Resource dynamics and positive and negative interactions between plants in arid systems

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Abstract

In arid systems, below-ground resources fluctuate from being plentiful during pulses of rainfall to limiting to plant growth during interpulses between rainfall events. The role of plant interactions in structuring plant populations within systems with widely fluctuating resource levels is widely debated. I propose that the overall outcome of interactions along a temporal gradient of resource availability changes from positive during interpulses to negative during pulses.

I examined negative interactions between four co-dominant chenopod shrubs in arid *Acacia papyrocarpa* woodlands. Two chenopod shrubs, *Enchylaena tomentosa* and *Rhagodia spinescens*, occur almost exclusively beneath canopies. *Atriplex vesicaria* and *Maireana sedifolia* occur both beneath and in open sites between trees. Contrary to predictions, negative interactions were more intense when conditions were least productive. The intensity of competition between shrubs growing beneath canopies changed significantly over time and was least intense during a large pulse and most intense during a long interpulse. Competition was more intense in open sites than in the more fertile sites under trees. However, differences in soil fertility between sites did not explain the difference in competition intensity between sites.

Positive interactions between *Acacia* and *Enchylaena* and *Atriplex* seedlings also changed in intensity over time. Changes in positive interactions along temporal gradients depended on the facilitation mechanism. Supporting my prediction, microclimate modification by *Acacia* facilitated the survivorship of seedlings during interpulses in a dry year. However, modification of soil properties by *Acacia* facilitated seedling emergence and growth during pulses. *Enchylaena* grew more when protected by *Acacia* canopies but canopies had neutral to negative effects on *Atriplex* growth. Carbon uptake in pot-grown *Atriplex* seedlings was reduced when grown under light levels similar to those occurring beneath *Acacia* canopies. Carbon uptake in *Enchylaena* was not affected by shading when plants were well-watered but when plants were water stressed, high light levels had photoinhibitory affects.

Plant interactions seem to be most intense at the beginning of interpulses when plants are competing for diminishing water, or survivorship is enhanced in the favourable microsites provided by other plants. Later in the interpulse, interactions become less intense as conditions become more stressful and therefore survivorship and growth are affected more by abiotic conditions than plant interactions. In this system, positive interactions have an important role in determining the distribution of four dominant chenopod shrubs.

Declaration

This work contains no material which has been accepted for the award of any other degree or diploma in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text.

I give consent to this copy of my thesis, when deposited in the University Library, being available for loan and photocopying.

Jane Prider

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CHAPTER 1

Introduction and Literature review: Plant interactions along spatial and temporal resource gradients

Introduction

Competition has long been a focus of ecological theory and research (see reviews by Connell 1983, Schoener 1983, Fowler 1986a, Goldberg and Barton 1992, Goldberg *et al.* 1999). Conceptual and mechanistic theories about competition have developed around the limitations imposed by resources (for discussion see Huston and DeAngelis 1994). The role of competition in regulating populations and communities under varying environmental conditions and resource levels is still widely debated. Grime (1973), Southwood (1977, 1988), and Greenslade (1983) argue negative interactions become more important as stress decreases or resource levels increase. However, Tilman (1988) and Newman (1973) argue the intensity of negative interactions will not change along a resource gradient.

More recently, positive interactions or facilitation have been reconsidered as important processes in communities (Callaway 1995). Studies show positive interactions are frequently observed in stressful environments, and this stress may be a result of low resource levels, frequent disturbance, high consumer pressure, or extreme physical conditions (see reviews by Hunter and Aarsen 1988, Callaway 1995, Callaway and Walker 1997, Brooker and Callaghan 1998). Plants can have positive effects on their neighbours by modifying resources, protecting them from disturbance or herbivores or ameliorating harsh physical conditions. Facilitation occurs when any of these mechanisms has a positive effect on the performance of a neighbouring plant.

Resource gradients

Resource gradients occur when the availability of resources required for plant growth vary in either space or time. The distribution of plants along such gradients is constrained by their physiological tolerances of resource levels and conditions along the gradient, and biological interactions (Cornelius *et al.* 1991). Biotic factors, such as competition, are proposed to limit plant distributions at the optimal end of the gradient whereas abiotic factors limit distributions at the harsher end of the gradient (Gurevitch 1986, Wilson and Keddy 1986, Reader 1990, Greiner La Peyre *et al.* 2001). However, a simple trade-off between competitive ability and stress tolerance (*sensu* Grime 1977) has not been supported in empirical studies (e.g. Donovan and Richards 2000, Emery *et al.* 2001, Jurjavcic *et al.* 2002). The dominant species at any point along a gradient may be the species that is the best competitor under that set of environmental conditions (Tilman 1982, Emery *et al.* 2001, Greiner La Peyre *et al.* 2001). The consideration of positive interactions (or facilitation) further alters the importance of biotic interactions along resource gradients (Callaway 1997). Positive interactions between plants have been frequently observed at the more stressful end of gradients where the physical presence of a plant may increase resource levels or ameliorate the harsh conditions for neighbouring plants (Greenlee and Callaway 1996, Choler *et al.* 2001, Pugnaire and Luque 2001).

Resource gradients in arid systems

In arid systems water frequently limits plant growth. These systems are driven by pulses of rainfall and are characterised by fluctuating levels of below-ground resources. Soil water fluctuates from being plentiful during pulses that follow rainfall events, to limiting to plant growth during interpulses between rainfall events. As the interval between pulses becomes greater, water availability becomes increasingly restricted to pulses and system productivity declines (Noy-Meir 1973). The frequency and magnitude of rainfall events or pulses may have effects different to the overall amount of resource that is supplied per growing season. Thus, although there is a resource gradient from low to high water availability between interpulses and pulses, there is also temporal heterogeneity within pulses associated with the size and frequency of individual rainfall events (Ehleringer *et al.* 1999).

With declining water availability plants become more widely separated, although below-ground cover may be continuous (Burke *et al.* 1998). With sparser plant spacing resources tend to accumulate around plants (Burke *et al.* 1998). This may result from the redistribution or concentration of resources by physical and biotic processes (Belsky and Amundson 1998). At the landscape scale, the distribution of resources becomes more spatially heterogeneous as resource inputs into the system decline. In arid and semi-arid systems, topography is important in creating spatial resource gradients at large spatial scales (Tongway and Ludwig 1990), but at smaller scales these gradients are commonly created by the physical presence of plants (Tongway and Ludwig 1994). Scarce or limiting resources become concentrated around plants and after rainfall the availability of resources in these patches becomes above the threshold for plant establishment and growth (Tongway 1990). This is important because patches unoccupied by plants may not reach these threshold levels (Noy-Meir 1981).

Gradients and plant interactions

The role of competition in arid systems has been addressed recently in mathematical (Chesson and Huntly 1997) and conceptual theory (Goldberg and Novoplansky 1997). These theories have recognised that fluctuating resources may be a particularly important mechanism for promoting coexistence and determining competitive hierarchies in harsh or unproductive systems. However, neither of these theories considers the role of positive interactions. Other conceptual theories that have described the role of positive and negative interactions along resource or stress gradients have not considered the effects of fluctuating resources (Bertness and Callaway 1994, Callaway and Walker 1997, Holmgren *et al.* 1997, but see Brooker and Callaghan 1998). As positive interactions are frequently observed in arid systems, where plant growth is controlled by pulsed resource inputs, this scale of temporal gradient may provide insights into the balance between positive and negative interactions. During interpulses abiotic conditions may have more negative effects on plant performance than competitive effects. However, if habitat modifications by plants ameliorate harsh abiotic conditions, plant interactions may be more important overall in structuring vegetation in harsh environments.

Thesis scope

In this research, I use experimental approaches to examine plant interactions along spatial gradients and pulse-driven temporal gradients. The study system is arid *Acacia papyrocarpa* open woodland, located on the northern Eyre Peninsula, South Australia. There is some evidence that *A. papyrocarpa* modifies its undercanopy environment by increasing the availability of nutrients (Facelli and Brock 2000) and soil moisture (Grey-Smith 1987, Facelli and Brock 2000), and altering substrate characteristics such as soil bulk density (Barnes 1993). This creates spatial resource gradients between undercanopy sites and the matrix habitat. The distribution of several plants is positively associated with the undercanopy environment of *A. papyrocarpa* (Tester *et al.* 1987, Barnes 1993, Facelli and Brock 2000). These modifications and spatial associations suggest facilitative relationships between these species and *A. papyrocarpa*. Facilitation may be particularly important in this environment where rainfall is unpredictably low and variable.

Competitive relationships have not been examined extensively in these woodlands (but see Wotton 1993 and Harris and Facelli in press). Depending on the response of competition intensity to resources, the intensity of negative interactions may differ between undercanopy microhabitats and open spaces and the effects of spatial and temporal gradients may be interactive. I use a guild of perennial chenopod shrubs to examine plant interactions in this system. These shrubs form the dominant plant cover and the various species have different distributions in relation to tree canopies. These distributional differences may reflect the overall balance between positive and negative interactions for these species in *A. papyrocarpa* woodlands.

In this review, I use evidence primarily from manipulative field experiments in semi-arid to arid systems to examine how resource gradients affect the relative intensity of negative and positive plant interactions. I first describe how plants respond to temporal resource gradients of pulsed water supply and how plants create spatial resource gradients that facilitate the performance of neighbouring plants. These processes have implications for the balance between positive and negative interactions. Facilitation and competition are likely to occur simultaneously and researchers have developed conceptual models to describe the balance between these interactions along environmental gradients (Bertness and Callaway 1994, Callaway and Walker 1997, Holmgren *et al.* 1997, Brooker and Callaghan 1998). However, these models do not describe explicitly how interaction intensity may change along a resource gradient driven by pulse phases of water input. I conclude this chapter by outlining a conceptual model that describes the relationship between positive and negative plant interaction intensities and pulse and interpulse phases. In the remaining chapters of the thesis, I test the predictions of this model and explore some of the underlying mechanisms of competition and facilitation.

Temporal gradients and the supply of resources

Most arid systems are characterised by a heterogeneous water supply, in the frequency and magnitude of rainfall events and in how water is distributed in the soil profile and across the landscape (Noy-Meir 1973). Temporal variations in rainfall input create spatial variation in soil water content with soil depth depending on how rainfall events are distributed and on soil characteristics. Larger rainfall events recharge deeper soil layers although this may only occur during the winter months when evaporation and transpiration rates are low (Ehleringer *et al.* 1999, Reynolds *et al.* 1999). Water reserves deeper in the soil profile may be retained throughout interpulses (Sharma 1976). Smaller rainfall events do not penetrate beyond the upper soil layers and these layers become quickly depleted in soil moisture during interpulses.

Pulse and interpulse intervals also control nutrient availability. Temperature and precipitation have a strong influence on the physical and chemical processes of soil formation and biological activity within the soil (Cowling 1978, Garner and Steinberger 1989). Much of the available nitrogen and phosphorus in arid soils is recycled through leaf litter so seasonal patterns of litter fall can limit the amount and temporal availability of these nutrients (Charley 1978). As rainfall initiates nutrient release from litter and ion uptake by roots, the mineral cycle is also temporally pulsed (Charley 1978) with pulses of nutrients available after soil wetting (Lee *et al.* 1983, Chapin 1988). The magnitude of rainfall events (Charley and Cowling 1968) and temperature (Whitford *et al.* 1986, Steinberger *et al.* 1990) are also important. Small precipitation events that initiate mineralisation of organic N, but are ineffective for plant growth, result in nutrient accumulation in the upper soil layers (Trumble and Woodroffe 1954, Charley and Cowling 1968). However, rainfall may trigger mineralisation only in seasons when temperatures are optimal (Whitford *et al.* 1986).

Plant responses to pulsed resources

Plants differ in their ability to utilise temporal and spatial variations in soil resources. Schwinning and Ehleringer (2001) suggested that plants in water-limited systems were 'moisture pattern specialists' adapting resource uptake patterns to water availability through the soil profile. Some species take up relatively little pulse water, i.e. from small rainfall events, (Ehleringer *et al.* 1991, Flanagan *et al.* 1992) but this may depend on the season, switching to deeper soil moisture sources later in the growing season (Evans and Ehleringer 1994). This switch may prevent these species from utilising pulse water outside the typical growth season (BassiriRad *et al.* 1999). However, plants that use unseasonal pulses further partition the soil water resource (Gebauer and Ehleringer 2000). Pulse water usage also depends on life form (Ehleringer *et al.* 1991, Harrington 1991). For example, grasses are more likely to use pulse water than shrubs (Sala *et al.* 1989, Golluscio *et al.* 1998). Depending on plant size, phenology and resource demand, what constitutes a pulse for one species may not necessarily be a pulse for another species (Harris and Facelli in press). The frequency of pulses may also be important. Some plants may respond to a cluster of small rainfall events, whilst others may respond to a single, large rainfall event but this will depend on the timing and predictability of rainfall events. Growth responses to nitrogen pulses can also depend on the magnitude of the pulse. The growth response may be greater when the same total amount of nitrogen is supplied in larger pulses than at a constant supply (Bilbrough and Caldwell 1997) or in smaller pulses (Yoder and Caldwell 2002). Within water-limited systems, most nutrient resources are restricted to the surface soil layers (Charley and Cowling 1968, Nishita and Haug 1973, Cowling 1978). Plants that respond to moisture pulses are therefore able to utilise nutrient sources in the upper soil layers. In some species, different parts of the root system acquire nitrogen than water (Gebauer and Ehleringer 2000) but resource uptake will depend on soil conditions (Hamerlynck *et al.* 2000, Hamerlynck *et al.* 2002). This diversity of pulse utilisation has consequences for resource partitioning and the temporal dynamics of plant interactions (Tilman 1997).

Spatial gradients: habitat modification and facilitation

Soil resources vary vertically through the soil profile but they may also vary horizontally when redistributed by physical means, or concentrated by the physical presence of plants. Considerable evidence has demonstrated that the presence of trees and shrubs modifies the microenvironment beneath their canopies. Apart from differences in temperature and light climate, plants can also alter the amount of below-ground resources in their undercanopy environment (e.g. Belsky *et al.* 1989, Breshears *et al.* 1997a). This increase in resource levels may supersede the requirements of the plant itself, resulting in elevated levels of resources in these habitats. This creates spatial heterogeneity of resources at the landscape scale, such that resource-rich patches or fertility islands are interspersed within a matrix of resource-poor habitats. As these patches are plant-created, they are also dynamic, related to the life cycles of the plants themselves (Aguiar and Sala 1999, Facelli and Brock 2000). At the whole-plant scale, these patches create resource or stress gradients; high resource/low stress microsites associated with plants and low resource/high stress microsites in the matrix habitat between plants.

Below-ground resource enrichment

Several processes can increase water availability in soils beneath plant canopies. The amount of water that reaches the soil beneath canopies depends on the size and timing of rainfall events (Pressland 1973, Belsky *et al.* 1989). During small rainfall events much of the water is intercepted by the canopy and subsequently evaporates (Pressland 1973, Vetaas 1992, Breshears *et al.* 1997a). During larger rainfall events water is redirected along plant branches and roots and may concentrate beneath plant canopies (Pressland 1973, Haworth and McPherson 1995, Martinez-Meza and Whitford 1996). The effectiveness of rainfall may be increased beneath canopies as the accumulation and subsequent breakdown of organic matter increases soil macroporosity that may improve the infiltration and retention of water (Joffre and Rambal 1988, Pugnaire *et al.* 1996). The hydraulic redistribution of water via root systems can also increase soil water content in the upper soil layers, particularly when steep water potential gradients develop in the soil profile (Richards and Caldwell 1987, Williams *et al.* 1993). The litter layer and canopy shading may also reduce evaporation of soil water, although water intercepted by these layers may at times reduce the amount of water reaching the soil (Breshears *et al.* 1997a). The shade cast by plant canopies can also modify the under-canopy microclimate by reducing soil and air temperatures and increasing humidity (Parker and Muller 1982, Belsky *et al.* 1989, Franco and Nobel 1989). These modifications may positively benefit plants growing in these microhabitats by reducing evaporative stresses (see review by Callaway 1995).

By altering the microclimate and substrate properties, sites beneath plant canopies can provide conditions for the accumulation of nutrients. The nutrient status of soils beneath canopies can be improved when litter or undercanopy herbaceous plants decompose (Kellman 1979, Vetaas 1992). Canopy microhabitats can also provide more suitable environments for soil microbia where the microclimate is modified and soil conditions may be moister (Cowling 1978, Steinberger *et al.* 1990). These sites may also promote microbial activity because of a greater availability of organic substrates (Correll 1967, Alon and Steinberger 1999). Plant canopies act as the foci for animal activity that can also increase nutrient levels through depositions of waste (Dean *et al.* 1999). Nitrogen levels may be higher in soils beneath species with N-fixing symbionts or associated with mycorrhizae (Carrillo-Garcia *et al.* 1999). Free-living nitrogen fixing bacteria may provide more nitrogen input into arid systems but their effects may be greater in less disturbed undercanopy microsites (Evans and Ehleringer 1993). Nutrient pumping by root systems also transfers nutrients from deeper soil layers to shallow soil layers (Richards and Caldwell 1987).

Facilitation mechanisms

Facilitation can occur when plant performance is improved by any of these modification mechanisms. The mechanism may depend on the stresses within a system. For example, in water-limited systems, mechanisms that reduce heat and desiccating conditions will be more common (Holmgren *et al.* 1997). There may be a combination of factors that improve the water relations for plants growing beneath canopies, including both microclimatic and soil effects. Improvement to plant-water relations is the most often-cited facilitation mechanism. This has been demonstrated indirectly by showing that plants are not facilitated if watered (Jong and Klinkhamer 1988, Kitzberger *et al.* 2000, Ibáñez and Schupp 2001). It has also been the inferred positive effect of canopy shading through a reduction in evaporative demand (Frost and McDougald 1989, Weltzin and Coughenour 1990, Pugnaire *et al.* 1996, Rousset and Lepart 2000, Anderson *et al.* 2001). Increased water availability through hydraulic lift has been shown to improve growth of herbs beneath *Acer* trees (Dawson 1993, Emerman and Dawson 1996).

Microclimate may interact with soil effects to produce higher nutrient loads that in turn may reduce water stress for plants. A combination of increased organic matter and shade may increase the activity of soil microbiota (Steinberger *et al.* 1990), especially if shade reduces the depletion of soil moisture (Wilson and Wild 1995 cited by Belsky and Amundson 1998). Whether a plant can take advantage of higher nutrient levels under the canopy can depend on the responses to other resources such as water and light availability (Franco-Pizaña *et al.* 1996, Rice and Nagy 2000). Plants may only be able to take advantage of increased nutrients beneath canopies when water is not limiting to growth (Bisigato and Bertiller 1999, Tielbörger and Kadmon 2000b). Although fertilised plants may more rapidly deplete water reserves because they are growing faster (Wadleigh and Richards 1953), higher nutrients may improve water use efficiency (Gordon *et al.* 1999, Wright *et al.* 2001). Interactive effects of shade and nutrients may be mediated through changes in soil temperature (Carrillo-Garcia *et al.* 2000) and reductions in water stress (Shumway 2000). Very few studies have demonstrated that increased nutrients alone are the primary facilitation mechanism. Maron and Connors (1996) showed that N-fixing shrubs might have positive effects on the growth of undercanopy herbaceous plants by increasing nitrogen availability.

Although increases in below-ground resources beneath plant canopies may have positive effects on plants, reduced light levels beneath plant canopies can have negative effects on carbon gain (Kitzberger *et al.* 2000, Forseth *et al.* 2001, Walker *et al.* 2001). Shade-tolerant species may be more able to take advantage of increased below-ground resources (Rice and Nagy 2000). Shading reduces radiation loads and can have positive effects on shaded plants by preventing photoinhibition under conditions when carbon fixation is limited by temperature or water stress (Greenlee and Callaway 1996, Egerton *et al.* 2000, Kitzberger *et al.* 2000). Shading may have negative effects on plant growth but positive effects on survival (Kitzberger *et al.* 2000). For example, the reduction of radiation beneath desert plants facilitates the establishment of cactus seedlings (Turner *et al.* 1966, Franco and Nobel 1989).

Positive effects may also be indirect (Miller 1994). For example, reductions in light levels may exclude competitive, light-demanding species from below canopies. Plants may establish under canopies where potential competitors have been excluded (Callaway 1992, Kellman and Kading 1992, Rice and Nagy 2000). By excluding light-demanding grasses, isolated shrubs or trees may facilitate the spread of other woody plants into grassy systems (Li and Wilson 1998).

Facilitation and gradients

Bertness and Callaway (1994) proposed that the frequency of positive interactions increased with physical stress. This can occur when the amelioration of stress by neighbouring plants by habitat modification favours plant performance to a greater extent than competition for resources restricts plant performance (Bertness and Callaway 1994, Callaway and Walker 1997). Both quantitative (Goldberg *et al.* 1999) and qualitative reviews (Hunter and Aarsen 1988, Callaway 1995, Callaway and Walker 1997, Brooker and Callaghan 1998) have shown that positive interactions are more frequent in unproductive environments than productive environments. Callaway (1997) also suggested that positive effects would become stronger as abiotic stress increases.

In water-limited systems, positive interactions are more frequently observed during years of lower rainfall. In experiments repeated in wetter years and drier years, facilitation of survivorship was more frequently observed in the drier year (Casper 1996, Greenlee and Callaway 1996, Ibáñez and Schupp 2001). Frost and McDougald (1989) also found that trees facilitated herbaceous biomass production during a drier year but not a wetter year. Kitzberger *et al.* (2000) found that shrubs facilitated the establishment of *Austrocedrus* in average years, but not wetter years, during the driest year establishment did not occur at all, either under shrubs or in spaces between shrubs. However, not all studies support this pattern. Tielbörger and Kadmon (2000b) found that annual plant reproduction was facilitated more during a wet year than a dry year and similarly, Casper (1996) found that shrubs facilitated herb reproduction less during a dry year than a wetter year.

Greenlee and Callaway (1996) pointed out that temporal variation in stress caused greater variations in interaction intensity than spatial variation in stress. They found that the intensity of facilitation differed between years of varying rainfall but not between sites of varying stress. They also found that this interaction was more intense for survival than for growth although too few plants survived to enable complete comparisons of final biomass. However, other studies have found that spatial gradients have effects on positive interactions. Biomass production (Pugnaire and Luque 2001), plant abundance (Tewksbury and Lloyd 2001), and seedling establishment (Parciak 2002) were higher beneath canopies at high stress sites but not at low stress sites.

There is some evidence that facilitation of survival increases with increasing abiotic stress (typically associated with water availability), especially temporal variations in stress. The facilitation of growth and reproduction may depend on the facilitation mechanism, the life stage, or the physiology of the interacting species. For example, higher nutrient levels beneath plants may only be beneficial to plants growing in this microhabitat when water is not limiting. Therefore, facilitation will occur during the more productive periods following rainfall (e.g. Tielbörger and Kadmon 2000b). If the facilitation mechanism is a reduction in evaporative demand, then facilitation may occur during interpulses when water availability is low and the system is least productive (e.g. Frost and McDougald 1989). This mechanism may be more important for young seedlings that may be more sensitive to stresses than more mature plants (e.g. Franco and Nobel 1989).

Competition and gradients

Competition along resource gradients has been an area of intensive ecological research. In sites that produce large standing crop there is a high demand for resources and competition intensity may be high (Grime 1973, Huston 1979). In less productive sites where biomass and resource depletion are low, and the demands on the limited resource base are reduced, competition intensity could decline (Grime 1973, Taylor *et al.* 1990). However, although competition for light may decline with decreasing productivity and standing crop, competition for below-ground resources may actually increase. If so, total competition will not change along productivity gradients, but will shift from predominantly above-ground in productive systems to below-ground in unproductive systems (Newman 1973, Tilman 1988). Despite extensive empirical research, there is still no consensus on how the intensity of competition changes with increasing below-ground resource levels (Casper and Jackson 1997).

Many experiments have demonstrated that competition intensity does change along resource gradients, yet there is little agreement about the direction of these changes. Along spatial resource gradients within the same system there are roughly equal numbers of field studies that have shown competition to be relatively more intense in the less fertile site (Fowler 1990, Davis *et al.* 1998, Pugnaire and Luque 2001) as in the more fertile site (Gurevitch 1986, Kadmon 1995, Greenlee and Callaway 1996, Jurjavcic *et al.* 2002). Similarly, in a meta-analysis of interaction intensity along productivity gradients, interactions varied in intensity in sites with low standing crop from strongly positive to strongly negative, although at high standing crop they were consistently negative (Goldberg *et al.* 1999). Along temporal gradients, some studies have shown competition occurs more frequently, or with more intensity, after rainfall or artificial watering in water-limited systems (Cable 1969, Gurevitch 1986, Kadmon and Shmida 1990, Wotton 1993, Kadmon 1995, Dunbar and Facelli 1999). However, a similar number of studies have found competition to be more intense during the dry season (Fonteyn and Mahall 1981, Manning and Barbour 1988, Welden *et al.* 1988, Flores-Martínez *et al.* 1998) or at low irrigation (Davis and Pelsor 2001, Goldberg *et al.* 2001).

The discrepancy between these studies has been attributed to a number of factors including, the use of absolute measures of competition intensity rather than relative measures (Grace 1995), the use of artificial versus experimental gradients (Goldberg and Barton 1992, Kadmon 1995), disagreements on when resource supply exceeds demand (Davis *et al.* 1998, Reynolds 1999), and differences in the frequency and magnitude of resource inputs (Goldberg and Novoplansky 1997).

Pulsed resources and competition

Goldberg and Novoplansky (1997) hypothesised that temporal changes in resource supply in unproductive environments will have different consequences for plant interactions depending on the amplitude of these temporal changes and the responses of individual plants to this dynamic. Plants experience two distinct phases - a pulse when most resource uptake and growth occurs, and an interpulse phase when resource supply is reduced and most stress-induced mortality occurs (Goldberg and Novoplansky 1997). The intensity and importance of competition will depend on the demands made on resources during these phases. Goldberg and Novoplansky (1997) predict that demands on resources occur during pulses so competition will be intense at these times. If resource availability during interpulses is also affected by plant uptake, then competition will also be intense during these periods and there may be little fluctuation in competition intensity over time (Goldberg and Novoplansky 1997). Competition during interpulses will depend on the plants ability to utilise rainfall pulses outside the main growing season (Ehleringer *et al.* 1999) but may also occur if plants compete for different resources at different times. For example, competition for soil water may not be intense immediately following a rainfall pulse, but may increase in intensity as the interpulse begins and water becomes limiting (Grubb 1992). Competition for nutrients may occur during pulses when most nutrient uptake is coupled to water uptake (Grubb 1992, Goldberg and Novoplansky 1997).

Resource competition is inextricably linked to the supply and demand for resources (Taylor *et al.* 1990, Huston and DeAngelis 1994). Whether competition intensity changes over time will depend on how plants can deplete resources as their availability declines. The supply of below-ground resources is limited by their rates of transport through the soil medium (Huston and DeAngelis 1994). Zones of depletion around plant roots may have little effect on resource supply to other roots when there is a low supply of resources in the soil pool or alternatively, when there is a plentiful supply of nutrients and water (Huston and DeAngelis 1994). Fluctuations in resource supply can potentially have complex effects on competition. As the length of the interpulse increases, plants may be less likely to continue resource uptake and therefore, the length and intensity of pulse and interpulse phases may be more important than the absolute amount of resources available over time (Novoplansky and Goldberg 2001). If abiotic conditions during interpulse phases have a greater effect on plant performance, then competition may be of overall lesser importance (Goldberg and Novoplansky 1997) as suggested by Grime (1973). This is supported by several field studies in arid systems that found plant performance during interpulses to be influenced more by abiotic conditions than plant interactions (Cable 1969, Knoop and Walker 1985, Fowler 1986b, Harrington 1991, Casper 1996, Briones *et al.* 1998, Donovan and Richards 2000, Harris and Facelli in press).

Fluctuations can allow many species to coexist when different species are favoured by different sets of environmental and competitive conditions (Chesson and Huntly 1989, Chesson 1994, Pacala 1996). Since species responses to resources and competition are non-linear (Levins 1979, Armstrong and McGehee 1980, Chesson and Huntly 1993, Chesson 1994), competitive hierarchies may change over time in response to resource heterogeneity. For example, one species may respond to small, frequent pulses and another to large, infrequent pulses but with intermediate fluctuations in pulse magnitude and frequency both species can persist (Sala *et al.*

1989, Tilman 1997). Fluctuations may weaken competitive interactions by reducing biomass when conditions are poor (Fowler 1988). The biomass or population size of many plants in arid systems is reduced during resource shortages, thereby lessening the likelihood of overlapping resource acquisition zones with neighbouring plants following rains. Population growth may increase when favourable conditions for growth coincide with low competition intensity (Chesson and Huntly 1989). These conditions are likely to co-occur when species are low in abundance, for example, after a rainfall event following a long interpulse. However, species must be able to persist when conditions are poor so they may take advantage of "good" conditions when they occur (i.e. the storage effect of Warner and Chesson 1985). Although fluctuating resource levels and harsh abiotic conditions may weaken plant interactions, interactions still play an important role in structuring species assemblages (Chesson and Huntly 1997). Even weak competitive interactions may lead to competitive exclusion as harsh conditions can decrease tolerance of competition and abundant species will experience competition when conditions are "good" (Chesson and Huntly 1989, 1997).

Whether competition intensity changes in relation to resource levels may depend on the nature of resource inputs, i.e. their frequency and magnitude, species responses to these inputs, and the measured plant response. Mechanistic approaches are therefore important in understanding the relationship between resource levels and interaction intensity (Tilman 1988).

Balance between facilitation and competition

Competition and facilitation commonly co-occur although facilitative interactions may not be observed as competitive interactions are stronger (Callaway and Walker 1997, Brooker and Callaghan 1998). A meta-analysis of plant interactions demonstrated that positive interactions were as common as negative interactions although positive interactions were stronger at low standing crop (Goldberg *et al.* 1999). In unproductive systems, positive interactions may outweigh any negative interactions or weaken the intensity of these interactions. If this is the case, interactions may become less intense as resource levels decrease (as in the Grime hypothesis). However, this may be a result of a decrease in the intensity of positive interactions at high resource levels, although negative interaction intensity may remain constant along this gradient (as in the Tilman hypothesis) (Goldberg *et al.* 2001, Pugnaire and Luque 2001).

Temporal shifts

Studies that have examined shifts in interactions over time have found positive interactions to be overall more intense at lower resource levels and negative interactions to be more intense at higher resource levels (Greenlee and Callaway 1996, Pugnaire and Luque 2001). Pugnaire and Luque (2001) found this change in interaction intensity was due to facilitation decreasing in intensity with increasing resource levels but competition intensity remaining constant. By manipulating soil nutrients, Rebele (2000) found that competition was more intense at high productivity and facilitation was more intense at intermediate levels of fertility. The positive benefits of neighbours may also outweigh the negative effects, making facilitation overall more important. For example, in annual plant communities, survivorship was lower beneath shrubs but reproduction and seedling emergence was higher, producing overall a greater abundance of annuals beneath shrubs (Tielbörger and Kadmon 1995). Facilitation by shrubs was overall more important for annual plant distribution.

Plant life stage

Interaction effects may depend on the life stage of the interacting species (see review by Callaway and Walker 1997). Neighbouring plants can facilitate seedling establishment, but further growth of seedlings is inhibited by either competition or reduced light levels beneath canopies (Franco and Nobel 1989, De Steven 1991a, b, Franco-Pizaña *et al.* 1996, Anderson *et al.* 2001, Rebollo *et al.* 2001, Ganade and Brown 2002). Competitive effects may also be reversed with plant life stage. This has been well documented in the 'nurse plant syndrome' where larger plants provide protection or improved conditions for seedlings in their early stages of development, but these plants eventually outcompete their nurse plant as they mature (Yeaton 1978, McAuliffe 1984 690, Valiente-Banuet *et al.* 1991a, b, Callaway 1992, Flores-Martínez *et al.* 1994, 1998, Rousset and Lepart 2000). Interactions may also change with the maturity of the beneficial plant (Callaway *et al.* 1991, Kellman and Kading 1992). Habitat modification by older plants may have a greater facilitative effect than younger plants, for example, when nutrients accumulate over time beneath the canopy (Pugnaire *et al.* 1996, Facelli and Brock 2000, Pugnaire and Lazaro 2000, Tewksbury and Lloyd 2001).

The shifts between positive and negative effects on emergence, growth and survival suggest that different mechanisms are important at different life stages (Goldberg *et al.* 2001). Commonly, neighbours have neutral to positive effects on plant survival but negative effects on growth

(Callaway *et al.* 1996, Casper 1996, Goldberg *et al.* 2001, Howard and Goldberg 2001, Maestre *et al.* 2001, Rebollo *et al.* 2001, Tonioli *et al.* 2001, Ganade and Brown 2002). However, the competitive effects on growth may vary temporally depending on rainfall inputs (Tielbörger and Kadmon 2000b, Goldberg *et al.* 2001). Even within a growth season, interactions may change between positive and negative depending on the phenology of interacting species and their ability to capture resources (e.g. rooting depth) (Cable 1969, Holzapfel and Mahall 1999). Moreover, if competitive effects on growth occur during pulses, then this interaction may lead to competition-induced mortality during pulses. For example, Aguiar *et al.* (1992) found that competition-induced reductions in growth during spring pulses affected survival in the following summer interpulse. Plants that were less affected by competition were larger and were more likely to survive because they had access to water supplies deeper in the soil profile (Aguiar *et al.* 1992). Such observations may lead to the false conclusion that abiotic conditions during interpulses are more important overall than competitive interactions. Competition may be overall important under different circumstances, either by having a negative effect on plant performance during either pulses or interpulses or when there is a correlation between competitive reductions in growth during a pulse and plant performance during interpulses (Goldberg and Novoplansky 1997).

Fertility islands

Habitat modification by plants may produce fertility islands where resources are concentrated relative to the surrounding matrix. Although there may be interactions between the facilitator and understorey plants, there may also be interactions between plants growing within the fertility island. Fertility islands may have a higher density of plants or greater plant biomass than the matrix habitat (Facelli and Brock 2000, Pugnaire and Lazaro 2000, Tewksbury and Lloyd 2001). As closer-spaced or larger plants could have overlapping resource depletion zones, competition may be intense in these sites. Moreover, depending on plant responses to resource gradients, the intensity of interactions in these habitats may also differ from matrix habitats. Of the few studies that have compared competition intensity between plants in both these habitats, two found no effect (Parker and Muller 1982, Tielbörger and Kadmon 2000a) and another found competition was more intense in the fertility island (Rice and Nagy 2000). If competition is frequently more intense in fertility islands, then this may buffer the positive interaction between the facilitating plant and its understorey species.

Physiology

Many of the shifts in the direction of interactions between plants relates to gradients of moisture and light. Trade-offs between drought and shade tolerance has been proposed as one of the primary facilitation mechanisms (Smith and Huston 1989), dependent on the physiology of plants growing in these microhabitats (Holmgren *et al.* 1997). There may be a threshold or point of balance where positive effects outweigh negative effects such that an increase in some resources (such as soil moisture and nutrients) beneath the canopy may outweigh the negative effects of a reduction in light availability (Holmgren *et al.* 1997). However, plants growing under canopies in water-limited systems may have a lower demand for water because of reduced evaporative demand in canopy microclimates making trade-offs unimportant (Holmgren 2000). Water stress can increase with irradiance and shading can improve water relations in dry soils (Holmgren 2000). If canopy microclimates increase water availability or reduce water stress for plants growing beneath their canopy, then there will be differences in the water relations of plants growing in microsites associated with plant canopies and removed from plant canopies. The shoot water potential of shrubs (Hay 1998, Maestre *et al.* 2001), perennials (Shumway 2000) and grasses (Amundson *et al.* 1995) was higher under canopies than in the open. Other studies have demonstrated that improvements in plant water status do not necessarily equate with higher water use efficiencies for plants growing beneath canopies (Forseth *et al.* 2001, Loik and Holl 2001). A reduction in carbon assimilation in shaded microsites can restrict growth (Forseth *et al.* 2001), although the maintenance of higher tissue water status may prolong plant survival. However, reductions in photosynthetic rates with water stress are likely to be greater under high irradiation. Therefore, shading will have positive effects when water becomes limiting (Holmgren 2000).

Conceptual model

The importance placed on competition as an organisational force has often led to the neglect of the consideration of facilitation and interactions with environmental factors. It is the inter-relationship between biotic interactions and abiotic factors that determines the structure of vegetation (Tilman 1990). Brooker and Callaghan (1998) developed a conceptual model that attempts to combine these ideas. They examined the relationship between plant interactions and disturbance over a temporal or spatial gradient. They predicted facilitation would dominate where disturbance was high whereas competition would dominate where disturbance was low. The outcome of these interactions would change with distance along a spatial or temporal gradient of disturbance regime. Although they chose not to include 'stress' as an environmental factor in this model, due to the debate on the relationship between stress and competition, Bertness (1998) in his review of this model argued it would be quite valid to do so. Indeed, a period without rainfall may be described as a disturbance. A model by Bertness and Callaway (1994) that did not include spatial or temporal dynamics showed how the frequency of positive interactions through habitat amelioration increased along a gradient of increasing physical stress whereas the frequency of competitive interactions decreased. By combining the concepts in the models of Brooker and Callaghan (1998) and Bertness and Callaway (1994) with the competition hypothesis of Goldberg and Novoplansky (1997), I have developed a unified conceptual model (Fig. 1.1).

This model predicts the outcome of plant interactions in relation to the temporal dynamics along a water resource availability gradient. However, the relationships may equally apply to other stresses or resource availabilities along a spatial gradient. This depiction of the model more accurately represents relationships in an unproductive environment where there is an obvious difference between pulses and interpulses. These fluctuations may occur at a number of temporal scales and the scale will depend on the growth rates or life span of the species of interest. This model predicts positive interactions will be more intense as water availability decreases. This will occur when plants ameliorate water stress or increase soil water availability for neighbours during interpulses. Negative interactions will either remain equally intense along the gradient or decrease in intensity during interpulses. This will depend on whether plants are able to reduce resource availability to neighbouring plants during interpulses as well as pulses or only during one of these phases.

There is an interaction between plant interactions and changing water availability such that the balance between competition and facilitation changes over time. Both models predict that interactions will become overall negative during pulses but will become overall neutral to positive during interpulses. The models predict temporal shifts in the direction of interactions but this balance may also be affected by the life stage or physiology of the interacting species.

General research aims

I explore the dynamics of plant interactions at the spatial scale of patches associated with the canopies of mature *A. papyrocarpa* trees and temporal scales encompassing pulse and interpulse cycles. The general aims of this research are to test the predictions of my conceptual model and some of the mechanisms that may explain these predictions.

1. To examine the growth responses of plant species to spatial and temporal resource gradients. (Chapter 3)

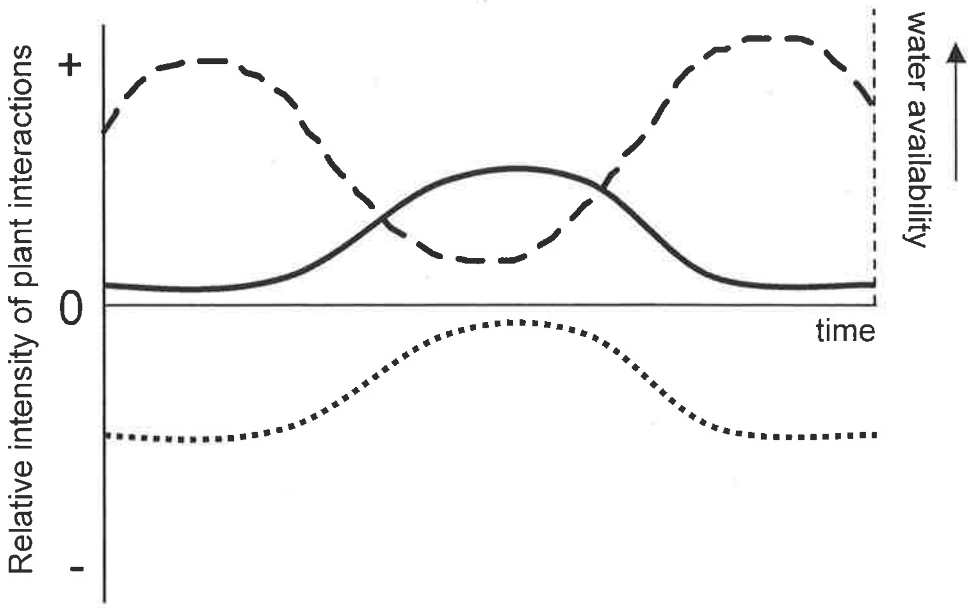
2. To determine whether the competitive response of chenopod shrubs changes in response to the dynamics of resource inputs. (Chapters 4 & 5)

3. To determine if there is a facilitative relationship between *A. papyrocarpa* and chenopod shrubs growing beneath its canopy and if so, its mechanism. (Chapter 6)

4. To examine whether interactions between *A. papyrocarpa* and understorey shrubs change over time in relation to pulses and interpulses. (Chapter 6)

5. To investigate how the responses of chenopod shrubs to resource gradients are affected by their life stage or physiology. (Chapters 6 & 7)

A)



B)

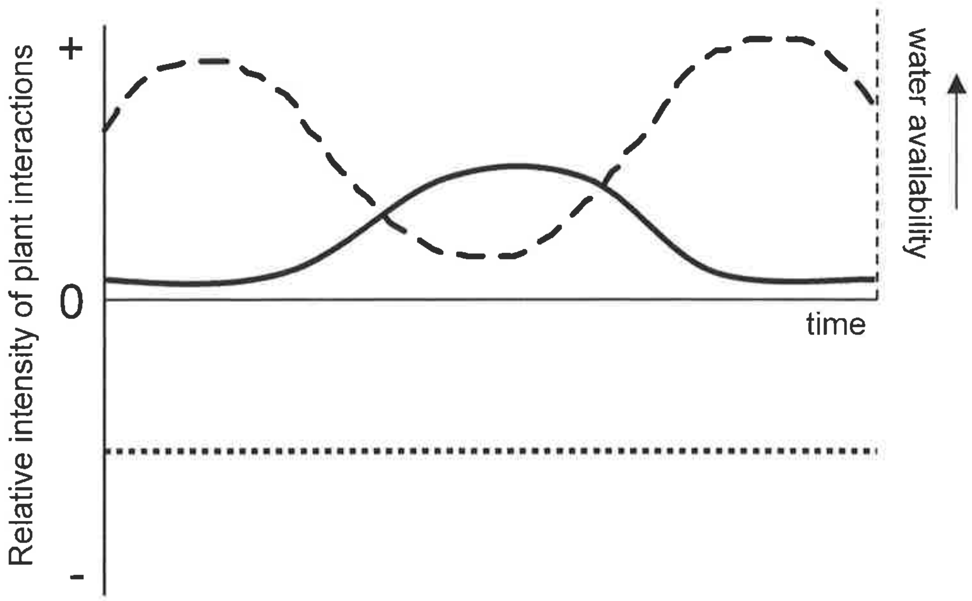


Fig. 1.1 A conceptual model of the dynamic relationship between water availability and plant interactions. The dashed line (---) represents pulses of high water availability alternating with interpulses of low water availability (right y-axis). The direction of plant interactions changes along the left y-axis, from neutral or no interactions at 0. The intensity of facilitation (—) and competition (....) may change in relation to pulses and interpulses (A) or competition may remain of equal intensity throughout pulses and interpulses (B).

CHAPTER 2

Study site and study species

Introduction

Due to a combination of low, unpredictable precipitation, low humidity, high insolation and high evaporation arid systems occupy a considerable proportion of the Australian continent (Fox 1999). Arid systems in the north of the continent are dominated by summer rainfall patterns, whilst those in the south are dominated by winter rainfall. In southern arid systems low-pressure cells from northerly tropical weather systems can produce large summer rainfall events but their occurrence is extremely variable and unpredictable (Fox 1999). The southerly winter depressions typically produce smaller, more predictable rainfall events (Fox 1999). These rainfall patterns affect the distribution of vegetation types in arid systems in Australia. Summer rainfall supports grasses whereas winter rainfall supports shrubs. On alkaline or sodic soils where there is some winter rainfall chenopod shrublands form the dominant vegetation, occupying 7% of inland Australia (Leigh 1994). These shrublands are used extensively for grazing (Orchard and Wilson 1999). *Acacia* species are the dominant trees across arid to semi-arid Australia (Johnson and Burrows 1994). These plants have an important functional role in these systems. Through physical and biological processes resources become concentrated around larger shrubs and trees (Charley 1978, Tongway and Ludwig 1990, Tongway and Ludwig 1994, Facelli and Brock 2000). These plants stabilise these systems by tightly recycling nutrients, modifying the local microclimate, and improving and stabilising soils (Tongway 1990).

Study site

I conducted field surveys and experiments at Middleback Station (32°57'S, 137°24'E), 16 km northwest of Whyalla, South Australia. The station is used for wool production, with most paddocks stocked at a rate of one sheep per six hectares. Small paddocks and conservative stocking rates have preserved perennial cover in paddock locations away from watering points (Lange *et al.* 1984). I conducted field surveys and experiments in Overland Paddock and the adjacent Railway Paddock. These paddocks are on low, gently undulating calcrete plains

(Twidale and Campbell 1985). Soils are structureless red-brown calcareous earths of clay-loam texture or desert loams, underlain at 40cm depth by a layer of small calcium carbonate concretions in a matrix of soft calcareous earth (Jessup and Wright 1971). The formation of surface crusts on these soils can impede the infiltration of rainwater but where disturbed, soils become powdery and loose when dry (Wright 1985). Soils are of low fertility and are saline, particularly at depth (Wright 1985).

