous Forest, northern Japan. *Annals of Botany* **77**, 529-537.

Kubota, Y., and Hara, T. (1996b). Recruitment processes and species coexistence in a sub-boreal forest in Northern Japan. *Annals of Botany* **78**, 741-748.

Lamont, B. B. (1978). Biophysical constraints to the rehabilitation of mine wastes. *In* "Rehabilitation of Mined Lands in Western Australia." pp. 37-45, Perth.

Laverty, T. M. (1992). Plant interactions for pollinator visits: A test of the magnet species effect. *Oecologia* **89**, 502-508.

Lee, W. G., and Fenner, M. (1989). Mineral nutrient allocation in seeds and shoots of twelve *Chionochloa* species in relation to soil fertility. *Journal of Ecology* **77**, 704-716.

Lemaire, G. and Millard, P. (1999). An ecophysiological approach to modelling resource fluxes in competing plants. *Journal of Experimental Botany* **50** (330), 15-28.

Levine, J. (1999). Indirect Facilitation: Evidence and predictions from a riparian community. *Ecology* **80**, 1762-1769.

Levitt, J. (1972). "Responses of plants to environmental stresses," Academic Press, New York.

Luken, J. O. (1990). "Directing ecological succession," Chapman and Hall, New York.

Macias, F. A., Castellano, D., and Molinillo, J. M. G. (2000). Search for a standard phytotoxic bioassay for allelochemicals. Selection of standard target species. *Journal of Agricultural and Food Chemistry* **48**, 2512-2521.

Macias, F. A., Oliva, R. M., Varela, R. M., Torres, A., and Molinillo, J. M. G. (1999). Allelochemicals from sunflower leaves cv. Peredovick. *Phytochemistry* **52**, 613-621.

Mack, R. N., and Harper, J. L. (1977). Interference in Dune Annuals: Spatial Pattern and Neighbourhood Effects. *Journal of Ecology* **65**, 345-363.

Malcom, C. V., Clarke, A. J., Dantuono, M. F., and Swaan, T. C. (1988). Effects of plant spacing and soil conditions on the growth of five Atriplex species. *Agricultural Ecosystems and Environment* **21**, 265-280.

Malik, A. R., Anderson, D. J., and Myerscough, P. J. (1976). Studies on structure in plant communities.VII* Field and experimental analyses of *Atriplex vesicaria* populations from the riverine plain of New South Wales. *Australian Journal of Botany* **24**, 265-280.

Mann, J. (1987). "Secondary Metabolism," 2nd/Ed. Clarendon Press, Oxford.

Mansfield, T. A., and Jones, M. B. (1976). Photosynthesis: leaf and whole plant aspects. *In* "Plant structure, function and adaption" (M. A. Hall, ed.), pp. 443. The MacMillan Press Ltd, London.

McConnaughay, K. D. M., and Bazzaz, F. A. (1991). Is physical space a soil resource? *Ecology* **72**, 94-103.

McNaughton, S. J. (1978). Serengeti ungulates: Feeding selectivity influences the effectiveness of plant defence guilds. *Science* **199**, 806-807.

Mitchell, A. A., and Wilcox, D. G. (1998). "Arid shrubland plants of Western Australia," 2nd/Ed. University of Western Australia Press, Perth.

Morgan, J. W. (1995). Ecological Studies of the Endangered *Rutidosis leptorrhynchoides*. II.* Patterns of Seedling Emergence and Survival in a Native Grassland. *Australian Journal of Botany* **43**, 13-24.

Mueller-Dombois, D., and Ellenberg, H. (1974). "Aims and methods of Vegetational Ecology," New York.

Nernberg, D., and Dale, M. R. T. (1997). Competition of five native prairie grasses with *Bromus inermis* under three moisture regimes. *Canadian Journal of Botany* **75**, 2140-2145.

Newman, E. I. (1973). Competition and diversity of herbaceous vegetation. *Nature* **244**, 310.

Newman, E. I., and Miller, M. H. (1977). Allelopathy among some British grassland species II. Influence of root exudates on phosporous uptake. *Journal of Ecology* **65**, 399-411.

Nilsson, M. C., Zackrisson, O., Sterner, O., and Wallstedt, A. (2000). Characterisation of the differential interference effects of two boreal dwarf shrub species. *Oecologia* **123**, 122-128.

