Facilitation and Fertile Islands:
linking canopy effects with plant interactions.

Graeme T. Hastwell

Thesis submitted for the degree of
Doctor of Philosophy

Department of Environmental Biology
University of Adelaide, Australia

July 27, 2001

Contents

Abstract

Plant community composition and soil nutrient levels under tree canopies frequently differ from that found in the open spaces between trees. While there is some evidence suggesting that these differences may be due to factors associated with the presence of trees, rather than simply being the result of pre-existing heterogeneity, the processes giving rise to this phenomenon are poorly understood. The issue of biogenic modification of the environment is of considerable theoretical interest and has important implications for the management of natural resources. Consequently, this thesis investigates the question of whether trees generate heterogeneity in resources and plant community composition, and seeks to identify some of the canopy processes that may be responsible.

I investigated the association between woody perennial plants and heterogeneity in soil resources and plant communities in an arid chenopod shrubland. A field survey revealed that soil nutrient levels (organic carbon, total nitrogen and available phosphorus) were higher under canopies of the small clonal tree *Alectryon oleifolius* than in areas outside canopy edges. Soil nutrient levels and plant litter densities were also positively correlated with canopy size. Nutrient levels differed with aspect, while correlations between nutrients changed with distance from the trunk, suggesting that shading by canopies influences nutrient cycling processes.

A second survey found that whereas the soils and plants under the smallest trees did not differ from those found in open areas, species composition and soil organic carbon levels under larger trees did differ. This is consistent with fertile islands being created by cumulative biological processes. Evidence suggested that fertile islands may develop when shrubs establish in the shade of trees and trap litter, thereby concentrating nutrient cycling.

I used artificial canopies to test the effects of shade and rainfall redirection on emergence of the annual forb *Carrichtera annua* and the perennial grass *Danthonia caespitosa*. Although emergence rates were very low, significantly more seedlings emerged in shaded plots than in unshaded plots, and emergence was sometimes higher under larger canopies than smaller canopies. No effects of rainfall redirection were detected.

I tested the effects of shading on *Enchylaena tomentosa* seedlings in order to verify the prediction that facilitation becomes stronger as environmental stress increases. Patterns of survivorship and growth differed. As predicted, shading reduced mortality rates in summer, but not during winter and spring. However, while shading consistently increased *E. tomentosa* growth rates, the difference between shaded and unshaded seedlings did not differ between seasons. Thus facilitation of growth did not change as stress increased.

I used graphical models linking modification by plants with plant performance to investigate the strength of interactions along environmental gradients. These models show that facilitation will not always be stronger under adverse conditions, and that it may show complex patterns of change.

My results confirm that modification of soil resources and plant community composition occurs in the vicinity of *A. oleifolius*. The magnitude of this modification increases with canopy size, and varies with both distance and direction from the tree trunk, suggesting that modification is the result of cumulative processes with shading being an important factor. Support for this view was provided by experimental tests of the effects of shading on emergence of *C. annua* and *D. caespitosa*, and on growth of *E. tomentosa*. Clearly, tree canopies are an important source of heterogeneity in both physical resources and plant community composition. Their effects on neighbouring plants increase with canopy size, while the generation of heterogeneity in soil resources appears to depend on both size and time.

Declaration

I declare that this work contains no material that 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 also give consent to this thesis being available for photocopying and loan if accepted for the award of the degree.

Graeme T. Hastwell
July 27, 2001

Acknowledgements

First and foremost My supervisor, José M. Facelli, fostered an intellectual environment that encouraged me to develop ideas and to find my muse. I feel privileged to have had the benefit of his guidance and support.

Making models Yvonne Stokes of the Department of Applied Mathematics provided valuable comments and most of the algebraic analysis in Chapter 7. Russ Sinclair also supplied thoughtful suggestions on an earlier draft.

'Twas all for noughts Bill Venables of the Department of Statistics provided help with some particularly nasty data. Following his departure for CSIRO and the withdrawal of statistical consulting for postgraduates, Alan Welsh (ANU) and the participants of the Extra Zeroes workshop at Biometrics99 provided much-needed encouragement and support.