Climate

The area experiences an arid climate with an average annual rainfall at Middleback station of 217 mm (75 year average) though this has ranged from 91mm to 511mm. I obtained rainfall data from A. Nicolson at Middleback Station, located approximately 2 km from Overland Paddock and 8 km from Railway Paddock. The monthly rainfall is evenly distributed throughout the year, although summer rainfall events are typically larger and less frequent whereas winter rainfall is more reliable but rainfall events are smaller. The long-term monthly averages show no differences between months but the cooler months, May to October, typically have more rain days (3-4) than the warmer months, November to April (1-2 rain days). Mean annual temperatures range from a daily maximum of 28.9°C in January to a daily minimum of 7.3°C in July (Australian Bureau of Meteorology). During this study the summer of 2002 was cooler than the previous two summers (Fig. 2.1A). The monthly rainfall average was frequently less than the long-term monthly average, with two months of exceptionally high rainfall in 2001 (Fig. 2.1B).

Vegetation

The vegetation of the region is chenopod shrubland or low open *Acacia papyrocarpa* woodland (Specht 1972). Less common tree species include *Alectryon oleaefolium* and *Myoporum platycarpum*, interspersed with large monospecific groves of *Casuarina pauper*, a clonal tree. Tree cover ranges from 0-10% with a maximum height of 10 m. In Overland Paddock *A. papyrocarpa* density is 48 trees ha^{-1} (Reid 1984). The mid-understorey of the woodlands comprises a shrub layer of woody, semi-succulent chenopod shrubs. These shrubs, although appearing mesic in character have leaves with a low stomatal frequency, a low transpiration rate and low osmotic potential (Wood 1934). They are thus quite drought-tolerant. They provide a vegetative cover of from 10-30%. The dominant understorey shrubs are *Atriplex vesicaria* and *Maireana sedifolia*. They occur with equal frequency beneath *A. papyrocarpa* canopies and in the intercanopy spaces (Facelli and Brock 2000), although *Atriplex vesicaria* is more commonly found beneath *M. platycarpum* canopies (Tester *et al.* 1987). A distinctive berry-fruited chenopod flora occurs beneath *A. papyrocarpa*, which includes *Enchylaena tomentosa*, *Rhagodia spinescens* and *Chenopodium gaudichaudianum* (Barker 1972). These species rarely occur beyond tree canopies (Tester *et al.* 1987, Facelli and Brock 2000), with the latter two species occurring more frequently under *A. papyrocarpa* than other trees (Tester *et al.* 1987). Perennial shrub cover under *A. papyrocarpa* ranges from 30% under sparse canopy cover to 60% under dense canopy cover (Facelli and Brock 2000). During favourable seasons with adequate rainfall, an ephemeral flora occupies the lower understorey. This flora includes the native grasses *Austrodanthonia caespitosa*, and *Austrostipa* spp. and numerous forbs and short-lived perennials. There are no ephemerals that germinate only in summer although there are several species which establish only in response to winter rains (Nicolson 1985). Ephemeral species also show different distributions in relation to *A. papyrocarpa* (Barnes 1993) and shrub canopies (Pound 1998, Harris and Facelli in press). In undisturbed areas, but not beneath *A. papyrocarpa*, there is a cryptobiotic crust of predominantly lichens (Rogers and Lange 1971).

Species descriptions

Acacia papyrocarpa

Acacia papyrocarpa is a slow-growing, long-lived tree that has a large spreading canopy (Lange and Sparrow 1992). Trees may live for longer than 360 years with the canopy attaining its maximum extent after approximately 250 years (Ireland 1997). Growth occurs during late spring to midsummer but declines to almost zero during the winter months (Maconochie and Lange 1970). Trees attain a maximum height of 10 m although most mature trees at the study site reach a height of 6-7 m with a canopy radius of 5-6 m (M. Escoto Rodriguez, unpublished data). Trees are patchily distributed, occurring frequently in small, uneven-aged groves of up to six trees with contiguous canopies, or as isolated individuals (Lange and Purdie 1976).

Soils under mature *A. papyrocarpa* canopies have higher total nitrogen (Correll 1967, Facelli and Brock 2000), soil organic carbon, available phosphorus, total phosphorus and sulphur than matrix soils (Facelli and Brock 2000). Although nitrogen-fixing nodules have not been found on *A. papyrocarpa* roots, soils from these woodlands were capable of fixing nitrogen when supplied with an energy source, indicating the presence of free-living nitrogen-fixing bacteria (Correll 1967). Soil water content may be seasonally higher beneath trees than in adjacent open spaces, particularly during summer at shallow depths (Grey-Smith 1987, Facelli and Brock 2000). Soils from beneath canopies have lower water retention and bulk density than open soils (Grey-Smith 1987, Barnes 1993) and the depth of the evaporation front is lower in soils under canopies (Grey-Smith 1987).

Atriplex vesicaria

Atriplex vesicaria is a small, woody shrub that grows to a height and width of 60-70 cm. The shrub has a half-life of 11 years but re-establishes readily from seed (Crisp 1978). The root system is shallow and fibrous, extending 1- 2 m from the shrub centre and rarely to a depth of 1.5 m (Jones and Hodgkinson 1970). Most roots are confined to the top 15 cm of soil (Sharma 1976), and the shrub is commonly found growing on soils with a confined rock layer at shallow depths (Carrodus and Specht 1965). At Middleback, root excavations revealed that roots did not extend past the calcrete horizon at 40 cm depth.

Atriplex vesicaria shoots have a low osmotic potential (Carrodus and Specht 1965) and carbon gain can be maintained to water potentials of –10 MPa although leaf expansion does not occur at water potentials less than –3 MPa (Coleman 1982). *Atriplex vesicaria* utilises the C4 carboxylation pathway (Chapman and Jacobs 1979). Leaves are short-lived (Williams 1979), and along with roots are drought-deciduous (Osborn *et al.* 1932). Leaves and shoots grow rapidly after rains (Williams 1979). *Atriplex vesicaria* leaves accumulate NaCl and this is thought to improve radiation reflectance properties, reducing heat gain during the hotter months (Sinclair and Thomas 1970). Younger leaves accumulate more NaCl and non-structural carbohydrate than older leaves but older leaves are shed first during drought (Black 1956b, Williams 1979, Coleman 1982). *Atriplex vesicaria* is dioecious and reproduction is opportunistic, occurring after adequate rainfall in any season (Williams 1979). Wind or ants disperse *A. vesicaria* seeds (Briese and Macauley 1981).

Maireana sedifolia

Maireana sedifolia is a medium-sized woody shrub, growing to a height and width of 1.5 m. The shrub is long-lived with a half-life of 150 years, with infrequent establishment from seed (Crisp 1978). The shrub is slow growing (Wotton 1993), with a low photosynthetic capacity and low photosynthetic rates, but is able to gain carbon to water potentials of –10 MPa (Hay 1991). *Maireana sedifolia* has an extensive root system with a lateral extent of 5-6 m and a vertical extent of up to 2 m (Osborn 1935). It is commonly confined to areas where there is deep infiltration of water after rainfall (Carrodus and Specht 1965). However, at Middleback, root excavations revealed that roots rarely extend beyond the calcrete layer. Unlike *A. vesicaria*, leaves are retained during all but the most severe droughts (Wotton 1993). *Maireana sedifolia* leaves have a silvery, hairy covering with good reflective properties that reduces radiation absorption and hence leaf-heating during the summer months (Sinclair and Thomas 1970). The dioecious shrubs usually fruit during autumn after above average summer rainfall (Wotton 1993). Germination of seed is drought-sensitive, hence seedling establishment only occurs during extended periods of good rainfall (Wotton 1993). Wind or ants, the common dispersal agents of other dry chenopod fruits, probably disperse seed (Briese and Macauley 1981).

Enchylaena tomentosa

Enchylaena tomentosa is a soft, woody shrub that can grow to a height of 1 m and a width of 1.5 m. The leaves are succulent and covered with fine hairs. *Enchylaena tomentosa* has fleshy fruits that are bird dispersed (Tester *et al.* 1987). It commonly fruits from autumn to spring but fruits may also be found after heavy rainfall in late spring or summer (Reid 1984).

Rhagodia spinescens

Rhagodia spinescens is a sprawling woody shrub that can grow to a height of 1.5 m and to widths of more than 2 m. The leaves are silvery and mealy. *Rhagodia spinescens* can continue to gain carbon at low water potentials and has high photosynthetic rates when water is not limiting (Chapman and Jacobs 1979). The fleshy seeds are bird-dispersed and are produced from summer to autumn, though reproduction may be flexible following rains (Reid 1984).

Throughout this thesis where there is no confusion with other species I will refer to these five species by their generic name.

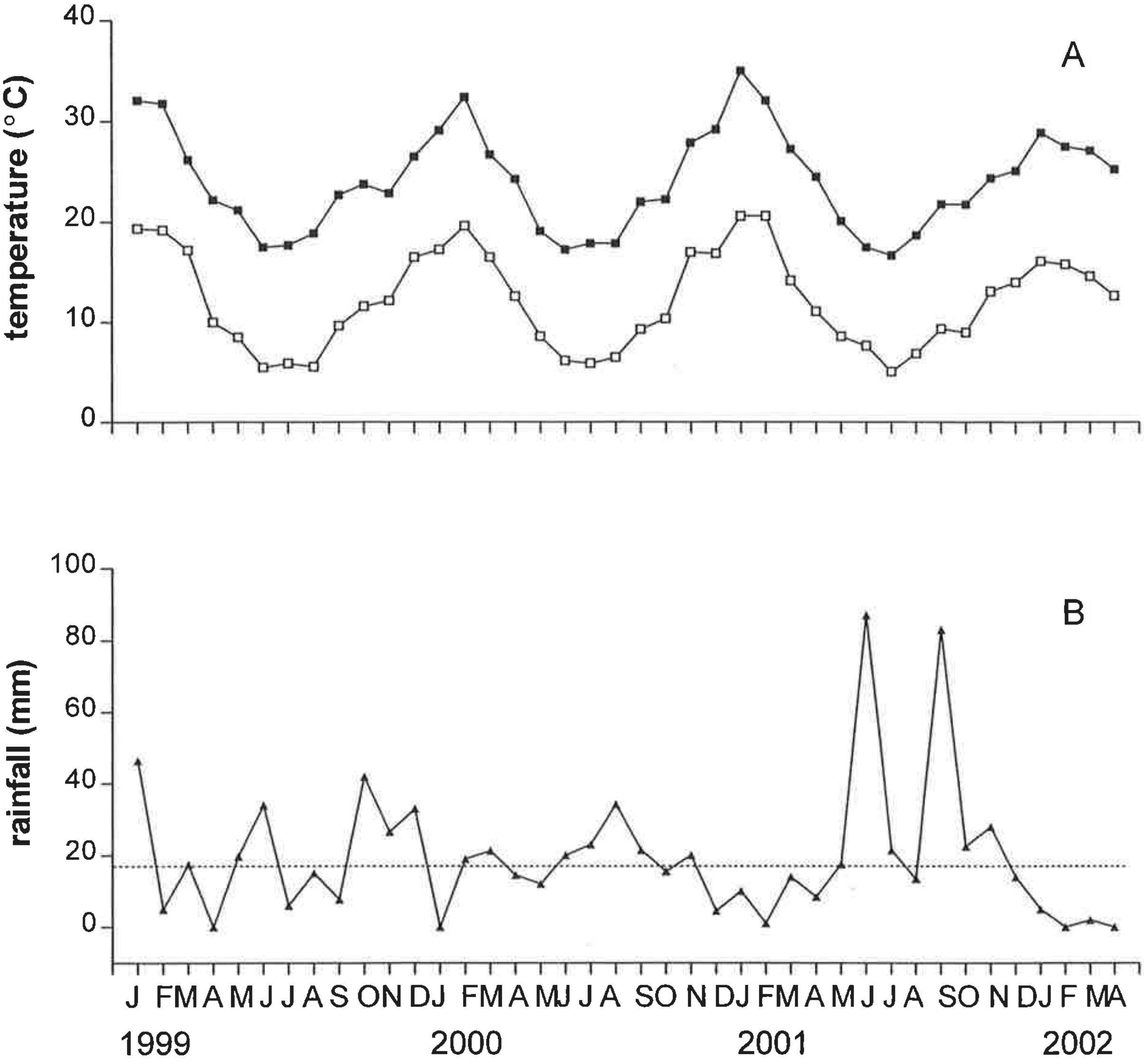


Fig. 2.1 A) Mean maximum and minimum monthly temperatures and B) total monthly rainfall for the duration of this study. The dashed line shows the long-term monthly rainfall average. Temperature data from Whyalla automatic weather station (Australian Bureau of Metereology). Rainfall data recorded by the Nicolson family at Middleback Station.

CHAPTER 3

Vegetation responses to pulses and patchiness

Introduction

In arid systems, water is only available for plant growth in pulses that begin after rainfall events. Average productivity decreases as the frequency and predictability of these pulses decreases (Noy-Meir 1973). Pulses alternate with interpulses of varying duration when water becomes limiting to ecosystem processes. As plant nutrient uptake is coupled to water uptake (Cowling 1978), soil resources fluctuate from being comparatively plentiful during pulses to limiting during interpulses. Plants therefore experience consecutive periods of favourable growing conditions during pulses, deteriorating growing conditions as soils dry out during interpulses, to potentially lethal conditions during drought (Westoby 1980). The frequency and magnitude of pulses is also important. Although total rainfall inputs may be the same, a series of small frequent events may affect plant growth differently to fewer but larger events by sustaining actively growing plant tissue over longer time periods (Novoplansky and Goldberg 2001). However, the magnitude of plant growth responses to a pulse is not only proportional to the magnitude of the rainfall input and its distribution in time, but also the levels of other factors which influence growth, such as soil nutrients, light and temperature (Ludwig and Whitford 1981, Noy-Meir 1981, Bilbrough and Caldwell 1997).

Although topographic, edaphic and microclimatic factors further modify water availability (Ayyad 1981), plants can also modify how water is distributed throughout the soil profile. The amount of rainfall that penetrates plant canopies and is redirected through stem and root flow to the soil is dependent on the magnitude of rainfall events (Parker and Muller 1982, Joffre and Rambal 1988, Evans and Ehleringer 1994, Haworth and McPherson 1995, Breshears *et al.* 1997a, Breshears *et al.* 1997b). Reductions in evaporation of soil moisture through canopy shading and litter layers may be important for retaining soil moisture into interpulses (Facelli and Brock 2000). Potentially, plants may modify soil water content by different mechanisms during pulses than during interpulses. The extent to which soil water content differs between canopies and the matrix habitat is thus influenced by temporal variations in rainfall inputs and climatic conditions.

By increasing the availability of resources in their immediate environment, some plants can facilitate the growth of neighbouring plants (Callaway 1995). This increase in resource levels has the potential to affect the diversity and productivity of systems (Levin 1974, Hacker and Gaines 1997, Aguiar and Sala 1999). Plant-created patches may affect species diversity by either creating new habitat or modifying the habitat so that less stress tolerant species can persist (Hacker and Gaines 1997). These modified habitats may also buffer conditions during interpulses, ameliorating stress for plants growing there when resources are in limiting supply (Bertness and Callaway 1994).

In this chapter I aim:

1) To characterize the spatial and temporal heterogeneity of soil water resources beneath *Acacia papyrocarpa* trees and in adjacent open spaces.

2) To determine whether the spatial gradients associated with tree patches affects ephemeral and perennial shrub diversity and productivity.

3) To examine patterns of plant growth in relation to rainfall pulses to answer the following questions:

    i) Does the magnitude and timing of perennial shrub growth responses to pulses differ between species?

    ii) How does spatial heterogeneity associated with tree patches affect these responses?

    iii) How does the magnitude and timing of pulses affect ephemeral plant standing biomass?

Methods

Study site

I conducted the surveys in Overland Paddock, in an area of the paddock with a relatively homogeneous topography on a gently undulating calcrete plain. In order to make spatially explicit comparisons between sites associated with *Acacia* and corresponding intercanopy (open) spaces I selected trees of a similar size or age class (age class V to VI after Lange and Purdie

1976) and with similar canopy density. Both tree age and canopy cover can affect resources beneath *A. papyrocarpa* and vegetation patterns (Facelli and Brock 2000). Trees in these age classes show the maximum modification to soil properties in the undercanopy microenvironment, in contrast to the matrix habitat between trees (Facelli and Brock 2000). For each survey I selected appropriate trees occurring within a 10 m belt transect oriented along a random bearing.

In this study, and all subsequent experiments, I have used the term "site" to distinguish between microenvironments under *A. papyrocarpa* canopies (canopy sites) and the adjacent matrix habitat between trees (open sites).

Soil water content

At six weekly intervals, from August 1999 until late November 2001, I measured soil water content at depths of 5, 20, and 35 cm, under *Acacia* canopies and in adjacent open sites. I did not sample soils below 35 cm as a layer of calcium carbonate occurs at 40 cm and shrub root excavations revealed that shrub roots were typically confined above this layer. I collected soil samples along a random bearing 2 m from the tree bole under canopies, and 2 m beyond the canopy edge in open sites. I collected 15 samples at each depth in each site. I determined soil water content gravimetrically by weighing fresh weight of soil and dry weight after oven drying samples at 105°C for at least 48 hours. Daily rainfall records were kept by A. Nicolson at Middleback Station, located approximately 3 km from Overland Paddock.

Biomass surveys

In October 1999, 2000 and 2001, I sampled ephemeral biomass in plots under *Acacia* canopies and open sites. I included perennial forbs and grasses in this category as these species commonly persist only as rootstock during rainless periods. I located open sites between 5 m and 25 m from the canopy edge at random bearings from each sampled tree. I sampled ephemerals from 1 m^2 plots in each site but due to their patchy distribution I subdivided the plot into sixteen 0.25 m^2 subplots, evenly distributed in a regular array within a 2.5 m radius centred on the tree bole under canopies and in a similar array in open sites. I removed the above-ground biomass of ephemerals at ground level; pooled samples for each 1 m plot in each site and later dried and weighed each species separately. I sampled 25 plots in each site each year.

In another location within Overland Paddock in August 1999, I sampled the perennial shrub leaf biomass. I sampled each species separately in paired plots 2 m by 2 m located under *Acacia* trees or in adjacent open spaces. I located plots a minimum of 1 m from the tree bole under canopies and at a random distance between 2 and 20 m from the canopy edge, at random bearings from the tree centre, in open sites. I estimated the leaf biomass of common shrubs using the Adelaide technique (Andrew *et al.* 1979) and I harvested less common shrubs at ground level, stripped their leaves from their stems, dried and weighed leaf samples. I sampled 39 pairs of sites.

In January 2001, at different locations each centred on an *Acacia* tree, I sampled root biomass. I collected samples from two separate transects along random bearings from the tree centre. I collected two samples under tree canopies, 1 m and 2 m from the tree bole, and two samples 5 m and 10 m beyond the canopy edge. I sampled roots by hammering 150 mm lengths of 100 mm diameter PVC pipe into the ground until flush with the surface. I removed soil intact within pipes and retrieved roots by sieving the soil through a 1 mm sieve. As I could not retrieve very fine roots by dry sieving, I retrieved them from half of the 24 replicate transects by washing through a 0.3 mm sieve. I separated roots into three size classes, < 1 mm diameter, 1 – 2 mm diameter, and > 2 mm diameter, before oven drying and weighing.

I oven-dried all plant material at 85°C for at least 48 hours.

Perennial shrub growth

I measured the shoot growth of the four commonest perennial shrubs, *Atriplex vesicaria*, *Maireana sedifolia*, *Enchylaena tomentosa* and *Rhagodia spinescens* in sites beneath *Acacia* canopies and in adjacent open sites for the former two species. I used paint to mark shoot tips 20 mm from the apical meristem, on five shoots on ten shrubs of each species in each site. I measured the growth of this primary shoot and any side shoots repeatedly at six weekly intervals concurrently with soil moisture measurements. I re-marked shoots 20 mm from the tip when their length exceeded 40 mm and marked new shoots when any marked shoot died. I calculated the shoot elongation rate of each shrub as the average change in length of the five marked shoots between measurement times. I fenced each shrub to exclude large vertebrate grazers (rabbits, sheep and kangaroos). Eight *Enchylaena* plants and four *Rhagodia* plants died over the course of measurements and I replaced them with different shrubs under the same *Acacia* canopy. No *Atriplex* or *Maireana* plants died.

Analyses

I tested the effects of site on soil water content over the measurement period separately for each measurement depth using non-parametric multivariate analysis of variance procedures (NPMANOVA\, Anderson, 2001, McArdle and Anderson 2001). I square root-transformed data to eliminate heterogeneous variances. I could not include the data from 6/6/01 in this analysis as only nine samples could be collected on this occasion. I analysed this data set by ANOVA testing the effects of site, depth and their interaction.

I used linear regression to examine the relationship between rainfall and soil water content. I calculated separate linear regressions for soil water content at each depth in each site as the dependent variable and rainfall at different lag intervals, ranging from one week to 12 weeks prior to collecting soil samples as the independent variable. I used the mean soil water content at each sampling occasion for these regressions as these data were normally distributed (Underwood 1997), after the removal of an outlier (June 2001), when I sampled soil water content immediately after a large single rainfall event.

I used the Shannon Weiner Index (Shannon 1948) to quantify ephemeral and perennial diversity for each plot using the formula:

$$H'_j = - [\Sigma\ p_i\ (\ln p_i)]$$

where p_i is the proportion of species *i* in plot *j*. I compared ephemeral diversity and species richness in each site using two-tailed t-tests. Due to the highly left-skewed distributions of the ephemeral biomass data, and the large variation between years, I tested biomass for each year separately. I tested the effect of site on total above-ground biomass, and grass and forb biomass separately using Mann Whitney tests, but adjusted significance levels to account for the number of tests (n) on the same data set ($\alpha' = \alpha/n$; Underwood 1997).

I tested the effects of site (canopy or open) on perennial species richness, perennial species diversity, total perennial leaf biomass, and the proportion of leaf biomass per species in each plot with non-parametric Wilcoxon Kruskal-Wallis tests (WKW tests) or Kruskal-Wallis tests (KW tests, GraphPad Prism Ver. 3.02). I compared the perennial root biomass at increasing distances from the tree bole, using separate ANOVAs for the three size classes of roots. Where there was no significant difference between distances, I pooled root biomass in canopy and open sites and tested the effect of site.

I tested the differences between shoot elongation rates of all species under canopies, and *Atriplex* and *Maireana* shoot growth responses in canopy and open sites over the measurement period, by repeated measures MANOVA. I log-transformed data as variances were heterogeneous and the data were not normally distributed. I used an adjusted univariate F-test (Geisser-Greenhouse) when comparing model effects between different measurement periods (time) as the sphericity condition was not met. Where there were significant differences in shoot elongation rates over time, either between species under canopies, or between sites for *Atriplex* and *Maireana*, I tested each measurement time separately by one-way ANOVA, adjusting alpha values to account for repeated tests on the same data set.

I used JMP IN Ver. 5.0.3. software (SAS Institute) for all analyses, unless otherwise indicated.

Results

Pulses

Daily rainfall totals over the past four years highlight the variable nature of water inputs to this system, with no distinct seasonal patterns emerging (Fig. 3.1). Rainfall was below the long-term average of 217 mm only in 2000 (Table 3.1). In 2001 a high proportion of the rain fell during the winter months, but lower proportions of rain fell during the winters of other years (Table 3.1). Rainfall was distinctly pulsed during the extent of this study (Fig. 3.2A). Pulses occurred at different times of the year over the duration of this study. The pulse occurred in late spring-early summer in 1999, during early spring in 2000, and winter-spring in 2001 (Fig. 3.2A). Pulses in 1999 and 2000 comprised several smaller rainfall events, whilst the larger pulse in 2001 included several small and three large rainfall events (Fig. 3.1).

Soil water content

Soil water content increased with depth but fluctuated at all depths over the measurement period (Fig. 3.3). Soil water contents at 20 and 35 cm varied consistently over most of the sampling period, with soil water contents typically from 3-5% greater deeper in the soil profile (Fig. 3.3). A seasonal pattern is evident in comparisons between soils under canopies and those in the open. During the summer months, soil water content was higher under canopies, but during winter to spring soil water content was greater in open sites (Fig. 3.3). However, over the measurement period soil water content beneath tree canopies did not differ significantly from open sites at depths of 20 and 35 cm (Table 3.2). At 5 cm depth there were significant differences between sites (Table 3.2), with soil water content higher beneath canopies. Although the analysis did not include a time effect (non-normal distributions prevented this), plots showed that at shallow depths canopy soils were moister during the summer months and open soils were moister during winter/spring (Fig. 3.3). In June 2001, soils in canopy sites had higher water contents than soils in open sites at all soil depths (Table 3.3).

Soil water content at 5 cm depth in open sites was linearly correlated to rainfall that occurred up to six weeks prior to measurements (Table 3.4). Up to 48% of the variation in soil water content was explained by the previous six weeks rainfall. Under canopies, soil water content was linearly related to rainfall occurring from two to eight weeks before measurement (Table 3.4). Rainfall four weeks prior to soil moisture measurements explained most variation, yet rainfall that occurred up to eight weeks prior to measurements still explained 28% of the variation. Soil water content at 20 cm depth showed a significant linear relationship to the previous 8 and 12 weeks rainfall in both sites (Table 3.4). At 35 cm depth there was no significant linear correlation between rainfall and soil water content.

Diversity

The species recorded during surveys are listed in Appendix 1. Sites beneath *Acacia* canopies on average supported the same number of woody perennial and ephemeral species as open sites (Table 3.5). Canopy plots had significantly higher perennial shrub diversity but open plots had significantly higher ephemeral diversity (Table 3.5).

Biomass

There were more ephemerals in 2001 than in 1999 or 2000, although this was because of increased numbers of forbs rather than grasses (Fig. 3.4). In 1999, open sites supported significantly more ephemeral biomass than canopy sites, but in 2001, canopy sites had more ephemeral biomass than open sites (Fig. 3.4A). Forb biomass was significantly greater in canopy sites in 2000 and 2001 (Fig. 3.4B). Grass biomass was significantly higher in open sites than canopy sites in 2001 (Fig. 3.4C).

Significantly more perennial leaf biomass was produced in sites beneath canopies than open sites (WKW test, $\chi^2 = 44.10$, $P < 0.0001$), with means ± 95% CI of 63.81 ± 15.21 g m^{-2} leaf biomass under canopies and 43.35 ± 8.65 g m^{-2} in the open. The bulk of the perennial shrub biomass in

Overland Paddock consisted of the four common chenopod species but their spatial distribution differed. In canopy sites, all four shrubs had similar proportions of biomass per area basis, although there was a significantly greater proportion of *Rhagodia* biomass than other less common species (KW statistic = 10.22, $P = 0.04$, Fig. 3.5). In open sites, there was proportionally less *Enchylaena* and *Rhagodia* biomass than *Atriplex*, *Maireana* and all other species combined (KW statistic = 77.76, $P < 0.0001$, Fig. 3.5).

There was a gradient in fine root biomass from the inner canopies of trees to outer spaces well removed from trees (Table 3.6). Fine root biomass (<1 mm diameter) was higher within 1 m of the tree bole than 2 m, but there was no difference in fine root biomass in open sites 5 m and 10 m from the canopy edge (Fig. 3.6). The biomass of roots between 1 and 2 mm in diameter was significantly greater under canopies than open sites but did not differ with distance from the tree bole (Table 3.6, Fig. 3.6). The biomass of roots larger than 2 mm in diameter did not differ significantly between sites (Table 3.6, Fig. 3.6).

Perennial shrub growth

Shoot growth of the four common chenopod shrubs responded rapidly to rainfall pulses and growth rates decreased gradually as each interpulse progressed (Fig. 3.2). Maximum shoot elongation rates during 1999 and 2000 occurred during spring to early summer in response to rainfall peaks in spring. The growth peak in 2000 was less than in 1999 for all species, even though rainfall pulses were of similar magnitude both years (Fig. 3.2). Shoot elongation rates also peaked during spring in 2001, although rainfall pulses occurred in both winter and spring (Fig. 3.2). The shoot elongation rates of the four species growing under canopies differed significantly, although these differences were not consistent over time (Table 3.7). *Enchylaena* and *Rhagodia* responded more rapidly to a winter rainfall event in 2001 than *Atriplex* and *Maireana*. Shoot elongation rates of the former two shrubs were significantly higher than *Atriplex* and *Maireana* in July and September 2001, and *Maireana* continued to have lower shoot elongation rates than *Enchylaena* and *Rhagodia* in October 2001 (Fig. 3.2). Other differences between species occurred in August 1999, during an interpulse, and January 2000 where growth was in response to summer rainfall (Fig. 3.2). *Maireana* shoot elongation rates differed between sites (Table 3.7), but were only significantly greater under *Acacia* canopies on two measurement occasions, in October 1999 and October 2000 (Fig. 3.2D). Site had no significant effect on *Atriplex* shoot elongation (Table 3.7).

Discussion

Soil water content

Variation in soil water content within the soil profile resulted from temporal pulse inputs and spatial modifications of these inputs mediated by the presence of plants. Canopies of *Acacia* trees significantly modified soil water content over the duration of this study. The effects were seasonal and depended upon the timing of sampling and soil depth. For example, the June 2001 measurements were taken the day after a 47 mm fall of rain. Soil beneath canopies held more water than open soils on this occasion but the effect was greater at 35 cm depth. This suggests that textural changes to soils beneath canopies increase infiltration rates (Cowling 1978). On similar but treeless soils supporting *Atriplex*, infiltration of rainfall beyond 30 cm soil depth is limited (Carrodus and Specht 1965), even immediately following large rainfall events (Sharma 1976). Higher soil water content under canopies at the end of summer suggests decreased evaporation of soil moisture over the summer months. These results support the findings of Facelli and Brock (2000) that soil water contents at shallow depths under *Acacia papyrocarpa* canopies were higher in March preceded by a month without rain. They found this occurred under dense canopied trees, but under sparse canopied trees there was no significant difference to open sites. Hence, shading may be important for preventing evaporational losses from shallow soil depths, increasing the period of time soil moisture is available under canopies. The thickness of the litter layer may also reduce evaporative losses as sparse canopied trees produce less litter than dense canopied trees. I found that increases in soil water content at shallow depths under *Acacia* canopies persisted for longer after rainfall events. Rainfall events explained variations in soil water content at 5 cm depth under canopies for up to two months, whereas in open sites rainfall events explained only more immediate variability in soil moisture.

Deeper soil moisture usually reflects long-term or seasonal inputs, but may also depend on the time of year of rainfall events (Reynolds *et al.* 1999). However, I found no correlation between rainfall events up to three months prior to measurements and the water content of deeper soil layers. Infiltration to this depth may require the input of a single large or several smaller rainfall events in quick succession (Reynolds *et al.* 1999), hence the soil moisture peaks coinciding with rainfall inputs to November 1999 and June 2001. I found that the soil water content at 35 cm depth remained above 50% field capacity (assuming field capacity was reached after the heavy rainfall in June 2001), so presumably water could have been available to plants throughout the year at this depth (see Chapter 8 for relationship between soil water content and carbon uptake). Evaporative losses from depths greater than 10 cm are low in arid systems, particularly when the uppermost layer dries out (Noy-Meir 1973). However, even when rainfall inputs are high, transpirational losses of soil water may deplete soil water reserves at the rooting depth of plants (Milton 1995). This may explain the low soil water contents at 20-35 cm depth during October 2000 and 2001, periods when plant growth and therefore transpirational losses were likely to be high. Higher soil water contents in open sites in cooler months could be the result of the lack of penetration through the canopy or litter layer of smaller rain showers at this time.

Pulse effects on biomass production

The timing and size of pulses differed between the three years of this study. This produced differences in ephemeral biomass and perennial shrub growth between years, although peak ephemeral biomass production was more closely linked to the size of pulse inputs than perennial shrub growth. Although there was not a large difference in rainfall proportions during the warmer months in the three years of this study, a large proportion of the rain in 2001 fell during the cooler months. The greatest ephemeral biomass was also produced during this year suggesting that ephemeral biomass production is controlled by winter rainfall. There are no forb species at Middleback that require high temperatures for germination but some germinate only at low temperatures (Nicolson 1985). The ephemeral flora could be described as a winter flora, requiring rainfall pulses during the cooler months, but this needs confirmation from studies over long time scales. For example, the single large winter rainfall event in 2001 may also have affected the ephemeral response, i.e. the magnitude of this event may have been more important than the timing. The grass biomass response to pulses was more modest and showed no distinct changes over the three years. Grass production may have been limited by seed input. Consecutive years of low grass production could have reduced the seed bank, weakening the responses to the large 2001 rainfall pulse. In addition, grass biomass was sampled in October and grasses, especially *Austrodanthonia caespitosa* and *Austrostipa* spp., may have not reached their biomass peak by this stage.

Although peak perennial shoot growth was related to rainfall peaks, the differences in shoot elongation rates between years did not always reflect differences in pulse regimes. *Enchylaena* and *Rhagodia* shoot elongation rates were greater after the largest pulse (2001) than other pulses, although this response did not occur in *Atriplex* and *Maireana*. Rainfall pulses were of similar magnitude in 1999 and 2000 (see Fig. 3.2A) but growth in all species was less in the latter year probably because of low rainfall in the preceding six months. Spring and summer rain in 1998/1999 may have enabled the larger growth response to spring rains in 1999. Rainfall over the summer months may sustain either leaf or root biomass to enable plants to respond to subsequent rainfall. This "carry-over" effect, where production is greater in a wet year preceded by a wet year rather than a dry year, has been found in semi-arid grasslands (Lauenroth and Sala 1992, O'Connor *et al.* 2001, Oesterheld *et al.* 2001). Carry-over effects may potentially be greater in semi-arid to arid shrublands as perennial shoots have long-life spans. In addition, *Atriplex* and *Maireana* store carbohydrates that accumulate when water uptake is too low to support growth but are sufficient to maintain positive carbon uptake (Coleman 1982). For these species, growth patterns could reflect longer-term seasonal dynamics rather than recent pulse events. In a long-term study of chenopod biomass dynamics, Noble (1977) found *Atriplex* biomass was correlated to rainfall of the previous 42 months and *Maireana*, the previous 24 months, whereas herbaceous biomass correlated best to the previous 12 months rainfall.

Enchylaena and *Rhagodia* had higher shoot elongation rates during pulses, but I found they were more likely to die during interpulses, probably from stresses associated with high temperatures and low water availability. Half of these deaths occurred in March 2001 after a summer with very low rainfall. In contrast, *Atriplex* and *Maireana* had slower growth rates during pulses but were able to survive the interpulses over the course of this study. In terms of plant strategies there appears to be a trade-off between faster growth immediately after a pulse and the ability to survive or continue growing during interpulses (Westoby 1980). This has implications for plant competition (Goldberg and Novoplansky 1997, Novoplansky and Goldberg 2001). All four species may be good competitors, *Enchylaena* and *Rhagodia* because of superior ability to pre-empt resources (faster shoot elongation rates), and *Atriplex* and *Maireana* with their tolerance of low resource levels (Grace 1991, Gordon *et al.* 1999). Such differences in resource usage or partitioning may enable these four species to co-exist under *Acacia* canopies. Although *Enchylaena* and *Rhagodia* have limited survivorship during drought, seedlings may readily replace dead plants. Such mechanisms would enable these shrubs to persist in this system with unpredictable pulses of rainfall. Variations in pulse inputs may also change competitive hierarchies. Pulse-utilisers may be better competitors during years with more frequent pulses but more stress-tolerant species may be better competitors during long interpulses (Tilman 1997, Novoplansky and Goldberg 2001). Alternatively, stress-related deaths during interpulses may select for stress-tolerant or stress-avoiding adaptations (e.g. resprouting or regenerating from seed) that could lessen the importance of competition in pulsed systems (Grime 1979).

Effects of patchiness

As soil moisture differences between sites were not large, higher growth rates of *Maireana* shrubs growing under canopies was probably not the result of greater soil water availability in these sites. Reduced evaporative demand and higher nutrient availability in these sites could have contributed to higher shoot elongation rates. The increases in soil water content beneath canopies may not have been enough to improve plant growth in these sites, but the differences may have been enough to affect other soil processes, especially the activity of soil microbiota (Cowling 1978). Soil microflora may remain active for longer after rainfall events under canopies and together with lower temperatures in these sites, and high litter loads the labile nutrient pool would be much higher (Garner and Steinberger 1989). When rains occur above the threshold for plant response these nutrients may then be readily utilized. Such effects may explain the higher forb biomass in 2000 and 2001, and greater perennial leaf and root biomass under tree canopies. Although facilitation is predicted to be more frequently observed when conditions are more stressful (Bertness and Callaway 1994), I found forb biomass was greater under canopies in both a dry year (2000) and a wet year (2001). This may be explained by the extensive growth during the wetter year of some species (e.g. *Sisymbrium erysimoides*, *Zygophyllum ammophilum*) largely restricted to canopy microenvironments. It seems that when water is not limiting to growth these species may be advantaged by the increased nutrients beneath canopies.

The higher perennial diversity under canopies was related to the even proportions of the four most common shrubs in these sites. Lower diversity in open sites may be explained by the absence of *Enchylaena* and *Rhagodia* in most plots. There may be two reasons for an increase in diversity in the presence of tree canopies. The physical presence of a species (such as *A. papyrocarpa*) can create a habitat that is otherwise absent or rare in a system, or may modify the habitat to enable less stress tolerant species to persist (Hacker and Gaines 1997). Such effects may produce differences in species composition and diversity between canopy and intercanopy habitats (Belsky *et al.* 1989, Facelli and Brock 2000, Tewksbury and Lloyd 2001, Tester, 1987). In this system, microenvironments beneath *Acacia* canopies appear to favour the persistence of species such as *Enchylaena* and *Rhagodia*. This may be a result of improved resources or conditions for growth and survival.

Although the number of ephemeral species did not differ between sites, open sites were more diverse. Canopy sites were dominated by a few species that constituted a high proportion of the biomass. Barnes (1993) found seed banks of soils beneath *A. papyrocarpa* canopy were more diverse than seed banks in open soils, but this was based on numbers of germinating plants rather than biomass. Plants that achieve greater size can dominate habitats, not necessarily those species that germinate in the greatest numbers. Although canopies had positive effects on perennial and forb biomass they had negative effects on grass biomass. The shady microenvironment or thick litter layers beneath tree canopies may be less suitable for grass establishment in this system.

Summary and conclusions

Most growth, of both perennial and ephemeral plants, occurred in 2001 in response to a large rainfall event. Shoot elongation of all four perennial species was related to pulses of rainfall, irrespective of the timing of this rainfall. However, the magnitude of perennial shrub growth responses is likely to reflect longer-term rainfall inputs in addition to recent pulse events. All species grew concurrently, although *Enchylaena* and *Rhagodia* had greater shoot elongation rates than *Atriplex* or *Maireana*. These species are co-dominant in sites beneath *Acacia* canopies, and *Atriplex* and *Maireana* co-dominate open sites. These species may therefore potentially compete for soil resources.

Soil water content was modified beneath canopies, especially in the summer months at shallow soil depths. Soil water content at shallow depths also showed a significant relationship to rainfall pulses. In deeper soils there were no differences between sites in soil water content, although infiltration rates may be faster in soils beneath *Acacia* canopies. Canopy sites were more productive than open sites with greater root and leaf perennial biomass and at times greater forb biomass. Soil moisture differences between canopy and open sites were probably not large enough to explain the differences in production in the two sites. Higher nutrient levels and the amelioration of harsh physical conditions during the summer months under tree canopies may explain these vegetation responses.

Resource inputs and biomass production in this system are pulse-driven, yet interaction with plant-created patches alters this dynamic. The response of ephemeral and perennial plants to rainfall fluctuations was site specific. Spatial and temporal resource gradients can have different effects on processes in this system, which can not be predicted simply from an examination of only one of these gradients. Plant interactions in particular may demonstrate complex interactions between space and time and will be examined in the subsequent chapters.

Table 3.1 Total annual rainfall and cool season rainfall totals at Middleback Homestead for the three years of this study and the year prior to the study (1998).

Year	Total rainfall (mm)	Rainfall (May to Sep) (mm)
1998	331.4	112.7
1999	253.1	83.5
2000	205.6	111.0
2001	320.5	222.5

Table 3.2 Separate NPMANOVAs testing the effect of site on soil water content at three soil depths. Significant difference between sites at $**\alpha < 0.01 > 0.001$.

Depth	Source	df	SS	*F*	*P*
5 cm	site	1	6.713	2.767	0.002**
	error	26	63.080		
20 cm	site	1	4.793	1.154	0.302
	error	26	107.945		
35 cm	site	1	1.980	0.586	0.878
	error	26	87.924		

Table 3.3 ANOVA testing the effect of site and soil depth and their interaction on the soil water content measured on 6/6/2001. * Significant difference between treatments at α < 0.05 > 0.01.

Source	**df**	SS	***F***	***P***
Site	1	2.043	5.666	0.021*
Depth	2	1.002	1.390	0.259
Site/depth	2	1.854	2.570	0.087
Error	48	17.309		

Table 3.4 Coefficients of determination (r^2) for linear regressions between lag rainfall and mean soil water content measured at three different soil depths in sites under *Acacia papyrocarpa* canopies and in adjacent open spaces. Significant linear relationships at * α < 0.05 > 0.01, and ** α < 0.01 > 0.001.

		Lag rainfall (weeks)					
Site	**Depth**	**1**	**2**	**4**	**6**	**8**	**12**
canopy	5 cm	0.13	**0.32***	**0.39****	**0.25***	**0.28***	0.15
	20 cm	0.01	0	0.04	0.21	**0.27***	**0.27***
	35 cm	0	0.05	0.03	0.08	0.16	0.10
open	5 cm	**0.31***	**0.46****	**0.48****	0.22	0.16	0.12
	20 cm	0.02	0.13	0.12	0.20	**0.39****	**0.29***
	35 cm	0	0.12	0.02	0.07	0.18	0.15

Table 3.5 Means ± 95% CI and results of Wilcoxon Kruskall-Wallis tests comparing perennial and ephemeral species richness and diversity in canopy and open sites. Significant difference between treatments at ** $\alpha < 0.01 > 0.001$ and *** $\alpha < 0.001$.

	Species richness	**Species diversity**
Perennial		
canopy	3.46 ± 0.36	0.76 ± 0.09
open	3.46 ± 0.45	0.40 ± 0.11
WKW χ^2	0.006	19.601***
Ephemeral		
canopy	8.52 ± 1.29	1.01 ± 0.14
open	9.44 ± 1.83	1.36 ± 0.20
WKW χ^2	0.577	9.221**

Table 3.6 ANOVAs testing the effects of distance from the tree bole (a) or site (b, c) on separate size classes of root biomass. Significant difference between treatments at *** α < 0.001.

Root diameter	**Source**	**df**	SS	***F***	***P***
< 1mm	Distance	3	6.157	11.130	< 0.001***
	Error	40	7.376		
1-2 mm	Site	1	6.868	20.876	< 0.001***
	Error	94	30.924		
2 mm	Site	1	0.004	0.030	0.862
	Error	94	12.920		

Table 3.7 Repeated measures MANOVAs testing the shoot elongation rates of the four species in sites under canopies and the effects of site on the shoot elongation rates of *Atriplex* and *Maireana*, at different measurement times. Significant difference between treatments at * $\alpha < 0.05 > 0.01$, ** $\alpha < 0.01 > 0.001$, *** $\alpha < 0.001$.

Source	**num df**	**den df**	***F***	***P***
All species				
Species	3	24	6.766	0.002**
Time	9.15	219.69	60.261	<0.001***
Time/species	27.46	219.69	2.634	<0.001***
Atriplex				
Site	1	17	2.198	0.157
Time	7.76	131.93	44.353	<0.001***
Time/site	7.76	131.93	1.221	0.252
Maireana				
Site	1	17	6.815	0.018*
Time	8.77	149.03	28.293	<0.001***
Time/site	8.77	149.03	3.132	0.002**

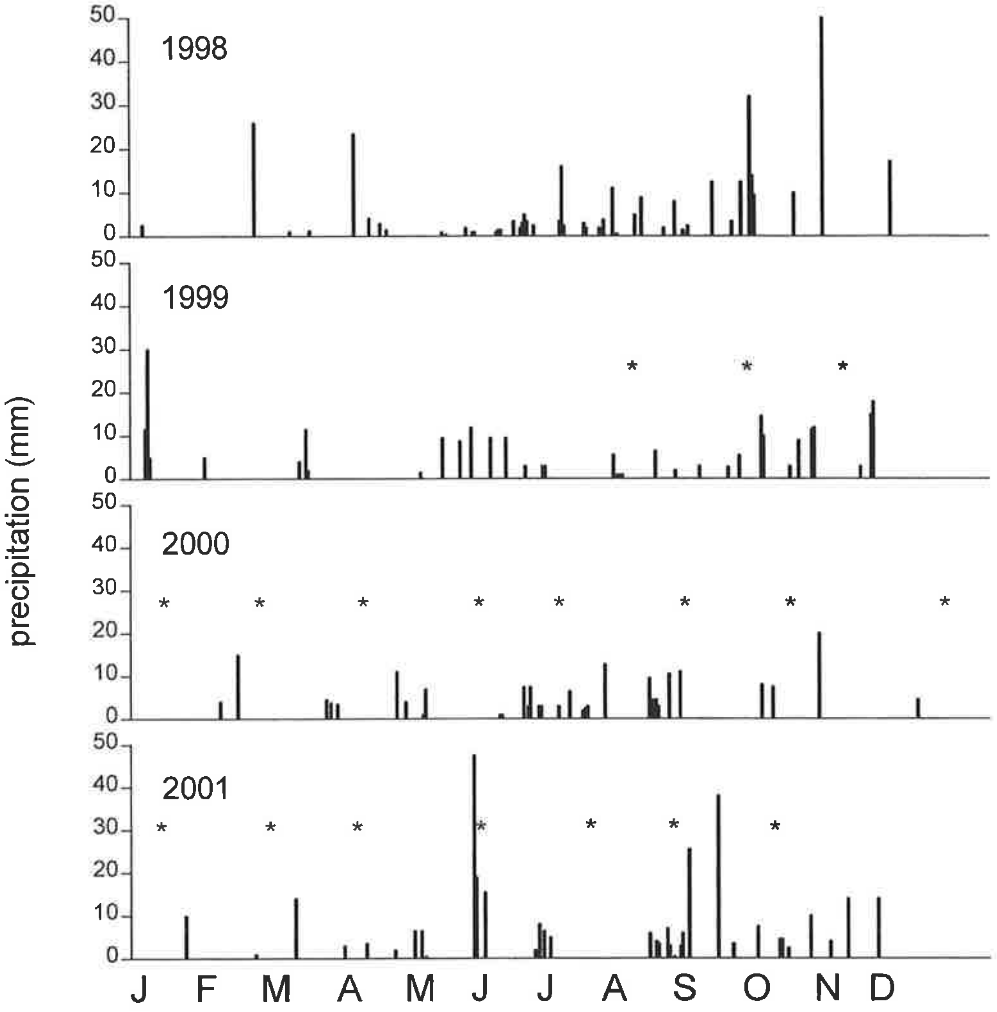


Fig. 3.1 Daily precipitation over the duration of this study (1999-2001) and the previous year (1998): * indicate soil water content and plant growth sampling dates.