Novoplansky, A., and Goldberg, D. E. (2001). Effects of water pulsing on individual performances and competitive hierarchies in plants. *Journal of Vegetation Science* **12**, 199-208.

Olofsson, J., Moen, J., and Oksanen, L. (1999). On the balance between positive and negative plant interactions in harsh environements. *Oikos* **86**, 539-543.

Osborne, J. M., and Brearley, D. R. (1997). "Placer (Granny Smith) Waste Dumps 1996 Revegetation Assessment: 1992 and 1993 seedings." Curtin University of Technology, Perth.

Osborne, J. M., Fox, J. E. D., and Mercer, S. (1993). Germination response under elevated salinities of six semi-arid bluebush species (Western Australia). *In* "Towards the rational use of high salinity tolerant plants." (H. Leith and A. A. Masoom, eds.), Vol. 1, pp. 323-338. Kluwer Academic Publishers, Netherlands.

Osborne, J. M., Schatral, A., and Brearley, D. M. (1994). "Laboratory studies on the germination and viability of seed sown on waste rock dumps at the Placer (Granny Smith) Gold Mine in 1994.." Curtin University of Technology, Perth.

Ott, L. (1988). "An introduction to statistical methods and data analysis.," PWS-Kent Publishing Company, Boston.

Oxley, R. E. (1975). The perennial chenopod pasture lands of Australia. *In* "Studies of the Australian arid zone IV. Chenopod shrublands." (R. D. Graetz and K. M. W. Howes, eds.), pp. 1-4. Commonwealth Scientific and Industrial Research Organization, Deniliquin.

Pake, C. E., and Venable, D. L. (1995). Is coexistence of Sonoran desert annuals mediated by temporal variability in reproductive success? *Ecology* **76**, 246-261.

Pake, C. E., and Venable, D. L. (1996). Seed banks in desert annuals: implications for persistence and coexistence in variable environments. *Ecology* **77**, 1427-1435.

Pantastico-Caldas, M., and Venable, D. L. (1993). Competition in two species of desert annuals along a topographic gradient. *Ecology* **74**, 2192-2203.

Parr-Smith, G. A. (1982). Biogeography and evolution in the shrubby Australian species of *Atriplex* (Chenopodiaceae). *In* "Evolution of the flora and fauna of arid Australia" (W. R. Barker and P. J. M. Greenslade, eds.), pp. 291-299. Peacock Publications, Prewville, South Australia.

Parr-Smith, G. A., and Calder, D. M. (1975). *Atriplex vesicaria* Heward ex Benth. and related species: taxomony and variation. *In* "Studies of the Australian arid zone IV. Chenopod shrublands" (R. D. Graetz and K. M. W. Howes, eds.), pp. 17-28. Commonwealth Scientific and Industrial Research Organization, Deniliquin.

Perrson, H. (1978). Root dynamics in a young Scots pine stand in Central Sweden. *Oikos* **30**, 508-519.

Peterson, C. J., and Squiers, E. R. (1995). Competition and succession in an aspen-white-pine forest. *Journal of Ecology* **83**, 449-457.

Phillips, D. L., and MacMahon, J. A. (1981). Competition and spacing patterns in desert shrubs. *Journal of Ecology* **69**, 97-115.

Pielou, E. C. (1960). A single mechanism to account for regular, random and aggregated populations. *Journal of Ecology* **48**, 575-584.

Pons, T. L. (1991). Dormancy, germination and mortality of seeds in a chalk-grassland flora. *Journal of Ecology* **79**, 765-780.

Pringle, H. J. R., Vreeswyk, A. M. E. V., and Gilligan, S. A. (1994). "An inventory and condition survey of rangelands in the north-eastern Goldfields, Western Australia.," Rep. No. 87. Department of Agriculture, Western Australia, Perth.

Pugnaire, F. I., and Haase, P. (1996). Comparative physiology and growth of two perennial grass species in a semi-arid environment. *Annals of Botany* **77**, 81-86.

Pugnaire, F. I., Haase, P., Incoll, L. D., and Clark, S. C. (1996a). Response of the tussock grass *Stipa tenacissima* to watering in a semi-arid environment. *Functional Ecology* **10**, 265-274.