Sew, a needle pulling thread Learning to sew was perhaps the skill I least expected to acquire during my Ph.D. Wendy Telfer provided sewing lessons and a loan of her treasured sewing machine. My seams may not have been straight, but they withstood the test of arid zone time.

Making shadecloth grow David Bigham and Andrew Barritt made a number of suggestions that improved the design of the artificial canopies.

A big thankyou Lachlan MacLachlan and Brian Pumper unhesitatingly provided access to Koonamore Station, and witnessed my activities with (I think) some amusement. Their support for the department's research activities is greatly appreciated.

Field help Many friends and fellow students generously volunteered time and effort, often under physically demanding conditions. This group of hardy souls included Ted Bullen, Wendy Telfer, David Bigham, Natalia Wilczynski, Jeff Cox, Greg Hay, Tanja Lenz, Christian Hodgson, and Gael Fogarty. Jessica Moyle-Croft, who is

not very hardy, came along too.

For blood, sweat and beers Glenys Wood, David Ladd and Paull Wood fearlessly wielded crowbars, shovels and posthole diggers. This special hand-picked team had what it took to erect a grove of artificial trees and provide a Thai feast every night.

Sowing the seeds Anne Bartlett and Martin Purvens spent days on hands and knees planting fifteen thousand seeds ...one at a time. Martin is currently convalescing in Antarctica.

Some liked it hot Jim Trice and Jane Prider each accompanied me on many field trips, including the notorious 50°C trips of January 1999 and 2000. Their contributions to my project were invaluable; Jim for knots and coffee, Jane for demonstrating the art of the possible.

Closer to home Joe Wiskich and David Christophel provided laboratory and image processing facilities respectively, while Peter Gordon introduced me to the arcane arts of scanning.

Three cheers! For all the departmental support staff. In particular David Ladd, Lidia Mischis, Richard Norrish and Marilyn Saxon did much to make my work easier and more pleasant.

The mud stuck Colin Rivers of the Department of Soil Science introduced me to soil analysis methods and provided laboratory facilities.

Spot the mistake Thanks to Richard Williams and Tanja Lenz for proofreading several chapters of this thesis. Jane Prider had the unenviable task of wading through the early drafts of the big complex ones - I expect to return the favour one day soon!

Many other friends and family members contributed in ways that were less tangible but no less important. Their support is much appreciated.

Chapter 1

Plants as agents of change: the influence of woody perennials on their surroundings.

1.1 Introduction

The capacity of plants to change their environments in biologically important ways was recognised early in the history of ecology (Clements, 1916; Watt, 1947). However, ecologists have not been consistent in the way they have viewed the plant-environment relationship. Much effort was expended seeking explanations for regional-scale distribution of plant species and vegetation communities, with particular emphasis on edaphic and climatic factors (Specht, 1972; Mueller-Dombois and Ellenberg, 1974; Ellenberg, 1988). Smaller scale patterns tended to be overlooked, so the possibility that plants may contribute to the creation of their environments was rarely considered. More recent work shows that while soil and climatic factors may satisfactorily explain global and regional plant distributions, they are less useful at smaller scales (Holling, 1992; Turner, 1989).

Other factors have contributed to the loss of interest by ecologists in the potential for plants to modify their environments. In particular, the emphasis on competition since the 1950s resulted in an intellectual atmosphere where the possibility of positive interactions between plants was almost never considered (Bertness and Callaway, 1994; Callaway, 1995). However the importance of such interactions has recently been reassessed (Bertness and Leonard, 1997; Holmgren et al., 1997; Brooker and Callaghan, 1998). Facilitation is no longer viewed as a curiosity, but is now considered to be a widely occurring process that may be at least as important as competition in shaping some communities (Callaway, 1995; Bertness and Leonard, 1997; Holmgren et al., 1997; Rousset and Lepart, 1999).

Many studies have found that the soils and the plant communities that occur beneath the canopies of woody perennial plants differ substantially from those from the spaces between canopies (Zinke, 1962; Garcia-Moya and McKell, 1970; Tiedemann and Klemmedson, 1973; Charley and West, 1975; Kellman, 1979; Barth, 1980; Bernhard-Reversat, 1982; Belsky et al., 1989; Dunham, 1991; Guttierrez et al., 1993). In fact, very few published studies failed to detect large differences in soil fertility or species composition. Differences between canopy and open soils and plant communities have been reported from a range of habitats and for a variety of plant lifeforms.