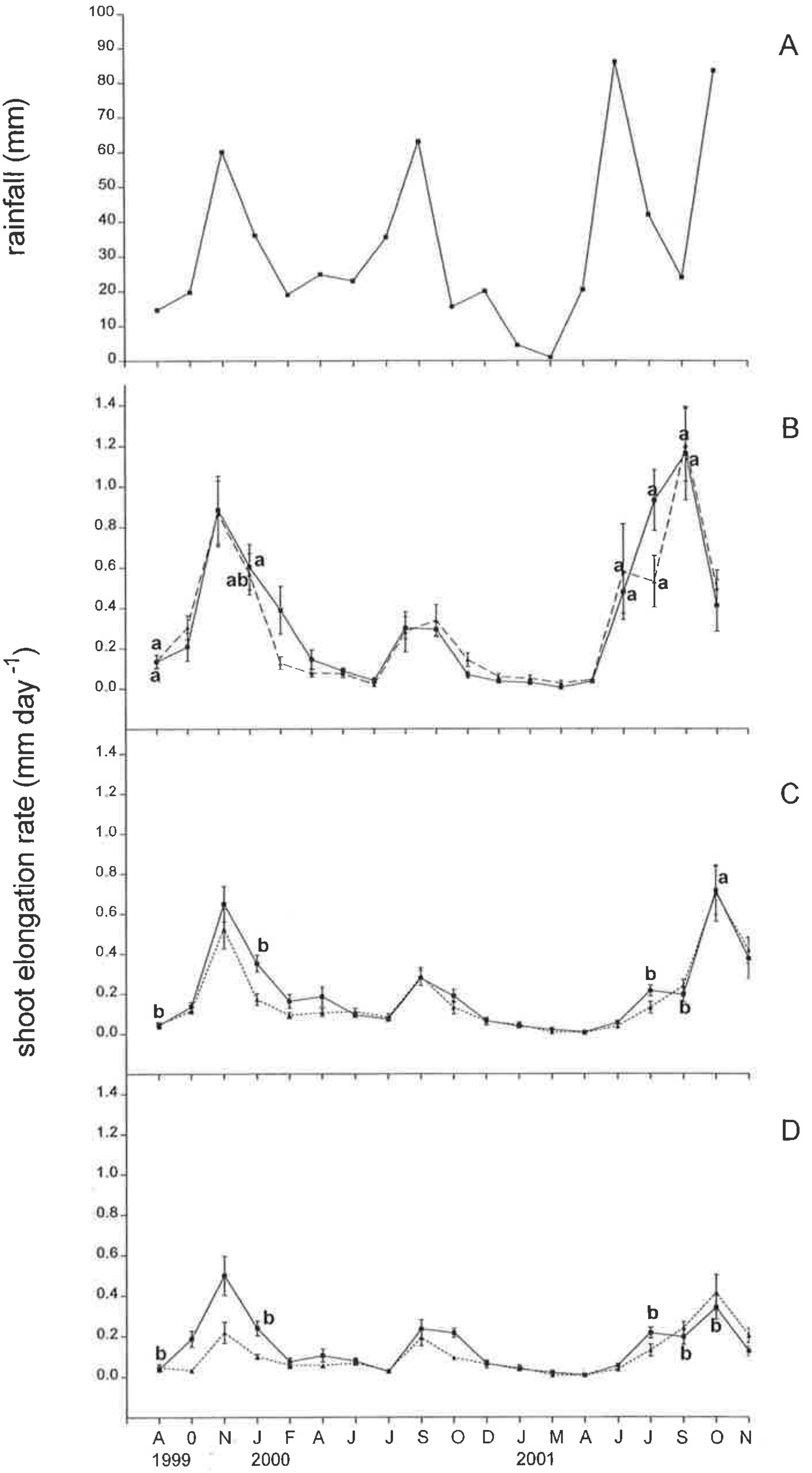


Fig. 3.2 A) Precipitation totals for the six week period preceding soil water content and plant growth sampling; B) shoot elongation rates (mean ± 1SE) of *Enchylaena* (—) and *Rhagodia* (----), and C) *Atriplex* and D) *Maireana* under *Acacia* canopies (—) and in adjacent open sites (····). Data points labelled with different letters indicate significant differences between species shoot elongation rates on that measurement occasion, for plants growing under *Acacia* canopies (Tukey-Kramer HSD tests).

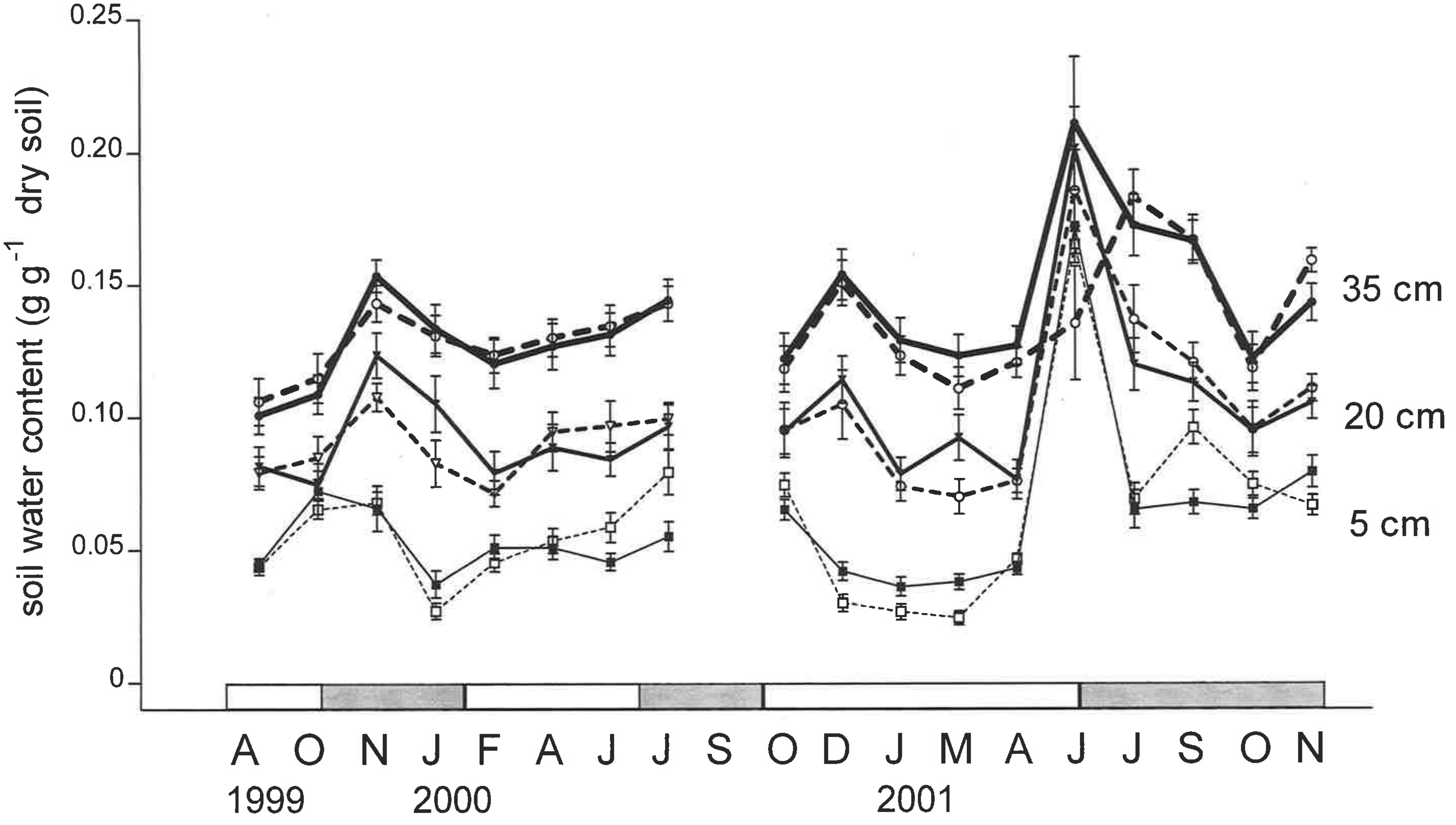


Fig. 3.3 Soil water content (mean ± 1SE) at three soil depths under *Acacia* canopies (—) and in adjacent open sites (----). The shaded horizontal bars on the x-axis represent pulse periods, the unshaded portions, interpulses. Data were not collected in September 2000.

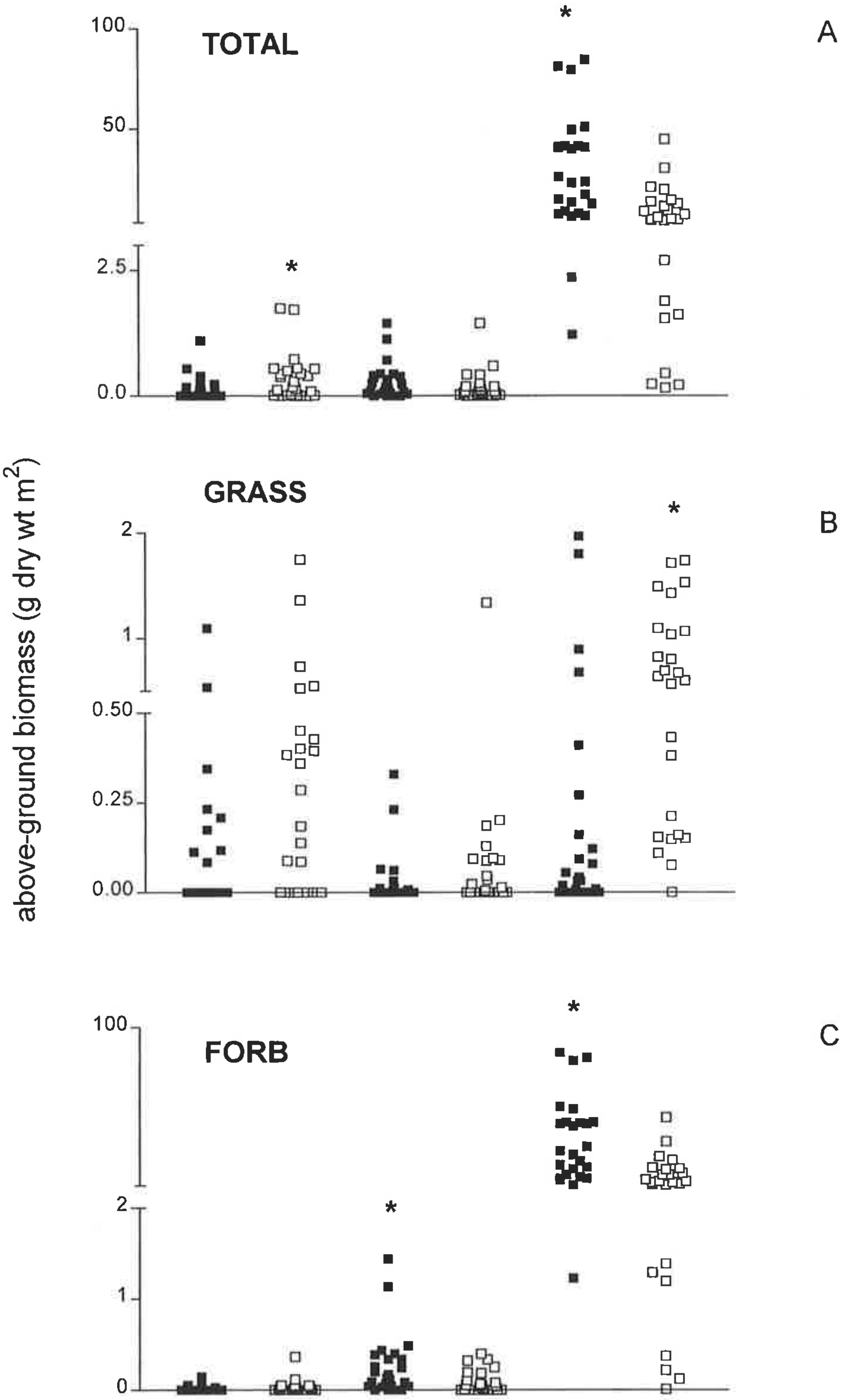


Fig. 3.4 Scatterplots of A) total above-ground biomass of ephemerals, and separated into B) above-ground grass biomass and C) above-ground forb biomass in sites beneath *Acacia* canopies (closed squares) and open sites (open squares) sampled in October in three years. * Denotes that biomass was significantly greater within year at $\alpha < 0.017$ (Mann Whitney tests). Note split axes and different axis scales in each graph.

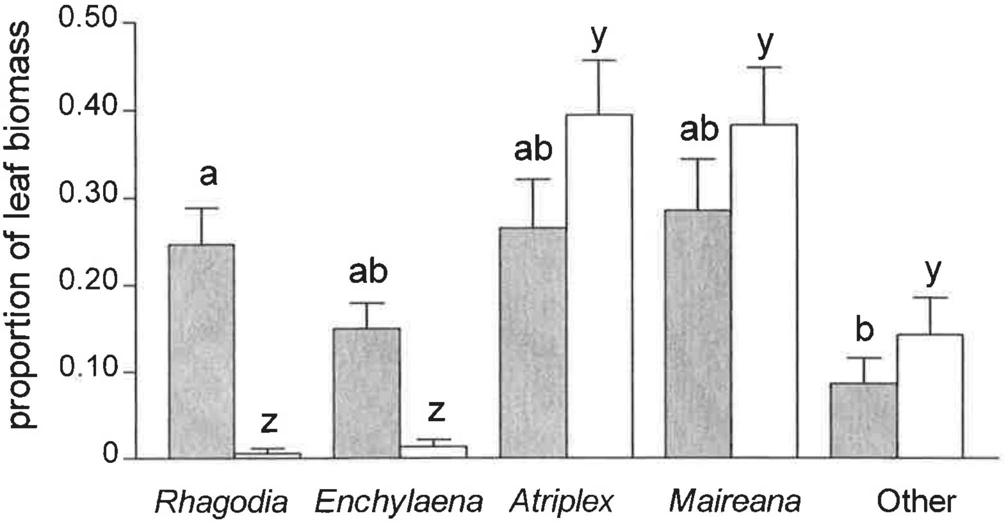


Fig. 3.5 Proportions (means + 1 SE) of the total leaf biomass of four dominant chenopod species and other perennial species combined, in 4 m^2 plots located under *Acacia* canopies (shaded bars) and in adjacent open spaces (unshaded bars). Bars labelled with different letters within sites were significantly different at a < 0.05 (Dunn's test, GraphPad Prism, Ver. 3.02).

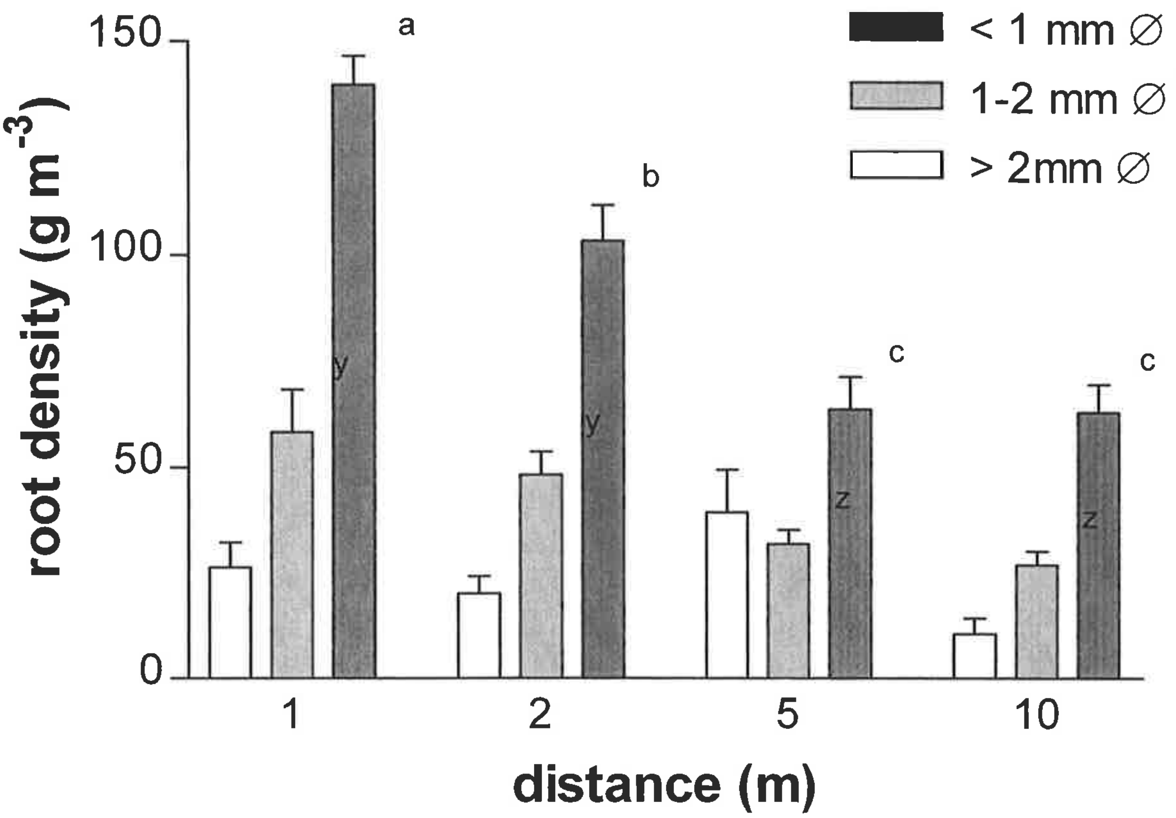


Fig. 3.6 Mean (+ 1 SE) biomass of different root size classes at varying distances from the tree bole (1 m and 2 m) and canopy edge (5 m and 10 m). Columns labelled with different letters within each size class were significantly different at $\alpha < 0.05$ (Student's t tests, null hypothesis 1, 2 > 5, 10).

CHAPTER 4

Changes in competition intensity along temporal and spatial resource gradients

Introduction

The variable and unpredictable nature of rainfall events in arid systems makes it difficult to predict the outcome of competitive interactions. Goldberg and Novoplansky (1997) suggested that competition will be important if competitive effects on resource uptake after rainfall pulses affects plant performance during interpulses between rainfall events, or if plants control resource availability during both phases. They argued that competition would be less important when plant survival during interpulses is independent of resource uptake by neighbouring plants. However, Chesson and Huntly (1997) demonstrated that although environmental fluctuations may weaken competition intensity, competition might still be an important force controlling the distribution and abundance of species. It is difficult to measure the importance of competition, particularly for long-lived shrubs. It requires some measure of the fitness of the population, e.g. natality and mortality (Welden and Slauson 1986). However, relative measures of competition intensity (e.g. growth) can be more accurately measured and give some indication of the importance of competition relative to other processes affecting fitness. For example, competition may not be very intense, but if there are no other factors affecting plant fitness competition may be important.

The intensity of competition along a resource gradient will depend on the demands made on resources at varying rates or levels of resource supply. Competition will be intense when plants reduce the resources available to other plants above the rate of depletion by abiotic factors. Competition may be more intense during pulses as during this period most resource uptake and growth takes place (Goldberg and Novoplansky 1997). But if plants continue resource uptake into interpulses, competition intensity may not change over time. In addition, in patches where plants are able to achieve the highest growth rates, such as fertility islands, competition may be more intense (Rice and Nagy 2000).

Even if fluctuations in resources do not affect competition intensity they may affect the competitive ranking of species (Novoplansky and Goldberg 2001). A review by Goldberg (1996) has shown that there are no clear patterns in the consistency of competitive rankings between the same species growing in environments differing in resource availability . However, Keddy *et al.* (2000) suggested that competitive rankings between species are more likely to change in infertile habitats dominated by root competition. In fertile habitats competitive hierarchies result from competition for light and the plant that can grow larger will suppress neighbours, resulting in asymmetric competition (Keddy *et al.* 2000). Root competition is more symmetric than shoot competition, with the largest plant not necessarily being the best competitor (Blair 2001). Therefore traits apart from the ability to grow fast may confer below-ground competitive ability, and the most competitive trait may change with resource inputs. For example, a plant that is a good competitor when resources are plentiful during pulses, may be a poor competitor when resources are scarce in interpulses. Competitive hierarchies will therefore depend on the length and magnitude of pulse phases rather than the absolute amount of resource input within a typical growth season (Novoplansky and Goldberg 2001).

At Middleback, the distribution of perennial shrubs in sites varying in fertility or abiotic stress will enable me to examine potential changes in the intensity of plant interactions along temporal and spatial resource gradients. The aims of this chapter are:

1) To test the two alternative predictions of my conceptual model (Fig. 1.1):
    i) that competition will be more intense during pulses, or
    ii) that competition will be of equal intensity during pulses and interpulses.
2) To compare competition intensity between shrubs growing in the more fertile sites under *Acacia* trees with the less fertile open sites.
3) To further explore the link between resource availability and competition by examining the correlation between competition intensity and soil water content.
4) To determine if the competitive hierarchies of the four co-dominant chenopod species change over time in relation to pulse phases.

Methods

Experimental design

I conducted this experiment in Overland Paddock, Middleback Station. This paddock has a high tree density and distant from the watering points all four chenopod shrubs can be found growing beneath tree canopies. In sites beneath *Acacia* canopies, I tested the responses of the four chenopod species, *Atriplex*, *Maireana*, *Enchylaena* and *Rhagodia*, to the removal of all neighbouring plants. In open sites, I also tested the responses of *Atriplex* and *Maireana* to neighbour removal: *Enchylaena* and *Rhagodia* do not occur in open sites.

I selected two similar sized mature shrubs of each species beneath each *Acacia* canopy, with ten replicate pairs (or ten *Acacia* sites) for each species. I also selected ten replicate shrub pairs of *Atriplex* and *Maireana* in open sites between trees, at a random distance from the canopy edge and a random bearing from the tree bole. These shrubs were located at least 2 m beyond the edge of canopies with shrub pairs located a similar distance apart as the shrub pairs under canopies. I randomly selected one of the shrub pairs in each site as a control, to monitor shrub responses with neighbouring plants present. The other shrub (treatment), had the above-ground biomass of neighbouring shrubs removed at the soil surface for a 2 m radius from the target shrub stem or centre and annual plants hand weeded over the course of the experiment. I used these shrubs to monitor responses with neighbouring shrubs absent (competition-free). I fenced each plant to exclude large vertebrate herbivores.

Response variables

I marked five shoots on each shrub with a paint mark, 20 mm from the base of the apical meristem. I measured the length of these stems and any secondary branches arising within this stem portion at six weekly intervals from August 1999 until November 2001. An estimate of the shoot elongation rate for each shrub was the average of these five marked stems. On each measurement occasion, I recorded the reproductive status of marked stems as the presence or absence of flower buds, flowers or fruits, and calculated the frequency of these observations over the 19 measurement occasions (reproductive frequency). New stems were marked when stems died over the course of the experiment and I re-marked shoots when their primary or secondary stem length exceeded 40 mm. I recorded shrub deaths and replaced any shrubs that died by another shrub beneath the same tree. Fourteen shrubs died in sites under trees but no shrubs died in open sites.

I calculated competition intensity as the difference between the shoot elongation rates of plants without neighbours (treatment) and plants with neighbours (control) in each site, either under a tree canopy or in the open. As I was primarily interested in proportionate changes that resulted from my manipulations of neighbouring plants, I calculated relative competition intensity (RCI). This allowed me to compare competition intensity between times when plants were growing at different rates and between species that grow at different rates. RCI was calculated using the lognormal response ratio (lnRR; Hedges *et al.* 1999):

$$\mathrm{RCI}_{\mathrm{SE}} = \ln \mathrm{SE}_{\mathrm{T}} - \ln \mathrm{SE}_{\mathrm{C}}$$

where SE is the shoot elongation for T, treatment shrubs and C, control shrubs within each site. RCI increases with increasingly positive values of RCI. Some measurements could not be included in the analysis because shoot elongation was either less than or equal to zero or a plant had died. On most occasions this only required the removal of a single data point, although in March and April 2001, up to four data points had to be removed for each species in each site. Pooling growth into pulse and interpulse phases according to rainfall patterns (see Fig. 3.2A) eliminated this difficulty. This produced a pulse and interpulse phase for each of the three years of the study.

I also calculated the RCI for reproductive frequency. Due to the high number of zero values I did not use lnRR but used the formula:

$$\mathrm{RCI}_{\mathrm{Rf}} = \mathrm{Rf}_{\mathrm{T}} - \mathrm{Rf}_{\mathrm{C}} / \mathrm{Rf}_{\mathrm{T}}$$

where Rf is reproductive frequency in T, treatment and C, control shrubs.

Analyses

I tested the effects of competitors on shoot elongation using non-parametric MANOVA procedures (Anderson 2001). In this analysis I was interested in whether competition occurred and not in how its intensity may have changed over time. The data set was too large to test all factors together using this program hence I performed separate one-way tests for each species in each site. I log transformed data prior to analyses to satisfy assumptions of homogeneous variances. Where tests were non-significant I performed a power analysis, but used the mean shoot elongation rate for each shrub across all measurement times for these comparisons. I examined the least significant values (LSV) in these tests, which gives an estimate of the difference in mean shoot elongation rate between treatment and control shrubs required for a significant result given the same standard error. Significance values were set at $\alpha < 0.05$ for this analysis.

I tested whether RCI $_{SE}$ changed over time and differed between species growing beneath canopies using repeated measures MANOVA. I also used this procedure to test the effects of site (canopy or open) on the RCI $_{SE}$ of *Atriplex* and *Maireana* plants, and included time and species effects in these models as well. I used RCI $_{SE}$ measured on each occasion and pooled into pulses and interpulses for these analyses.

I used the mean RCI $_{SE}$ of each species in canopy sites in the three pulses and interpulses to test for the concordance of competitive hierarchies between pulses and interpulses. I used Kendall's coefficient for these analyses to test for rank differences between pulses and interpulses in each year (Zar 1999).

I used correlation techniques to examine the relationship between RCI $_{SE}$ and the availability of soil water at three depths in the soil profile (from Chapter 3). I calculated separate correlations for each species in each site. I also compared the log shoot elongation of control plants with the log shoot elongation of treatment plants over the experimental period using correlation. I used the average shoot elongation rates on each measurement occasion for each species in each site to construct scatter plots. I constructed density ellipses around the scatter plot of these values to examine patterns of competition when plants were growing at different rates. If competition has no effect on shoot elongation then the points in the scatter plot should approach a slope equal to one. When data are plotted with controls on the abscissa and treatments on the ordinate then points lying above the line of slope equal to one indicate that treatment plants grew better than their paired control plants, or that competition occurred. This relationship can be examined along the entire range of growth rates. I have demonstrated that plants grow in response to rainfall inputs (Chapter 3), therefore this relationship also demonstrates competitive responses in relation to resource gradients, with increasing rainfall correlated to increasing growth rates.

The reproductive frequency data for each species were not heteroscedastic, so I performed separate ANOVAs for each species, testing the effects of competition, and including a site effect in the case of *Atriplex*. *Maireana* data was also heteroscedastic between treatments so I tested competition and site effects independently using Welch's ANOVA. I tested RCI $_{Rf}$ between species growing under canopies by ANOVA and I used a separate ANOVA that included the effect of site on the RCI $_{Rf}$ of *Atriplex* and *Maireana*.

I used log-rank tests to test for differences between survivorship curves for plants with and without neighbours, testing species separately (GraphPad Prism Ver. 3.02). For those plants that died I tested whether they had reduced growth or more intense competition in the census period prior to death using t-tests. In these cases I subtracted the shoot elongation rate or RCI $_{SE}$ for the dead shrub from the average value for that treatment and tested the null hypothesis of no difference between the dead shrub and all other shrubs in that treatment.

I used JMP IN Ver. 4.0.3 (SAS Institute) for all analyses, unless otherwise indicated.

Results

Shoot elongation

For all species growing beneath canopies, competition had no significant effect on shoot elongation (Table 4.1). Over most of the experimental period plants growing beneath *Acacia* canopies without neighbours had higher shoot elongation rates than plants with neighbours (Fig. 4.1), but growth rates were variable and a power analysis showed that the power to detect significant differences was low (Table 4.2). In addition, the difference between the least significant value and the actual value were very low for *Atriplex*, *Maireana* and *Enchylaena*, and within the expected range of precision using my growth measurement technique (Table 4.2). In open sites *Atriplex* and *Maireana* plants without neighbours had significantly greater shoot elongation rates than plants with neighbours (Table 4.1, Fig. 4.1). Relative competition intensity (RCI $_{SE}$) did not change significantly over time, and did not differ significantly between species or between sites in the case of *Atriplex* and *Maireana* (Table 4.3, Fig. 4.2).

When the data were pooled into pulse and interpulse growth phases, some clearer patterns emerged. For plants beneath canopies, there were no significant differences in RCI $_{SE}$ between species but RCI $_{SE}$ did change significantly over time (Table 4.4). During the last year of the study (2001) when there was a long interpulse culminated by a strong pulse, competition was more intense during the interpulse (Fig. 4.3A). This pattern also occurred the year before but the differences were not as marked (Fig. 4.3A). Pair-wise comparison tests were not powerful enough to detect significant differences between treatments though.

Comparisons of RCI $_{SE}$ between sites for *Atriplex* and *Maireana* revealed that competition was relatively more intense for plants in open sites than under canopies, although there were no significant differences between species or over time (Table 4.4). However, as in canopy sites, RCI $_{SE}$ was weakest during the pulse of 2001 (Fig. 4.3B). Competition in open sites was twice as intense as in canopy sites for these two species over the duration of this study (means ± 1 SE, RCI $_{SE}$ open 0.46 ± 0.06, canopy 0.18 ± 0.07).

There was no significant hierarchical ranking of competitive ability for species growing in canopy sites (Friedman's test, $\chi^2_{r\ 4,\ 6} = 0.8$, $P > 0.05$). Hierarchical rankings changed randomly across all pulse and interpulse intervals. The changes in rankings between pulse and interpulse phases were also random. There was no significant difference between species competitive rankings in pulses and interpulses (Friedman's test, $\chi^2_{r\ 4,\ 3} = 2$, $P > 0.05$).

Competition and soil moisture

Enchylaena and *Maireana* competition intensity was negatively correlated to soil moisture, i.e there was a decrease in RCI $_{SE}$ with increasing soil moisture (Table 4.5). In canopy sites, competition intensity was correlated to soil water content at shallow soil depths for both species. In open sites, competition intensity in *Maireana* was correlated with deeper soil water supplies. A large proportion of the correlations were negative, suggesting that competition intensity decreased with increasing soil water resources (Table 4.5). Scatter plots of growth of plants with competitors and without competitors illustrate this (Fig. 4.4). There was a general trend for plants to be unaffected by competitors when they were growing at their maximum; growth approached the line with a slope equal to one. As conditions became less conducive for growth, the slope became less than one, and there was a trend for plants without neighbours to grow more than plants with neighbours. *Atriplex* plants growing under canopies showed an exception to this pattern, being unaffected by competitors when growing conditions were poor, but with a slope becoming greater than one as growing conditions improved (Fig. 4.4C).

Reproduction

The presence of neighbouring plants had significant effects on the frequency of occurrence of reproductive structures in *Atriplex*, *Rhagodia* and *Maireana* (Tables 4.6, 4.7). Plants of these three species growing beneath canopies without neighbours more frequently had reproductive structures present than plants growing with neighbours (Fig. 4.5). *Atriplex* reproduction was also significantly more frequent in plants growing without neighbours present in open sites, but the presence of competitors did not significantly reduce *Maireana* reproduction in open sites (Fig. 4.5). There were differences in RCI_{Rf} between species growing under canopies (Table 4.8). Competition was relatively more intense for *Rhagodia* and *Maireana* reproduction than *Enchylaena* (Fig. 4.6). The RCI_{Rf} did not differ between sites for either *Atriplex* or *Maireana* (Table 4.8).

Survival

There were losses to mortality in *Enchylaena* and *Rhagodia* plants over the course of the experiment, but not the other two species. Plants without competitors more frequently survived, although survivorship curves comparing competition treatments were not significantly different for either species (Fig. 4.7). Fifty percent of deaths were recorded in March 2001, during the longest and most severe interpulse. Other deaths typically occurred at the ends of interpulses, including a further three deaths at the end of the interpulse in 2001. For shrubs that died, there were no clear patterns of either reduced shoot elongation or more intense competition in the census period preceding death when compared to other shrubs in those treatments (one sample t-tests, $t \neq 0$, $n = 14$: shoot elongation rate $t = 1.64$, $P = 0.12$; RCI_{SE} $t = 0.74$, $P = 0.48$).

Discussion

Growth of the four dominant chenopod shrubs in this system responded similarly to the presence of competitors. Both spatial and temporal data demonstrated that competition intensity decreased with increasing resource availability. Growth was least affected by competition during periods or in sites where plants could potentially grow at the fastest rates. Competition intensity in fertility islands beneath *Acacia* canopies was less intense than in open sites. There were temporal changes in competition intensity in canopy sites that appeared to be related to pulse magnitude and interpulse length. Competition was weak during a large pulse and most intense during the longest interpulse. Such patterns were also observed in open sites, although competition was intense during both pulse and interpulse phases in these sites.

Spatial responses

I found that competition was more intense in open sites, contrary to my prediction that it would be more intense in the more fertile or less stressful sites beneath *Acacia* canopies. I did not detect significant improvements in shrub growth for plants growing beneath canopies in the absence of neighbours. Variability in growth rates reduced the power of statistical tests to detect competition effects but there was other evidence to suggest that competition also occurred under canopies. Competition intensity changed significantly over time in canopy sites, so at times competitive effects on shoot growth were significant beneath canopies. Competition also affected reproduction in plants growing beneath canopies. Once shrubs produce reproductive structures, typically on branch tips, shoot elongation is arrested. This may explain the lack of a significant difference in growth but a significant difference in reproduction between competition treatments for most species.

Although the removal of neighbours may have only minor affects on above-ground growth, minor effects on root growth may be much more important. If shoot growth is correlated with root growth, which is the case for *Atriplex vesicaria* (Coleman 1982) and some other arid perennial shrubs (Reynolds *et al.* 1999), then minor differences in growth rates may be important for the acquisition of below-ground resources. Although plants in arid systems are sufficiently spaced that shoots rarely compete for light, root systems are likely to be much more extensive and to have overlapping depletion zones. Competition may only increase with fertility when increases in shoot biomass result in competition for light. Tilman (1988) suggested that plants would compete for below-ground resources when light was not limiting to growth. Although plant density beneath canopies is greater than in the open (Facelli and Brock 2000) canopies of neighbouring shrubs do not frequently overlap, hence competition between shrubs for light would not be intense for plants growing beneath canopies. Competition may be more intense between widely spaced shrubs in open sites than shrubs in canopy sites because below-ground resources, especially nutrients, are in lesser supply in open sites. My data indicate that competition intensity increases with decreasing resource availability.

Temporal responses

Contrary to my prediction, competition appeared to be relatively more intense during interpulses than pulses for plants growing beneath canopies. There were clear trends for competition intensity between shrubs under canopies to increase during interpulses on all occasions but the first pulse and interpulse. This pattern may not have been observed during the first year of the study as shrub removal may have initially increased the resources available to treatment shrubs, causing an initial growth spurt in competitor-free shrubs during the first pulse. Although, responses to pulse frequency were similar in both sites, competition intensity did not change significantly over time in open sites. Plants in open sites competed for resources during both pulses and interpulses. Plants in open sites may be competing for nutrients during pulses, as nutrient mobilisation requires soil moisture (Bengtsson *et al.* 1994), and water during interpulses as soils dry out (Grubb 1992). If plants under canopies were not nutrient-limited, this may explain the lack of competition observed during the final pulse.

The intensity of competition was linked to the frequency or magnitude of pulses and interpulses. When pulses and interpulses were of short duration (during 1999 and 2000) competition intensity did not differ between the two phases. I found reduced competition during a large pulse that followed a long interpulse. During severe interpulses there is loss of plant biomass so resource acquisition zones of neighbouring plants will not overlap. Although I did not measure below-ground biomass, *Atriplex* and *Maireana* have drought deciduous roots (Coleman 1982) and it is possible *Enchylaena* and *Rhagodia* roots may also be lost in dry periods. *Enchylaena* and *Rhagodia* deaths were also more likely to occur during long interpulses. Above-ground biomass, and presumably root biomass, is replaced during pulses but early in the pulse whilst biomass is accumulating there will be little overlap of resource acquisition zones. However, as the interpulse begins plants will be at their maximal size and will compete for diminishing resources. Small but frequent pulses may sustain plant biomass (Novoplansky and Goldberg 2001) such that competition may occur during both pulses and interpulses. Thus during years with more evenly distributed rainfall competition may be more intense than during drier years or years with large interpulses, regardless of rainfall in the following pulse. Therefore the total rainfall during a growing season may be less important than pulse or interpulse frequency.

To date there is limited experimental evidence of changes in competition intensity with changes in pulse frequency. In a glasshouse experiment competitive hierarchies changed with pulse frequency, such that a fast growing species was a better competitor in a frequent pulse competitive regime, and a slower growing species was a better competitor when interpulses were longer (Novoplansky and Goldberg 2001). Field experiments that examine temporal changes in competition intensity frequently examine differences between years with varying rainfall, but the distribution of this rainfall may be more important than its absolute amount. However, this approach has not been addressed in field competition experiments but it may explain some inconsistent results. For example, in comparisons of wetter and drier growth seasons competition more frequently has a negative effect on plant growth or reproduction during the wetter season (Cable 1969, Gurevitch 1986, Casper 1996, Greenlee and Callaway 1996), but it has been found to be more intense during a drier season (Flores-Martínez *et al.* 1998).

As water is assumed to be the most limiting resource in arid systems many field experiments have examined the effects of competition on plant water relations. These experiments typically measure plant water relations spanning wetting and drying cycles so a re-examination of these experiments may give insights into relative competition intensity in different pulse phases. Wotton (1993) examined the water potential of *Maireana sedifolia* with and without neighbours over two years and a close examination of her data reveals that competition was more intense during the interpulse of the wetter year than the drier year. There was frequently no significant competition effect when water potential was measured after rainfall events, during pulses or during a severe interpulse (Wotton 1993). Briones *et al.* (1998) did not detect competition in removal experiments between three species in the Chihuahuan desert during the interpulse of a year with low precipitation. Fonteyn and Mahall (1981) found differences in the xylem potential of *Ambrosia* shrubs with and without competitors during an interpulse, but not immediately following a large rainfall event. Competition between *Atriplex vesicaria* and *Orbea variegata*, a stem succulent, was not detected during an interpulse or at the beginning of a pulse, but occurred later in the pulse (Dunbar and Facelli 1999).

These results support the hypothesis that competition intensity responds non-linearly to temporal changes in resource availability. Competition may be weak or non-existent when resources are very limiting, or in ample supply (Grubb 1992, Huston and DeAngelis 1994, Davis *et al.* 1998). In arid systems, where competition is primarily for below-ground resources, competition is most likely to affect plant performance in 'average' seasons (Knoop and Walker 1985) when rainfall is neither extremely low (Casper 1996), extremely high, or distributed in such a pattern as to produce pulse and interpulse phases with these characteristics. Below-ground competition intensity along an abiotic stress or resource gradient may follow a parabolic curve (Welden *et al.*

1988), with competition most intense at intermediate levels of abiotic stress or resources. Increasing temporal heterogeneity may therefore weaken negative plant interactions in unproductive systems (Fowler 1988), as below-ground competition will not occur when resources are extremely plentiful or extremely scarce. Goldberg and Novoplansky (1997) suggested that competition during the previous pulse could affect survival during the following interpulse, but I did not detect any such link. I suggest that competition will be most intense at the beginning of each interpulse as this is when biomass will be at its maximum and resources will start to become limiting. Although survivorship may not be affected until later in the interpulse, competition during the early interpulse is perhaps more important than competition during the previous pulse.

Species responses

I found no differences in species competitive responses, with the exception of reproductive frequency, which was not affected by competition in *Enchylaena*. Temporal fluctuations can promote coexistence if different species are favoured by environmental conditions that fluctuate over time (Chesson 1985). Coexistence of the four shrubs at equal dominance beneath canopies (Chapter 3) could be attributable to different growth responses and life history strategies. *Enchylaena*, *Rhagodia* and *Atriplex* grow more rapidly in response to rainfall events than *Maireana* (Chapter 3), but are also more likely to lose biomass during interpulses. *Maireana* is thus more tolerant of low resource levels but is unable to respond quickly to resource inputs. Although *Enchylaena* and *Rhagodia* losses to mortality were more frequent, seedlings more readily replace these shrubs than *Atriplex* or *Maireana*. These different combinations of strategies may lead to different hierarchies of competitive ability at different combinations of interpulse and pulse severities, but the unpredictability and variability of these phases will in the long-term result in the coexistence of these four species beneath canopies. However, I did not detect any changes in competitive hierarchy using shoot growth data.

I only examined competition between adult plants in this study but competitive effects may vary with plant life stage (Weltzin and McPherson 1997, Howard and Goldberg 2001). For example, during pulse periods, competition between newly establishing shrub seedlings and emerging annuals may be important. Additionally, severe interpulses that result in reduction in adult plant biomass may create competition-free niches for newly establishing seedlings in the subsequent pulse (Miriti *et al.* 2001). Such patterns may further reinforce the differences in competition intensity between pulse phases. Competition between annuals and mature shrubs may also occur and the early interpulse phase would appear to be the most crucial time, as annuals would be fully developed by this stage. Although there was a large growth of annuals in 2001 in response to the pulse (Chapter 3), competition was not more intense on this occasion. However measurements were only taken until the end of this pulse and not into the following interpulse.

Soil moisture

The links between competition and soil moisture were very tenuous, and highlight difficulties in relating plant responses to environmental parameters. Although I found shrub growth closely tracked pulse inputs, the same pattern did not hold for soil moisture (Chapter 3). As soil moisture measurements are instantaneous and represent the soil moisture at a particular instant in time they may not reflect the soil moisture conditions between plant growth measurement intervals. Integrated measurements of soil moisture may give a more accurate indication of soil moisture conditions between growth measurement intervals, although more frequent measurements of plant and soil water status may give a more accurate picture of whether plants are competing for water at different times during pulses and interpulses. However, plant water status may be less informative about how important competition is in terms of population regulation or community structure. Measurements of growth rates, survivorship, and reproduction may give more information about these processes but these responses may not necessarily reflect the preceding pulse and interpulse conditions. For example, *Maireana* and *Atriplex* growth is correlated more closely to rainfall in the previous two to four years respectively than more recent rainfall events (Noble 1977).

Correlations between competition intensity and soil moisture may offer some insights into the mechanisms of competition. *Maireana* RCI was correlated with water at different depths in the two sites. Soil moisture may be available at shallow depths for longer under canopies (Chapter 4), hence competition for this resource during interpulses. There would be an advantage in maintaining root activity at shallow depths under canopies, as this is where the highest nutrient levels are found. The cooler temperature under canopies (Chapter 6) may prolong root survival in these sites. In open sites, shallow roots may be shed earlier during interpulses, hence RCI is correlated with deeper soil moisture in open sites. *Enchylaena*, like *Maireana* appears to compete for soil moisture at shallow depths under canopies as well. For *Rhagodia* and *Atriplex* the correlations between RCI and soil moisture were not significant under canopies, suggesting no competition or competition for other resources.

Summary and conclusions

Both my spatial and temporal data provide no support for the prediction that competition increases in intensity as resource availability increases. My data imply that competition intensity may decrease with resource availability in an arid system and this is supported by both temporal and spatial changes in competition intensity. Plants control below-ground resources during both pulses and interpulses, but as resource demand during interpulses is much greater than resource supply, competition intensity increases in intensity at these times. Although plants may have very limited growth during interpulses, the availability of resources during this period appears to be controlled by plants and not just abiotic factors. Such minor differences in resource uptake during these periods may therefore have important impacts on overall plant fitness.

My evidence suggests that competition between mature shrubs in arid systems responds non-linearly to rainfall inputs. Below-ground competition intensity is inversely related to pulse frequency or intensity, but below a threshold of pulse amplitude competition is weak. Therefore competition is most intense when pulses are of intermediate intensity or frequency. Greater insight into this relationship could be gained by measurement of plant responses to different pulse regimes in glasshouse or field experiments. However, I believe it is important to measure a number of plant responses, from changes in root, shoot and reproductive biomass to finer scale physiological responses, such as carbon uptake or xylem water potential.

Table 4.1 Separate one-way NPMANOVAs testing the effects of competition on shoot elongation for each species in canopy and open sites. Shoot elongation significantly greater in treatment shrubs (without neighbours) at * $\alpha < 0.05 > 0.01$, ** $\alpha < 0.01 > 0.001$.