Pugnaire, F. I., Haase, P., and Puigdefabregas, J. (1996b). Facilitation between higher plant species in a semiarid environment. *Ecology* **77**, 1420-1426.

Pugnaire, F. I., Haase, P., Puigdefabregas, J., Cueto, M., Clark, S. C., and Incoll, L. D. (1996c). Facilitation and succession under the canopy of a leguminous shrub, *Retama sphaerocarpa*, in a semi-arid environment in south-east Spain. *Oikos* **76**, 455-464.

Pugnaire, F. I., and Luque, M. T. (2001). Changes in plant interactions along a gradient of environmental stress. *Oikos* **93**, 42-49.

Pyankov, V. I., Gunin, P. D., Tsoog, S., and Black, C. C. (2000). C4 plants in the vegetation of Mongolia: their natural occurrence and geographical distribution in relation to climate. *Oecologia* **123**, 15-31.

Rayment, G. E., and Higginson, F. R. (1992). "Australian laboratory handbook of soil and water chemical methods," Inkata Press, Melbourne.

Reichenberger, G., and Pyke, D. A. (1990). Impact of early root competition on fitness components of four semiarid species. *Oecologia* **85**, 159-166.

Rew, L. J., Froud-Williams, R. J., and Boatman, N. D. (1995). The effect of nitrogen, plant density and competition between *Bromus sterilis* and three perennial grasses: the implications for boundary strip management. *Weed Research* **35**, 363-368.

Rhodes, I., and Stern, W. R. (1978). Competition for light. *In* "Plant Relations in pastures" (J. R. Wilson, ed.), pp. 175-189. Commonwealth scientific and industrial research organisation, Melbourne.

Rice, E. L. (1974). "Allelopathy," Academic Press, New York.

Ross, M. A., and Harper, J. L. (1972). Occupation of biological space during seedling establishment. *Journal of Ecology* **60**, 77-88.

Russell, G., Jarvis, P. G., and Monteith, J. L. (1990). Radiation absorption by canopies and stand growth. *In* "Plant canopies: their growth, form and function" (G. Russell, B. Marshall and P. G. Jarvis, eds.), pp. 178. Cambridge University Press, Cambridge.

Ruthven, D. C. (2001). Herbaceous vegetation diversity and abundance beneath honey mesquite (*Prosopis glandulosa*) in the South Texas Plains. *Texas Journal of Science* **53**, 171-186.

Saxena, A., Singh, D. V., and Joshi, N. L. (1996). Autotoxic effects of pearl millet aqueous extracts on seed germination and seedling growth. *Journal of Arid Environments* **33**, 255-260.

Schatral, A., and Osborne, J. M. (1996). "Seed quality and germination characteristics: 1996 seeding mixture for waste rock dumps. Placer (Granny Smith) Gold Mine.." Curtin University of Technology, Perth.

Sharma, M. L. (1976). Soil water regimes and water extraction patterns under two semi-arid shrub (*Atriplex* spp.) communities. *Australian Journal of Ecology* **1**, 249-258.

Sharma, M. L. (1982). Aspects of salinity and water relations of Australian chenopods. *In* "Contributions to the ecology of halophytes" (D. N. Sen and K. S. Rajpurohit, eds.). Dr W. Junk Publishers, The Hague.

Shaybany, B., and Kashirad, A. (1978). Effect of NaCl on growth and mineral composition of *Acacia saligna* in sand culture. *Journal of the American Society for Horticultural Science* **103**, 823-826.

Short, D. C., and Colmer, T. D. (1999). Salt tolerance in the halophyte *Halosarcia pergranulata* subsp. *pergranulata*. *Annals of Botany* **83**, 207-213.

Short, N. (1998). "Root exploration studies: A comparison of the rooting systems of *Atriplex* and *Maireana* species. Biology Project 301." Curtin University of Technology, Perth.

Silander, J. A., and Pacala, S. W. (1985). Neighborhood predictors of plant performance. *Oecologia* **66**, 256-263.

Silverton, J., and Wilson, J. B. (1994). Community structure in a desert perennial community. *Ecology* **75**, 409-417.

Sinclair, A. R. E. (1989). Population regulation in animals. *In* "Ecological Concepts." (J. M. Cherrett, ed.), pp. 197-241. Blackwell, Oxford, UK.