Species	**Error SS (18 df)**	**Model SS (1 df)**	***F***	***P***
Canopy sites				
Atriplex	129.667	11.078	1.538	0.128
Maireana	113.664	8.605	1.363	0.173
Enchylaena	162.371	13.244	1.468	0.106
Rhagodia	185.771	16.780	1.626	0.111
Open sites				
Atriplex	117.317	15.792	2.423	0.006**
Maireana	109.689	10.434	1.712	0.047*

Table 4.2 Power analysis of the effect of neighbours on shoot elongation rates for plants growing under canopies. Tests were based on the mean difference in stem elongation rate between treatment and control shrubs over the entire measurement period. LSV, least significant value or mean significant difference required for significance at $^*\alpha < 0.05$.

Species	**Mean difference in shoot elongation rate (mm wk $^{-1}$)**	**LSV**	**Power**
Atriplex	1.25	1.36	0.30
Maireana	1.22	1.28	0.35
Enchylaena	1.20	1.36	0.21
Rhagodia	1.15	1.57	0.10

Table 4.3 Repeated measures MANOVAs testing the effects of species, time and their interaction on the relative competition intensity (shoot elongation) for all species growing in canopy sites and, the effects of species, site, time and their interaction on the relative competition intensity of *Atriplex* and *Maireana* for each measurement period. Model effects that include time use Greenhouse-Geisser epsilon adjusted degrees of freedom.

Source	**num df**	**den df**	***F***	***P***
Canopy – all species				
Species	3	4	0.755	0.58
Time	3.25	13	0.783	0.53
Time/species	9.75	13	0.740	0.68
Atriplex, Maireana				
Site	1	7	0.117	0.74
Species	1	7	0.226	0.65
Site/species	1	7	1.107	0.33
Time	4.94	34.57	1.566	0.20
Time/site	4.94	34.57	0.899	0.49
Time/species	4.94	34.57	0.608	0.69
Time/species/site	4.94	34.57	0.811	0.55

Table 4.4 Repeated measures MANOVAs testing the effects of species, time and their interaction on the relative competition intensity (shoot elongation) for all species growing in canopy sites and, the effects of species, site, time and their interaction on the relative competition intensity of *Atriplex* and *Maireana* during pulse and interpulse periods. $^{\#}$ Pillai's trace. Significant difference between treatments at *$\alpha < 0.05 > 0.01$.

Source	**num df**	**den df**	***F***	***P***
Canopy – all species				
Species	3	36	0.081	0.97
Time	5	28	3.334	0.017*
Time/species$^{\#}$	15	90	0.833	0.64
Atriplex, Maireana				
Species	1	35	0.160	0.69
Site	1	35	4.175	0.049*
Species/site	1	35	1.286	0.27
Time	5	31	1.385	0.26
Time/species	5	31	1.698	0.17
Time/site	5	31	0.698	0.63
Time/species/site	5	31	0.313	0.90

Table 4.5 Pearson product-moment correlation values for the linear relationship between competition intensity (RCI $_{SE}$) and soil moisture at depths of 5, 20 and 35 cm for the four species in canopy and *Atriplex* and *Maireana* in open sites over the course of the study. Significant correlation at * $\alpha < 0.10 > 0.05$, ** $\alpha < 0.05 > 0.01$.

	Soil moisture depth		
	5 cm	**20 cm**	**35 cm**
Canopy sites			
Atriplex	-0.10	0.05	0.12
Maireana	**-0.42***	-0.04	-0.26
Enchylaena	**-0.51****	-0.10	-0.18
Rhagodia	0.01	0.14	0.07
Open sites			
Atriplex	-0.20	-0.24	-0.34
Maireana	0.13	**-0.42***	**-0.49****

Table 4.6 Separate ANOVAs testing the effects of competitors on the frequency of occurrence of reproductive structures in *Enchylaena* and *Rhagodia*, and the effects of competitors, site and their interaction on the reproductive frequency of *Atriplex*. Significant difference between treatments at **α < 0.01 > 0.001.

Source	**df**	SS	***F***	***P***
Enchylaena				
Competitors	1	0.059	1.930	0.182
Error	18	0.554		
Rhagodia				
Competitors	1	0.681	11.394	0.003**
Error	18	1.075		
Atriplex				
Competitors	1	0.242	7.920	0.008**
Site	1	0.006	0.181	0.673
C/site	1	0.001	0.018	0.893
Error	36	1.099		

Table 4.7 Results of separate Welch ANOVAs testing a) the effects of competitors on *Maireana* reproductive frequency in canopy and open sites, and b) the effects of site on the reproductive frequency of *Maireana* with (+C) and without (-C) neighbours. Significant difference between treatments at * $\alpha = 0.05$, *** $\alpha < 0.001$.

Source	**num df**	**den df**	***F***	***P***
a) canopy	1	10.41	4.856	0.050*
open	1	12.82	2.098	0.172
b) +C	1	17.10	0.040	0.844
-C	1	15.03	57.447	<0.001***

Table 4.8 Separate ANOVAs testing the effects of species on the $\mathrm{RCI}_{\mathrm{Rf}}$ for all species growing in canopy sites and, species, site and their interaction on the $\mathrm{RCI}_{\mathrm{Rf}}$ for *Atriplex* and *Maireana.* Significant difference between treatments at $*\alpha < 0.05 > 0.01$.

Source	**df**	SS	***F***	***P***
Canopy – all species				
Species	3	4.121	2.907	0.048*
Error	36	17.012		
Atriplex, Maireana				
Species	1	0.008	0.017	0.896
Site	1	0.685	0.620	0.251
Species/site	1	0.615	1.350	0.253
Error	36	16.404		

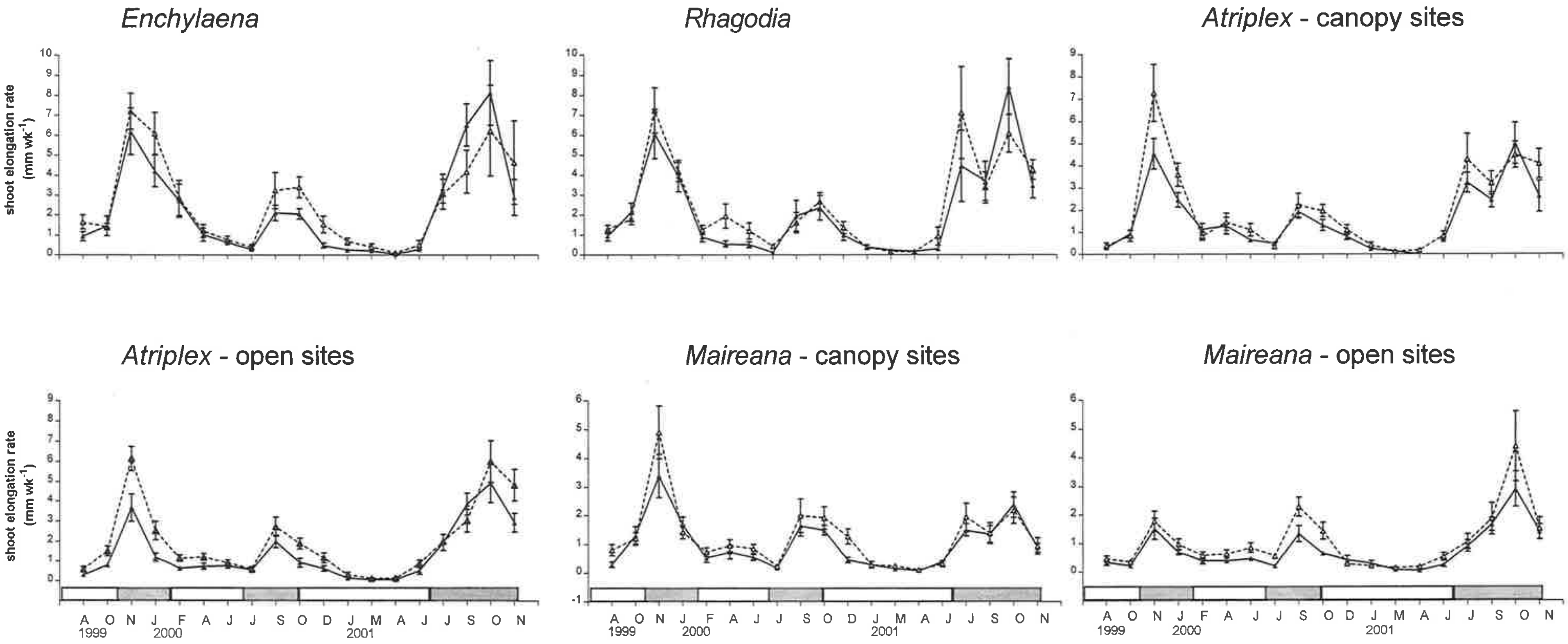


Fig. 4.1 Shoot elongation rates (mean ± 1 SE) for shrubs growing in sites beneath *Acacia* canopies and *Atriplex* and *Maireana* in open sites, with (—) and without (---) neighbours over the course of the experiment. The shaded horizontal bars on the x-axis represent pulse periods, the unshaded portions, interpulses.

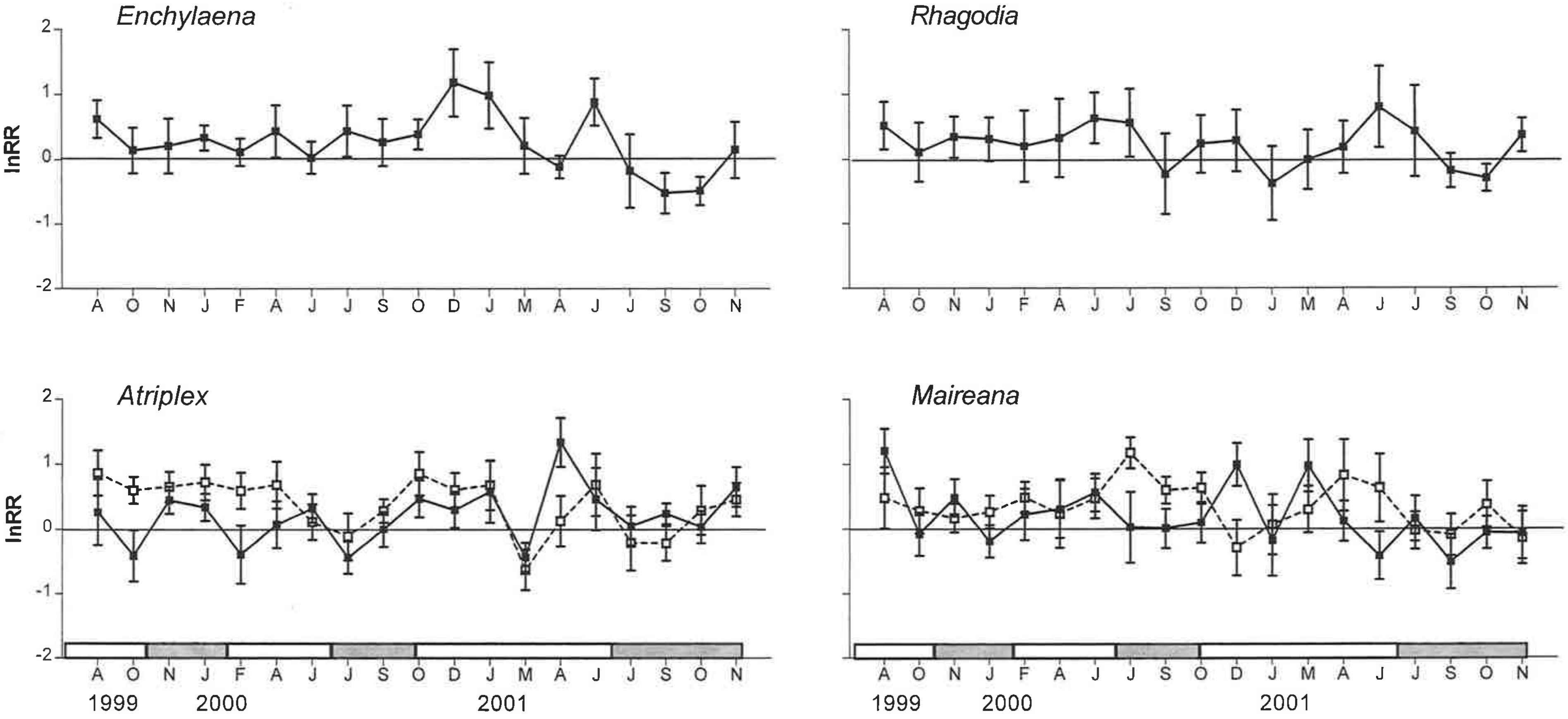


Fig. 4.2 Mean (± 1 SE) relative competition intensity of shoot elongation as measured by the log response ratio (ln RR) for shrubs growing in sites beneath *Acacia* canopies (—) or in open sites (---). The line at zero represents the point where shoot elongation of plants with neighbours equals that of plants without neighbours. The shaded horizontal bars on the x-axis represent pulse periods, the unshaded portions, interpulses.

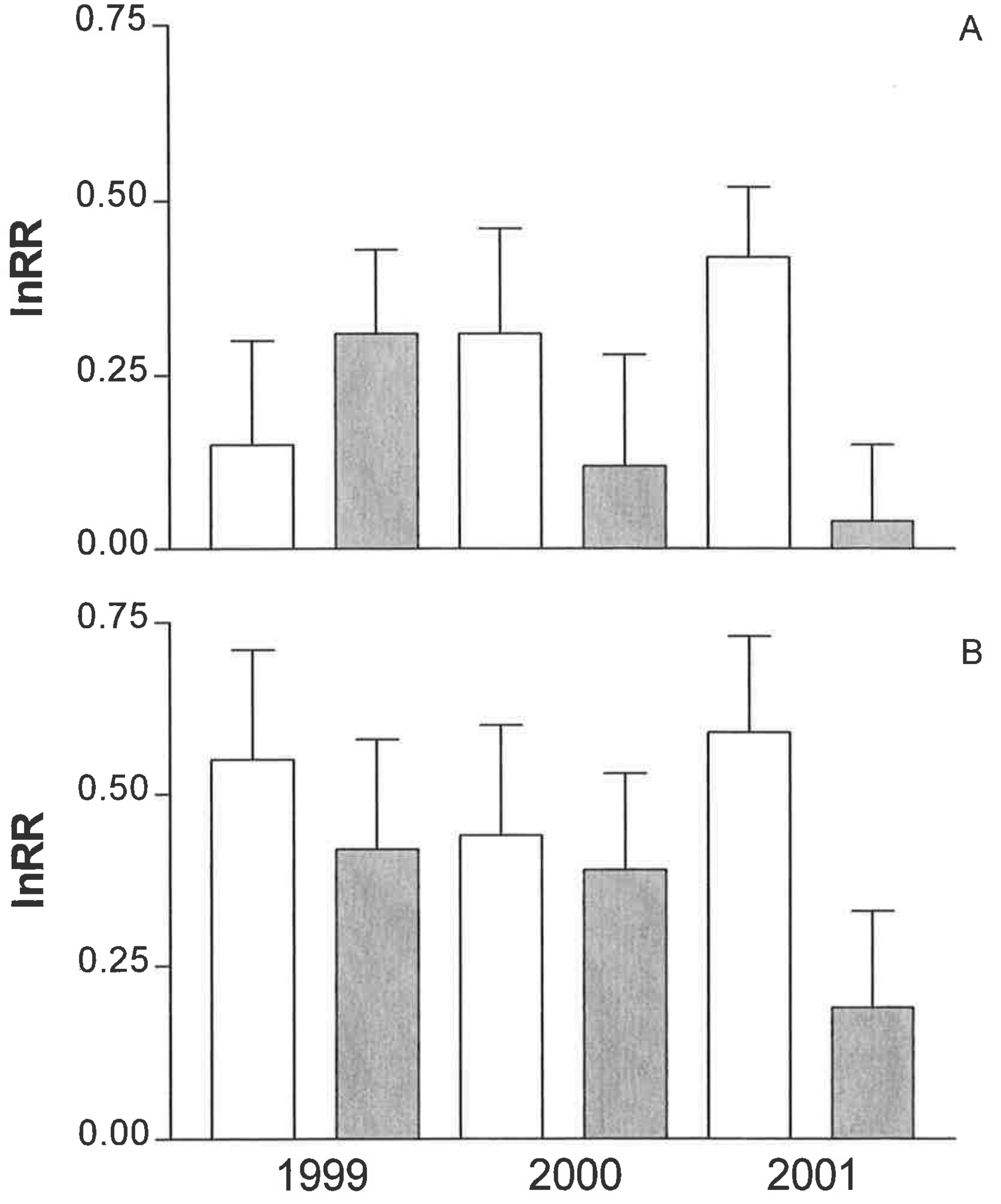


Fig. 4.3 Mean (+ 1SE) relative competition intensity of shoot elongation as measured by the log response ratio (ln RR) for all species combined in A) sites beneath *Acacia* canopies and B) open sites, during interpulse (unshaded bars) and pulse (shaded bars) periods.

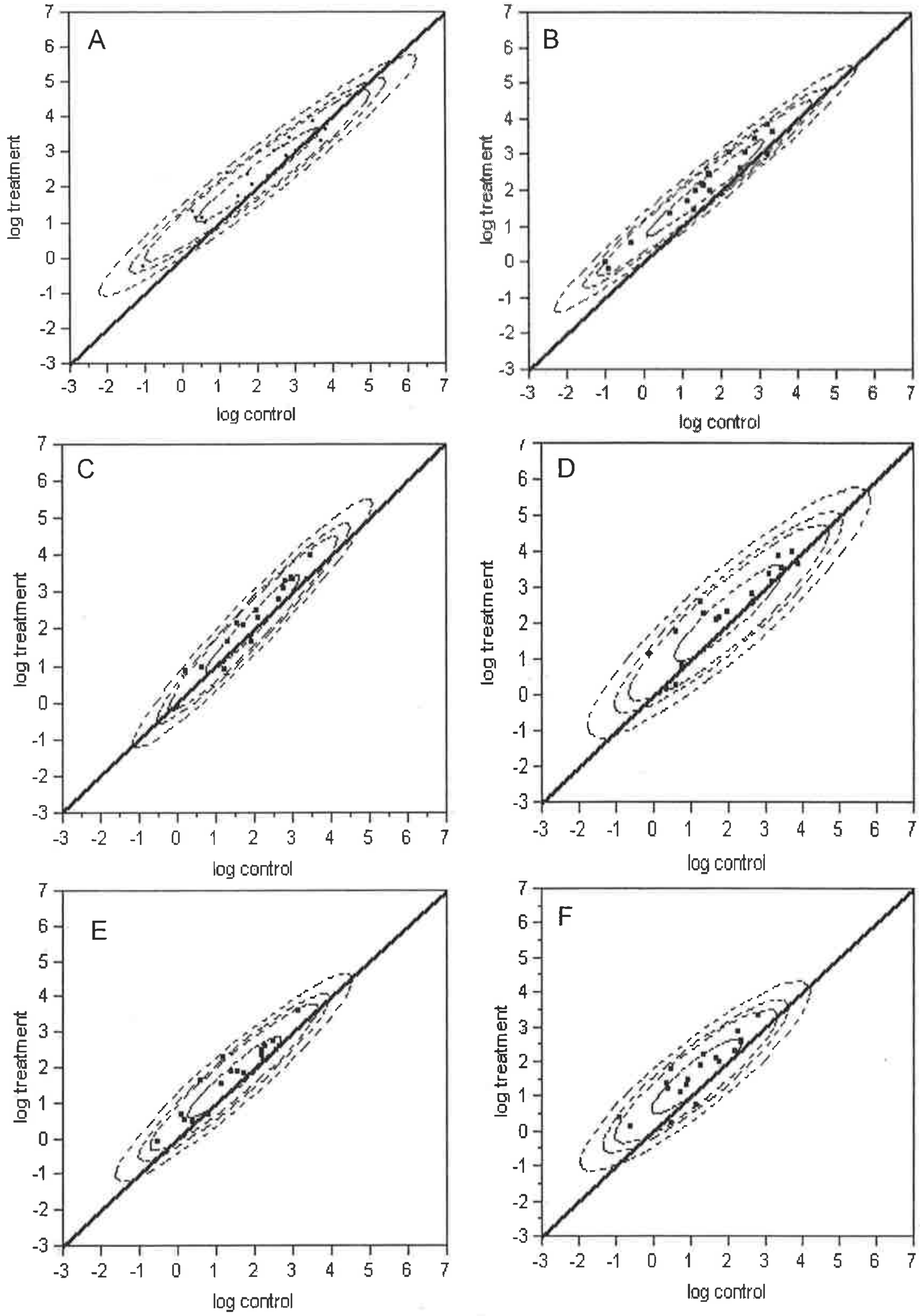


Fig. 4.4 Scatterplots of log growth of A) *Enchylaena*, B) *Rhagodia*, C) *Atriplex* and E) *Maireana* plants with neighbours (control) and without neighbours (treatment) growing beneath canopies and D) *Atriplex* and F) *Maireana* in open sites. Each point is the average growth of 10 replicates measured at the same time. The diagonal line represents a slope = 1 when control and treatment plants have the same growth. The dashed lines are bivariate normal ellipses enclosing from the inside out, 50, 90, 95 and 99 % of values.

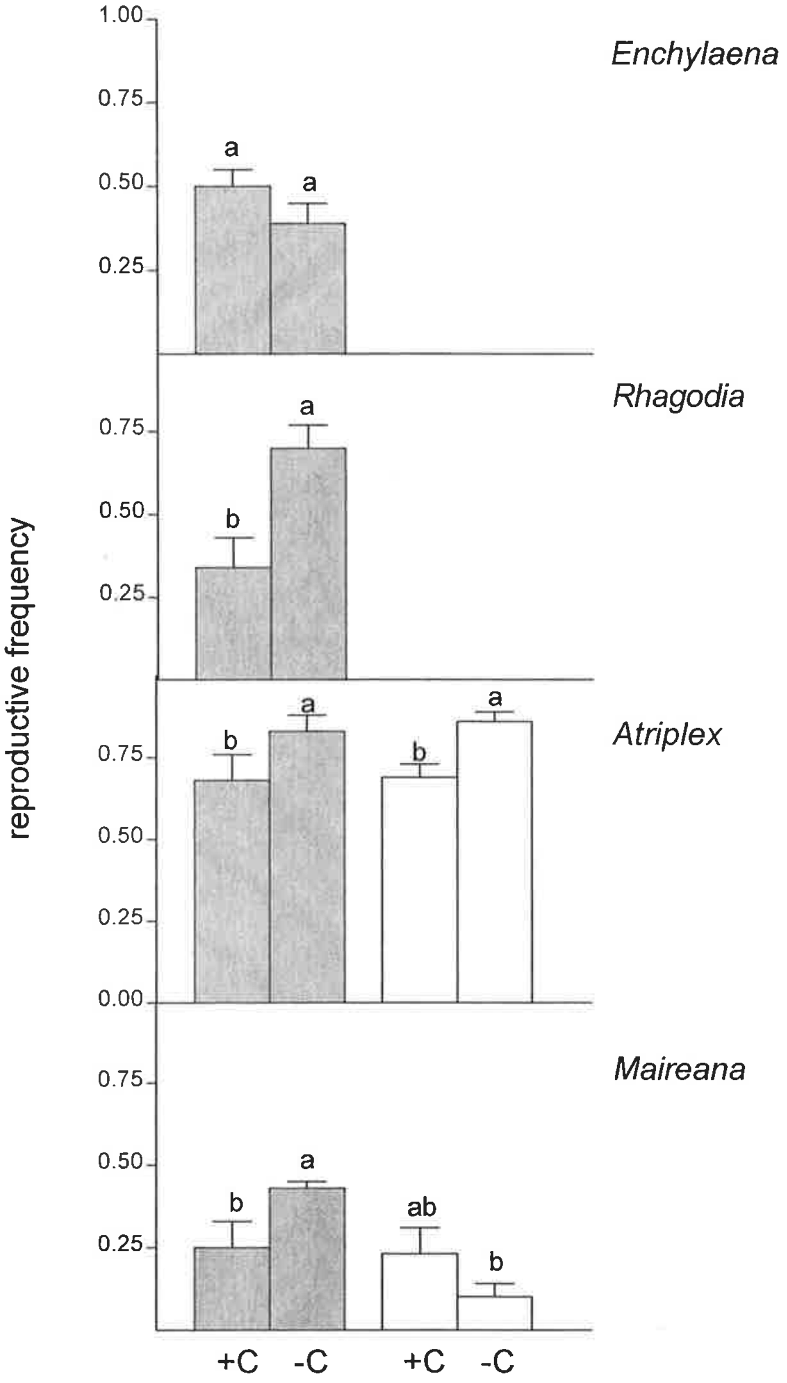


Fig. 4.5 Mean (+ 1SE) frequency that reproductive structures were observed on shrubs growing in sites under *Acacia* canopies (shaded bars) or in open sites (unshaded bars), with competitors (+C) and without competitors (-C), over the course of the experiment. Columns labelled with different letters were significantly different at $\alpha < 0.05$. (ANOVA, Welch ANOVA for *Maireana*. For statistical details see Tables 4.6 & 4.7).

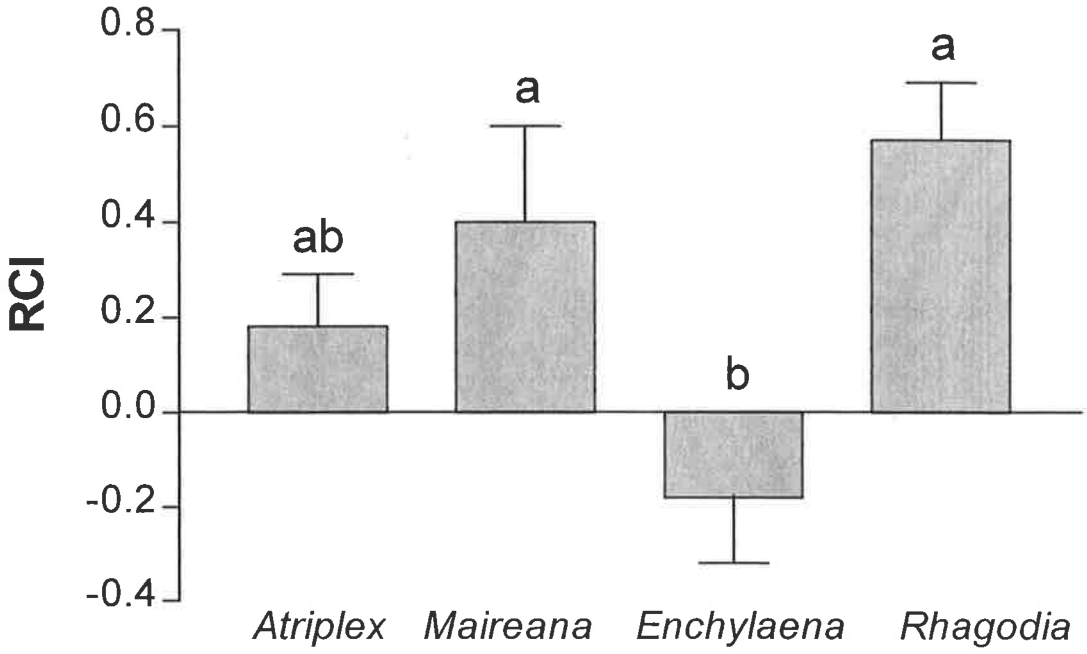


Fig. 4.6 Mean (+ 1SE) relative competition intensity (RCI) of reproductive frequency for the four species in sites beneath *Acacia* canopies. Columns labelled with different letters were significantly different at α < 0.05 (Tukey-Kramer HSD test).

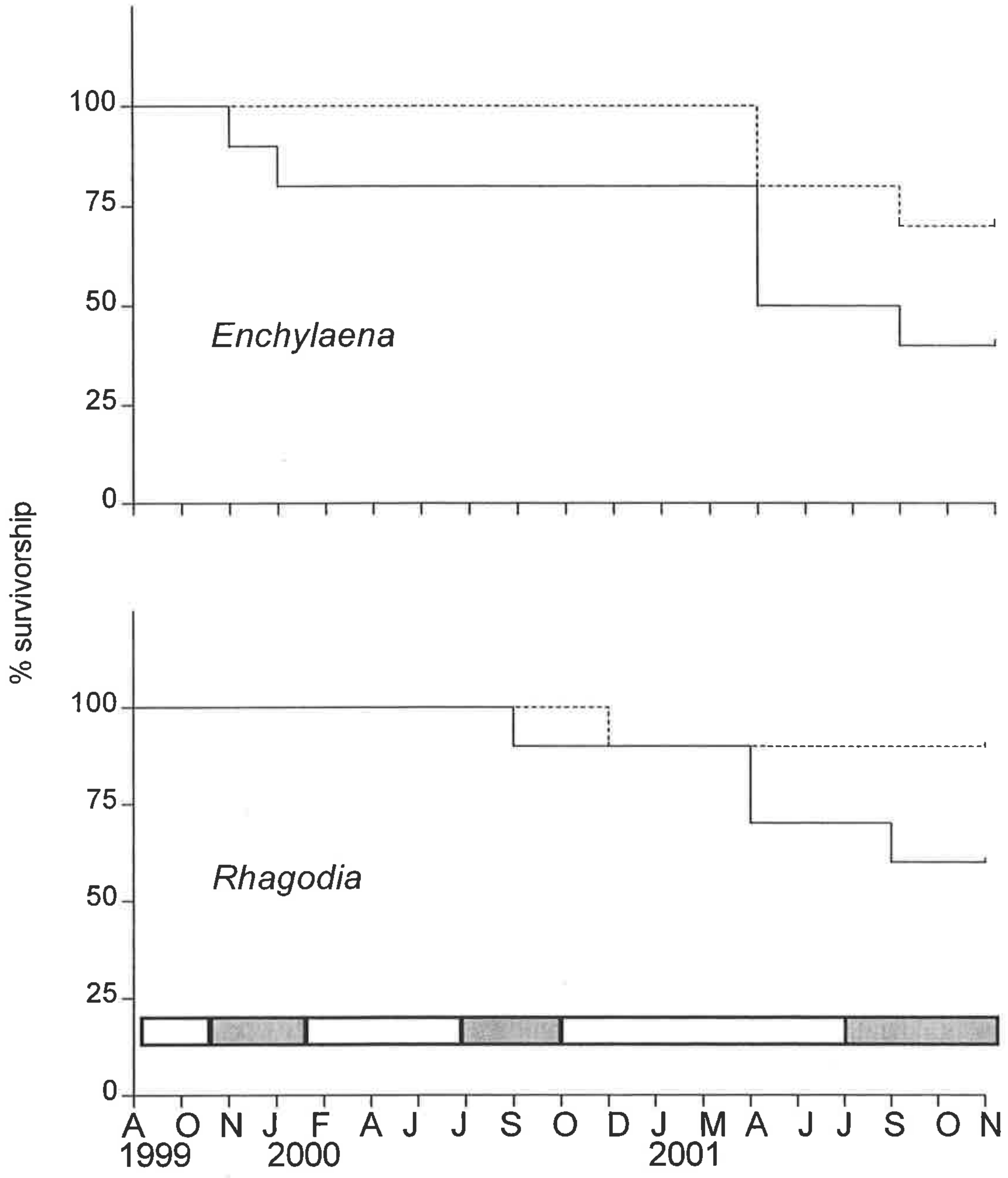


Fig. 4.7 Survivorship curves for *Enchylaena* and *Rhagodia* with competitors (—) and without competitors (---). The shaded horizontal bars on the x-axis represent pulse periods, the unshaded portions, interpulses. (Log rank tests comparing curves: *Enchylaena* $\chi^2 = 5.298, P = 0.15$; *Rhagodia* $\chi^2 = 2.076, P = 0.15$).

CHAPTER 5

The effects of nitrogen availability on the growth and response to competition of *Atriplex vesicaria*

Introduction

Although plant growth in arid systems is primarily limited by water availability, nutrients may also limit growth during rainfall pulses. Australian arid soils are low in nitrogen in relation to other arid systems worldwide (Charley and Cowling 1968). The effects of nutrients on competition, as distinct from competition for soil moisture, have been less frequently addressed in arid systems (Fowler 1986a). Competition intensity between plants in arid systems may not be affected by increases in nutrient availability if plants have a limited ability to respond to nutrient addition. In infertile sites plants commonly have traits leading to high nutrient retention rather than competitive ability for nutrient uptake (Aerts 1999). Thus they have low relative growth rates and a limited capacity to elevate nutrient uptake rates and therefore do not respond to nutrient additions by increasing growth rates (Chapin 1980, Aerts 1999). Rather than utilise N immediately for tissue growth, some species from low nutrient sites store N so the N content of tissue increases with N addition (Chapin 1980, Gerdol *et al.* 2002).

Mature *Atriplex vesicaria* leaves have a high N content (Beadle *et al.* 1957) but the N content of their litter is low suggesting efficient nutrient redistribution before leaf senescence. *Atriplex* also has a high relative growth rate when water and nutrients are available (Jones *et al.* 1970, Williams 1979). Osmond *et al.* (1980) hypothesised that this combination of high leaf nitrogen content and fast growth rates indicated that *Atriplex* might be very efficient at absorbing and utilising nutrients. They proposed that adaptations that allow it to persist and take advantage of temporal variations in nutrient supply are probably more advantageous than the ability to tolerate low nutrient levels. This suggests that not only would *Atriplex* respond to N addition by increasing growth rates but also it would be a good competitor for soil nutrients during pulses. There have been no field studies on the effects of N addition on *A. vesicaria* growth however *Atriplex vesicaria* plants grown in pots filled with soil from sites where it grows showed increased growth with additions of N and P (Cook, 1973 cited by Osmond *et al.* 1980). Natural populations of *Atriplex* growing in soils with *Acacia papyrocarpa* litter have higher leaf N than plants growing in litter-free soils, suggesting plants may store extra nutrients (Correll 1967) but this may be a long-term effect of growth in higher N soils. These findings suggest that *Atriplex* growth may be less nutrient-limited in the higher fertility sites beneath *Acacia* canopies.

Increased soil fertility beneath canopies may also explain the differences in competition intensity observed between sites in the previous competition experiment. Competition for nutrients may be more intense in the less fertile open sites. Several other studies have found that below-ground competition was more intense in sites (Wilson and Tilman 1993, Peltzer *et al.* 1998, Pugnaire and Luque 2001) or pot treatments (Welbank 1961, Rebele 2000) with lower fertility. There was no correlation between *Atriplex* competition intensity and soil moisture in either site, therefore competition for soil moisture may not be important for this species. Depending on the balance between above- and below-ground competition, fertility islands associated with tree canopies may have an indirect positive effect on plant growth by reductions in competition intensity. My data suggests that competition may be less intense in the fertility islands associated with *Acacia* trees (Chapter 4).

There is some evidence to suggest that *Atriplex* may compete with other plants for nutrients and the intensity of competition increases with decreasing soil fertility. This experiment explores the effects of N addition on *Atriplex* growth, leaf nitrogen content and competitive response. I tested two hypotheses. Firstly, that *Atriplex* growth is N limited in open sites but not in canopy sites; and secondly, that competition is more intense in open sites than in canopy sites when growth is N limited. I predicted that only plants growing in open sites would respond to nitrogen addition, as the growth of these plants was nutrient limited, and this would be a saturating response (Pastor and Bridgham 1999). If competition for other resources was also important then there will be differences in the elevations of curves for plants growing with and without competitors present (Fig. 5.1). To test these hypotheses I fertilised shrubs growing under the canopy and in open sites. I applied fertiliser at a range of application rates rather than at discrete rates, commonly used in ecological experiments, in order to contrast the response curves of different treatments. In addition, existing N-levels in this system are heterogeneous (Facelli and Brock 2000) therefore discrete fertiliser applications would not necessarily produce discrete levels of N-avaliability.

Methods

Experimental design

I used a factorial design to test the effects of competition and nutrients on the growth of shrubs in both canopy and open sites. I selected 80 mature *Atriplex* shrubs in Overland Paddock. I chose 40 shrubs beneath the canopies of *Acacia* trees, and 40 shrubs at open sites at a random bearing and distance from each tree, but at least 5 m and no more than 20 m from the canopy edge. For the competition treatments, I randomly allocated shrubs within each site as competition control or treatment shrubs. There were no significant differences between the mean initial sizes of shrubs in each treatment although shrubs varied in size (biomass estimated using equation (1); ANOVA $F_{3,\,80} = 1.944, P = 0.130$). In target or no-competitor shrubs, on 16/7/01 I removed the above-ground biomass of neighbouring shrubs and all biomass of annuals from a 2 m radius around each shrub. I had to remove ephemeral plants and re-sprouting shrub shoots again on 4/9/01 and 18/10/01. Neighbouring shrubs and annuals remained in place around control shrubs.

Fertiliser application

For fertiliser treatments I applied fertiliser to every shrub. I calculated a nitrogen application rate that would deliver to each shrub a random quantity of nitrogen ranging from zero up to twice the nitrogen level found in soils beneath tree canopies. Applications of fertilizer were quantified to produce similar total amounts of available nitrogen in both canopy and open sites, although the range may be greater in open sites as there is less total nitrogen in these sites; canopy soils have up to 1.3 g N/kg of soil while open soils only have 0.4 g N/kg of soil (Facelli and Brock 2000). As selected shrubs were not all the same size I adjusted fertilizer application rates for estimated plant leaf biomass by multiplying application rates by the ratio between target shrub biomass and median shrub biomass for that site. I estimated plant leaf biomass using the Adelaide technique (Andrew *et al.* 1979). Shrub branch sub-samples or hand held units (HHU) are used to estimate biomass (B) or leaf dry weight. This yielded the following regression:

$$B = -0.72 + 0.78\ \mathrm{HHU}\ (r^2 = 0.995) \qquad (1)$$

I added nitrogen as slow release granular fertiliser (Native Garden Osmocote™ 17:1.6:8.7 N:P:K, Scotts Australia Pty Ltd), applied at rates of up to 16 g N/m^2 for median sized shrubs under canopies, and 27 g N/m^2 for median sized shrubs in open sites. I lightly cultivated an area of soil

50 by 50 cm around every shrub to a depth of 1 cm on 18/7/01, before applying the fertiliser and then covered it with the loosened soil. Plants received only natural rainfall, although large rainfall events the month before the application of fertiliser and during September maintained soil moisture at high levels during the peak growing season (see Figs 4.1 & 4.3).

I measured plant responses in relation to available nitrogen rather than the amount of applied fertiliser. I collected soil samples for nitrogen analysis from under each shrub on 5/9/01, immediately prior to the peak growth of *Atriplex* in 2001 (see Fig. 4.2). I collected a pooled sample of 70 g of soil from a depth of 5 cm at five locations under each shrub. I sifted air-dried samples through a 1.18 mm sieve. They were analysed for available nitrite/nitrate and available ammonium using 2 *M* Potassium chloride extractions (Agronomy and Farming Systems Analytical Laboratories, University of Adelaide). Available nitrogen (N) was the sum of nitrate/nitrite and ammonium concentrations.

Plant responses

I estimated plant growth using two methods. First, I measured shrub growth by estimating plant biomass using the Adelaide technique on 27/11/01, yielding the following regression:

$$B = -1.66 + 3.14 \text{ HHU } (r^2 = 0.993). \qquad (2)$$

I then calculated the increase in whole plant leaf biomass or relative growth rate (RGR) as:

$$RGR = B_{(t)} - B_{(t-1)} / B_{(t-1)} \cdot \text{days} \qquad (3)$$

where $B_{(t)}$ was the final leaf biomass at time t (from equation 2), and $B_{(t-1)}$ was the initial leaf biomass (from equation 1). Second, I measured individual shoot growth by marking ten shoots on each shrub with a paint mark at a distance of 20 mm from the base of the most distal leaves immediately after fertilizer application in July 2001. I harvested a further sample of 40 shoots of 20 mm length from 20 non-experimental shrubs in each site, dried and weighed each shoot, and used the average shoot weight for each site as an estimate of the initial biomass of marked shoots. I harvested marked shoots at the paint mark on 27/11/01, and dried them to constant weight. I used equation (3) to determine shoot RGR with $B_{(t)}$ as final shoot biomass and $B_{(t-1)}$ as the estimated initial shoot biomass.

I used these shoots to determine leaf N content of each shrub. I removed all the leaves from the stems and ground the leaves to a powder. The total nitrogen content of the homogenised sample was estimated using the Kjeldahl digestion technique (Waite Analytical Services, University of Adelaide).

Analyses

I used ANCOVA to explore differences in nitrogen availability between sites and competition treatments after fertiliser addition, with fertiliser application rates as the covariate. I transformed these data before analyses to satisfy assumptions of normality and linearity between the covariate and each response variable. I used a non-parametric procedure (Wilcoxon-Kruskal Wallis test) to test the effect of site on the ratio of nitrite/nitrate: ammonium.

To test the effects of N-addition on plant growth, I used non-linear regression of available N as the independent variable and shrub growth indices (either shoot or shrub RGR) as the dependent variable for each competition and site treatment. I fitted the data to a rectangular hyperbola with the following equation:

$$\text{Growth rate} = B_{\max} \cdot N / (Kd + N) \tag{4}$$

Where $B_{\max}$ is the maximum or plateau growth rate, and Kd is the amount of total available N where growth rate is half of $B_{\max}$ (Fig. 5.1). It is also possible that high concentrations of nitrogen may have a negative effect on plant growth (Haynes 1986, Pastor and Bridgham 1999). If this is the case then a quadratic equation may provide a better fit for the data (Underwood 1997). This model is of the form:

$$\text{Growth rate} = A + B \cdot N + C\,N^2 \tag{5}$$

where N is available nitrogen and A, B, and C are constants. I used F tests to determine which curve gave the best fit to the data. I used GraphPad Prism software (Ver. 3.02, GraphPad Software, San Diego, Ca.) for all non-linear analyses.

I analysed leaf N content in the same manner but only used the hyperbolic equation. In this case I predict that only plants in open sites will store nitrogen with increasing N availability, so the responses should be similar as for growth (Fig. 5.1). However, I also predict that this response will only occur if there are no significant growth responses to available N.

I also analysed the data by grouping available N into five levels: < 20, 20-40, 40-70, 70-100 and > 100 mg N/ kg soil. I chose these levels to distribute sample sizes as evenly as possible across treatments. These levels were used as an effect in analysis of variance procedures. I used an ANOVA model testing the effects of site, competition and available N and their interactions on shoot RGR and leaf N content. There was a significant positive correlation between initial shrub size and shrub RGR therefore I tested the same model effects on shrub RGR by ANCOVA, with initial shrub size as a covariate. I transformed variables for these analyses to meet the assumptions of ANOVA and ANCOVA. I used JMP IN (Ver. 4.0.3) software for all analyses of variance and covariance.

Results

Available nitrogen

There was a significant positive linear relationship between the rate of fertiliser application and total available N in both sites (Fig. 5.2). Competition treatments had no significant effects on available N (Table 5.1); nitrogen was not reduced to lower levels in treatments with neighbouring plants present. Although more fertiliser was added to open sites, the overall amount of available N did not differ between sites (Table 5.1). Canopy soils were significantly depleted in ammonium in relation to nitrite/nitrate (W-KW test, $Z = -3.39$ $P < 0.001$) with canopy soils having less ammonium than open sites (marginal significance, Table 5.1) but there was no significant difference in the concentration of nitrate/nitrite between sites (Table 5.1, Fig. 5.3). The range of available N was also greater in open sites but the range was greater towards the maximum values rather than the minimum values (Fig. 5.3).

Plant responses

Neither shoot or shrub RGR, or leaf N content responses to available N showed a good fit to a hyperbolic model in any of the treatment combinations (Table 5.2). Although hyperbolic curves provided better fits than quadratic equations for growth parameters (Table 5.3), no function satisfactorily described the relationship between nitrogen availability and growth rates or leaf N content (Fig. 5.4). Shoot RGR showed the best fit to the model for plants without competitors or plants in open sites (highest R^2 values), but model parameters had large confidence intervals (Table 5.2).

By grouping available N into five levels some significant effects of soil nitrogen status on plant growth were detected. Site, competition and soil fertility had significant effects on shoot RGR (Table 5.4a). Plants in both sites responded similarly to available N, as the interaction between N level and site was not significant (Table 5.4a). Shoot elongation rates were significantly greater for plants growing in soils in the range 20 – 40, 70 – 100 and > 100 mg N/ kg soil than in soils with less than 20 mg N/ kg soil (Fig. 5.5). Shoot RGR was also greater in plants growing in open sites and for plants growing without neighbours (Fig. 5.6A).

Competition and site had significant effects on shrub RGR, but soil fertility had no significant effect (Table 5.4b). Plants growing without neighbours and plants growing in open sites had higher RGR than plants with neighbours or plants beneath *Acacia* canopies (Fig. 5.6B). Nutrient addition and neighbours had the same effects on shrub RGR in both sites, as the interactions were not significant (Table 5.4b). In addition, smaller plants had higher relative growth rates than larger plants (Fig. 5.7A). It was not possible to calculate relative competition intensity using this experimental design. However, the RGR of plants with neighbours in open sites was 74% of the RGR of plants without neighbours, but in canopy sites it was 86% (Fig. 5.6B); therefore there was some evidence that competition was more intense in open sites.

Plants in canopy sites had significantly higher leaf N contents than plants in open sites (Fig. 5.7B), but the level of available N had no significant effect on leaf N content (Table 5.4c). *Atriplex* growing in canopy sites had leaf N contents of 2.35 ± 0.06% (mean ± 1 SE) and in open sites of 1.91 ± 0.04%. *Atriplex* plants without neighbours had significantly higher leaf N contents than plants with neighbours (Table 5.4c).

Discussion

Atriplex responded to nutrient addition by increasing individual shoot growth but I did not detect a response in whole shrub RGR to an increase in available N, nor did plants accumulate N in leaf tissue. The site in which plants were growing had significant effects on plant nitrogen status and growth rates. Plants growing under canopies had higher leaf N content but plants in open sites had higher growth rates. However, these differences may reflect variation in light climate between the two sites rather than trade-offs between N accumulation and growth. Neighbouring plants negatively affected the RGR and leaf N content of *Atriplex* in both sites, but the effects of neighbours on RGR was greater in open sites.

Responses to nitrogen addition

The results suggest that *Atriplex* responds to very small increments in available N, but any additional nutrients have little further effect on growth, i.e. N uptake becomes rapidly saturated. Adding nutrients increased the growth rate of individual shoots but probably did not affect the growth of new shoots from the base of the plant or on existing stems, as nutrient addition did not improve overall RGR. This growth may have been supported by carbohydrate reserves that accumulate over the dry season in *Atriplex* (Coleman 1982), or mobilisation of existing N reserves in the plant, with nutrient uptake supporting apical growth. Alternatively, measurements of individual shoot growth could be made more accurately than whole shrub growth rates. The coarser growth measurements may not have been sensitive enough to detect changes in growth rate with N addition.

The effects of nutrient addition did not differ between sites despite differences in background nutrient content. It was predicted that plant growth in canopy sites would not be nutrient-limited and growth would be at its plateau position. The range of available N in canopy sites was similar to that in open sites. There were also low values for available N in canopy sites in addition to open sites, therefore plants may have been N-limited in both sites. Soils in canopy sites were ammonium depleted although equal amounts of ammonium and nitrate were added. Cooler soil temperatures and higher organic matter in canopy soils may have increased the activity of soil bacteria, with losses of ammonium to nitrification (Haynes 1986). Plants preferentially take up ammonium when temperatures are cooler (Haynes 1986) and this may also have lowered ammonium concentrations in canopy soils that may be cooler than open soils. The higher organic matter in canopy soils (Facelli and Brock 2000) may also increase the uptake and sequestering of N by microbial decomposers, decreasing its availability to plants. This may explain why canopy soils did not have more available N than open soils at low fertiliser application rates.

Leaf N content

Higher leaf N contents in plants in canopy sites may reflect the accumulation of N over longer time scales in these N-rich sites, and therefore the addition of N had no detectable effect on leaf N (reserve storage rather than accumulation, see Chapin *et al.* 1990). Leaf nitrogen contents of desert shrubs are similar to those of shrubs from more mesic systems, even though soil nutrients are inherently lower (Killingbeck and Whitford 1996, Reich *et al.* 1999). The temporal and spatial heterogeneity of soil resources in arid systems can result in instances of high nutrient availability in either space or time reducing selection pressures typical of consistently low-N environments (Killingbeck and Whitford 1996). This may lessen the importance of strategy shifts between high nutrient storage or retention and high RGR (Aerts and Chapin 2000). Because of the wide variability of plant responses to resource inputs in arid systems there will be plants that grow in response to nutrient pulses (such as *Atriplex*) and slow-growing species that store nitrogen in excess of growth requirements during these pulses.

Nitrogen content per leaf mass may be confounded by differences in leaf morphology with shading. *Atriplex vesicaria* leaves produced in shade are larger and thinner than high-light produced leaves (Black 1954) and have a greater specific leaf area (SLA, Chapter 8). Although SLA was not measured in this experiment, leaves produced in canopy sites were observed to be larger and thinner than leaves produced in open sites. SLA may be a function of a thicker leaf, a higher cell density, or a combination of these features (Witkowski and Lamont 1991). Leaf nitrogen concentration is not affected by leaf thickness so leaves with a larger SLA will have a higher N content; leaf N scales proportionally with leaf size (Garnier *et al.* 1997). However, if smaller, thicker leaves have a higher cell density, especially a greater proportion of N-free cell wall material, then leaf N will not scale proportionally with leaf size (Witkowski and Lamont 1991, Garnier *et al.* 1997). Leaves with a small SLA may have less N on a weight basis but similar N on an area basis as leaves with larger SLA.

The variation in thickness of *A. vesicaria* leaves is produced by changes in the layer of vesicular hair cells on the leaf surface (Black 1954). Shade-grown leaves have a thinner layer of these thin-walled cells than leaves grown in high-light or dry conditions (Black 1954). Cell size does not change with leaf size (Black 1956a) and in another species, *A. triangularis*, cell density does not appear to change with leaf thickness (Osmond *et al.* 1980). Therefore variation in the SLA of *A. vesicaria* with light climate may be a result of changes in leaf thickness and the density of the vesicular layer. Consequently leaf N concentrations per mass are expected to increase with increases in leaf area.

Although shade leaves had a higher N content on a mass basis the N content on an area basis may be similar or even greater in smaller, high-light grown leaves. This is because leaf N content per area is the quotient of leaf N content per mass and leaf area per mass (Wright and Westoby 2001). Differences in growth rates between sites are probably not correlated with leaf N content (negative in this case), and are more likely to be correlated with differences in light levels in the two sites.

Site effects

Plants grew more in open sites than under canopies, regardless of competition or nutrient status. This suggests that under conditions where nutrients and water do not limit growth reduced light levels beneath *Acacia* canopies may limit *Atriplex* growth. *Atriplex* carbon assimilation rates and biomass were reduced when grown under light levels similar to those found beneath *Acacia* canopies in a pot experiment (Chapter 8). Field studies have also shown that *A. vesicaria* shrubs in full sunlight have greater assimilation rates than shrubs under *Acacia* canopies, but only during the morning before they became water stressed (Hay 1998). Light limitations may also reduce the plants ability to elevate nutrient uptake capacity (Jackson and Caldwell 1992) or respond to patches of nutrient enrichment by increasing root growth into those patches (Bilbrough and Caldwell 1995).

Competition

The results from this experiment reinforces those from the previous competition experiment, demonstrating that competition does affect the above-ground growth of *Atriplex* and competition is more intense in open sites. The lack of an interaction between competition and available N provides support for the hypothesis of Osmond *et al.* (1980) that *Atriplex* may be able to utilise soil N more efficiently than its neighbours. Removal experiments measure competitive responses rather than competitive effects (Goldberg 1990). If *Atriplex* is more efficient at absorbing and utilising soil N than its neighbours then its response to neighbour removal may not change with increasing nutrients. However, intraspecific competition could affect resource uptake and removal of conspecific neighbours would therefore increase growth rates. But at Middleback, *Atriplex* occurs in mixed stands with other species and only a small proportion of the biomass removed from treatments were conspecifics. Intraspecific competition may not be very important in this system. As neighbour removal did improve *Atriplex* RGR, competition for other resources also affects *Atriplex* growth. However, as neighbours affected leaf N contents, there is some evidence that nitrogen uptake is affected by competition but this was not related to the amount of available N in the soil.

Sources of variability

Although *Atriplex* had a limited growth response to N addition, there was considerable variability in this response. One source of variability was initial plant size. I used naturally occurring plants, as I wanted to assess the competitive response of mature plants. Fertiliser added to small plants could have more effect on growth than fertiliser added to large plants, as it would be concentrated in the region of most roots. Although *Atriplex* has the greatest percentage of its root system immediately below the crown, roots can extend up to 2m from the shrub centre (Jones and Hodgkinson 1970). Measurements of available N taken from below the shrub crown may therefore not be representative of the N available to the entire root system and this effect would be magnified for larger plants.

Soil nutrient heterogeneity is a further source of variation. Nitrogen levels in soils similar to those occurring at the field site can fluctuate twofold at small spatial scales (Cowling 1978). This experiment also showed that responses to N-addition are likely to occur even after minor additions of fertiliser. More samples in the lower range of fertiliser application rates would enable a better description of the non-linear response to N-availability. Most ecological nutrient addition experiments examine growth responses at discrete fertiliser application rates, typically with levels of zero, low and high addition. Such application methods are more likely to detect differences between treatments than varying the gradient as I did, but they are limited in their applicability to what may happen under natural conditions.

Summary and conclusions

Atriplex growth responded to small increases in N but there was no evidence of N accumulation in leaves with N addition. Plants without neighbours had higher leaf N contents and this may have contributed to the higher growth rates of these plants although competition for other resources also occurred. Competition for N could be important for *Atriplex*, although because *Atriplex* may respond to very minor additions of N (or be very effective in elevating N uptake) more experiments in the range of small N additions are warranted. As there was no interaction between site, competition or nitrogen addition, higher competition intensities in open sites were not related to differences in N availability. However, the site that plants were growing in had significant effects on growth and leaf N content. Although plants growing beneath canopies had higher leaf N contents they grew less than plants in open sites. Plants beneath canopies had higher mass-based leaf N contents, but area-based leaf N may not have differed between plants growing in either site. The higher N levels beneath canopies may be important in improving the N status of plants in these sites enabling them to tolerate the lower light levels in these sites. Existing N and light levels beneath canopies may still be limiting to *Atriplex* growth when water is available. These effects will be explored in the following chapter.

Table 5.1 ANCOVAs testing the effects of site and competition (C) and their interaction on the availability of different forms of nitrogen in the soil. Each model has the amount of applied fertiliser (AF) as a covariate. * Marginally significant difference, open > canopy at $\alpha < 0.05$.

Source	**df**	SS	***F***	***P***
Total Nitrogen				
AF	1	187.467	22.747	<0.001
Site	1	5.691	0.691	0.409
C	1	9.383	1.139	0.289
Site/C	1	0.399	0.048	0.827
Error	75	618.107		
Ammonium				
AF	1	35.507	22.293	<0.001
Site	1	6.245	3.921	0.051*
C	1	3.467	2.177	0.144
Site/C	1	2.322	1.458	0.231
Error	75	119.454		
Nitrate/nitrite				
AF	1	11.553	17.608	<0.001
Site	1	1.729	2.636	0.109
C	1	0.781	1.190	0.279
Site/C	1	0.060	0.092	0.763
Error	75	49.207		

Table 5.2 Results of non-linear regression fitting separate hyperbolic curves for the responses of *Atriplex vesicaria* to nitrogen availability in sites beneath *Acacia* canopies or open sites, with neighbouring plants present (+ C) or removed (– C). B_{max} represents the maximum or plateau growth or leaf N content and Kd is the amount of available nitrogen when growth or leaf N content is half B_{max}.

Treatment	**B_{max} (± 95% CI)**	**Kd (± 95% CI)**	**R^2**
Shoot RGR (mg mg^{-1} d^{-1})			
Canopy – C	0.396 ± 0.201	12.63 ± 27.88	0.187
Canopy + C	0.234 ± 0.213	5.78 ± 42.52	0.009
# Open – C	0.583 ± 0.259	9.70 ± 23.99	0.149
Open + C	0.415 ± 0.197	11.28 ± 31.04	0.155
Shrub RGR (g g^{-1} d^{-1})			
Canopy – C	0.020 ± 0.005	2.07 ± 6.78	0.038
Canopy + C	0.016 ± 0.007	-0.35 ± 13.22	0.000
Open – C	0.036 ± 0.016	1.77 ± 11.28	0.013
Open + C	0.026 ± 0.006	0.80 ± 5.36	0.006
Leaf N content			
Canopy – C	2.43 ± 0.17	0.47 ± 1.38	0.030
Canopy +C	2.42 ± 0.38	1.95 ± 5.91	0.028
Open – C	2.04 ± 0.12	0.71 ± 1.16	0.101
Open +C	1.86 ± 0.18	0.62 ± 1.94	0.028

Table 5.3 F-tests comparing the fit of a hyperbolic and a quadratic model to the non-linear regression between *Atriplex* growth rates and available nitrogen. The null assumption is that the hyperbolic model is the best fit. The null hypothesis was not rejected at $\alpha < 0.05$. Treatment labels as in Table 5.2.

Treatment	**Quadratic model** **SS (df =17)**	**Hyperbolic model** **SS (df =18)**	***F***
Shoot RGR			
Canopy – C	0.447	0.513	2.509
Canopy + C	0.806	0.803	0.064
Open – C	1.388	1.346	0.531
Open + C	0.899	0.858	0.813
Shrub RGR			
Canopy – C	0.0009	0.0009	0.326
Canopy + C	0.0032	0.0015	0.052
Open – C	0.0111	0.0113	0.296
Open + C	0.0020	0.0021	0.702

Table 5.4 Results of a, c) ANOVA and b) ANCOVA testing the effects of site (S), competition (C), and level of available nitrogen (N) and their interactions on the responses of *Atriplex vesicaria* plants. Initial biomass was used as a covariate in the ANCOVA model. Significant difference between treatments at * $\alpha < 0.05 > 0.01$, ** $\alpha < 0.01 > 0.001$, *** $\alpha < 0.001$.

Source	**df**	SS	***F***	***P***
a) *Shoot RGR*				
S	1	0.306	7.038	0.010*
C	1	0.260	5.975	0.017*
N	4	0.503	2.894	0.029*
S/C	1	<0.001	<0.001	0.998
S/N	4	0.046	0.266	0.899
C/N	4	0.125	0.717	0.583
Error	64	2.784		
b) *Shrub RGR*				
Initial biomass	1	5.339	26.814	< 0.001
S	1	0.927	9.676	0.003**
C	1	2.011	10.102	0.002**
N	4	0.388	0.487	0.745
S/C	1	0.004	0.020	0.889
S/N	4	0.012	0.015	1.000
C/N	4	1.184	1.486	0.217
Error	63	12.554		
c) *Leaf N content*				
S	1	0.895	44.988	<0.001***
C	1	0.083	4.183	0.045*
N	4	0.106	1.327	0.270
S/C	1	0.023	1.168	0.284
S/N	4	0.062	0.777	0.544
C/N	4	0.083	1.046	0.391
Error	64	1.273		

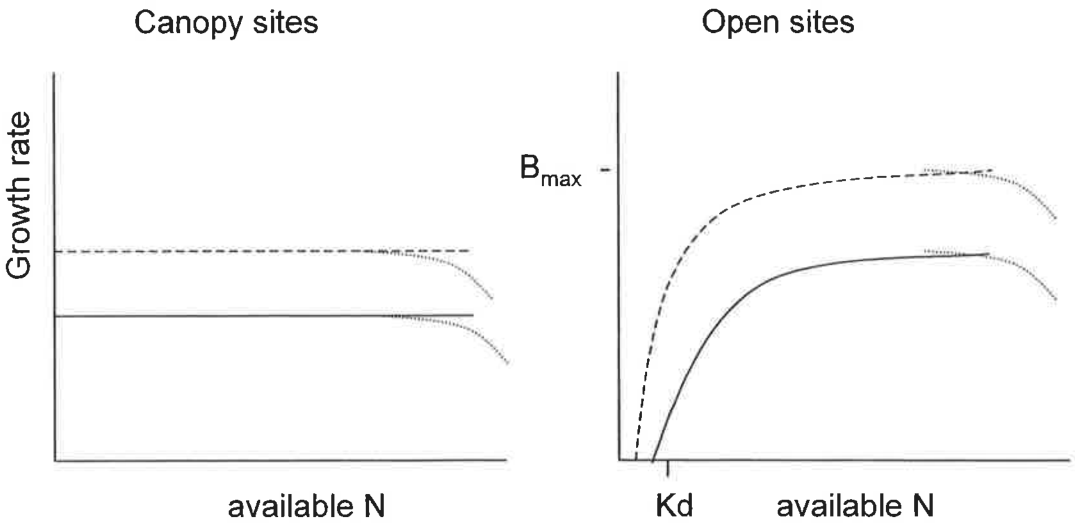


Fig. 5.1 Predicted relationships between growth and available nitrogen for plants growing with competitors (—) and without competitors (---) in sites beneath *Acacia* canopies and in the open. B_{max} is the plateau growth rate for the competitor free curve and Kd is the amount of available nitrogen when the growth rate is half its maximum. For open sites the curve is : Growth rate = $B_{max} \cdot N / (Kd + N)$. If high nutrient levels are toxic to plant growth curves will follow the dotted lines (……) and the curve equation is quadratic: Growth rate = $A + B \cdot N + C N^2$.

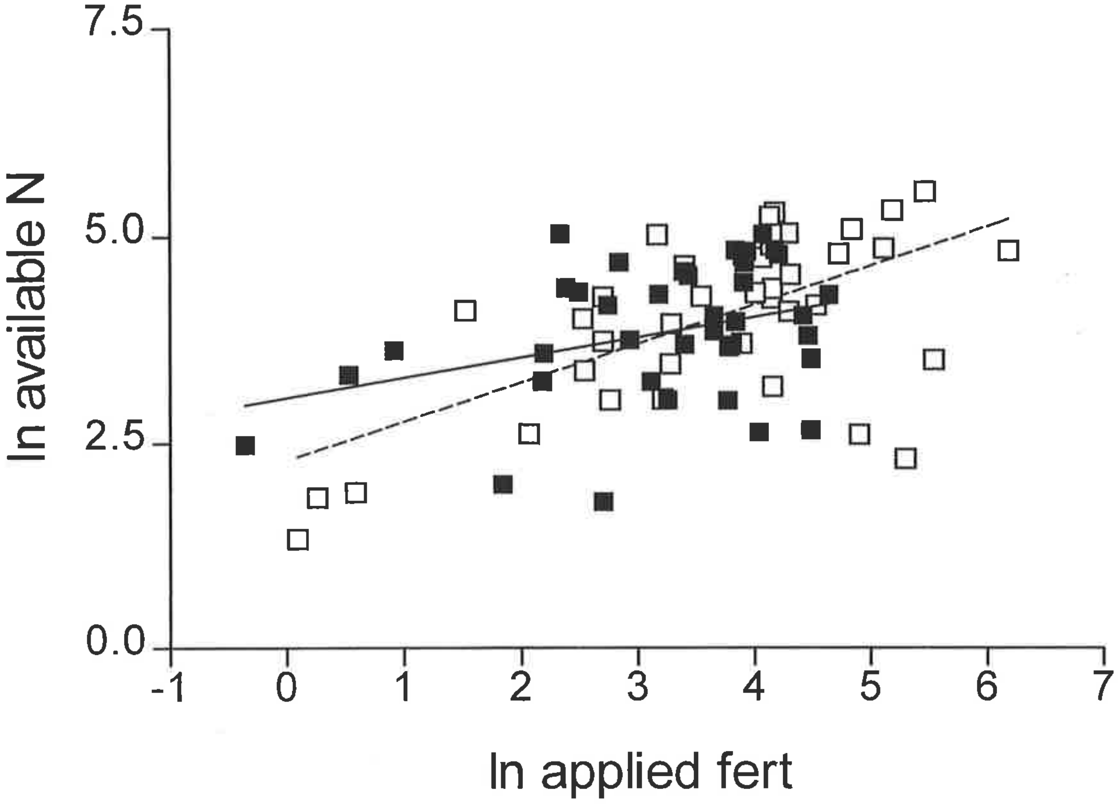


Fig. 5.2 Relationship between log normal fertiliser application rates and log normal available N in September 2001 in canopy sites (■—) and open sites (□---). The regression lines for each fit are: canopy, $y = 3.05 + 0.24x$, $r^2 = 0.11$ $P = 0.035$; open, $y = 2.93 + 0.47x$, $r^2 = 0.39$ $P < 0.001$. The slopes and intercepts for the two curves do not significantly differ. (Slopes $F = 2.33$ $P = 0.13$, intercepts $F = 0.01$ $P = 0.92$).

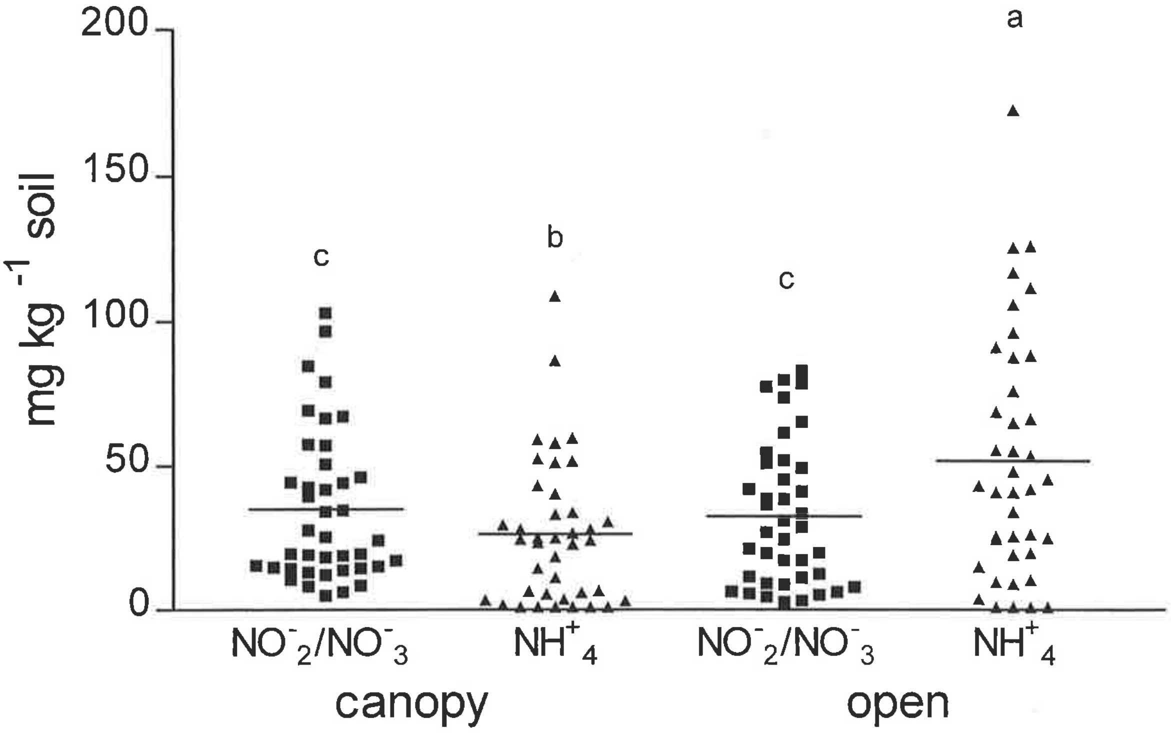


Fig. 5.3 Amounts of nitrite/nitrate (squares) and ammonium (triangles) in soils sampled from beneath *Atriplex* shrubs growing under canopies of *Acacia* (canopy) or in open sites (open). The horizontal bars are means. Columns labelled with different letters were marginally significantly different, nitrogen types analysed separately (site effect in ANCOVA anlaysis $\alpha = 0.051$, Table 5.1).

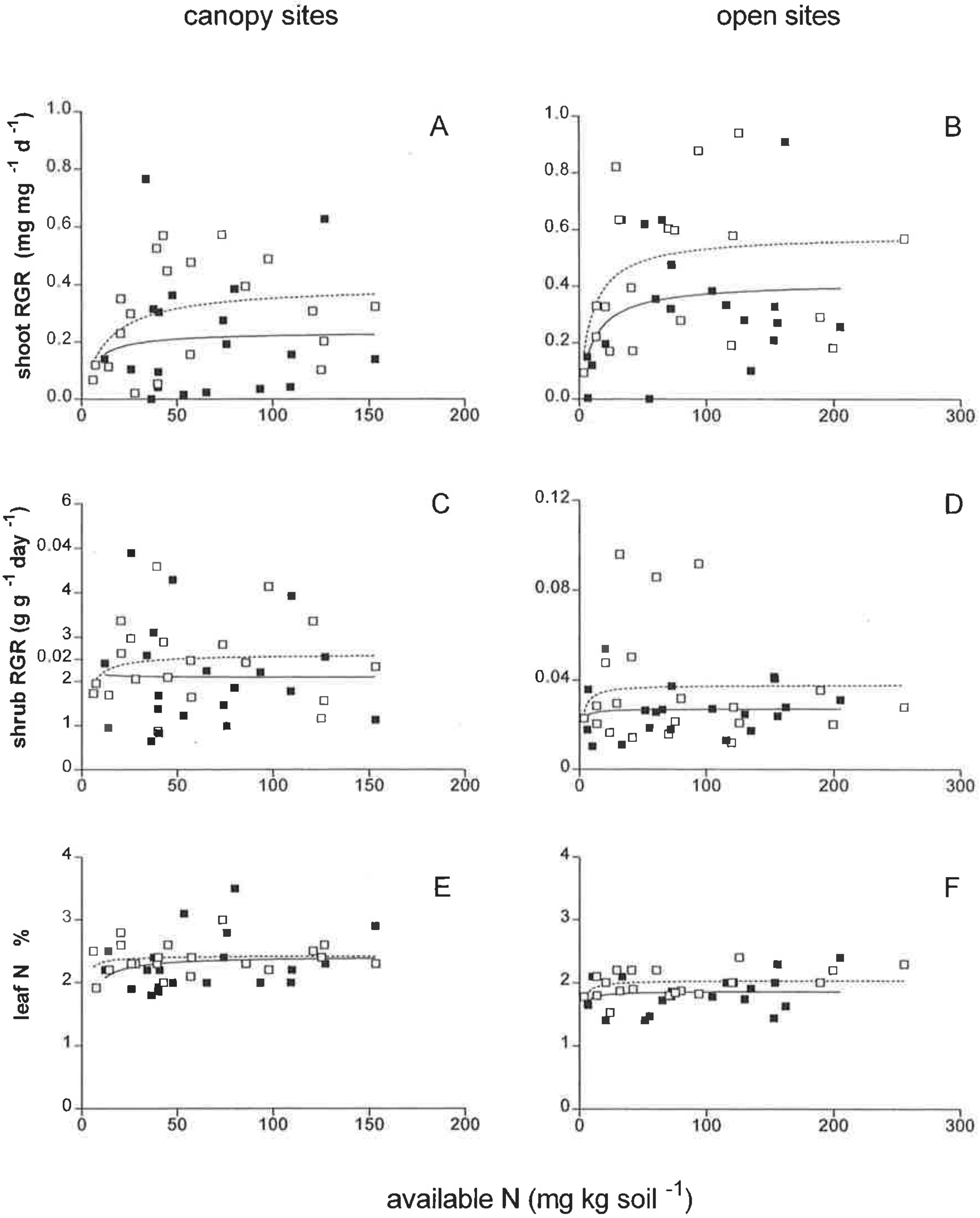


Fig. 5.4 Shoot RGR (A, B), whole shrub RGR (C, D), and leaf N content (E, F) in relation to available N in soil samples for *Atriplex* growing in sites beneath *Acacia* canopies and in open sites with (■—) and without competitors (□---). The curves fitted to the data points are rectangular hyperbolas (see Table 5.2 for curve parameters). The goodness of fit in each case is not better than the fit of a horizontal line . Note different x-axis scales for each site and different y-axis scales for C, D.

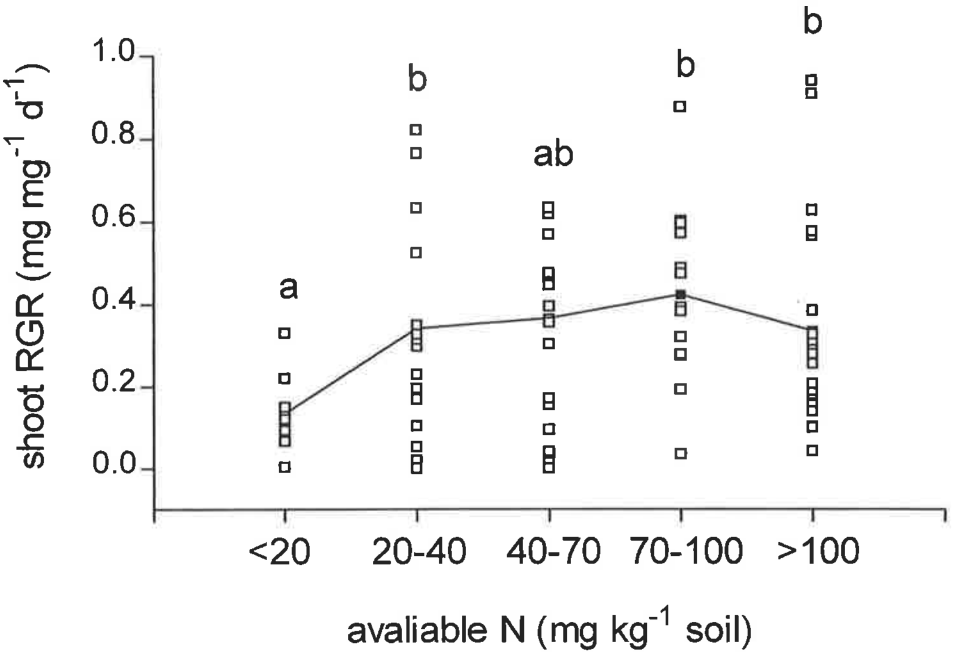


Fig. 5.5 Scatterplot of shoot relative growth rates in *Atriplex* at five levels of available N. The line connects the means. Columns labelled with different letters were significantly different at $\alpha < 0.05$ (Student's LSD tests; null hypothesis $1 < 2 < 3 = 4 = 5$).

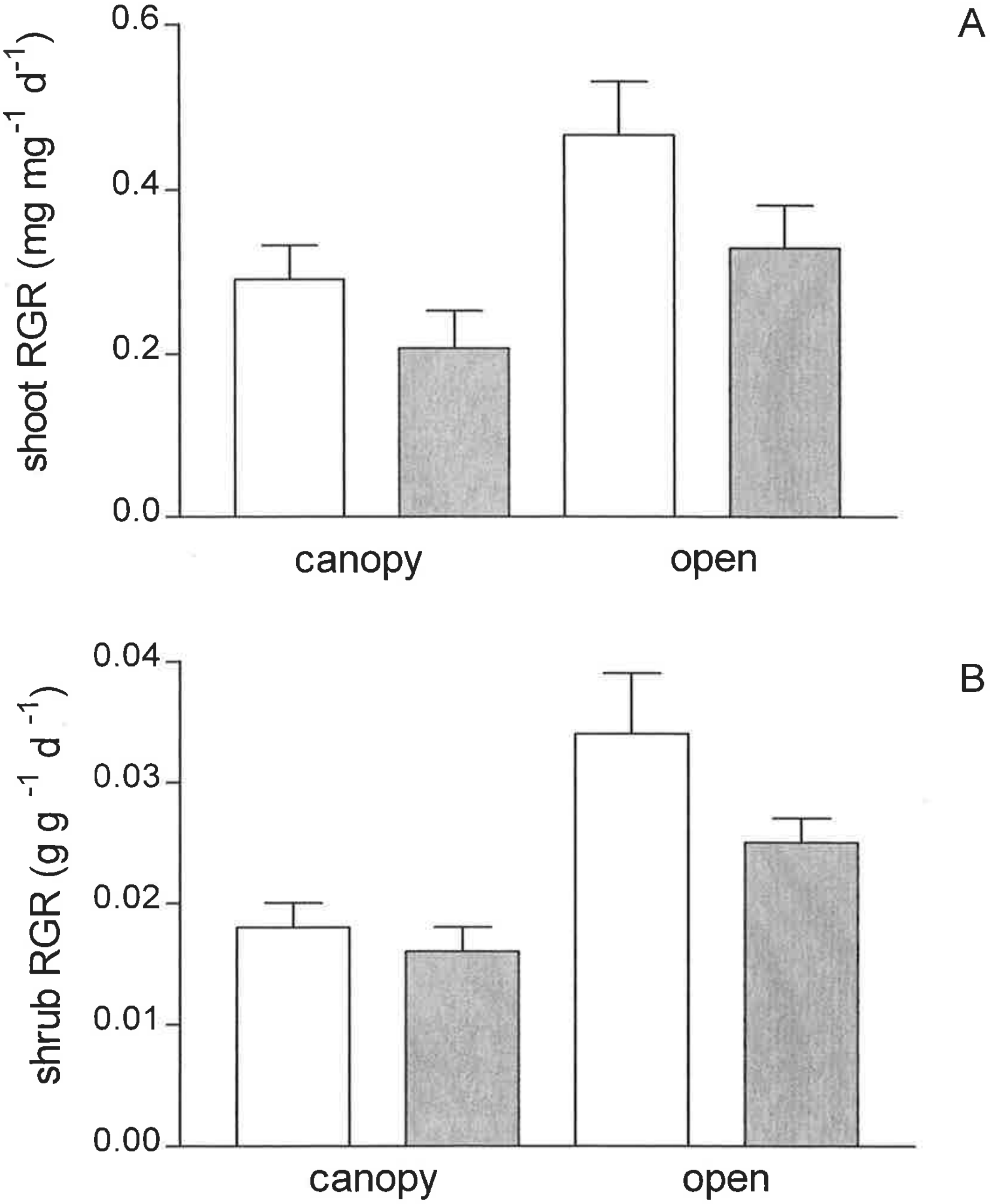


Fig. 5.6 Mean (+ 1 SE) of A) shoot relative growth rate (RGR) and B) whole shrub RGR of *Atriplex,* in canopy and open sites with neighbours present (shaded bars) or removed (unshaded bars). Growth was significantly greater in open sites and without competitors using both growth indices (ANOVA see Table 5.4).

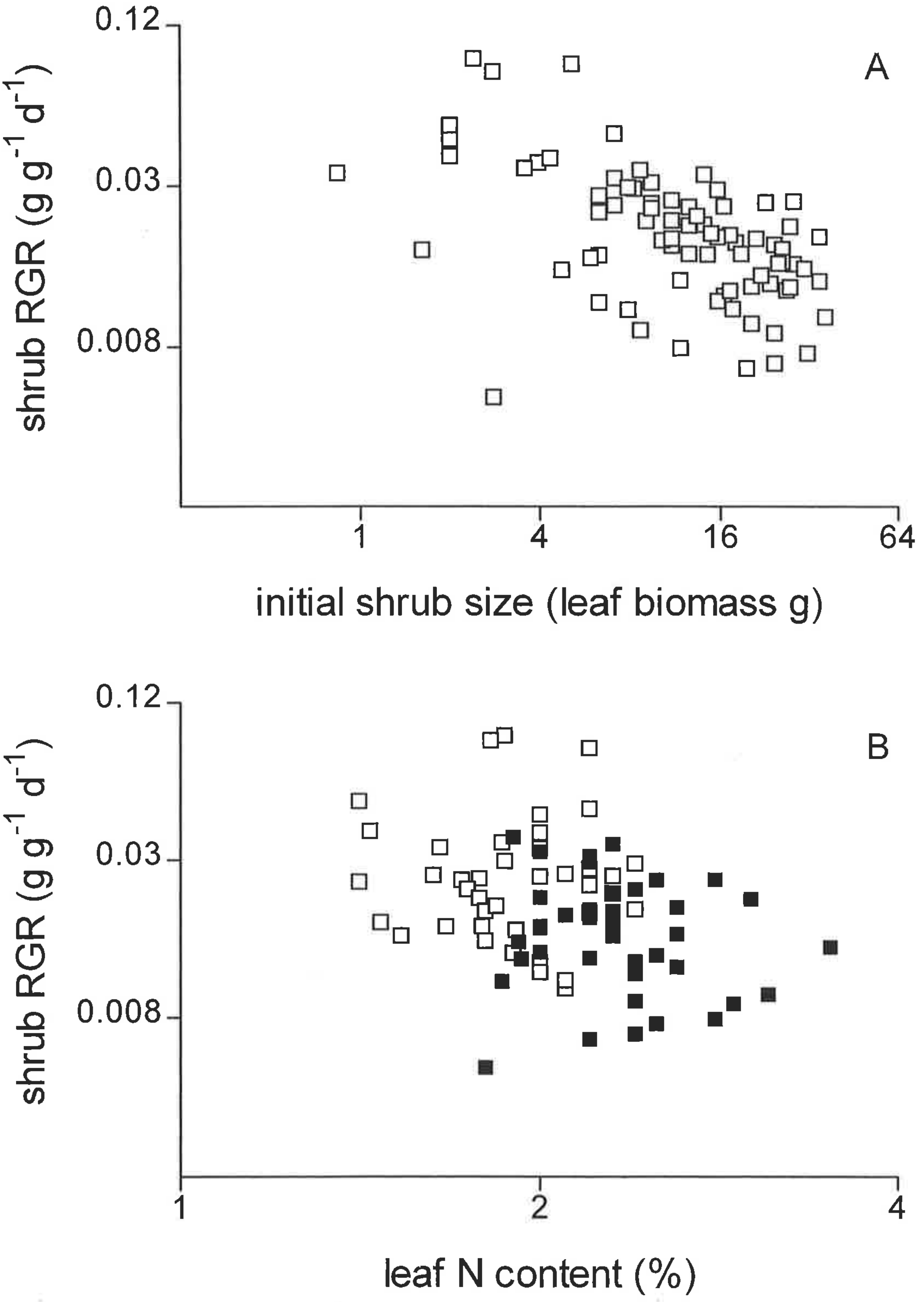


Fig. 5.7 The relationship between A) initial shrub size and shrub relative growth rate (RGR) for all experimental *Atriplex* plants and B) shrub RGR and leaf N content for *Atriplex* growing in open sites (unshaded squares) and canopy sites (shaded squares). Note log scales of both x- and y-axes.

CHAPTER 6

Temporal shifts in the effects of microclimatic and soil modifications by *Acacia papyrocarpa* on shrub performance

Introduction

The modifications of the environment produced by tree canopies may enhance the growth, survival or fitness of plants growing beneath them (Callaway 1995). The extent to which trees facilitate the growth of understorey plants at different times will depend on the differing requirements of these species for light and below-ground resources, and their tolerance of environmental conditions, at different life stages (Callaway and Walker 1997). This temporal variability occurs at different scales relevant to the life cycles of the interacting plants and can range from intra- and inter-seasonal scales to interannual or larger scales (Ehleringer *et al.* 1999).

Although shade can have a negative impact on plant growth, the positive benefits of other microclimatic or soil modifications beneath plant canopies could outweigh this (Holmgren *et al.* 1997). However, it is difficult to determine whether positive effects on plants growing beneath others are due to microclimatic or soil modifications. Either or both of these mechanisms may be important in producing positive effects on the performance of plants growing in this microhabitat. In arid systems where plant growth and survival can be frequently limited by water availability, reduction of water stress has important benefits for plants growing in the shade of other plants. Decreased evaporative demand beneath canopies and modified soil properties both have implications for plant-water relations. Water limitation is more common during the summer, when temperatures and radiation loads are high producing multiple stresses on plants at these times (Valladares and Pearcy 1997). Plant canopies in arid systems may ameliorate water stress in plants growing beneath their canopy through both direct and indirect means. The alleviation of other stress factors, such as thermal, radiation, and nutrient stresses, may lessen the impacts of water stress (Nilsen and Orcutt 1996, Valladares and Pearcy 1997).

Bertness and Callaway (1994) predicted that positive interactions would occur more frequently as conditions become more stressful. Interannual studies of interactions comparing wet years and dry years have frequently found positive interactions in the drier years and negative interactions during the wetter years (Greenlee and Callaway 1996, Kitzberger *et al.* 2000, Ibáñez and Schupp 2001). Similarly, comparisons of plant associations between low and high stress sites found that positive interactions were more frequent in high stress sites (Greenlee and Callaway 1996, Pugnaire and Luque 2001). In arid systems where rainfall is typically pulsed, there may be several changes in the direction of interactions within a year in response to rainfall inputs. However, very few studies have examined changes in interaction intensity within or beyond the main growing season (but see Holzapfel and Mahall 1999). Perennial woody plants that may sustain growth outside the main growing season (or between large rainfall pulses) have the potential to be positively affected differentially throughout the year. In addition, various life stages may have differential responses to the habitat modifications imposed by large trees. Newly emerged plant seedlings are the most vulnerable to desiccation therefore shading may promote establishment but have a negative or neutral effect on subsequent growth and the performance of the mature plant (Barnes and Archer 1996, Anderson *et al.* 2001).

In this experiment, I test the responses during early establishment phases of two woody perennial species to habitat modifications by *Acacia* canopies. I aim to determine whether soil or microclimate modification affect seedling emergence and the growth and survival of seedlings during their first summer, which may be one of the most stressful periods for plant establishment. I selected two species that had different distributions in relation to *Acacia*: *Atriplex vesicaria* and *Enchylaena tomentosa*. My second aim is to examine how the effects of facilitation change over time by comparing responses over a temporal gradient of increasing abiotic stress or resource shortage. My hypotheses, based on species distributions, are that *Acacia* will have an overall positive effect on *Enchylaena*, but an overall neutral effect on *Atriplex*. I predict that *Enchylaena* seedlings are unable to survive the stressful conditions occurring outside canopies, but *Atriplex* is able to tolerate conditions in both microsites. I expect positive interactions to be more frequent or more intense during the more stressful season, which in this system occurs during late summer to early autumn when temperatures are highest and soil moisture is lowest, due to high evaporation rates. I propose that the primary mechanism by which trees facilitate perennials is by ameliorating water stress through altering either microclimate and/or soil properties.

Methods

Study site

I conducted this study in Railway Paddock. Rainfall during the first year of this study (June 2000 to April 2001) was 170 mm, with 99 mm between June and September (winter to early spring). During the second year of this study (June 2001 to April 2002), there was 276 mm of rainfall, with 204 mm between June and September. The maximum winter temperatures in June were similar in 2000 and 2001 (17 °C) but summer maxima in January were higher in 2000 (35°C) than in 2001 (29 °C) (Fig. 2.1B).

Experimental design

I used manipulative field experiments to examine the effects of *Acacia* microclimates and soils on the emergence, growth and survival of *Atriplex* and *Enchylaena* seedlings. I established ten replicate blocks of two plots under an *Acacia* canopy and two plots in an adjacent open site. I placed plots under mature *Acacia* trees with continuous canopy cover and branches that did not reach the ground on the southern side of the tree. I chose this aspect to minimize variability in light climate between canopies and over time. I cleared two plots (1.5 m x 1m) on the southern side of trees and in open spaces adjacent to each tree but at least 15 m from any tree. I further subdivided each plot into six randomly assigned subplots (Fig. 6.1) each 25 cm by 25 cm with at least a 20 cm buffer between adjacent subplots. I established three types of subplot, replicated once in each plot. In the first subplot type (undisturbed control subplots), I did not manipulate soils. In the second subplot type (treatment subplots), I reciprocally transplanted soil between subplots under *Acacia* canopies and adjacent open subplots to test for soil and microclimatic effects independently. In the third subplot type (disturbed control subplots), I transplanted soils within sites to control for disturbance associated with the transplant process.

To transplant soils I cut slabs of soil to a depth of 25 cm with a spade, and shifted the slabs in as intact a state as possible. As this effectively severed neighbouring root connections, I also cut the edges of undisturbed subplots with a spade to 25 cm depth. I fenced each plot to exclude large vertebrate herbivores.

I raised seedlings of *Enchylaena* and *Atriplex* in a glasshouse in 0.13 L pots filled with potting mix. When the seedlings were two weeks old, I hardened them for one week outdoors before planting out. I planted three-week old seedlings of *Enchylaena* in three randomly assigned subplots per plot on 1-2 June 2000. I planted two seedlings in each subplot and thinned six weeks later to one seedling per subplot by removing the smallest live seedling. Where both seedlings in a subplot had died, I replaced them on 26 June. I planted four-week old *Atriplex* seedlings on 5-6 September as earlier seed germinations failed.

To aid initial seedling establishment and to reduce transplant shock, I watered transplanted seedlings with 1.5 L of water at three weekly intervals. This represents a fall of approximately 25 mm of rain (the average monthly rainfall for the region is 18 mm per month). I then continued these watering treatments in one plot under each tree and an adjacent open plot (i.e. within each block) from September 8 for *Enchylaena* and October 20 for *Atriplex*. The other plot received no further water.

As evaporation rates are high in this environment, I installed a drip irrigation system that delivered water at the rate of approximately 1 L per 24 hour period. I constructed drippers from 8 cm sections of microporous pipe connected to 6 mm polypipe. I used a cork borer to drill small holes within each water treatment subplot and buried porous pipe sections 10 cm below-ground. The pipes were gravity fed from a 20 L water container. Each plant received 3L of water over 3 days. I watered *Enchylaena* plants in this manner on October 20 and December 12, but buckets refilled after the December watering had not emptied by January, possibly because of pipe blockages, so the watering treatment was discontinued. I applied this watering treatment to *Atriplex* plants in October only and as there was no significant difference between watered and unwatered treatments, these treatments were pooled for analyses and watering treatments were not included in models for this species.

I established a separate set of subplots to examine seed germination of the two species, using 15 cm lengths of 9 cm diameter PVC pipe as subplots. I hammered these into the soil leaving 2 cm protruding from the soil surface. I manipulated soil in disturbed control and treatment subplots as described for seedling subplots, but shifted soil intact within pipes. Undisturbed control subplots remained *in situ* and all pipes remained in the ground. Sufficient rain to wet the soil to at least 15 cm depth did not occur until late August 2000. I installed pipes at this time and sowed 20 *Enchylaena* seeds from a commercial source (Blackwood Seeds, Murray Bridge, South Australia) or 40 locally collected *Atriplex* seeds in each pipe. In glasshouse germination trials, *Enchylaena* seeds had 85% viability and *Atriplex* seeds 52% viability. I watered all subplots with 200ml of water two days after sowing and again sixteen days later. I applied a watering treatment to half the plots with watered subplots receiving 200 ml of water on the 1st and 19th of October. In the three weeks following sowing 11 mm of rain fell. I repeated this experiment in 2001 immediately preceding heavy rainfalls in early June (66.5 mm) but I did not apply watering treatments. In the three weeks following seed sowing there was 21 mm of rain.

Canopy microclimate

I measured temperature and photosynthetic photon flux (PPF) under *Acacia* canopies and in adjacent open sites in November, January and February. I placed Quantum light sensors 1 metre from the northern side of the tree bole and in the open at least two metres from the canopy edge. Copper-constantan thermocouples were buried 10 cm below the soil surface adjacent to light sensors. I logged PPF at one minute intervals and temperature at two minute intervals for periods ranging from 12 hours (November light data) to two full days (January data). I used trees of similar age and size to experimental trees for this sampling. I measured volumetric soil moisture in each subplot type using a theta probe (Type ML2x, Delta-T devices, Cambridge) on one occasion, when I scored emergence in July 2001.

Response variables

I scored seedling emergence in 2000 on four occasions from September to December. I counted year 2001 seedling emergence three weeks after I sowed seeds in June and then thinned these plots to leave five seedlings in each plot. I monitored the survivorship of these seedlings until April 27, 2002.

I monitored the survival of transplanted seedlings at six weekly intervals from planting until April 24, 2001. Over this time period I also monitored the survival of forty naturally occurring *Atriplex* seedlings that appeared to be a cohort from winter 2000.