Sneesby, J. E. (1992). "Revegetation of the Westonia Tailings Dam: Field and laboratory investigations.." Curtin University of Technology, Perth.

Stoneman, G. L. (1992). Factors affecting the establishment of Jarrah (*Eucalyptus marginata*) from seed in the northern Jarrah forest of Western Australia. Ph.D. Thesis, Murdoch University.

Sumida, A., and Komiyama, A. (1997). Crown spread patterns for five deciduous broad-leaved woody species: ecological significance of the retention patterns of larger branches. *Annals of Botany* **80**, 759-766.

Summul, M., Kull, K., Oksanen, L., and Veromann, P. (2000). Competition intensity and its importance: results of field experiments with *Anthoxanthum odoratum*. *Oecologia* **125**, 18-25.

Thijs, H., Shann, J. R., and Weidenhamer, J. D. (1994). The effect of phytotoxins on competitive outcome in a model system. *Ecology* **75**, 1959-1964.

Tilman, D. (1982). "Resource competition and community structure," Princeton University Press, Princeton, New Jersey.

Tilman, D. (1988). "Plant Strategies and the Dynamics and Structure of Plant Communities," Princeton University Press, Princeton.

Tremmel, D. C., and Bazzaz, F. A. (1995). Plant architecture and allocation in different neighbourhoods: implications for competitive success. *Ecology* **76**, 262-271.

Turkington, R., Klein, E., and Chanway, C. P. (1993). Interactive effects of nutrients and disturbance: an experimental test of plant strategy theory. *Ecology* **74**, 863-878.

Valladares, F., and Pearcy, R. W. (1998). The functional ecology of shoot architecture in sun and shade plants of *Heteromeles arbutifolia* M. Roem., a Californian chaparral shrub. *Oecologia* **114**, 1-10.

Valladares, F., and Pugnaire, F. I. (1999). Tradeoffs between irradiance capture and avoidance in semi-arid environments assessed with a crown architecture model. *Annals of Botany* **83**, 459-469.

Vargas-Mendoza, M. C., and Fowler, N. L. (1998). Resource-based models of competitive interactions. I. Intraspecific competition in *Ratibida columnifera* (Asteraceae). *American Journal of Botany* **85**, 932-939.

Wagner, R. G., and Radosevich, S. R. (1998). Neighborhood approach for quantifying interspecific competition in coastal Oregon forests. *Ecological Applications* **8**, 779-794.

Walck, J. L., Baskin, J. M., and Baskin, C. C. (1999). Effects of competition from introduced plants on establishment, survival, growth and reproduction of the rare plant *Solidago shortii* (Asteraceae). *Biological Conservation* **88**, 213-219.

Weidenhamer, J. D., Hartnett, D. C., and Romeo, J. T. (1989). Density-dependent phytotoxicity: distinguishing resource competition and allelopathic interference in plants. *Journal of Applied Ecology* **26**, 613-624.

Weiner, J. (1980). The effects of plant density, species proportion and potassium-phosphorous fertilization on interference between *Trifolium incarnatum* and *Lolium multiflorum* with limited nitrogen supply. *Journal of Ecology* **68**, 969-979.

Weiner, J. (1988). The influence of competition on plant reproduction. *In* "Plant reproductive ecology; patterns and strategies" (J. L. Doust and L. L. Doust, eds.), pp. 229-245. Oxford University Press, Oxford.

Weiner, J., Kinsman, S., and Williams, S. (2000). Modeling the growth of individuals in plant populations: local density in a strand population of *Xanthium strumarium* (Asteraceae). *American Journal of Botany* **85**, 1638-1645.

Witkowski, E. T. F. (1991). Growth and competition between seedlings of *Protea repens* (L.) L. and the alien invasive, *Acacia saligna* (Labill.) Wendl. in relation to nutrient availability. *Functional Ecology* **5**, 101-110.

Yeaton, R. I. (1978). A cyclical relationship between *Larrea tridentata* and *Opuntia leptocaulis* in the northern Chihuahuan desert. *Journal of Ecology* **66**, 651-656.

Yeaton, R. I., and Cody, M. L. (1976). Competition and spacing in plant communities: The Northern Mojave Desert. *Journal of Ecology*, 689-696.

Zobel, K., and Zobel, M. (1988). A new null hypothesis for measuring the degree of plant community organization. *Vegetatio* **75**, 17-25.