To estimate plant size I measured plant height and width (distance between the tip of the widest pair of opposite leaves and the width perpendicular to this) at approximately six week intervals from September (*Enchylaena*) and October (*Atriplex*) until April. I used these dimensions to calculate plant volume. I determined initial plant size as the average size of twenty seedlings at the time of planting. After the final measurement I removed above-ground biomass at ground level, oven dried it at 85 °C to constant weight, and measured dry weight. Log transformations of April plant volume and shoot dry weight of each species had a significant linear relationship. Regressions for different treatments were not significantly different so I pooled the data for each species. The regression equations for each species were:

$$\text{Ln SDW}_{Enchylaena} = -3.712 + 0.576 * \ln V_{Enchylaena} \; (r^2 = 0.95, P<0.0001) \quad (1)$$

$$\text{Ln SDW}_{Atriplex} = -3.976 + 0.634 \ln V_{Atriplex} \; (r^2 = 0.94, P<0.0001) \quad (2)$$

where SDW is shoot dry weight (g) and V is shoot volume (mm^3).

As shoot volume demonstrated a good relationship with biomass, I used shoot volumes to calculate growth rates over the course of the experiment. I determined relative growth rates (RGR) between each measurement period as:

$$\text{RGR} = \frac{V_{(t)} - V_{(t-1)}}{V_{(t-1)} * \text{days}} \quad (3)$$

where V = shoot volume (mm^3) and t = time.

I quantified the intensity of facilitation by calculating the relative interaction intensity (RII). I assumed that *Acacia* canopies provide improved conditions for growth compared to sites away from the influence of canopies, i.e. they facilitate plant growth. Of interest here is whether the facilitative effect of canopies on the growth rate of plants growing beneath them changes over time. To calculate relative interaction intensity (RII) I treated adjacent canopy and open plots as matched pairs. I used the log-normal response ratio (lnRR; Hedges *et al.* 1999) to quantify relative growth differences between plants growing in the same soil type between each site. Prior to calculations I added a constant (k) to each RGR to eliminate any negative RGR by setting the lowest RGR as zero:

$$\text{lnRR} = \ln(\text{RGR}_{\text{canopy site}} + k) - \ln(\text{RGR}_{\text{open site}} + k) \quad (4)$$

To separate soil effects from microclimate effects I calculated RII in two ways. I calculated the combined effects of both mechanisms on RII by comparing plants growing in *in situ* soils in the two sites, i.e. undisturbed control subplots. To isolate the effect of microclimate on RII I compared plants growing in the same soil type in the two sites. I only used measurement periods in which there was no significant difference between disturbed and undisturbed controls.

Analyses

I analysed the experiment as a split-plot design, with soil treatment (subplots) as the within-plot effect and blocks nested in each site as a random effect. Where there was no significant difference between disturbed and undisturbed control subplots I re-ran models pooling control subplots within each site. In these cases I tested differences in soil origin, i.e. soil from canopy or open. I analysed the data for each species separately as I did not plant them concurrently, with the exception of the 2000 seedling emergence data and the 2001-2002 survival data. I tested data for normality and heterogeneity of variances and transformed data when necessary to meet the assumptions of multivariate and univariate ANOVA. I iteratively removed highest-order interaction terms from models when they were not significant.

I analysed seedling emergence in 2000 using a logistic nominal regression, with the presence or absence of emerging seedlings within a subplot as a nominal response with two states. I could not estimate seedling emergence in 2000 within each subplot due to the very low proportions of germinating seed. I analysed the proportion of emerging seedlings in 2001 by ANOVA testing the effects of soil type and site and their interaction, but analysed species separately due to differences in seed viability.

I examined growth rates in three ways. I analysed RGR from the time of planting until the culmination of the experiment by ANOVA and used a second ANOVA model to compare RGR during the establishment period as I watered all plants during this period. Thirdly, I used repeated measures MANOVA to compare RGR across measurement periods when I applied watering treatments. I pooled the watering treatments in *Atriplex* models as I only watered these plants once and there was no significant difference between watered and unwatered treatments. I used an adjusted univariate F-test (Geisser-Greenhouse) when comparing model effects between different measurement periods (time), as the sphericity condition was not met. Where there were significant differences between treatments at different measurement periods I further tested model effects using separate ANOVAs for each measurement time. I adjusted alpha levels by the Bonferonni procedure for the number of times I applied tests to the same data set ($\alpha' = \alpha/n$). Due to *Enchylaena* deaths in open sites after January, I only analysed *Enchylaena* growth rates up until this point.

I used repeated measures MANOVA to analyse changes in RII over time. I could only use data from the establishment period (September) and December to compare RII for *Enchylaena* due to lack of survivors after this date and significant differences between controls in the October measurement period. To test the direction of the interactions for both species, i.e. whether tree canopies had positive, neutral or negative effects on plant growth, I performed individual Student's t-tests for each measurement period with a null hypothesis of a positive effect of canopies (one-tailed hypothesis, $t > 0$). I adjusted significance levels to account for repeated tests on the same data sets using the Bonferroni method.

I analysed biomass data with ANOVA. I estimated the biomass of *Enchylaena* plants in December from the regression equation (1) and this enabled the inclusion of a site effect in the analysis of biomass up until this measurement period. I used Cox's Proportional Hazards (JMP Ver. 3.1.4) to analyse the effects of canopy microclimate, soils and watering treatments on the survival of transplanted seedlings over time during the first year of the study. I tested the effects of canopy microclimate and soils on the proportion of seedlings (planted as seeds) alive in April 2002 using an ordinal logistic model. I used individual Likelihood-Ratio tests to compare differences between species within sites and differences between sites within species. Significance probabilities were set at $\alpha < 0.0125$ for these tests (Bonferonni correction).

I used JMP IN (Ver.4.0.3) for all analyses unless otherwise stated.

Results

Canopy microclimates

Acacia canopies modified undercanopy light climate and soil temperatures. Over the four days of measurements PPF under canopies averaged 20% PPF of full sun conditions (e.g. Fig. 62A). Soil temperatures beneath canopies remained relatively constant over 24 to 48 hour periods, averaging approximately 25 °C during January (Fig. 6.2B). Temperatures in open soils were higher than canopy soils during the measurement periods with soil temperatures increasing rapidly during late morning to early afternoon and cooling down slowly overnight (Fig. 6.2B). Maximum soil temperatures in open sites in January were 20°C greater than canopy soil temperatures. In July 2001, volumetric soil moisture did not differ significantly between soil types and sites, although it differed between experimental blocks (Table 6.1).

Seedling emergence

In 2000 seedling emergence was very low. Only 10% of subplots had emerging seedlings. There were no significant differences in emergence between species and sites, but there was a soil treatment effect (Table 6.2). Most emergence occurred in disturbed control subplots (canopy soils) under canopies, with no emergence in control subplots (open soils) in open sites (Fig. 6.3).

Seedling emergence was much higher in 2001 occurring in greater numbers in all subplots. There was an interaction between site and soil type (Table 6.3). For both species, the highest emergence occurred in canopy soils in open sites. Although *Atriplex* emergence was higher in canopy soils in both canopy and open sites *Enchylaena* emergence was only higher in canopy soils in open sites (Fig. 6.4A). Overall, *Acacia* had positive effects on the emergence of both species, as emergence was greater in canopy soils in canopy sites than open soils in open sites.

Growth

Early in the growing season I watered plants to encourage establishment. During this period there were no significant differences in *Atriplex* RGR between soil treatments and sites (Table 6.4) although there were trends for RGR to be higher in canopy soils in both sites during this period (see October, Fig. 6.5). In the establishment period, *Enchylaena* RGR was significantly higher beneath canopies and in canopy soils (Table 6.4, Fig. 6.6).

Over the entire experiment, canopy soil favoured the growth of *Atriplex*, independent of canopy microclimate effects (Table 6.5). From the time of planting until April *Atriplex* RGR and final shoot biomass was greater in canopy soils (Fig. 6.4). Although plants growing in canopy soils in open sites had more shoot biomass, the interaction between site and soil was not significant (Table 6.5). However, the overall effect of *Acacia* was positive, as growth was greater in canopy soils in canopy sites than open soils in open sites.

From the time of planting until December, the effects of soil type on *Enchylaena* RGR and estimated shoot biomass differed between sites (Table 6.6). *Enchylaena* plants grew less in open soils but this effect only occurred in open sites as canopy microclimates had positive effects on *Enchylaena* growth in open soil (Fig. 6.4). By April there was no difference in shoot biomass between *Enchylaena* seedlings growing in different soil types in canopy sites (ANOVA $F_{1,37} = 2.445$, $P = 0.128$). Watering had positive effects on the overall RGR and shoot biomass of *Enchylaena* until December but there was no interaction between water and soil type or site (Table 6.6). The final biomass of canopy grown *Enchylaena* seedlings was also higher in watered plots (ANOVA $F_{1,37} = 9.76$, $P = 0.004$).

Temporal responses

During the period after supplementary watering ceased the RGR of *Atriplex* changed significantly being highest in December (early summer) but falling to almost zero for the remainder of the measurement period (time effect, Table 6.7, Fig. 6.5). There were significant differences between sites and soil types during this period although this was not consistent over time (time/site and time/soil interactions, Table 6.7). In April (autumn), RGR was significantly higher in open sites and in canopy soils. Growth rates were very slow in these treatments (< 0.002 mm mm^{-3} d^{-1}) yet biologically significant as other treatments had negative growth at this time. During other measurement periods there were trends for RGR to be greater in canopy sites but these differences were not significant at $\alpha < 0.0125$.

I watered *Enchylaena* plants until December, and RGR was analysed over three periods, October, December and January. Soil treatments and watering had significant effects on RGR but these effects changed over time (Table 6.8). Like *Atriplex,* growth rates remained positive during October and December but declined to almost zero by January. There were significant differences between soil treatment subplots only during October when RGR in undisturbed control subplots was lower than in other subplots in both canopy and open sites. Growth rates significantly improved with the addition of water but there was also a site and water interaction in December and January (time/site/water interaction, Table 6.8). In December, watering increased *Enchylaena* growth rates in both canopy and open sites (Fig. 6.7). Watering appeared to have a greater effect on growth in open sites than for plants under canopies (Fig. 6.7). The effects of watering persisted after December as plants in watered plots had higher RGR in January, but only in canopy sites (Fig. 6.7).

Relative interaction intensity

The RII for the combined effects of microclimate and soils changed significantly over time for *Enchylaena* (MANOVA, time effect $F = 7.878$, $P = 0.021$). Soil type and watering had no significant effect on RII in the absence of microclimatic effects. RII did not change significantly over time for *Atriplex.*

There were changes in the direction of interactions over time, i.e. *Acacia* had positive, neutral and negative effects on RGR at different times. During the establishment period when all plants were watered (until September), canopy microclimates and soils had positive effects on *Enchylaena* growth (Table 6.9). During this period, *Acacia* microclimates had a neutral effect on *Atriplex* growth but the effects of soils under canopies were positive (Fig. 6.8). *Acacia* had neutral effects on both species during December, i.e. there was no difference in plant growth between open sites and beneath tree canopies (Table 6.9). Although the effects of canopy soil continued to be neutral for *Atriplex* for the remainder of the experiment, during January canopy microclimates had a significantly positive effect on plant growth (Table 6.9). In April, this interaction showed a reverse trend, with plants growing at relatively faster rates in open sites with negative microclimate effects (Fig. 6.8).

Survival

In the first year (2000-2001), survival of both *Atriplex* and *Enchylaena* seedlings was significantly higher in canopy sites than open sites (Likelihood-Ratio $\chi^2 = 5.351$, $P = 0.021$ and L-R $\chi^2 = 18.774$, $P < 0.001$ respectively). Most *Enchylaena* mortality occurred between November and January, particularly in open sites (Fig. 6.9B). Approximately 75% of seedlings of both species remained alive at the end of the experiment in canopy sites. By April, *Atriplex* survival in open sites was approximately 50% whereas *Enchylaena* survival was less than 25% (Figs 6.9A, B). Watering improved *Enchylaena* survival in open soils, but watering did not affect survival in canopy soils (Fig. 6.9C, site/soil type interaction L-R $\chi^2 = 3.869$, $P = 0.055$). There was no significant difference between the survival curves of a naturally occurring population of *Atriplex* plants and experimental seedlings planted in open sites (Logrank test, $\chi^2 = 0.1836$, $P = 0.668$).

In the second year (2001-2002), canopy microclimates had positive effects on *Enchylaena* survival but neutral effects on *Atriplex* survival (species/site interaction, Table 6.10). *Atriplex* survival tended to be consistently higher in open sites (Fig. 6.10B) although this was not significant (Table 6.10c). More *Enchylaena* seedlings survived than *Atriplex* seedlings under canopies, but in open sites this pattern was reversed (Fig. 6.10). The greatest proportion of *Enchylaena* seedlings died between January and April 2002 (Fig. 6.10A). Most *Atriplex* deaths occurred between July and September (Fig. 6.10B).

Discussion

My results show that habitat modifications by *Acacia* facilitate all aspects of *Atriplex* and *Enchylaena* establishment. Microclimatic modifications by tree canopies had positive effects on plant survivorship and growth, and soil modifications had a positive effect on seedling emergence and plant growth. However, responses to soil and microclimate modifications differed between species and changed over time. For *Enchylaena,* canopy microclimates were important, as plant performance did not significantly differ between soil types in canopy sites. Conversely, *Atriplex* emergence and growth responded positively to soil modifications and canopy microclimates had positive effects as stress increased.

Seedling emergence

Acacia soil properties had a positive effect on seedling emergence in 2001, but *Acacia* microclimates had a negative effect, as highest seedling emergence occurred in canopy soils in open sites. Almost 70 mm of rain fell in the 12 hours after I sowed seeds and soil moisture was the same in each subplot three weeks later, therefore soil moisture availability cannot explain the higher emergence in canopy soils. The textural qualities of canopy soils, e.g. lower bulk density and greater pore spaces, may enhance emergence because these soils may be less restrictive to early root growth (Greacen and Oh 1972, Stirzaker *et al.* 1996).

It seems unlikely that higher seedling emergence in open sites was a response to higher soil temperatures, as this would have increased emergence in open soils as well and this was not the case. Additionally, *Atriplex* has a low germination optimum temperature and higher temperatures have a negative effect on germination (Burbidge 1946). In glasshouse trials, Facelli and Brock (2000) also found that *Enchylaena* seedling emergence was greater in canopy soils in high light treatments, but light had no effect on emergence in open soils. When soil structure is unrestricting to root growth then light may be important for early seedling establishment. This effect was not as strong in *Enchylaena*, which has much larger cotyledons than *Atriplex*. If *Enchylaena* has greater seed reserves than *Atriplex*, it may be less dependent on carbon fixation (and hence light) in the period immediately following emergence from the soil.

In 2000, the highest emergence occurred in disturbed canopy soils in canopy sites. Disturbances to the soil could increase mineralisation and hence nutrient availability. Disturbances could also affect water infiltration and together with lower evaporation rates in canopy sites may have increased water availability in these subplots. This may explain why there was not such an effect in the same subplots in open sites. Higher emergence in canopy soils both years suggests that changes to soil properties beneath canopies is the primary facilitation mechanism for this process. Although comparisons between years are not conclusive, it is interesting that there was a positive canopy site effect on seedling emergence in the drier year (2000) but not in the wetter year (2001). This suggests that canopy microclimates may be important for early seedling establishment when conditions are more stressful. For example, Kitzberger *et al.* (2000) found that during wet years *Austrocedrus* established without the presence of shrub canopies, but during years with less rainfall, or average years, recruitment was a lot greater beneath shrub canopies.

Growth

Acacia modifications of soil properties had positive effects on plant growth. The lack of an interaction between watering and soil origin in *Enchylaena* biomass suggests that enhanced water storage and release in canopy soil (Facelli and Brock 2000) may not be the facilitation mechanism. Rather, the higher nutrient status of canopy soils may have allowed plants to achieve greater size.

There was a trend for growth rates and shoot biomass to be greater in open sites when plants were growing in canopy soils, which suggests that plant performance under canopies may be light-limited. This seemed to manifest when nutrients were not limiting to growth, as I did not observe negative shade effects in plants growing in open soils. Glasshouse and field experiments have demonstrated that shade has stronger suppressive effects on growth when below-ground resources are not limiting (Kozlowski 1949, Franco-Pizaña *et al.* 1996, Facelli and Brock 2000, Holmgren 2000, Anderson *et al.* 2001, Ludwig *et al.* 2001). For example, during April there were significant negative effects on *Atriplex* growth in canopy sites in canopy soils. This may be due to a rainfall event too small to penetrate the canopy, but large enough to provide water to plants growing in open sites. This produced a growth response in plants in open sites but only in the higher nutrient canopy soils, but plant growth under the canopy may have been water-limited. This reinforces findings from the nutrient addition experiment where I found reduced growth under canopies when below-ground resources were not limiting (Chapter 5).

Facilitation may occur more frequently for plants that are able to photosynthetically acclimate to light, than for shade-intolerant plants that have reductions in carbon gain under shaded conditions (Parker and Muller 1982, Shumway 2000, Forseth *et al.* 2001). Canopies may not have a positive effect on *Atriplex* when water and nutrients are not limiting due to a higher light requirement, which may balance out the benefits of more nutrients under canopies at this time. When increased availability of below-ground resources increases plant performance to the same extent that shading reduces it, canopies may have neutral effects. *Atriplex* is a C4 species and shows a marked reduction in carbon fixation when grown under shaded conditions (Chapter 7). As water becomes limiting the effects of shade on the reduction of transpirational losses may tip the balance and enhance growth under canopies (Holmgren 2000, Ludwig *et al.* 2001).

Enchylaena plants responded differently to canopy microsites. Early in the growing season, *Enchylaena* plants growing in canopy soils in canopy microsites had higher growth rates than other treatments. Thus when water and perhaps nutrients were not limiting shade had no negative effects on growth. Shading also had no effect on the final biomass of glasshouse grown *Enchylaena* (Facelli and Brock 2000). Later in the growing season, plants growing in open soils beneath canopies reached a similar size to those growing in canopy soils. The benefits of canopy microclimate had become greater than the benefit of canopy soils. The positive effects of reductions in heat and atmospheric water stresses could occur early in the growing season when soil water may still be available. The larger plants growing in canopy soils may have greater transpirational water loss; therefore growth rates may be reduced earlier than the smaller plants in open soils.

Survival

Canopy microsites were important for seedling survival of both species during the drier first year of this experiment. However, in the wetter, cooler second year of the experiment *Acacia* microsites did not facilitate *Atriplex* survival, although they still had positive effects on *Enchylaena* survival. During the first season of this experiment I recorded most deaths between November and January, when temperatures were high and soil water content low. This contrasts with the second year of the study when deaths occurred later in the season between January and April. Although plants survived longer into the interpulse in 2002, survival percentages were similar between years by April. Regarding *Enchylaena*, it appears that higher survival beneath canopies may be a function of reductions in water stress, as watering plants growing in open soils in open sites improved survival. A lack of a water effect on survival in canopy soils may be due to superior root growth in these soils allowing plants to access water stores deeper in the soil profile, or the improved water exchange capacities of these soils (Facelli and Brock 2000). Reductions in radiation or temperature stresses beneath canopies may also be an important factor affecting *Enchylaena* and *Atriplex* survival during the summer months.

Older *Atriplex* seedlings may be more tolerant of water stresses than *Enchylaena* plants. More plants were able to survive without the protection of *Acacia* canopies during both the interpulses of this study. During the wetter second year, most *Atriplex* deaths occurred during the pulse. Very young seedlings are therefore sensitive to other stresses. These seedlings did not appear to be damaged by invertebrate herbivores. These deaths may have resulted from competition for light with ephemerals that established beneath canopies in the wetter year (see Chapter 3). I did not observe early seedling deaths in the first year of the study when there was limited ephemeral growth.

Temporal responses

I observed changes in canopy effects over time, which differed between the two species studied. The effects of canopy microclimate on *Atriplex* growth rates were positive during late summer to early autumn, neutral when plant growth was at its highest in spring, and slightly negative in late autumn. Similarly, canopy microclimates had positive effects on *Atriplex* survival during the drier year and neutral effects during the wetter year. This fits with classic predictions that facilitation is more likely to occur when conditions are more stressful (Bertness and Callaway 1994) and supports my conceptual model of increasing intensity of positive interactions during interpulses. It also supports other studies in water-limited systems that have shown facilitation of survival to be more frequent in a drier year than a wetter year (Casper 1996, Greenlee and Callaway 1996, Ibáñez and Schupp 2001).

Most studies examining temporal shifts in plant interactions typically examine these on annual scales. Plant responses are examined over different growth seasons in years with varying conditions, although some studies have examined patterns over different periods of the growth season (e.g. Holzapfel and Mahall 1999) and between high and low stress sites (Greenlee and Callaway 1996, Pugnaire and Luque 2001). However, species such as *Atriplex* do not have strong seasonal growth patterns and are able to grow at any time of the year, typically in response to rainfall (Noble 1977, Williams 1979). Examining interactions at finer time scales is thus important for species with such growth patterns providing new insights into interactions under varying conditions.

The combined effects of canopy microclimates and soils had positive effects on *Enchylaena* growth, even when water was not limiting to growth during the establishment period. Canopy facilitation resulted from the additive effects of soil and microclimate modifications. Until December, *Enchylaena* plants grew equally well in both environments when growing in canopy soils. However, by late summer plants were unable to survive outside the protection of the canopy. Thus *Acacia* canopies facilitated *Enchylaena* growth in the cooler months and plant survivorship during the hotter months. These positive effects were independent of pulse size; *Acacia* facilitated *Enchylaena* survival during interpulses following small and large pulses.

Acacia also had a positive effect on *Atriplex* growth during the establishment period but in this instance, soil effects were the mechanism and microclimate had a neutral effect.

These observations do not seem to fit with classical predictions for positive interactions, but there is growing evidence to suggest that the facilitation of plant growth is more intense when conditions are more conducive to growth. In studies with annuals, plant canopies can facilitate growth during periods or years when water is more plentiful (Holzapfel and Mahall 1999, Tielbörger and Kadmon 2000b, but see Pugnaire and Luque 2001). With perennial plants, Tewkesbury and Lloyd (2001) found that plants beneath trees in more mesic sites were much larger than conspecifics in open sites when compared with xeric sites within an arid system. Coupling of nutrient and water uptake could explain these patterns as low water potentials reduce rates of microbial release of nitrogen and phosphorus, decrease root growth and the mass flow of nutrients through the soil (Cowling 1978, Coomes and Grubb 2000). Therefore, the growth benefits of increased nutrients beneath canopies may only be realized when soil water content is high. In drier sites or during dry years plants may not benefit from the increased nutrients found under other plant canopies.

The effects of watering also changed over time. Water may be available for longer after rainfall or artificial irrigation under canopies because of greater infiltration (Cowling 1978), slower evaporative losses and the lower evaporative demand of plants in these microhabitats. Under the hypothesis that canopy microclimates have positive effects on plant performance by reducing water stress, watering plants in open sites should have more effect than watering plants in canopy sites, which is what I found in early summer (December 2000). Later in the season (January 2001), only plants under the canopy continued to realize the benefits of extra water; plants in open sites did not grow. Ibáñez and Schupp (2001) also found that watering during a dry summer had an effect on woody plant survivorship for seedlings growing under canopies, but did not improve survivorship in the open. In my experiment, the frequency of the watering applied may not have been sufficient to sustain growth when temperatures and evaporative rates were high.

Summary and conclusions

The dynamic combination of resources and conditions occurring beneath tree canopies provides a microenvironment that has positive effects on the establishment of these two species. Canopies facilitated *Enchylaena* growth during the peak of the growing season, probably by ameliorating temperature, heat and radiation stresses. It appears that *Enchylaena* requires the microenvironment created by *Acacia* or other trees in this system, in order to establish. However, canopy cover appears to be more important than canopy soils for the persistence of *Enchylaena*. *Enchylaena* occurs only sporadically in sites with dead *Acacia* where some soil differences can persist for some decades (Facelli and Brock 2000). Canopies were essential for seedling survivorship over the summer when seedling deaths were most likely due to water stress. On the other hand, although *Acacia* had positive effects on *Atriplex,* this species appeared less dependent on *Acacia* during the establishment phase. Canopy soils enhanced *Atriplex* seedling emergence and growth and canopy microsites improved seedling survivorship during the drier year. The positive effects of *Acacia* occurred during more stressful periods. Canopy microclimates had positive effects during interpulses, but as in *Enchylaena,* the positive effects of canopy soils were more likely to occur during pulses. Light may limit growth during the peak growing seasons for *Atriplex* but not for the more shade-tolerant *Enchylaena*. The contrasting distributions of *Enchylaena* and *Atriplex* is thus linked to their ecophysiological tolerances and the environmental changes produced by trees. Unlike *Enchylaena*, *Atriplex* also appears tolerant of the microclimatic conditions in intercanopy spaces. In the next chapter, I will examine the physiology of these two species under conditions simulating the light climate and soil conditions of canopy and open sites, to determine how physiological responses to microhabitat modifications relates to the distribution of these species.

Table 6.1 ANOVA testing the effects of site and soil type on the volumetric soil moisture measured in June 2001.

Source	**df**	SS	***F***	***P***
Block [site]	16	181.101	2.517	0.003
Site	1	13.263	2.949	0.105
Soil type	1	5.587	1.242	0.268
Site/soil type	1	12.317	2.739	0.102
Error	88	395.76		

Table 6.2 Nominal logistic Wald tests on the effects of species, site, watering and soil treatment on the emergence of *Enchylaena* and *Atriplex* seedlings in 2000. Significant difference between treatments at * $\alpha < 0.05 > 0.01$.

Source	**df**	**Wald $\chi 2$**	***P***
Block[site]	18	11.939	0.840
Species	1	2.148	0.143
Site	1	0.014	0.907
Water	1	0.248	0.618
Treatment[site]	4	9.862	0.043*

Table 6.3 ANOVAs testing the effects of site and soil type on the emergence of *Atriplex* and *Enchylaena* seedlings in 2001. Significant difference between treatments at ** $\alpha < 0.01 > 0.001$, *** $\alpha < 0.001$.

Source	**df**	SS	***F***	***P***
Atriplex				
Block[site]	16	0.079	0.490	0.946
Site	1	0.136	13.512	0.002**
Soil type	1	1.000	99.178	<0.001***
Site/soil type	1	0.133	13.139	<0.001***
Error	88	0.887		
Enchylaena				
Block[site]	16	0.367	0.756	0.729
Site	1	0.004	0.121	0.733
Soil type	1	0.901	29.725	<0.001***
Site/soil type	1	0.346	11.429	0.0011**
Error	88	2.667		

Table 6.4 Results of ANOVA testing the effects of site, soil type and their interaction on the RGR of *Atriplex* and *Enchylaena* during the establishment period. Significant difference between treatments at * $\alpha < 0.05 > 0.01$, ** $\alpha < 0.01 > 0.001$.

Source	**df**	SS	***F***	***P***
Atriplex				
Block [site]	18	10.923	0.231	1.000
Site	1	2.119	0.807	0.381
Soil type	1	6.650	2.533	0.115
Site/soil type	1	0.498	0.190	0.664
Error	98	257.278		
Enchylaena				
Block [site]	18	16.352	0.597	0.983
Site	1	10.907	7.165	0.015*
Soil type	1	11.966	7.860	0.006**
Site/soil type	1	0.747	0.491	0.485
Error	89	135.486		

Table 6.5 ANOVA testing the effects of site and soil type on a) the overall RGR and b) the final biomass of *Atriplex* seedlings. Significant difference between treatments at * α < 0.05 > 0.01.

Source	**df**	SS	***F***	***P***
RGR				
Block[site]	18	< 0.001	< 0.001	1.000
Site	1	1.500	0.611	0.445
Soil type	1	12.767	5.197	0.026*
Site/soil type	1	5.802	2.362	0.131
Error	50	122.838		
Final biomass				
Block[site]	18	17.877	0.854	0.633
Site	1	0.201	0.189	0.666
Soil type	1	5.171	4.444	0.040*
Site/soil type	1	2.059	1.769	0.189
Error	56	65.161		

Table 6.6 Separate ANOVAs testing the effects of site, soil type and watering on the growth responses of *Enchylaena* to December. Significant difference between treatments at * α < 0.05 > 0.01, ** α < 0.01 > 0.001.

Source	**df**	SS	***F***	***P***
RGR				
Block[site]	18	90.871	1.684	0.064
Site	1	2.975	0.993	0.332
Soil type	1	24.871	8.297	0.005**
Water	1	18.307	6.107	0.231
Site/soil type	1	4.377	1.460	0.016*
Site/water	1	0.159	0.053	0.818
Soil type/water	1	3.728	1.244	0.269
Error	71	203.832		
December biomass				
Block [site]	18	20.069	1.000	0.471
Site	1	1.301	1.166	0.294
Water	1	7.388	6.623	0.012*
Soil	1	8.587	7.697	0.007**
Site/soil	1	3.971	3.560	0.063
Site/water	1	0.477	0.428	0.515
Soil type/water	1	0.059	0.053	0.819
Error	71	79.203		

Table 6.7 MANOVA testing the effects of site and soil on the RGR of *Atriplex* seedlings over time. # Degrees of freedom calculated using Greenhouse-Geisser epsilon adjustments. Significant difference between treatments at ** α < 0.01 > 0.001, *** α < 0.001.

Source	**num df**	**den df**	***F***	***P***
Block [site]	18	58	1.31	0.216
Site	1	58	0.35	0.557
Soil	1	58	1.44	0.235
Site/soil	1	58	0.50	0.484
Time	2.38#	138.2#	346.74	<0.001***
Time/site	2.38#	138.2#	17.93	<0.001***
Time/soil	2.38#	138.2#	4.80	0.006**
Time/site/soil	2.38#	138.2#	2.42	0.083

Table 6.8 MANOVA testing the effects of site, soil treatment and watering on the RGR of *Enchylaena* seedlings over time. # Degrees of freedom calculated using Greenhouse-Geisser epsilon adjustments. Significant difference between treatments at * $\alpha < 0.05 > 0.01$, ** $\alpha < 0.01 > 0.001$.

Source	**num df**	**den df**	***F***	***P***
Block [site]	17	48	1.68	0.08
Site	1	48	0.10	0.75
Treatment [site]	4	48	4.95	0.002*
Water	1	48	9.74	0.003**
Water*site	1	48	0.38	0.54
Time	1.53#	73.7#	42.62	<0.001
Time*site	1.53#	73.7#	1.26	0.28
Time*treatment [site]	6.14#	73.7#	2.56	0.03
Time*water	1.53#	73.7#	2.55	0.10
Time*water*site	1.53#	73.7#	3.65	0.04*

Table 6.9 Relative interaction intensities (RII: means ± 1 SE) quantifying the intensity of facilitation by *Acacia* trees on the growth of *Atriplex* and *Enchylaena* seedlings at each measurement time. RII was calculated for the single facilitation mechanism of microclimate (1) and both microclimate and soil effects combined (2). Student's t-tests test if the mean value is significantly greater than zero, where zero indicates a neutral effect of *Acacia* on shrub growth. * $t > 0$ at $\alpha < 0.0125$ (*Atriplex*) and $\alpha < 0.025$ (*Enchylaena*).

Measurement time	**RII (1)**	***t***	**RII (2)**	***t***
Atriplex				
October	-0.08 ± 0.47	-0.163	1.24 ± 0.41	2.989*
December	0.40 ± 0.21	1.931	0.48 ± 0.32	1.516
January	0.25 ± 0.10	2.602*	0.37 ± 0.31	1.168
March	0.13 ± 0.07	1.708	0.29 ± 0.16	1.818
April	-0.11 ± 0.06	-1.827	-0.10 ± 0.08	-1.371
Enchylaena				
September	1.51 ± 0.47	3.213*	1.64 ± 0.38	4.318*
December	-0.20 ± 0.43	-0.472	0.17 ± 0.35	0.486

Table 6.10 Likelihood-Ratio (L-R) tests of a) the effects of species, site, soil type and their interactions on the proportion of seedlings surviving until April 2002, and individual tests b) between species within each site and c) between sites within each species. Significant difference between treatment effects at * $\alpha < 0.0125$ (individual tests), ** $\alpha < 0.01 > 0.001$, *** $\alpha < 0.001$. For pairwise comparisons (b, c), A, *Atriplex*, E, *Enchylaena*, C, canopy site, P, open site.

Source	**df**	**L-R χ^2**	***P***	**Comparison**
a) Block[site]	16	26.326	0.050	-
Species	1	9.219	0.002**	-
Site	1	8.381	0.004**	-
Soil type	1	1.327	0.249	-
Species/site	1	31.783	<0.001***	-
Species/soil type	1	0.285	0.594	-
Site/soil type	1	1.271	0.260	-
b) Species - open sites	5	15.691	0.008*	A>E
Species - canopy sites	5	33.459	<0.0001*	E>A
c) Site - *Atriplex*	5	5.522	0.356	C=P
Site - *Enchylaena*	5	42.816	<0.0001*	C>P

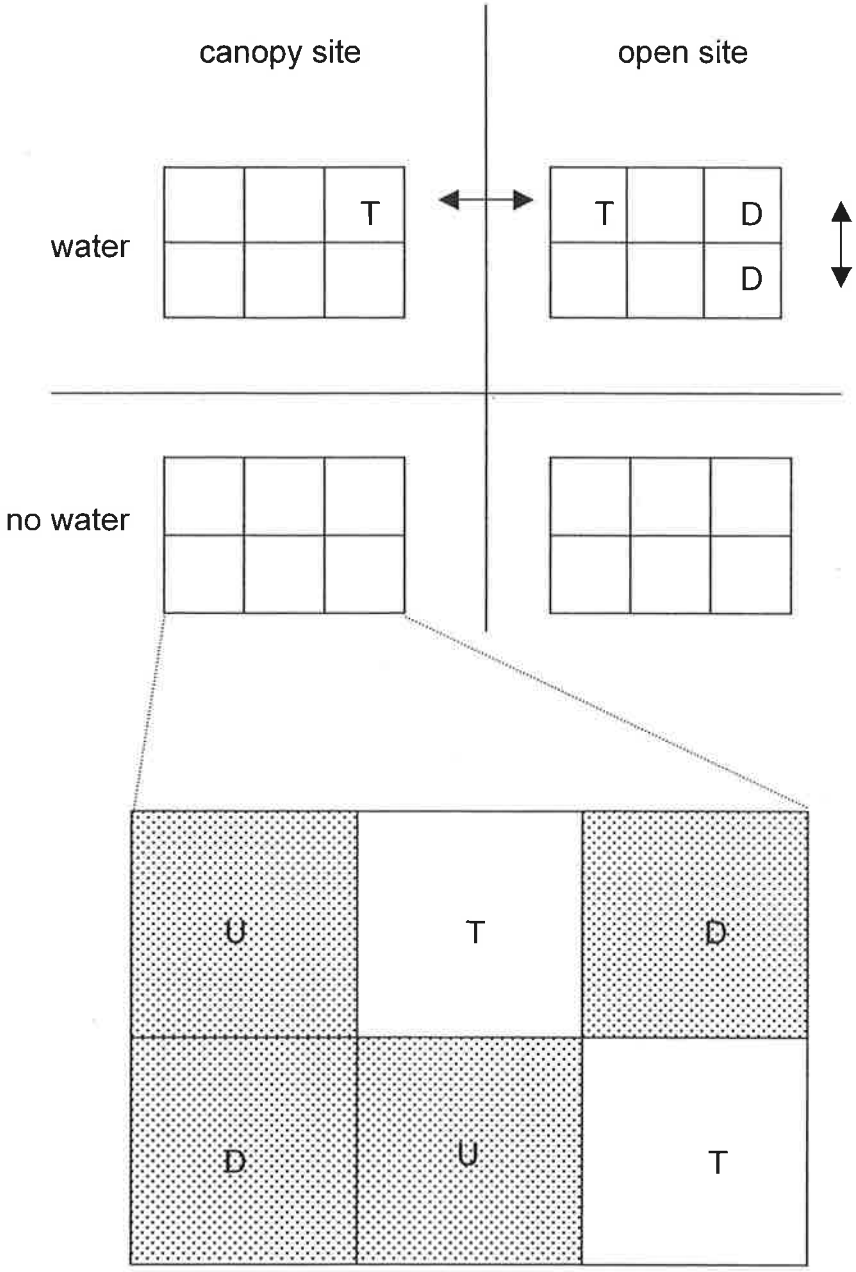


Fig. 6.1 Layout of experimental plots. Each plot was subdivided into six subplots, comprising undisturbed soils or undisturbed controls (U), soils transplanted within plots or disturbed controls (D), and soils reciprocally transplanted between sites (T). The arrows show soil transplants. In the enlarged example the shaded subplots would represent canopy soil, the unshaded subplots, open soil for a plot beneath the canopy.

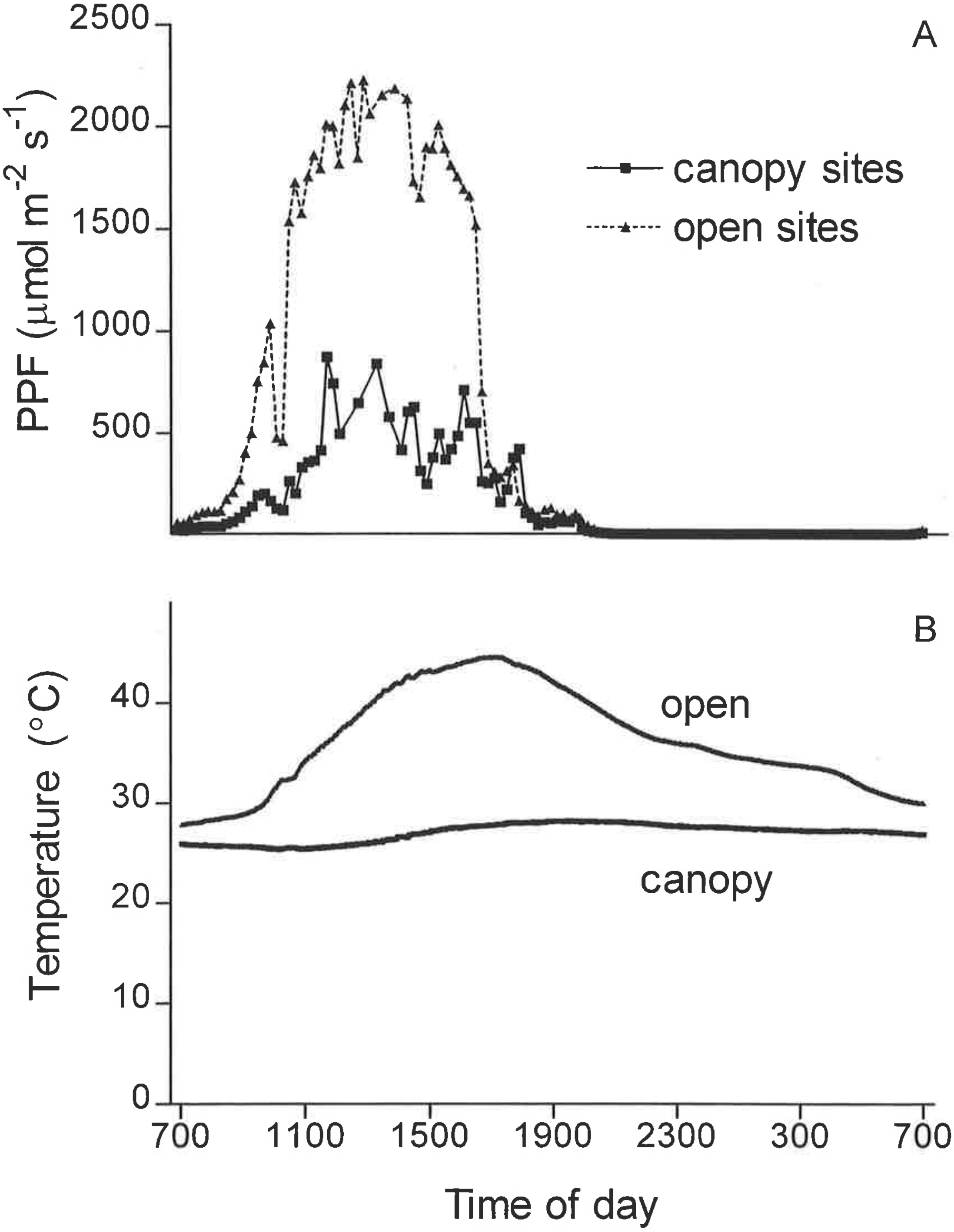


Fig. 6.2 Diurnal course of A) photosynthetic photon flux (PPF) and B) soil temperature at 10 cm depth in open unshaded sites and shaded sites under the northern side of an *Acacia* tree on 15 - 16 January 2000. PPF points represent the average for 15 minute intervals, with PPF measured every minute, and averaged for two quantum sensors in open sites and three sensors in canopy sites. Temperature points represent the average for two thermocouples in open sites and four in canopy sites measured at two minute intervals.

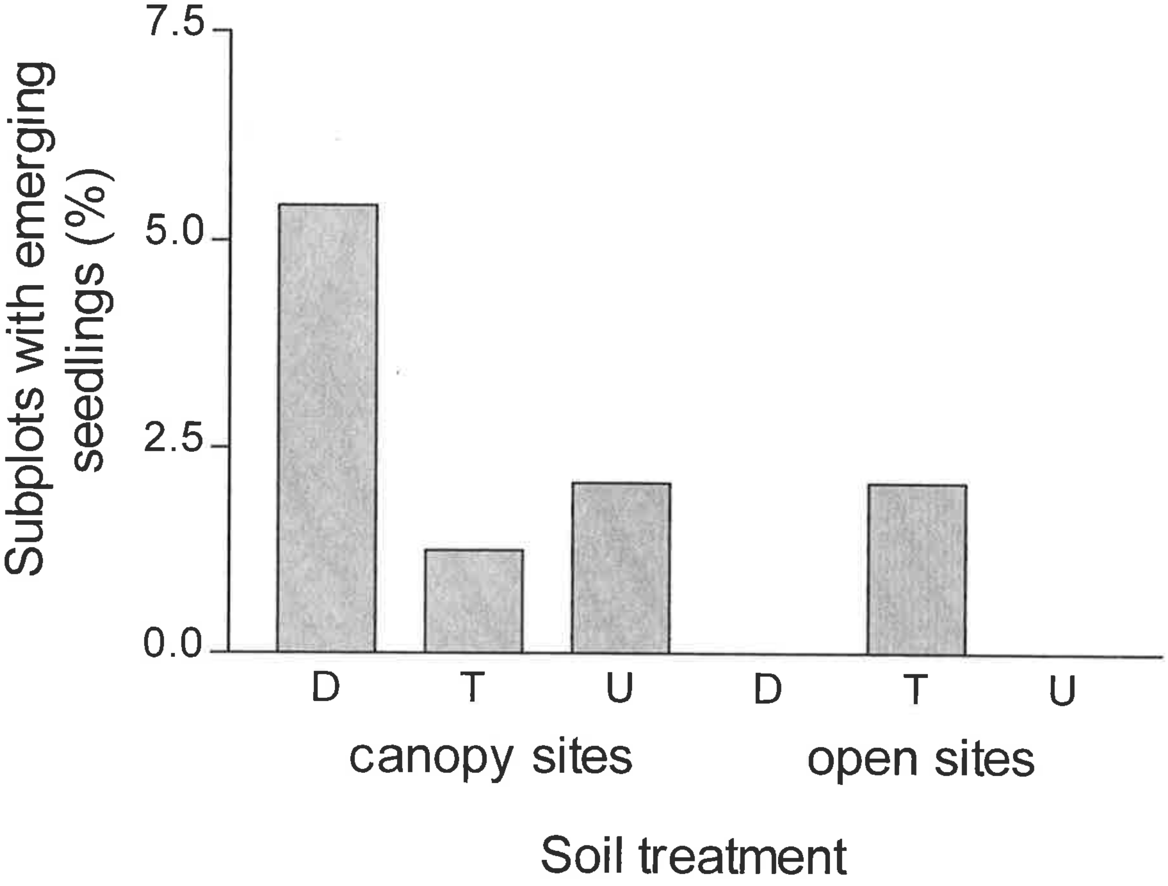


Fig. 6.3 The percentage of subplots with emerging *Atriplex* and *Enchylaena* seedlings in 2000. Soil treatments are; controls, both D, disturbed and U, undisturbed, comprising in situ soils, and transplant subplots T, with soils from alternate sites, i.e. open soils in canopy sites and canopy soils in open sites (see Fig. 6.1).

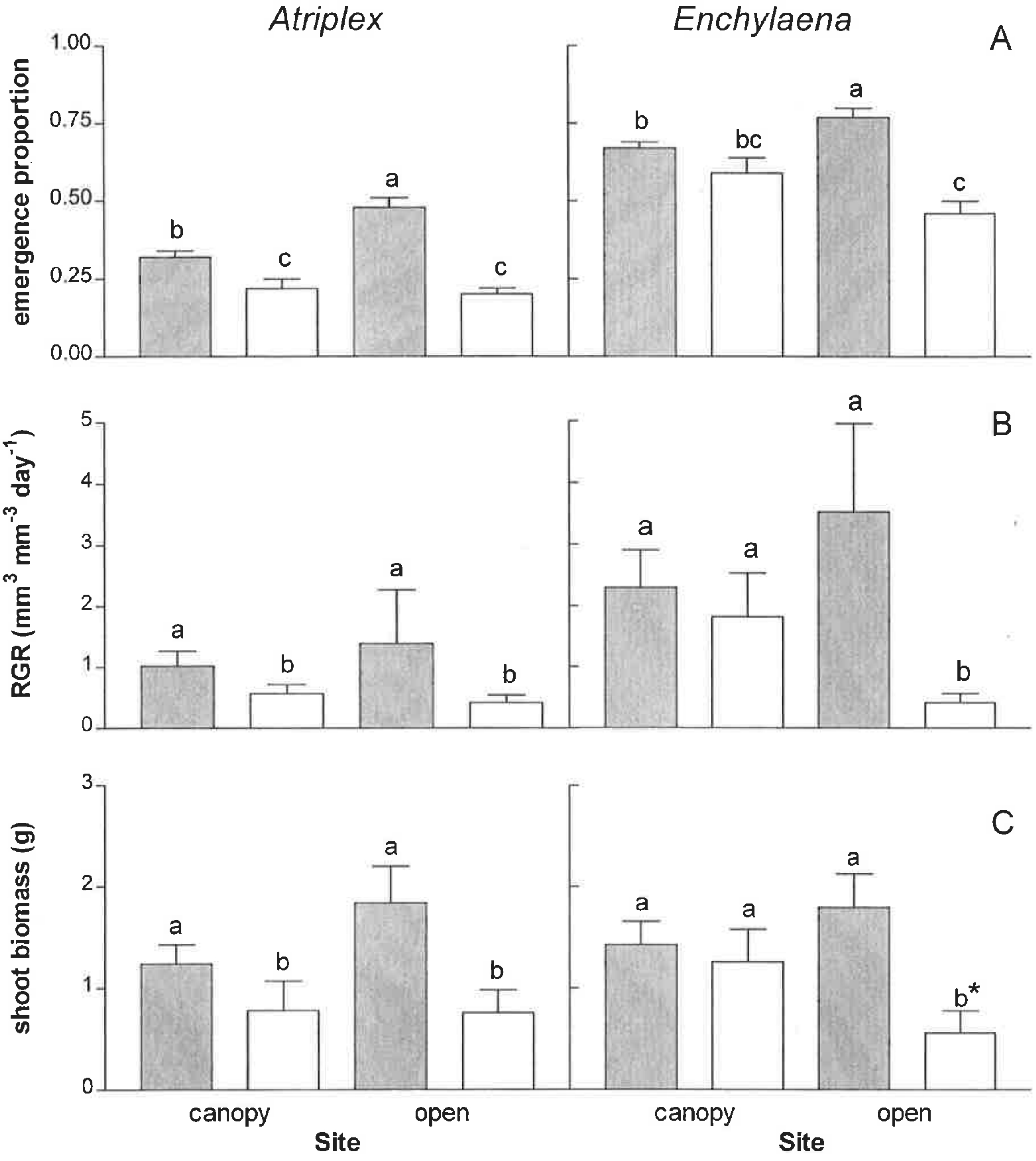


Fig. 6.4 Mean (+ 1SE) proportion of emerging *Atriplex* and *Enchylaena* seedlings in 2001 (A), and the relative growth rate (RGR, B) and shoot biomass(C) of transplanted seedlings in factorial combinations of canopy (shaded bars) and open soils (unshaded bars) and canopy and open sites. RGR and shoot biomass for *Enchylaena* are estimates from the time of planting (June) until December, for *Atriplex* from the time of planting (September) until April. Seedling emergence bars and *Enchylaena* RGR bars labelled with different letters were significantly different at *a* <0.01 (*Atriplex*) and *a* <0.05 (*Enchylaena*) (Tukey-Kramer HSD tests). *This difference was marginally significant (see Table 6.6).

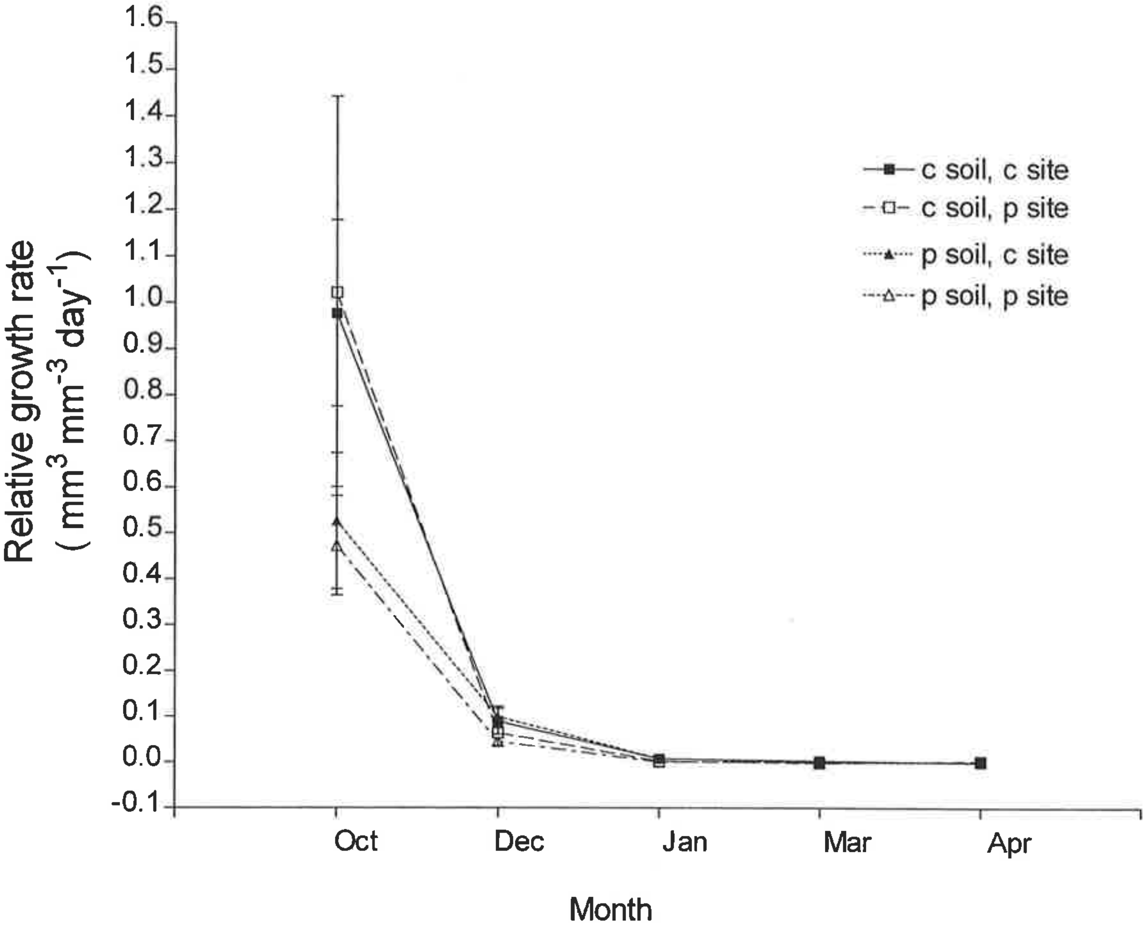


Fig. 6.5 Mean (± 1 SE) relative growth rate of transplanted *Atriplex* seedlings grown in canopy (c) and open (p) soils in canopy and open sites from the establishment period until April.

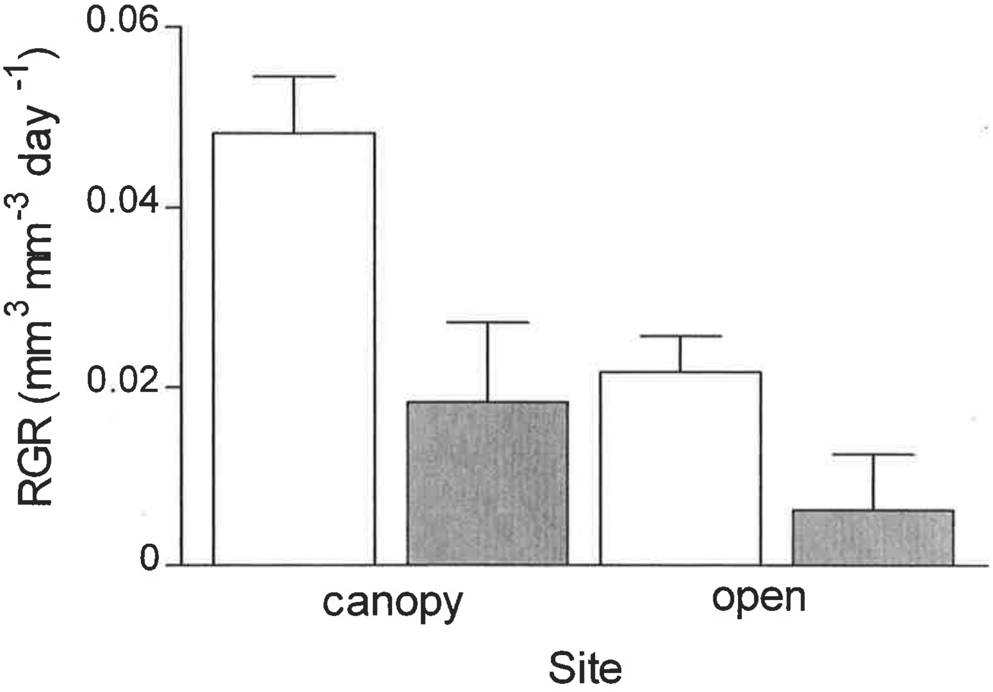


Fig. 6.6 Mean (+ 1SE) relative growth rate (RGR) of transplanted *Enchylaena* seedlings growing in two sites in canopy soil (unshaded bars) and open soil (shaded bars) during the establishment period (June to September) when all plants were watered.

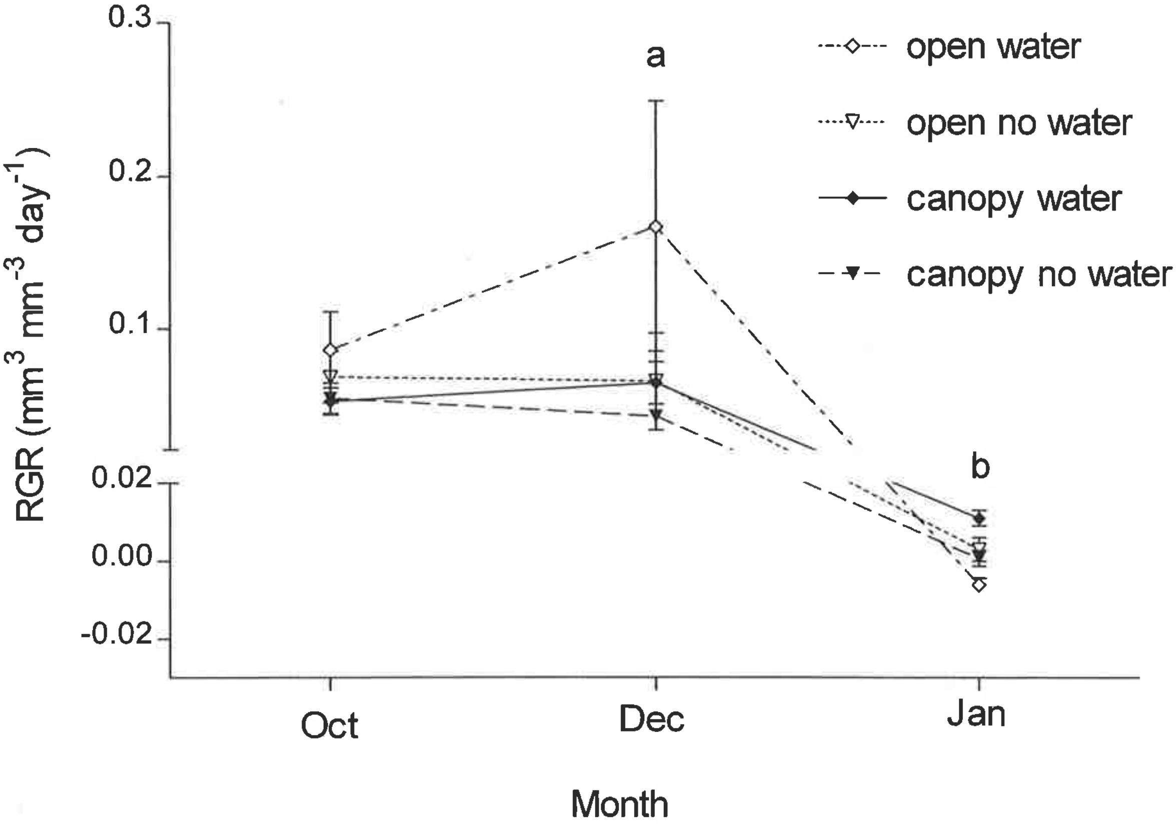


Fig. 6.7 Relative growth rate (RGR, means ± 1 SE) of transplanted *Enchylaena* seedlings in open and canopy sites, with and without supplementary watering. Note broken y-axis scale. a = significant difference between watering treatments within sites. b = significant effect of watering in canopy sites only (Tukey-Kramer HSD tests $a < 0.004$).

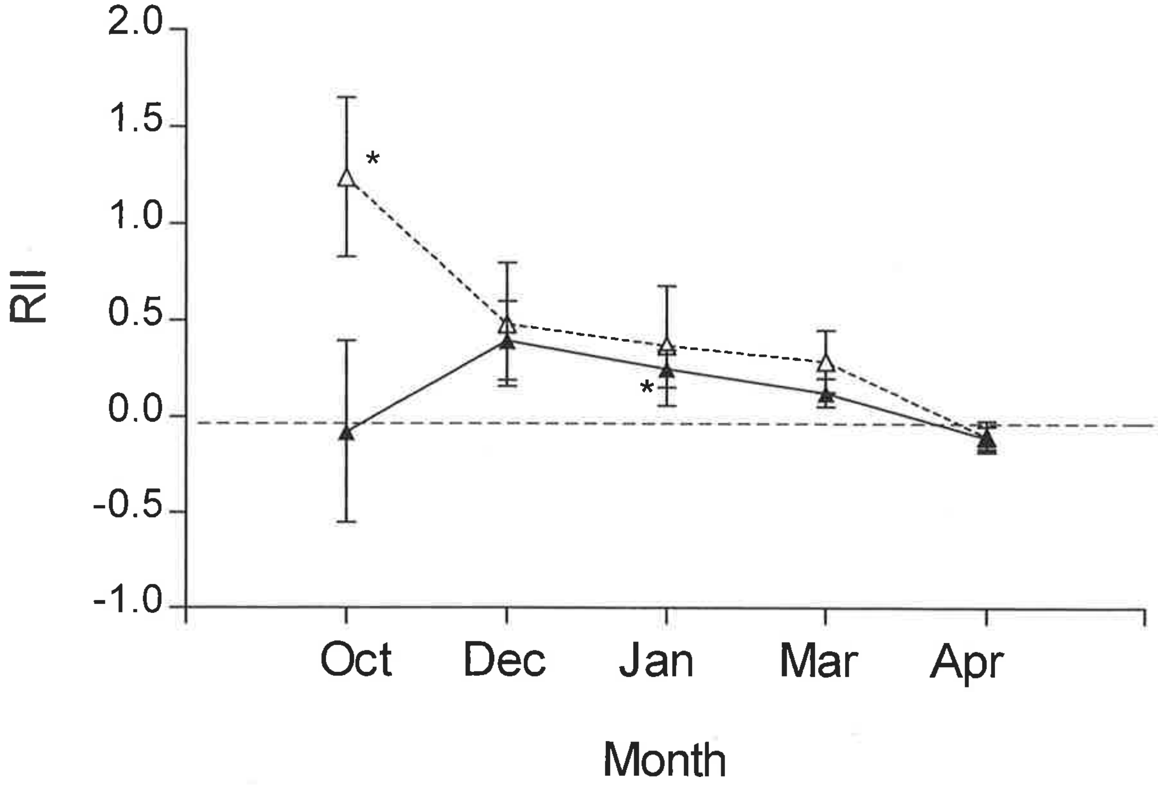


Fig. 6.8 *Atriplex* mean (± 1SE) relative interaction intensity (RII) or the relative difference in relative growth rate (RGR) between plants growing in canopy and open sites in the same soil type (solid line), that tests for a microclimate effect and in *in situ* soils (broken line) within each site that tests for combined soil and microclimate effects. The dashed line at zero marks where canopies have neutral effects on plant growth. * indicates values that are significantly greater than zero, i.e. RGR greater in canopy sites (see Table 6.9).

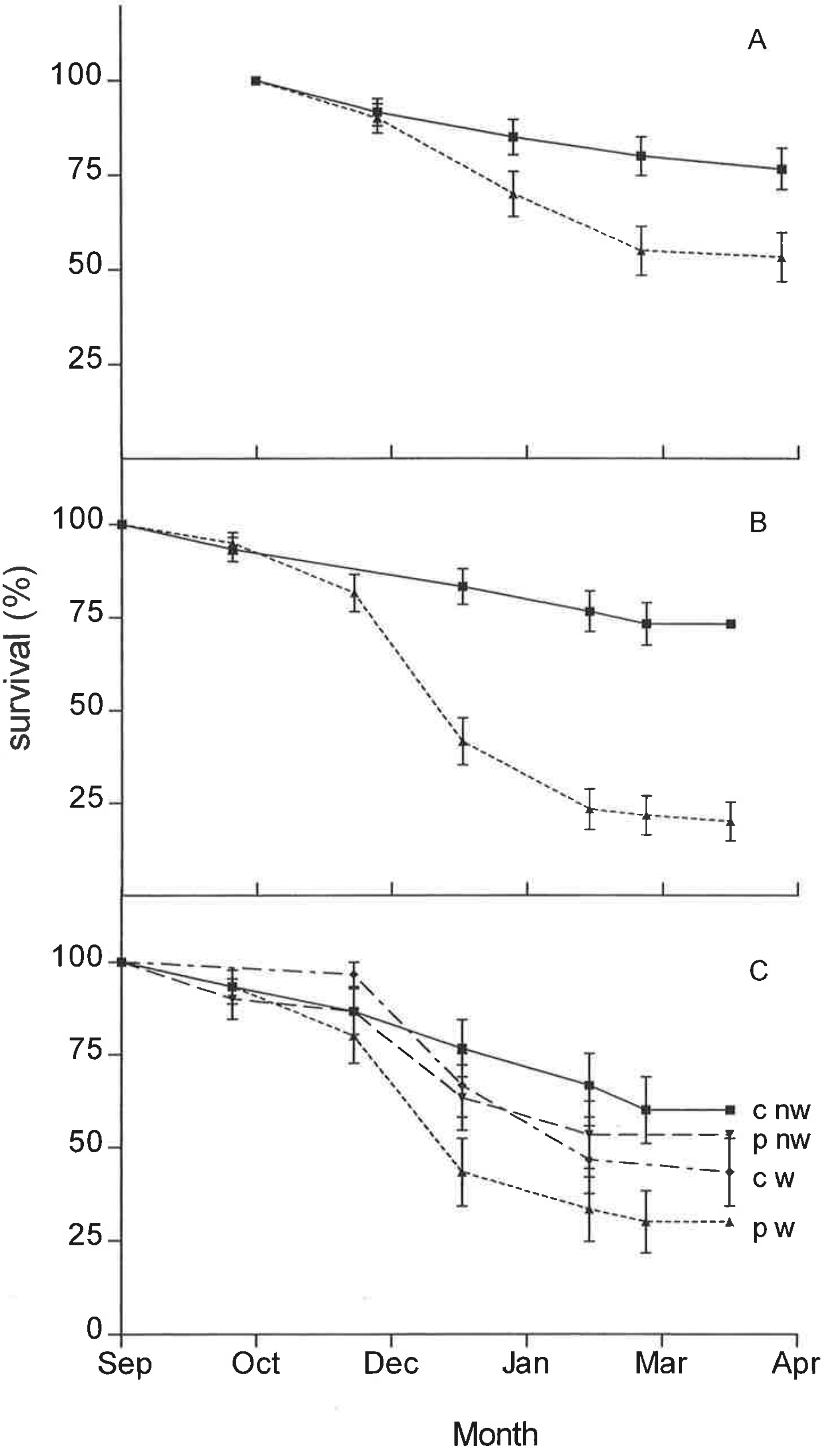


Fig. 6.9 Survival curves (mean ± 1SE) for A) *Atriplex* and B) *Enchylaena* in canopy sites (solid line) and open sites (broken line) and C) *Enchylaena* survival curves in two soil types (c, canopy soil and p, open soil) under two watering regimes, nw, no supplementary water, and w, supplementary water. Points represent survival fractions for each census and standard errors (GraphPad Prism, Ver.3.02).

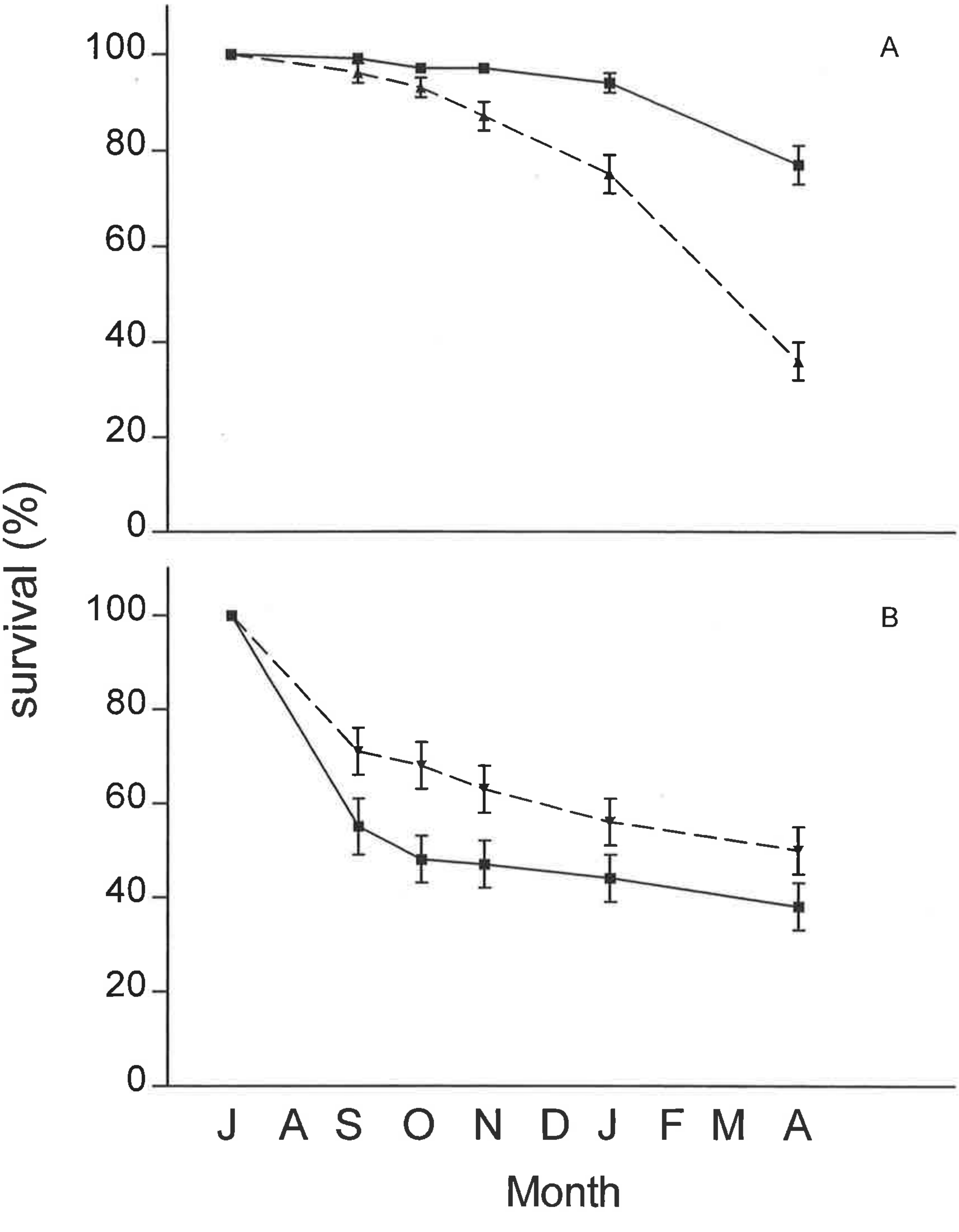


Fig. 6.10 Survival curves (mean ± 1SE) for A) *Enchylaena* and B) *Atriplex* seedlings germinated *in situ* in June 2001. For final survival percentages in April 2002 there was a significant site effect for *Enchylaena* but not *Atriplex* (see Table 6.9).

CHAPTER 7

Interactions between drought and light on the water relations and carbon gain of seedlings

Introduction

The relative abundances of resources required for plant growth are modified beneath plant canopies (see reviews by Hunter and Aarsen 1988, Belsky *et al.* 1989, Callaway 1995). Although light is reduced in this microhabitat, nutrient and soil moisture availability may be higher, and evaporative demands lower due to increased humidity or reduced temperatures. Such modifications may enhance or facilitate the growth of plants in this microhabitat (Callaway 1995). Whether a plant growing beneath the canopy of another is facilitated depends on its physiological tolerances and minimal resource requirements, especially for light and soil moisture at different life stages (Holmgren *et al.* 1997). Seedlings are particularly sensitive to resource shortages and stresses.

Researchers have examined the combined effect of shortages of light and soil moisture on the growth of temperate and tropical woodland and forest seedlings (Fisher *et al.* 1991, Veenendaal *et al.* 1996, Baruch *et al.* 2000, Poorter and Hayashida 2000, and review by Coomes and Grubb 2000). Many of these experiments have compared species that typically establish in canopy gaps with those that can establish in the deeply shaded understorey. Some researchers have found that plants growing in high light have greater sensitivity to soil moisture status; water limits growth when light is not limiting but light limits growth when water is not limiting (Kozlowski 1949, Fisher *et al.* 1991, Baruch *et al.* 2000, Holmgren 2000, Poorter and Hayashida 2000). However, the light climate beneath canopies in arid systems differs from that in many temperate or tropical systems. As rainfall decreases or the length of the dry season increases, light penetration through the canopy increases (Coomes and Grubb 2000). The shade cast by shrubs and trees in arid systems is not likely to be dense, but the effects of light reductions on the carbon gain of understorey plants in these systems has not received much attention. Whereas shade may be detrimental to seedling growth in mesic systems, shade may have a positive effect on seedlings in arid systems (Holmgren *et al.* 1997). In arid systems severe shortages of soil water often coincide with periods of high temperatures and high solar radiation, producing multiple stresses on plant performance.

Protection from high radiation loads in shaded microenvironments during drought may compensate for a loss of productivity due to reduced light levels when water is available.

Smith and Huston (1989) predicted that for forest systems there was a trade-off between shade-tolerance and drought-tolerance. Plants adapted to shaded conditions would be more sensitive to drought than plants adapted to higher irradiation. Their argument is based on biomass allocation patterns under dry and low light conditions. Plants growing in low light allocate a greater proportion of biomass to light capturing organs, creating a greater transpirational area and are thus susceptible to dry conditions. But under dry conditions proportionally more biomass is allocated to roots, which increases the ratio of respiring tissue hence the requirement for more light to maintain a positive carbon balance. Consequently, it has been hypothesised that growth and survival in shaded microenvironments only becomes viable with increased moisture availability in these sites (Holmgren *et al.* 1997). However, plants may be able to persist in shaded habitats in arid systems when reduced evaporative demands below canopies ameliorate water stress for plants growing there. Shading may therefore lessen the impacts of drought (Holmgren 2000). Alternatively, light and soil moisture may have independent effects, such that the effects of drought on plant performance may change proportionally with decreasing light availability (Sack and Grubb 2002).

In the previous experiment I showed how modifications to soils and microclimates by *Acacia papyrocarpa* had beneficial effects on plant growth, but canopy microclimates facilitated *Enchylaena* growth mainly during pulses and *Atriplex* growth mainly during interpulses. In this experiment I explore the physiological basis of these temporal differences in the effects of shade. I used pot grown seedlings to compare the physiological responses of these two shrub species and *Rhagodia spinescens* to an imposed water deficit when grown under light levels simulating the light conditions beneath *Acacia* canopies and the open sites between canopies. The study addresses the following questions:

1) Does light intensity affect physiological responses (shoot water potential, stomatal conductance, carbon gain) to water deficit?

2) Is the carbon gain of plants typically found only beneath canopies, i.e. *Enchylaena* and *Rhagodia*, sensitive to high light intensities, particularly during drought?

3) Is the carbon gain of plants found in high-light environments, i.e. *Atriplex*, affected by shade?

Methods

Experimental design

I grew seedlings of *Atriplex*, *Rhagodia* and *Enchylaena* from seed sourced from populations in areas with less than 400 mm annual rainfall (Supplier: Blackwood Seeds, Murray Bridge, South Australia). I sowed seeds in 0.3 L pots of topsoil collected from either under *Acacia* canopies (canopy soil) or from adjacent open spaces (open soil). Both soil types were used as soils differed in their water-holding and water-retention characteristics (Facelli and Brock 2000). This could affect water availability during the drought period. I fertilised each pot with 1.4 g of Osmocote™ slow release fertilizer (N:P:K 17:1.6:8.7; Scotts Australia Pty Ltd) so that nutrient effects were not included in this study. I established 200 seedlings of each species, giving 50 replicates for each treatment of soil type and light intensity. I maintained the pots outdoors. To reduce evaporation of soil water and to lower soil temperature I packed the pots into polystyrene foam boxes in random order and mulched each pot with a 20 mm layer of vermiculite. I provided shade to half of the pots with shadecloth that reduced incoming radiation to 20%. This represents a level of shading similar to that produced by *Acacia* trees at the field site (see Fig. 6.2). The remaining pots were grown in full sunlight. I watered seedlings every other day, unless the temperature was greater than 30 °C, in which case I watered daily. Only the surface soil of unshaded pots dried out between waterings. I hardened plants by omitting watering on two occasions prior to the imposition of drought conditions.

Plant responses

Measurements of shoot water potential, stomatal conductance and carbon gain commenced on the last day the plants were watered. I made daily measurements (two replicates per treatment) on unwatered plants until carbon gain was no longer positive. Because I aimed to examine plant responses to summer drought the drought period occurred during February 2000 (mean air temperature ± 1 SD, 36.2 °C ± 3.5). I measured photosynthetic rates and stomatal conductance on terminal shoots of four-month old plants using a Li-6200 Portable Photosynthesis System (Li-Cor Inc. Lincoln, Nebraska) at saturating light (1500 μmol m^{-2} s^{-1} for non-shaded plants, 1000 μmol m^{-2} s^{-1} for shaded plants). I determined these values by constructing light assimilation curves for three replicates of each species in each light treatment. I made measurements between 10 am and 1 pm outdoors, with shading provided by a voile cloth for the shaded treatments. Prior to all measurements, I equilibrated plants for 30 minutes in the light conditions under which the measurements were to be made. After these measurements I excised each shoot and immediately inserted it into a Scholander-type pressure chamber for measurement of shoot water potential. I determined the leaf area of measured shoots by scanning excised leaves and calculating scanned leaf area with an Optimas imaging program (Media Cybernetics, Ver. 5.2). I calculated gas exchange and stomatal conductance on a leaf area basis.

I cut the remaining above-ground biomass at ground level and dried it to constant weight at 85°C. Shoots on which leaf area had been determined were dried and weighed separately for determination of specific leaf area. I calculated specific leaf area as A/M ($cm^2\ g^{-1}$), where A is leaf area and M is leaf mass dry-weight. I weighed pots and then kept them moist until roots could be extracted, usually within five days. I determined the fresh and dried weight of roots. Soil from the pots was oven dried to constant weight at 105°C. I determined the soil water content in pots gravimetrically after first subtracting the weight of fresh roots from the initial soil weight.

Analyses

I used ANCOVA to test the effects of light treatment, soil type and species on each physiological variable as drought progressed. I used shoot water potential (Ψ_s), stomatal conductance (g_s) and carbon assimilation rate at saturating light (A_{max}) as dependent variables in separate analyses of covariance with percentage soil water content (SWC) as the covariate. I log transformed all physiological variables for analyses to satisfy assumptions of linearity. Significant differences in slopes in these models (interactions between the covariate and other effects in ANCOVA models) indicated different responses of the physiological variables over the drought period for different experimental treatments. Other significant effects in ANCOVA models, which did not include the covariate, indicated significant differences in the elevations or intercepts of the regression lines. In order to test differences between treatments at both low and high SWC I calculated values of dependent variables at two soil water contents, 8% and 20% of dry soil weight. I selected these soil water contents as I measured physiological variables across all treatments within this range. Additionally, the field capacity of soils was at a SWC of 24% soil dry weight and plants died when SWC fell below 5% dry soil weight. I used Tukey type tests (Zar 1999) for all post hoc multiple pairwise comparisons after ANCOVA.

I examined the relationship between stomatal conductance and photosynthetic rate with linear regressions on the log-transformed variables. I used ANOVA to test the effects of light treatment, soil type and species on shoot, root and total biomass, shoot proportion and specific leaf area. Drought treatments did not affect these variables as they represent growth over the period when seedlings were watered, and the imposed drought was short-term. I log transformed data to satisfy assumptions of homoscedasticity and normality. I used Tukey-Kramer HSD tests for post hoc comparisons.

I removed higher-order interactions where they were not significant. I used JMP IN Ver. 4.0.3 for all analyses unless otherwise indicated.

Results

Drought period

Over the nine to ten day drought period, in both soil types, SWC fell from a mean of 24% of soil dry weight across treatments on the final day of watering to a minimum of 8% of soil dry weight. Soil water content fell very quickly a day after the cessation of watering, but decreased at slower rates subsequently (Fig. 7.1). Over time, shaded soils maintained higher SWC than unshaded soils, however this does not affect the conclusions because I analysed physiological measurements as responses to SWC rather than time since last watered. Although *Atriplex* maintained positive carbon assimilation rates for the duration of this period, they had become negative in *Enchylaena* and *Rhagodia* after four days in unshaded conditions and after eight days in shaded conditions. Chamber temperatures during measurements were significantly higher in unshaded conditions than shaded conditions (means ± 1 SD, 38.7 ± 2.9 °C and 34.8 ± 3.0°C respectively; *ANOVA*, $F_{1,163} = 64.90$, $P < 0.001$). However, there was no significant linear relationship between temperature and photosynthetic rate over the measurement period and across the range of temperatures recorded ($r^2 = 0.003$, $P = 0.45$).

Shoot water potential

The relationship between shoot water potential (Ψ_s) and SWC over the drought period differed between light treatments for *Atriplex* and *Rhagodia* (significant species/shade/SWC interaction, Table 7.1), decreasing at a faster rate for plants growing under unshaded conditions (Fig. 7.2A). Shade-grown *Atriplex* plants had a much slower decline in Ψ_s over the drought period, and the fastest decline occurred in high-light grown *Rhagodia* (slope comparisons, Table 7.2). Droughted, shade-grown *Atriplex* plants had higher Ψ_s than all other treatments (Table 7.2) but Ψ_s did not differ between species grown in high light at low SWC (species/shade interaction, Table 7.1). For well-watered plants there was no significant difference in Ψ_s between light treatments for any of the species (Table 7.2).

Soil type affected the Ψ_s of well-watered plants growing in high-light treatments (soil/shade interaction, Table 7.1), being higher in open soils than canopy soils (Table 7.3). Although at low SWC plants growing in both soil types had higher Ψ_s when grown in shade (Table 7.3), the interaction between species and shade showed this was only significant for *Atriplex*. There were differences in Ψ_s between species growing in the different soil types (species/soil interaction, Table 7.1), but only at low SWC (Table 7.4).

Stomatal conductance

Stomatal conductance (g_s) fell at a slower rate over the drought period in shaded treatments (shade/SWC interaction Table 7.1, slopes 1.96 and 1.45, Fig. 7.2B). There was a light treatment effect on estimated g_s in *Atriplex* but not other species (species/shade interaction, Table 7.1). Stomatal conductance was significantly lower in shaded *Atriplex* plants at both high and low SWC (Table 7.2).

The relationship between SWC and g_s differed between species in different soil types over the drought period (species/soil/SWC interaction, Table 7.1). In *Enchylaena* and *Rhagodia* g_s fell at a more gradual rate in canopy soils. In *Atriplex* g_s fell at significantly slower rates in drying open soils (Fig. 7.3, slopes Table 7.2). The estimated g_s differed significantly between soil types at high and low SWC, but this was not consistent for all species (species/soil interaction Table 7.1). In well-watered soils *Rhagodia*, and *Enchylaena* g_s was higher in open soils (Table 7.4, Fig. 7.3). For *Atriplex* there was no difference between soil types at high SWC but at low SWC g_s was greater in open soils (Table 7.4, Fig. 7.3).

Photosynthetic rate

Maximum photosynthetic rates (A_{max}) were measured in well-watered unshaded *Atriplex* plants (12.84 μmol C m^{-2} s^{-1}), followed by *Rhagodia* (8.33 μmol C m^{-2} s^{-1}) and *Enchylaena* (5.81 μmol C m^{-2} s^{-1}). Positive carbon gain did not occur in most plants when soil water content dropped below 8% (Fig. 7.2C). A_{max} fell at a slower rate in plants growing in the shade (shade/SWC interaction, Table 7.1, slopes 0.74 and 0.48). There were species differences in A_{max} between light treatments at low and high SWC (species/shade interaction, Table 7.1). At high SWC only *Atriplex* plants were significantly affected by the light treatment under which they were grown, with A_{max} lower in shade-grown plants (Table 7.2). Although there was a trend for A_{max} to be higher in unshaded *Atriplex* than all other treatments, these differences were not significant (Fig. 7.3C, Table 7.2). At low SWC only *Enchylaena* plants were significantly affected by light treatment. High-light grown plants had stopped gaining carbon, whilst plants growing in the shade maintained carbon uptake (Table 7.2).

A_{max} was higher in *Atriplex* than other species over a wide range of g_s (Fig. 7.4). The relationship between g_s and A_{max} was strongest for *Rhagodia* ($r^2 = 0.70$, on transformed values) but changes in g_s only explained 48% ($r^2 = 0.48$) of the variation in A_{max} for *Atriplex* and 56% for *Enchylaena*. There were also differences between light treatments in the strength of this relationship. For *Atriplex* g_s explained 68% of the variation in A_{max} in unshaded treatments but 38% in shade treatments, for *Enchylaena* 83% and 33%, and *Rhagodia* 78% and 63% in unshaded and shaded treatments respectively.

A_{max} differed between soil types in the two light treatments but the differences between soil types were only significant at low SWC (soil/shade interaction Table 7.1). In dry soils carbon gain was negative in plants growing in canopy soil in unshaded conditions but there were no differences between other treatments, which all had positive carbon gain (Table 7.3).

Biomass

Shoot and root biomass differed between species, soil types and light treatments but there were interactions between pairs of these factors (Table 7.5). All species had less root biomass in shaded treatments yet only *Atriplex* shoot biomass was reduced when grown in shade (Fig. 7.5A). *Rhagodia* had less shoot biomass than the other two species and less root biomass under unshaded conditions (Fig. 7.5A). Shoot biomass was also affected by soil type. *Rhagodia* shoot biomass was significantly greater in canopy soils and there was also a similar trend for *Enchylaena* (Fig. 7.5B). *Enchylaena* plants growing in canopy soils had greater shoot biomass than *Atriplex* plants (Fig. 7.5B). Soil type also interacted with light treatment; shoot and root biomass was greater in canopy soils but only in unshaded treatments (Fig. 7.5C).

Atriplex and *Enchylaena* had similar proportions of shoot biomass but *Rhagodia* had a significantly greater proportion of shoot biomass (*ANOVA*, $F_{2,159} = 9.048$, $P < 0.001$). Shoot proportions and specific leaf area were significantly greater in shaded than unshaded treatments (*ANOVA*, $F_{1,159} = 253.300$, $P < 0.001$, and *ANOVA*, $F_{1,159} = 28.284$, $P < 0.001$ respectively).

Discussion

The effects of increasing water deficit on Ψ_s, g_s and A_{max} differed between light treatments. Plants had more gradual declines in Ψ_s (with the exception of *Enchylaena*), g_s and A_{max} over the drought period when grown in shade than when grown under high light. This suggests water stress is mitigated by shade during the summer months and that plants in shaded microclimates can maintain a positive carbon balance for longer into drought periods.

Water relations

Slower declines in g_s in shade, and high rates of g_s in unshaded, well-watered plants suggests that evaporative demand under shade was not as great as under high irradiance when ambient air temperatures are high. Leaf temperatures can be lower in shade where solar radiation loads are lower so plants are able to conserve more water and maintain higher tissue water status as less water is required for transpirational cooling (Schultz and Matthews 1997, Valladares and Pearcy 1997, Sawada *et al.* 1999 401). Stomatal conductance may also be lower in shade due to lower stomatal density in shade-grown leaves (Osmond *et al.* 1980, Valladares and Pearcy 1997, Lambers *et al.* 1998). This may explain the seemingly paradoxical result of a slower rate of decline in Ψ_s in shade treatments for *Atriplex* and *Rhagodia* in addition to the slower decline in g_s under these conditions.

The Ψ_s of *Atriplex* was very sensitive to shade, with shade-grown plants maintaining high Ψ_s even in very dry soils. Shade-grown *Atriplex* plants had very thin, lax stems as compared to the thicker, upright stems of plants grown in high light. Presumably xylem development (either the number and size of vessels) in shaded plants was not as extensive as in high light grown plants. For plants with poor hydraulic architecture, maintaining high tissue water status by decreasing water potential gradients may reduce the risks of cavitation (Schultz and Matthews 1997), which would increase stem survivorship, even though there may be reductions in growth.

Although shade-grown plants had higher proportions of shoot biomass than high-light grown plants, transpirational water losses per leaf area may not be greater in shade-grown plants, contrary to the predictions of Smith and Huston (1989). Reduced xylem formation (Shultz and Matthews 1993) and leaf vascularisation (Kozlowski 1949), and fewer stomata (Osmond *et al.* 1980, Valladares and Pearcy 1997) may reduce transpirational water losses due to anatomical differences between high and low light grown leaves. Coupled with reductions in water and heat stress in the shade, shade becomes an advantage as conditions become drier as it improves plant water relations (Holmgren 2000). Such effects may have enabled shaded *Enchylaena* and *Rhagodia* to continue gaining carbon longer into the drought period.

Carbon gain

Atriplex carbon gain was less affected by shoot water potential than the other two species. In high light treatments, *Atriplex* maintained higher photosynthetic rates over a broader range of Ψs than *Enchylaena* or *Rhagodia*. *Atriplex* also had a much higher leaf-level photosynthetic rate for a given g_s than the other two species and carbon gain was only equal between species at very low soil water content. Thus *Atriplex* had a much more conservative water use pattern or water use efficiency, being able to fix more carbon with less transpirational water loss. *Atriplex vesicaria* utilizes the C_4 carboxylation pathway whilst *Enchylaena* and *Rhagodia* are C_3 plants. Although the difference in water use efficiency between C_3 and C_4 species can be greater at high soil water contents than low soil water contents, C_4 plants use water more efficiently so they are able to remain physiologically active for longer into drought periods (Chapman and Jacobs 1979, Kalapos *et al.* 1996). In this study, *Atriplex* was able to gain carbon for longer into the drought period whereas photosynthesis ceased in high light grown *Enchylaena* plants soon after the imposition of drought. *Rhagodia* was able to maintain positive carbon gain to lower Ψ_s than *Enchylaena* but as in *Enchylaena* this point was rapidly reached after watering stopped. Both of these species showed less conservative water use strategies than *Atriplex*.

Decreases in A_{max} in unshaded plants over the drought period were influenced more by stomatal closure than shaded plants, at least for *Atriplex* and *Enchylaena*. Similar patterns have been found in other comparisons of shaded and unshaded plants (Lipscomb and Nilsen 1990a, 1990b, Niinemets *et al.* 1999, Sawada *et al.* 1999). Non-stomatal limitations to carbon assimilation are still poorly understood (Nilsen and Orcutt 1996). Damages to both carbon reduction and light harvesting functions in response to water stress may limit carbon assimilation under water stress in addition to damage via photoinhibition which is exacerbated by high light (Gamon and Pearcy 1990). It has been suggested that the reduced capacity for carbon reduction in shaded plants (Boardman 1977, Osmond *et al.* 1980) may predispose them to greater non-stomatal limitations during drought (Kubiske *et al.* 1996).

High irradiance had negative effects on *Enchylaena* carbon gain in very dry soils. Although most of the reduction in photosynthetic rate may be attributed to stomatal closure, observations of similar stomatal conductance between shaded and unshaded plants yet different photosynthetic rates suggested photoinhibitory effects. High temperatures or water stress can have similar or interactive effects on the inactivation of the photosynthetic apparatus at high irradiance (Bjorkman and Powles 1984, Powles 1984). The photochemistry of water stressed plants growing in shade can be less affected than water stressed plants growing under high irradiance (Gauhl 1979, Bjorkman and Powles 1984, Valladares and Pearcy 1997) although in other cases water stress was found to have no effect on photoinhibition (Gamon and Pearcy 1990, Valentini *et al.* 1995). Prolonged exposure to high temperatures that may be exacerbated by both high light and water stress can also have photoinhibitory effects (Ludlow and Bjorkman 1984, Gamon and Pearcy 1990, Valladares and Pearcy 1997). In this experiment, higher temperatures in unshaded conditions accompanied water stress so it is difficult to determine which factors were relevant. *Atriplex* also showed a minor photoinhibitory effect when water stressed as although conductance was higher in unshaded plants A_{max} did not differ between light treatments.

When water was not limiting, light limited carbon assimilation in *Atriplex* but not the other two species. Similar light-limiting effects have been observed for other species commonly found in high-light environments (Kozlowski 1949, Holmgren 2000). *Atriplex* may thus be at a competitive disadvantage when water is abundant under trees, but not during drought. At the field site *Atriplex* cover was significantly lower in the area adjacent to the trunk of dense canopied *Acacia* trees than the outer canopy zone of sparse canopied trees or immediately adjacent to trees (but not shaded) (Facelli and Brock 2000). *Rhagodia* and *Enchylaena* show the opposite pattern having more cover in the most shaded microenvironment (dense inner canopy) and decreasing in habitats with higher light (open sites) (Facelli and Brock, 2000). Although drought tolerance characteristics do not appear to de disadvantageous to *Atriplex* in shade, stomatal sensitivity to light could restrict carbon gain and hence growth and competitive responses under shaded conditions, particularly denser shade. There is not a clear demarcation zone between shaded canopy microenvironments and the unshaded matrix microenvironment in arid systems but rather a gradient exists between the two (Holmgren *et al.*, 1997; Moro *et al.*, 1997). This is in addition to the variation found beneath trees associated with aspect, canopy size (Tewksbury and Lloyd 2001) and canopy density (Facelli and Brock 2000). Gradients in light intensity beneath different *Acacia* canopies could have complex effects on the distribution of these three shrubs.

Soils

It was predicted that after the onset of drought soil moisture would be available for longer in canopy soils. Therefore Ψ_s, g_s and A_{max} would fall at slower rates in canopy soils. But this was only the case for *Enchylaena* and *Rhagodia* g_s. Well-watered *Enchylaena* and *Rhagodia* plants had lower estimated g_s in canopy soils. This was unexpected as it was predicted that more water would be available in well-watered canopy soils, allowing higher transpiration rates. One explanation could be due to root biomass that in both these species was greater in canopy soils. Roots that come in contact with a pot may produce ABA, triggering stomatal closure (Munns and Cramer 1996). Although well-watered plants growing in unshaded open soils had higher Ψ_s than other treatments the difference (0.2 MPA) was small, and not likely to be physiologically significant. This was possibly related to lower root biomass in these soils giving roots access to more soil water than in treatments with higher root biomass. With other physiological variables there were no consistent differences between soil types within shade treatments or within species, which are the most meaningful comparisons.

In unshaded treatments where soils dried out between waterings growth was poorer in open soils, but this was driven largely by the responses of *Enchylaena* and *Rhagodia* to the two soil types. It was predicted that growth would be poorer in open soils because of its higher bulk density (Barnes 1993). This would affect root penetration and water release (Greacen and Oh 1972, Hsiao 1973, Stirzaker *et al.* 1996). The effects of soil type on root penetration appear to be the most obvious causes of the growth and physiological differences observed between species. Unfortunately pot soil volumes may have not been enough to prevent the confounding effects of pot binding, so the effects of soil differences on physiological factors were unclear.

Summary and conclusions

Due to the controlling influence of water in arid systems, the effects of shade on the growth and water relations of plants is inextricably linked with the effects of water deficit. This study has demonstrated that the effects of shade become positive with increasing water deficit. Acclimation to shade provided protection against water and heat stress, but it was not possible in this experiment to separate these effects. Shading protected *Enchylaena* from photoinhibition when soils were very dry, yet carbon gain in *Rhagodia* and *Atriplex* was maintained over a wide range of Ψ_s. With no water deficit, shading reduced *Atriplex* carbon gain but not the carbon gain of *Enchylaena* or *Rhagodia*. *Atriplex* showed the most plastic response to shade, in terms of shoot architecture, biomass, Ψ_s, g_s and A_{max}. This species appears to be tolerant of a broad range of conditions, reflected in its wide distributional range in field conditions.

Rhagodia may be restricted to sites beneath canopies due to its high water usage. Stomatal conductance was very high in well-watered plants growing in full sun, and like in *Enchylaena* positive carbon gain was only maintained for a short time after the imposition of drought. Survivorship may therefore be reduced in open sites where water usage may be higher than in shaded sites because of higher evaporative demands. Similarly, *Enchylaena* survivorship may be restricted to sites beneath canopies due to the photoinhibitory effects of high irradiation loads and water stress in open sites during the summer months. Although textural differences between soil types did not appear to have any consistent effects on plant physiology in this experiment, with the exception of improvements in growth, increased nutrient levels under canopies can be a further factor impacting on plant performance in these sites.

Table 7.1 ANCOVAs of Ψ_s, g_s and A_{max} with soil water content (SWC) as the covariate in each case; testing the effects of species, shade and soil type and their interactions. Non-significant interactions have been removed from each model. All values were log transformed before analysis. Significant effects that include the covariate indicate different slopes, [1] see Table 7.2, [2] see Table 7.4 for multiple comparisons of slopes. Significant F values are labelled at the following probability values, * $\alpha < 0.05 > 0.01$, ** $\alpha < 0.01 > 0.001$, *** $\alpha < 0.001$. [#]Error SS (df)

		Physiological variable					
		Ψ_s		g_s		A_{max}	
Source	**df**	SS	*F*	SS	*F*	SS	*F*
SWC (covariate)	1	47.134	538.80***	96.289	274.17***	11.915	236.74***
Species	2	0.645	3.69*	1.321	1.88	0.239	2.38
Soil	1	0.663	7.57**	1.840	5.24*	0.567	11.27***
Shade	1	0.770	8.80**	1.648	4.69*	0.054	1.08
Species/soil	2	0.732	4.19*	4.261	6.07**	0.252	2.51
Species/shade	2	1.076	6.15**	5.193	7.39***	0.431	4.28*
Soil/shade	1	0.687	7.85**	0.743	2.12	0.335	6.65*
Species/SWC	2	1.122	6.41**	5.503	7.84***	-	-
Soil/SWC	1	0.131	1.50	2.125	6.05*	-	-
Shade/SWC	1	1.016	11.62***	2.900	8.26**	0.796	15.82***
Species/shade/SWC [1]	2	1.036	5.92**	-	-	-	-
Species/soil/SWC [2]	2	-	-	3.190	4.54*	-	-
Error[#]		12.684 (145)		50.573 (144)		7.449 (148)	

Table 7.2 Estimates of measured physiological variables at high (20% soil dry weight) and low (8% soil dry weight) soil water content between different species (A, *Atriplex*, E, *Enchylaena* and R, *Rhagodia*) grown under unshaded (N) and shaded (S) conditions; and the slopes of the regressions between soil water content and each physiological variable. All estimates were calculated from regressions between the log transformed soil water content variable and log transformed physiological variable in each case and then back transformed. Values labelled with a different letter within rows were significantly different at $\alpha < 0.05 > 0.01$.

		Treatment					
Physiological variable	**Soil water content**	**AN**	**AS**	**EN**	**ES**	**RN**	**RS**
Ψ_S (MPa)	low	-6.92^{a}	-2.87^{b}	-5.34^{ac}	-4.81^{c}	-6.90^{ac}	-5.89^{ac}
	high	-0.84^{ab}	-0.95^{a}	-0.52^{abc}	-0.33^{c}	-0.42^{bc}	-0.86^{ab}
	slope	1.46^{a}	0.69^{b}	1.43^{ac}	1.47^{a}	1.72^{ad}	1.31^{c}
g_s (mmol H_2O m^{-2} s^{-1})	low	14.88^{a}	8.10^{b}	6.92^{ab}	12.01^{ab}	7.13^{ab}	10.09^{ab}
	high	67.79^{ac}	28.57^{b}	71.98^{ac}	22.33^{ab}	118.41^{c}	74.20^{ac}
	slope	1.52^{a}	1.25^{b}	2.34^{a}	1.31^{b}	2.81^{a}	2.00^{b}
A_{max} (μmol C m^{-2} s^{-1})	low	0.10^{ab}	0.44^{a}	-0.31^{b}	0.49^{a}	0.28^{a}	0.55^{a}
	high	6.93^{a}	3.11^{b}	3.90^{ab}	3.80^{ab}	4.76^{ab}	3.85^{ab}
	slope	0.81^{a}	0.46^{b}	0.85^{a}	0.51^{b}	0.65^{a}	0.49^{b}

Table 7.3 Estimates of measured physiological variables at high and low levels of soil water content between plants grown in canopy and open soils, in shaded and unshaded conditions. All estimates were calculated as described in Table 7.2. Values labelled with a different letter within rows were significantly different at $\alpha < 0.05 > 0.01$.

Physiological variable	**Soil water content**	**Treatment** **Canopy soil** **No Shade**	**Canopy soil** **Shade**	**Open soil** **No shade**	**Open soil** **Shade**
Ψ_S (MPa)	low	-7.44^a	-4.21^b	-5.81^a	-4.07^b
	high	-0.68^a	-0.69^a	-0.46^b	-0.61^a
A_{max} (μmol C m^{-2} s^{-1})	low	-0.27^a	0.46^b	0.46^b	0.49^b
	high	4.34^{ab}	3.04^a	6.74^b	4.06^{ab}

Table 7.4 Estimates of measured physiological variables at high and low levels of soil water content between different species (A,*Atriplex*, E, *Enchylaena* and R, *Rhagodia*) grown in canopy (C) and open (P) soils; and the slopes of the regressions between soil moisture and each physiological variable. All estimates were calculated as described in Table 7.2. Values labelled with a different letter within rows were significantly different at $\alpha < 0.05 > 0.01$.

		Treatment					
Physiological variable	**Soil water content**	**AC**	**AP**	**EC**	**EP**	**RC**	**RP**
Ψ_s (MPa)	low	4.70^{ab}	4.04^{b}	4.38^{bc}	6.36^{ac}	6.89^{a}	5.56^{ab}
	high	1.05^{a}	0.51^{ab}	0.51^{ab}	0.22^{b}	0.85^{a}	0.47^{ab}
	slope	1.03^{a}	1.20^{a}	1.27^{a}	1.79^{a}	1.45^{a}	1.49^{a}
g_s (mmol H_2O m^{-2} s^{-1})	low	8.04^{ab}	13.34^{b}	13.33^{b}	5.51^{a}	8.17^{a}	9.70^{ab}
	high	36.39^{a}	37.36^{a}	53.67^{a}	81.96^{b}	55.35^{ab}	164.75^{c}
	slope	1.51^{a}	1.13^{b}	1.39^{a}	2.70^{c}	1.91^{d}	2.83^{c}

Table 7.5 Separate ANOVAs testing the effects of species, shade and soil type on shoot, root and total biomass. Significant F values are labelled according to the following probability values, * $\alpha < 0.05 > 0.01$, ** $\alpha < 0.01 > 0.001$, *** $\alpha < 0.001$, $^1P = 0.06$. $^\#$ Error SS (df)

		Shoot biomass		**Root biomass**		**Total biomass**	
Source	**df**	SS	*F*	SS	*F*	SS	*F*
Species	2	9.823	13.72***	0.533	22.35***	11.611	16.06***
Soil	1	7.895	22.06***	0.218	18.29***	6.949	19.23***
Shade	1	6.759	18.89***	2.586	216.97***	17.918	49.58***
Species/soil	2	4.018	5.61**	0.032	1.33	4.129	5.71**
Species/shade	2	6.007	8.39***	0.303	12.69***	5.848	8.09***
Soil/shade	1	1.535	4.29*	0.137	11.49***	1.296	3.59^1
Error $^\#$		53.328 (149)		1.812 (152)		53.851 (149)	

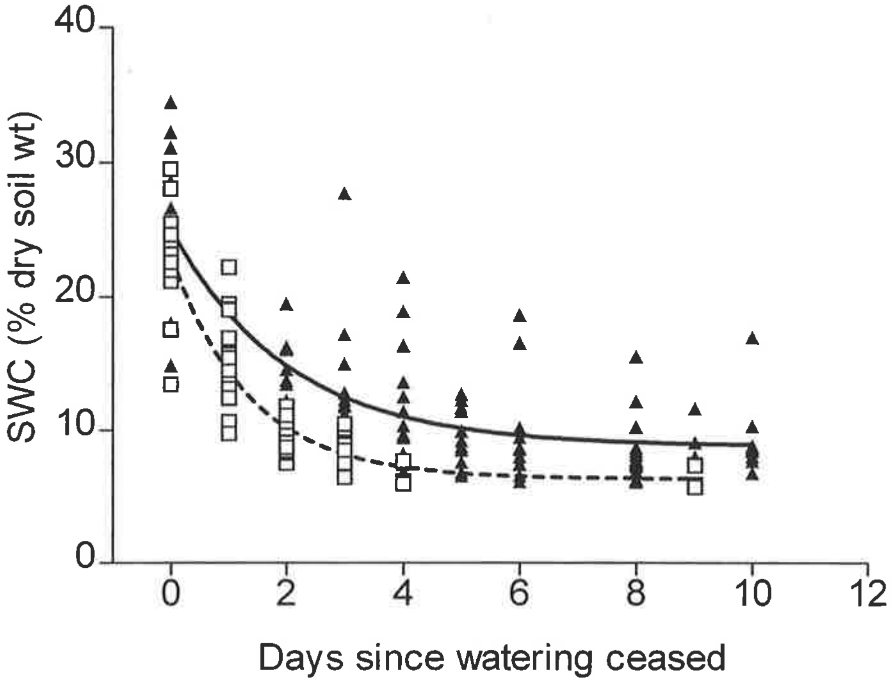
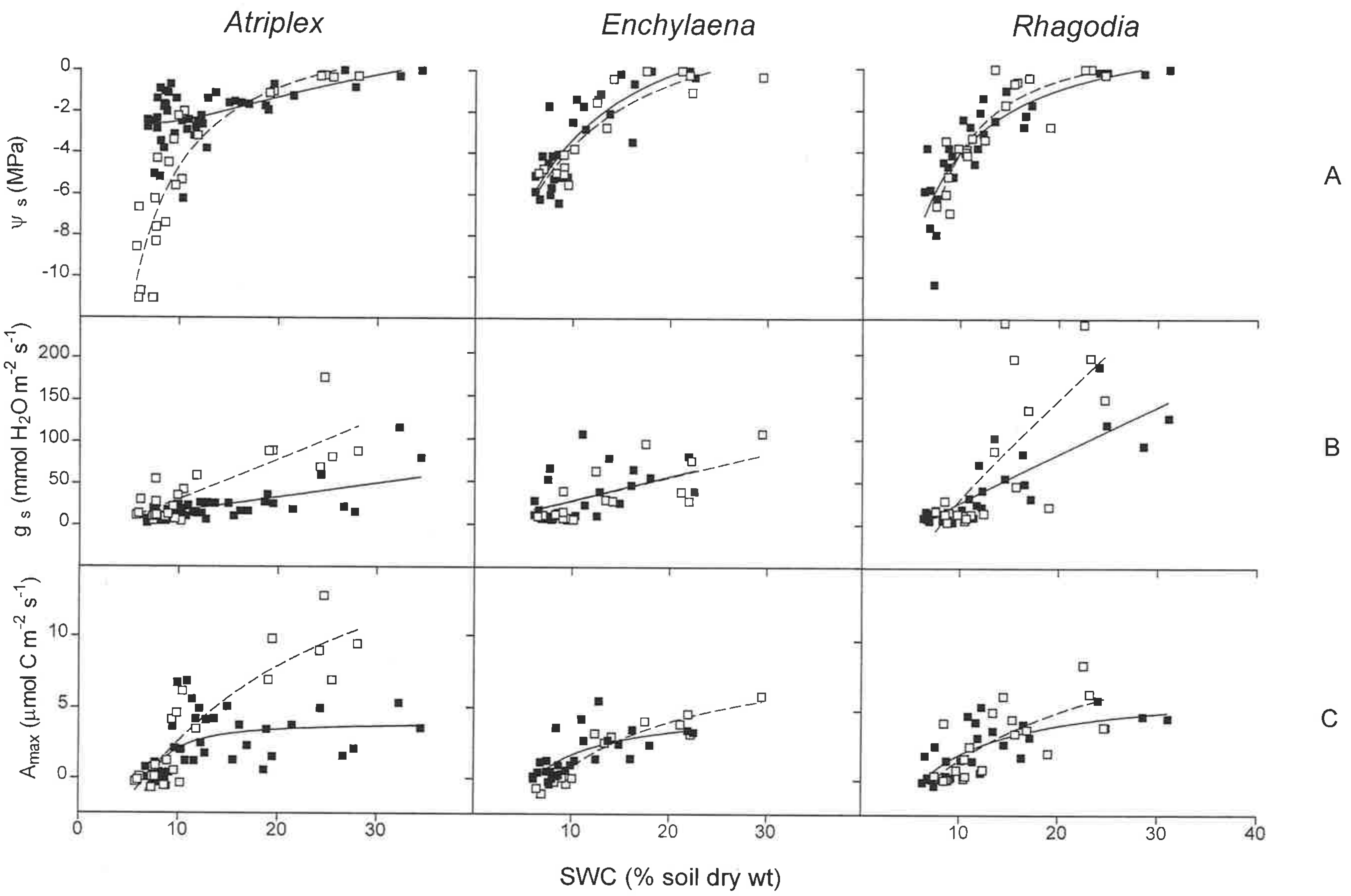


Fig. 7.1 Soil water content (SWC) as a percentage of dry soil weight for unshaded (□---) and shaded (■—) treatments over the drought period.


Atriplex
Enchylaena
Rhagodia
Ψ s (MPa)
0
-2
-4
-6
-8
-10
A
g s (mmol H2O m-2 s-1)
200
150
100
50
0
B
Amax (μmol C m-2 s-1)
10
5
0
C
0
10
20
30
40
SWC (% soil dry wt)

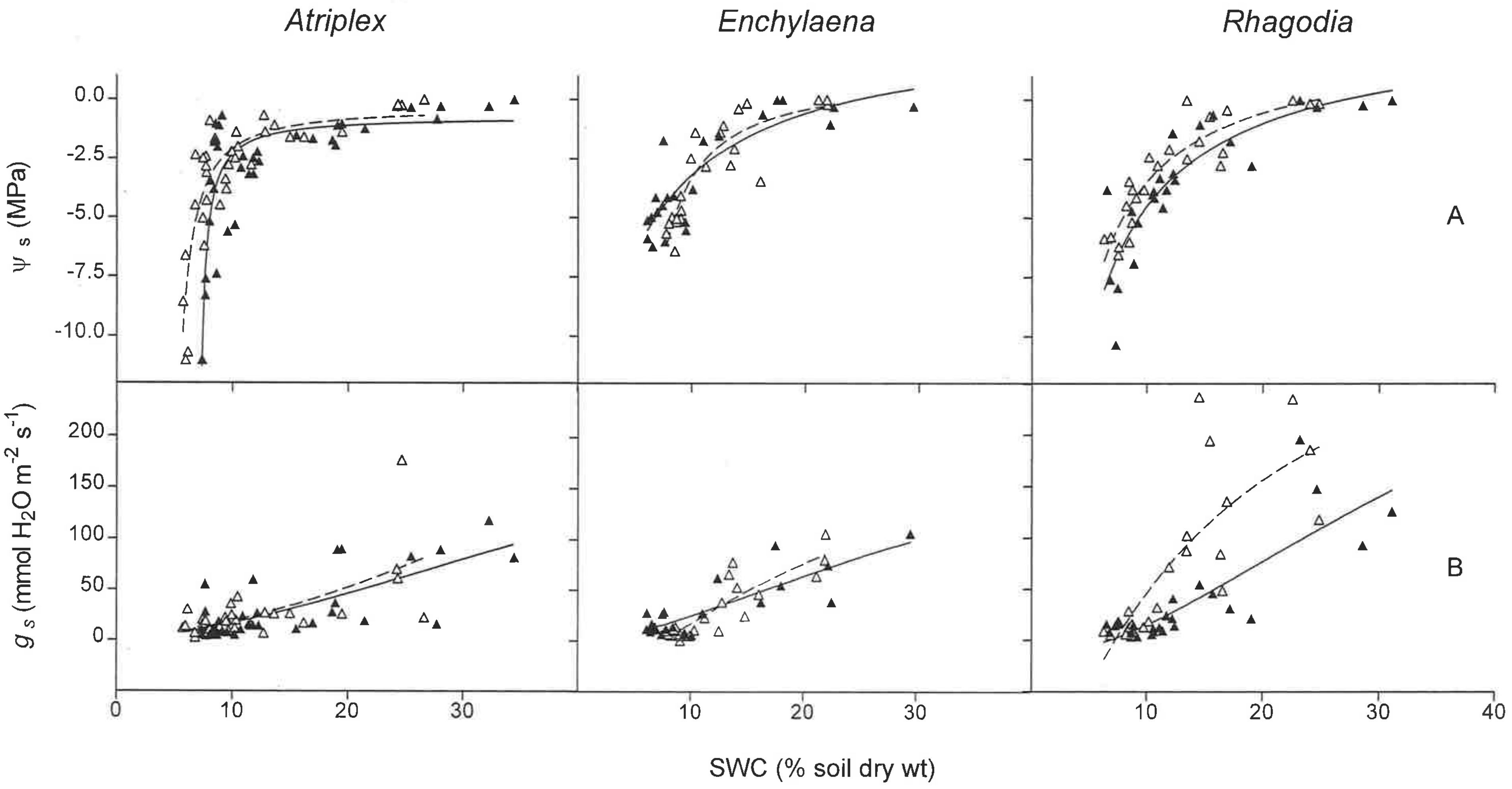


Fig. 7.3 Changes in A) Ψ_s, and B) g_s with increasing soil water content for *Atriplex*, *Enchylaena* and *Rhagodia* grown in canopy (▲—) and open (△ ---) soils. Curve fits are for illustrative purposes only (two site binding hyperbolas, GraphPad Prism, Ver. 3.02). See Table 7.4 for post hoc comparisons between treatments.

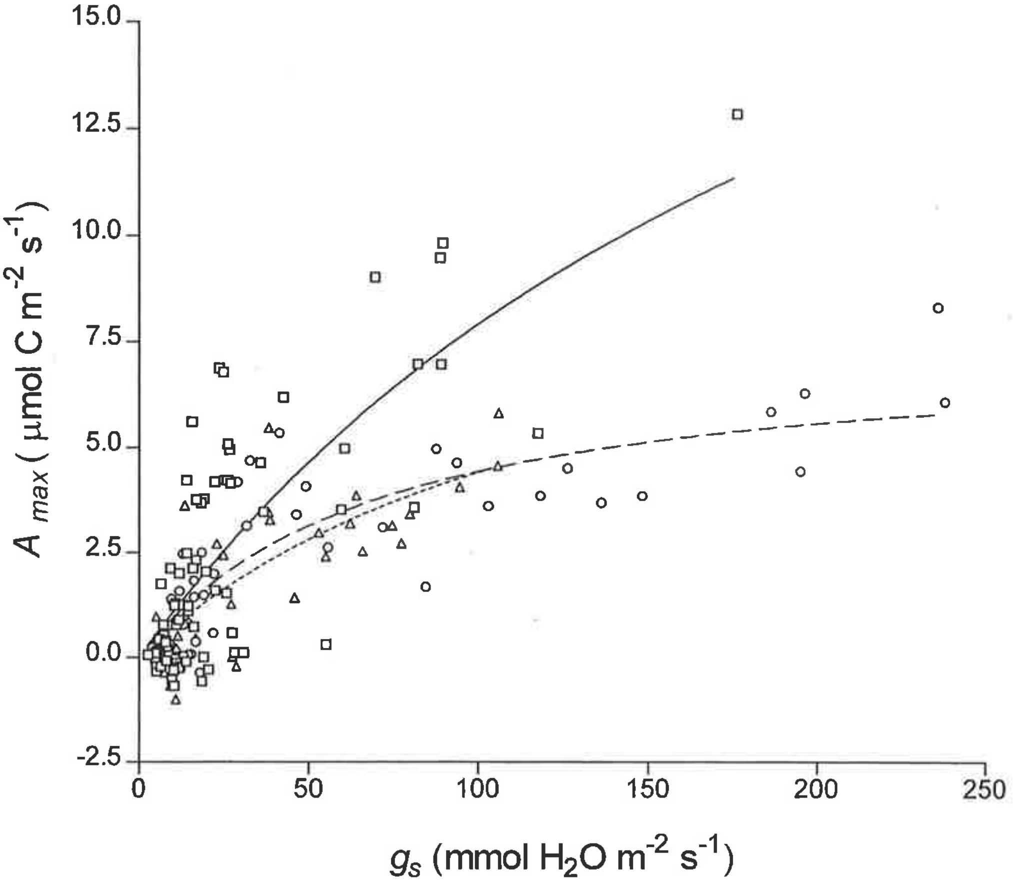


Fig. 7.4 Relationship between g_S and A_{max} for *Atriplex* (□ —), *Enchylaena* (Δ ....) and *Rhagodia* (o ----). Curve fits are for illustrative purposes only (two-site binding hyperbolas, GraphPad Prism, Ver. 3.0.2).

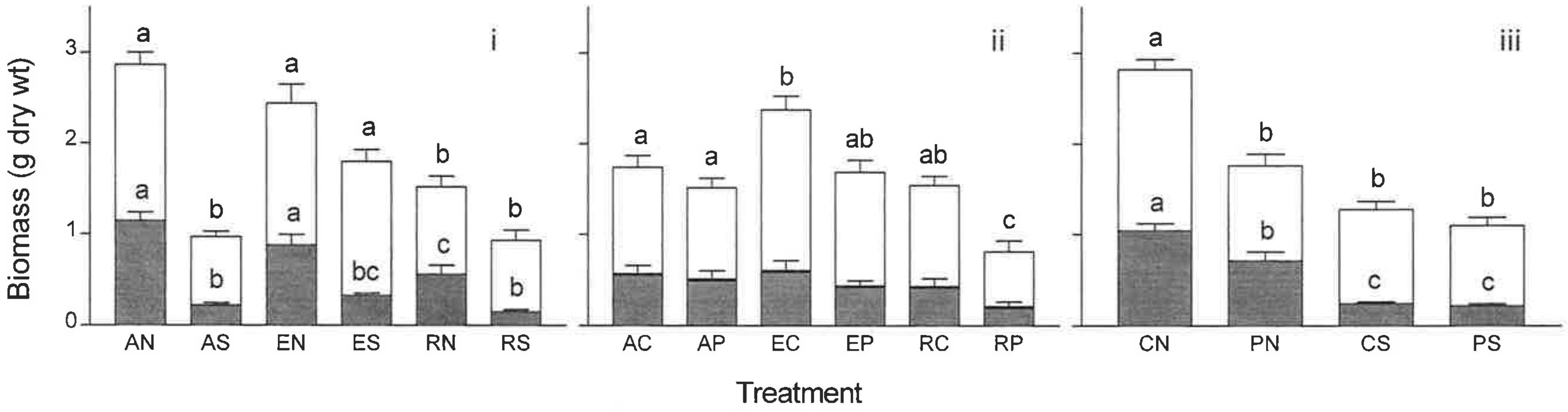


Fig. 7.5 Mean (+ 1SE) biomass of *Atriplex* (A), *Enchylaena* (E), and *Rhagodia* (R) plants grown in shaded (S) or unshaded (N) conditions and canopy (C) or open (P) soils, showing i) species/shade interaction, ii) species/soil interaction and iii) soil/shade interaction. The shaded parts of the columns indicate root biomass, the unshaded parts are shoot biomass. Column parts labelled with different letters indicate significant differences between either root or shoot biomass for each treatment combination where interactions were significant (Tukey-Kramer HSD tests, $\alpha < 0.05 > 0.01$).

CHAPTER 8

Summary and conclusions

Patchy vegetation is a striking feature of arid systems (Noy-Meir 1973, Aguiar and Sala 1999). At Middleback, patches beneath *Acacia* canopies provide a contrasting habitat to the matrix habitat, often with benign conditions and increased below-ground resources that are beneficial for the establishment and growth of other plants. These patches have effects on many system processes, but the main concern of this study was how these patches affected interactions between plants, and how this changed over time. For adult chenopod shrubs, competition was less intense beneath *Acacia* canopies particularly during rainfall pulses. *Acacia* facilitated the growth of shrub seedlings during pulses and seedling survivorship during interpulses, at least during a dry year. These changes in interaction intensity between pulse phases can be explained by temporal variation in resource availability and conditions in and beyond *Acacia* patches and the physiological responses of plants to these changes.

The nature of resource gradients

Temporal resource gradients in arid systems are stochastic as they are driven by unpredictable rainfall events. Rainfall at Middleback had no strong seasonal pattern; pulses of varying magnitude occurred at different times of the year. In both canopy and open sites it was expected that below-ground resources would fluctuate in relation to rainfall inputs. However, temporal changes in soil water content were asynchronous between sites under canopies and open sites. *Acacia* microsites had higher soil water content than open sites at shallow depths during the summer months. I found there was greater infiltration of water following a large rainfall event under *Acacia* canopies but canopy interception during smaller rainfall showers reduced soil water content in these sites compared with open sites. Although not examined in this study, these temporal fluctuations in soil moisture could also increase the difference in nutrient availability between the two sites. For example, microbial activity near the soil surface may continue for longer periods of time in the moister soils beneath canopies.

Amelioration of stresses beneath *Acacia* canopies is also time-dependent. The alleviation of water, radiation and temperature stresses occurs during interpulses in the warmer months.

Canopy sites had lower soil temperatures than open sites during summer and radiation was reduced by up to 80% in canopy shade. I found that the effects of these spatial changes in conditions on plant performance were temporally dependent. These changes had positive effects on plant survival during interpulses. Other spatial changes beneath canopies, such as increased nutrients and changes in soil properties, were also temporally dependent. The benefits of these changes were realised when water was available during pulses. Spatial and temporal variations in resources and conditions are therefore interactive.

Facilitation

My conceptual model predicted that positive interactions would be more intense during interpulses, but would decrease in intensity during pulses. I based this prediction on the premise that the primary facilitating mechanism was a reduction in water stress, the result of either reduced evaporative demand or increased availability of soil water in sites beneath plant canopies.

Patterns of survivorship agreed with this model, yet only when increased survivorship was mediated by canopy microclimates. *Atriplex* survival in the drier year, and *Enchylaena* survival both years supported the model. Canopy microclimate amelioration was the facilitation mechanism for survivorship, supporting the hypothesis that canopies may reduce water stress. *Acacia* did not facilitate *Atriplex* survival in the wetter year. Most deaths in this year occurred during the pulse, possibly as a result of competition from ephemerals. However, even at interannual scales the model was supported, facilitation occurred in the year with less water availability.

Facilitation effects on growth were more complex as they resulted from modifications of soils and microclimates. Disregarding soil modifications, canopy microclimates had positive effects on growth during pulses and interpulses but this response was species-specific. Canopy microclimates, probably by reducing water, heat and radiation stresses, had positive effects on *Atriplex* growth during interpulses. Canopy microclimates had neutral to negative effects on *Atriplex* growth during pulses, especially when below-ground resources were less limiting to growth (in canopy soils or after fertilisation). These results also support the conceptual model. However, canopy microclimates had positive effects on *Enchylaena* growth during pulses.

Enchylaena growth may also have been facilitated during interpulses but too few survivors in open sites prevented the analysis of this data.

Atriplex may not have been facilitated by canopy microclimates during pulses due to light limitations on growth. The carbon gain of this species was sensitive to reductions in light availability, unlike *Enchylaena* that showed no difference in carbon gain under different light levels. *Atriplex* (and possibly *Enchylaena*) growth may have been facilitated during interpulses due to stress effects on carbon gain when radiation loads are high and water availability low. *Atriplex* and *Enchylaena* showed some photoinhibitory effects in the pot experiment under drought conditions and high irradiation. Interactions between drought and shade explain the mechanism of facilitation between *Acacia* and *Atriplex* and *Enchylaena*, and why the effects change over time. The pot experiment showed that shade had positive effects as drought progressed. The effects of shade cast by *Acacia* canopies will differ over time as it depends on the availability of water and radiation loads. During interpulses, when water and heat stresses are greatest, shade has a positive effect by reducing the incidence of photoinhibition. Plants in the shade were able to continue gaining carbon for longer into the drought period. This may explain the positive effects of *Acacia* on *Atriplex* growth into the interpulse.

Soil modifications by *Acacia* had positive effects on growth during pulses. Facilitation was most intense for *Atriplex* and *Enchylaena* when grown in canopy soils and whilst being watered (during the establishment period). If changes to soil properties are the primary facilitation mechanism then facilitation may not increase in intensity as stress increases. Plants are able to take advantage of increased soil nutrients in canopy soils when water is not limiting and stresses are low.

At larger temporal scales, comparing between years, there was evidence of shifts between these two facilitation mechanisms. Canopy microclimates facilitated *Atriplex* and *Enchylaena* seedling emergence and ephemeral growth during the drier year, but canopy soils facilitated these processes during the wetter year. Facilitation of growth may therefore be most intense during either dry years, when canopy microclimates increase water availability or reduce evaporative demand, or wet years, when canopy soils provide improved conditions for growth when water is not limiting. Thus the conceptual model is supported at a number of temporal scales but only when the facilitation mechanism is a reduction in water stress. The intensity of these positive effects depends on the physiology of the beneficial species. Shade-tolerant species may benefit from canopy microclimates during pulses and interpulses.

Competition

My conceptual model predicted that competition would either be equally intense during pulses and interpulses or increase in intensity during pulses. This prediction was based on the assumption that resource uptake occurs primarily after pulses of rainfall therefore plants will compete for resources at this time. However, as some plants may continue positive carbon gain even when soil water content is very low, plants may potentially compete into interpulses. These predictions are based on the hypotheses of Goldberg and Novoplansky (1997).

I found that the first prediction, that competition was equally intense during both pulses and interpulses, was supported in open sites but not in canopy sites. Overall, competition was very variable in canopy sites and statistical tests were not able to detect any competitive responses. Competition intensity did change over time in canopy sites. The data for open and canopy sites showed trends for competition to be less intense during pulses than interpulses, contrary to the predictions of my model.

Competition may not be intense or detectable in neighbour removal experiments where the target plant has not been transplanted into the neighbourhood. Frequently, the regular spacing of shrubs in arid systems, as distinct from a random distribution, is purported as evidence for past competition (Fonteyn and Mahall 1981, Fowler 1986a). Of the chenopod shrubs at Middleback, *Maireana sedifolia* has a regular distribution in at least one site (Wotton 1993). If plants are regularly spaced or widely separated because of past competition, their present interactions with each other may be minimal as the existing spacing of shrubs reflects competition in the past. However competition was detected in open sites and in both sites in the second competition experiment. Competition between existing adult plants does occur in this system but is more intense in the less productive open sites and may also be more intense during less productive periods.

I found no difference in relative competition intensity between species. If each species has a different response to fluctuations in water availability this may promote coexistence (Chesson and Huntly 1997) or reduce the frequency of intense competition and hence the speed at which species are competitively eliminated (Huston 1979). Pulse and interpulse amplitude are therefore important. When pulses and interpulses were not extreme, i.e. not of large magnitude or length, then competition intensity remained equally intense over time. Competition intensity was reduced during the large pulse in 2001 but competition intensity was high during the preceding interpulse. Early interpulses seem to be the critical period, when competition is most intense. Competition may be least intense at the height of the pulse or at the height of the interpulse. This is consistent with the hypothesis that competition will be least intense when resource supply exceeds demand (Huston and DeAngelis 1994). This will occur when resources are plentiful, or alternatively when harsh conditions reduce resource demand. I suggest below-ground competition is more intense under moderate pulse amplitudes, i.e. pulses of moderate length or magnitude (Fig. 8.1).

The distribution of rainfall within a year may have more impact on plant interactions than the total annual rainfall. During years with small, frequent pulses competition may be more intense than during years with fewer, large pulses even though the total rainfall input may be the same. However under these circumstances competition may be intense but not important for population persistence. Big pulse years may provide good growing conditions (after rainfall pulses) with reduced competition intensity for pulse growers, but this will not favour stress-tolerators. During large interpulses growing conditions may be poor and competition may be intense but this will favour stress-tolerators and pulse growers will be disadvantaged. At average pulse/interpulse amplitudes slightly different combinations will favour different species and coexistence will be promoted. At a number of scales, a response may change when resources are uniformly distributed in time or space to when the same amount of resources are patchily distributed or heterogeneous (Noy-Meir 1981). This may include individual species responses (Bilbrough and Caldwell 1997), plant interactions (Novoplansky and Goldberg 2001) and system responses such as diversity and productivity (Noy-Meir 1981). It is a fruitful area for further research.

The balance between competition and facilitation

It is not possible to make a definitive statement about the overall balance between positive and negative interactions in these woodlands as interactions were examined between different structural elements; competition was examined between chenopod shrubs and facilitation was examined between *Acacia* and shrubs. The effects of *Acacia* canopies on the growth and survival of *Enchylaena* plants was overall positive. Even taking into account possible competitive effects of *Acacia*, *Enchylaena* plants grew more and survived longer when under *Acacia* canopies.

Acacia also had an overall positive effect on *Atriplex* growth possibly because increased nutrients in these microsites compensated for a decrease in light availability.

I believe plant interactions play an important role in determining the distribution patterns of species in this system. At the patch scale the positive interactions between *Acacia* and other vegetation components control the structure of this system. Fertility islands associated with *Acacia* canopies buffer against competition, as competition was less intense beneath canopies. This further increases the importance of positive interactions in this system. However, negative interactions may have a role in determining the spacing and abundance of individuals.

I have shown that facilitation affects seedling establishment and growth, and the growth and reproduction of *Maireana* adults. I did not determine the effects of competition on seedling establishment, growth and survival. The response of seedlings to competition may have further effects on the abundance and distribution of these chenopod shrubs. Howard and Goldberg (2001) found that competition had the greatest effects on the germination and growth of old-field seedlings and this had the most influence on species abundance. However, competition at the seedling stage may not be very important for drought-tolerant woody perennials. For example, the survival of adult *Atriplex vesicaria* is more important for population persistence than recruitment (Hunt 1995). Recruitment events in arid systems may be controlled by large rainfall events, during which times competition may not be very intense. The effects of competition on abundance may be most intense during the juvenile stages, when the resource depletion zones of roots begin to overlap. Shorter-lived plants that rely on frequent recruitment, such as *Enchylaena* and *Rhagodia*, may be more affected by competition than *Atriplex* and *Maireana*. Competition between perennial seedlings and ephemerals that establish after rainfall pulses could be an area for further research. I found that *Atriplex* seedlings had poor survivorship during pulses under canopies, possibly as a result of competition from ephemerals. The only study of this process I have found reports an observation of competition between *Atriplex vesicaria* seedlings and annual *Atriplex* seedlings during sowing trials in chenopod shrublands (Muirhead and Jones 1966). Increased resources under canopies may produce greater competition because of closer spaced individuals. This may affect the growth of new seedlings in these sites, but survival may be greater overall in these sites due to the ameliorating effects of the canopy during interpulses.

Conclusions

This study supports the existing literature that positive interactions are more frequent when stress increases, but only when the facilitation mechanism mitigates that stress. Improvements in soil nitrogen status do not show this response to stress. Under this mechanism positive effects may manifest whilst conditions are the most conducive to growth, which will not be the most stressful periods. Shade-tolerant plants are more likely to benefit from the increased below-ground resources under canopies. Temporal variation in positive interactions along a water gradient therefore depends upon the type of habitat modification and the physiological responses of species at different life stages. I have shown that positive interactions are important in influencing the distribution of species in this system and may be fundamentally important for the persistence of some species, e.g. *Enchylaena tomentosa.*

The results of competition experiments do not support Tilman's hypothesis of equal competition intensity across a resource gradient (Tilman 1988), but the mechanism he described did not occur in this system. There was not a switch between competition for above-ground resources at high resource levels to below-ground resources at low resource levels. However, in canopy microsites there may be alternation between competition for above- and below-ground resources at different life stages that interact with pulse phases. Competition for light may occur at seedling stages during pulses of large magnitude that promote ephemeral growth whilst competition for below-ground resources may occur in older plants. In these older growth phases there may be a temporal switch between competition for nutrients during pulses and water during interpulses. This would be an interesting area for further research. In support of Grime's hypothesis (Grime 1973), this research found no evidence that competition affects the persistence of adult populations of chenopod shrubs in this arid system. But contrary to his hypothesis, competition may have a role in determining abundance through acting on juvenile stages. This can readily be tested in short-lived shrubs with frequent seedling recruitment, e.g. *Atriplex, Enchylaena* and *Rhagodia*.

Habitat patches such as those created by *Acacia papyrocarpa* significantly influence plant interactions in this system and demonstrate how interactions between biotic and biotic processes affect vegetation patterns. I have used a unique approach in this study be integrating pulse and interpulse resource dynamics with existing positive and negative plant interaction theory. We can only really understand plant interactions by examining the mechanisms that affect these processes, and appreciate those different mechanisms may be important at different times. This is particularly evident in arid systems where there is such a contrast between resource availability and conditions during pulse and interpulse phases. Studies that cover different temporal and spatial scales may reveal further complexities in the vegetation dynamics of patchy systems.

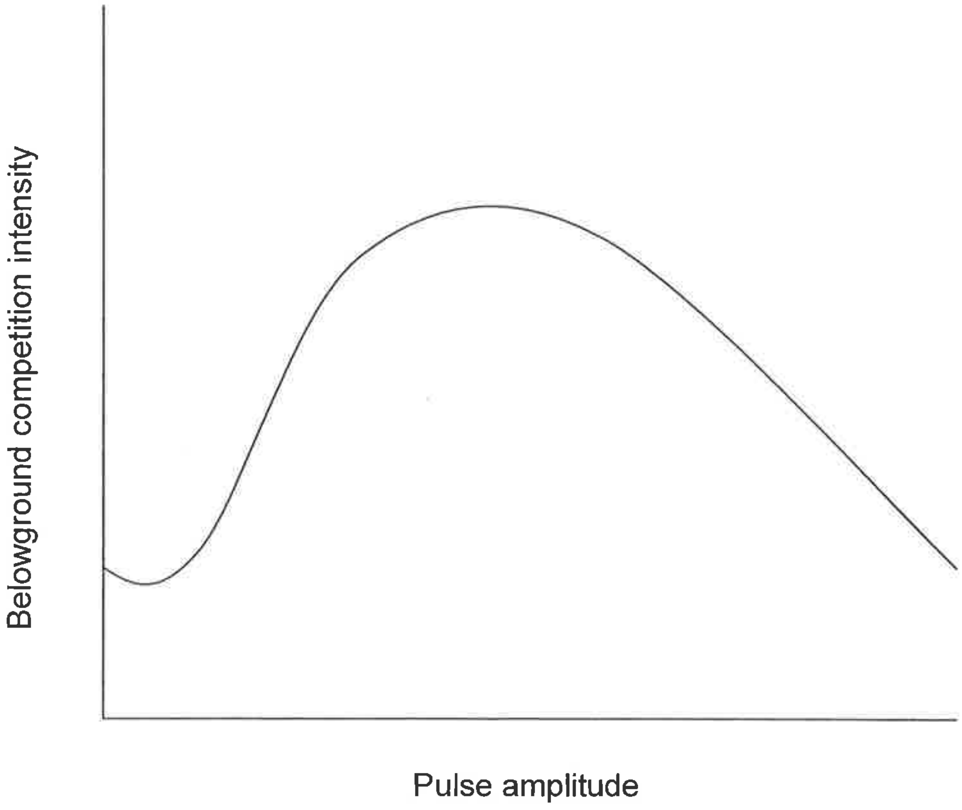


Fig. 8.1 The predicted relationship between belowground competition intensity and pulse amplitude. Pulse amplitude includes pulse magnitude and/or frequency.

Appendix 1

Species list of forbs, grasses and perennial shrubs indicating their presence under canopies (C) or in the open (P) during field surveys. Perennial shrubs were only sampled in 1999. Species nomenclature follows Jessop and Toelken (1986).

	1999		2000		2001	
	C	P	C	P	C	P
Forbs						
Actinobole uliginosum						✓
Alyssum linifolium			✓		✓	✓
Atriplex holocarpa					✓	✓
Brachycome lineariloba				✓	✓	✓
Bulbine semibarbarta				✓		✓
Calandrinia eremaea			✓	✓	✓	✓
Calotis hispidula			✓	✓	✓	✓
Carrichtera annua	✓	✓	✓	✓	✓	✓
Carthamus lanatus?					✓	
Chamaesyce drummondii						✓
Crassula colorata			✓	✓	✓	✓
Daucus glochidiatus						✓
Erodium cygnorum		✓	✓			✓
Galium sp.					✓	
Gnephosis burkittii						✓
Goodenia pusilliflora						✓
Harmsiodoxa blennodioides			✓	✓	✓	
Herniaria hirsuta				✓	✓	✓
Ixiochlamys nana				✓		✓
Lepidium sp.			✓		✓	
Lotus cruentus						✓
Medicago minima		✓		✓	✓	✓
M. polymorpha						✓
Mesembryanthemum nodiflorum			✓	✓	✓	✓
M. crystallinum						✓
Omphalolappula concava						✓
Oxalis corniculata					✓	✓
Parietaria debilis?					✓	✓
Plantago drummondii					✓	✓
Salsola kali				✓	✓	✓
Senecio glossanthus					✓	✓
Sisymbrium erysimoides?	✓		✓		✓	
Spergularia rubra			✓			✓

	1999		2000		2001	
	C	P	C	P	C	P
Forbs (cont.)						
Tetragonia eremaea	✓		✓	✓	✓	✓
Thysanotus baueri			✓			✓
Vittadinia cuneata					✓	✓
Wahlenbergia sp.						✓
Zygophyllum ammophilum	✓		✓		✓	✓
Z. crenatum?						✓
Species A				✓		
Species B	✓					
Grasses						
Austrodanthonia caespitosa	✓	✓	✓	✓	✓	✓
Austrostipa elegantissima			✓		✓	✓
Austrostipa sp.	✓	✓		✓	✓	✓
Bromus rubens				✓		✓
Eragrostis sp					✓	✓
Lophochloa pumila						✓
Pentaschistis airoides				✓		✓
Vulpia bromoides						✓
Species C					✓	
Perennial shrubs						
Atriplex stipitata	✓	✓				
A. vesicaria	✓	✓	-	-	-	-
Chenopodium gaudichaudianum	✓	✓	-	-	-	-
Enchylaena tomentosa	✓	✓	-	-	-	-
Eremophila scoparia	✓					
Eriochiton sclerolaenoides	✓	✓	-	-	-	-
Lycium australe	✓					
Maireana georgei		✓	-	-	-	-
M. pyramidata	✓	✓	-	-	-	-
M. sedifolia	✓	✓	-	-	-	-
M. trichoptera		✓	-	-	-	-
Maireana sp.	✓		-	-	-	-
Rhagodia spinescens	✓	✓				
R. ulicina	✓	✓				
Sclerolaena diacantha		✓	-	-	-	-
S. lanicuspis		✓	-	-	-	-
S. obliquicuspis	✓	✓	-	-	-	-
S. patenticuspis		✓	-	-	-	-
Sclerolaena sp.		✓	-	-	-	-

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