The ubiquity of these phenomena suggest that they may be the consequence of ecologically fundamental interactions. Alternatively, the observed patterns may merely be the consequence of pre-existing differences in the abiotic environment. In both cases it is important to consider the consequences of this heterogeneity for productivity and species diversity at larger scales.

This chapter reviews the known differences in soils and plant communities associated with the presence of perennial plants. It also considers processes that may be important in generating these differences, and attempts to place these observations into a conceptual context. Emphasis is placed on the importance of canopy characteristics in several processes of local modification. The role of facilitation in shaping community structure is explored, and the potential consequences for local and regional biodiversity is discussed.

1.2 The effects of plants on resources

Considered in the simplest terms, plants require four different types of resources - light, water, carbon and nutrients - for plant growth and reproduction (Coomes and Grubb, 2000; Poorter and Nagel, 2000). The acquisition or redirection of these resources by plants can alter their local availability, affecting neighbouring plants (Goldberg and Novoplansky, 1997; Goldberg et al., 1999). Ecologists interpret the resulting changes in fitness or growth as competition or facilitation.

Of the four essential types of resources, carbon is the least likely to be depleted by terrestrial plants. As plants do not compete for carbon dioxide in terrestrial systems, carbon will receive little further discussion in this review.

1.2.1 Differentiation between canopy and roots

There is a pronounced spatial segregation of resource acquisition between above- and below-ground plant organs. Light and carbon are the province of the above-ground organs, with leaves and phyllodes usually being the organs of acquisition. The aboveground structures may also increase soil resource acquisition by directing precipitation or airborne nutrients towards the roots (Mauchamp and Janeau, 1993; Whitford et al., 1997). The below-ground organs are responsible for the uptake of water and nutrients in plants other than epiphytes.

1.2.2 Light

Plant canopies can alter both the spectral quality and the intensity of light by interception (Turner, 1960; Parker and Muller, 1982; Georgiadis, 1989; Belsky et al., 1989; Callaway et al., 1991; Ryel et al., 1994; Breshears et al., 1997; Martens et al., 2000) and by selective transmission and reflection (Howard, 1966; Pearman, 1966). The zone in which the canopy modifies light is determined by the direction and diffusivity of the incident light, by the shape of the canopy and by the shape of the surface on which the shadow falls (Ryel et al., 1993; Cescatti, 1997). In natural systems the light source is the sun or skylight, so the size, shape and location of the zone of modification also depends on the latitude, the time of day and the time of year.

Canopy structure may also affect the light quality in under-canopy habitats. Canopies usually contain small gaps, creating sunflecks on the ground below (Curtis and Kincaid, 1984; Lee, 1987; Chazdon, 1988; Kursar and Coley, 1993). The light within a sunfleck may be little modified, or it may be of lower intensity and different spectral quality than ambient light. The small size of sunflecks ensures that any given point will not be exposed to an individual fleck for very long. Nevertheless, sunflecks are important to the survival and productivity of under-canopy plants in deciduous and tropical forests (Curtis and Kincaid, 1984; Chazdon, 1988). Evidence suggests that sunflecks begin to make a significant contribution to overall photosynthetic productivity when the light intensity below canopies falls below 10-20% of full sunlight (Chazdon, 1988; Ryser and Eek, 2000). However, the ability of under-canopy plants to utilise sunflecks varies considerably between species (Curtis and Kincaid, 1984; Chazdon, 1988).

The relationship between light intensity and photosynthetic production means that photosynthetic rates in below-canopy habitats may be lower, resulting in decreased assimilation and productivity (Amundson et al., 1995; Holmgren et al., 1997; Holmgren, 2000). However, photoadaptation, a process in which the concentration and arrangement of light-harvesting molecules and photosynthetic pigments within the plants' leaves are changed, introduces a degree of plasticity which permits partial compensation for differences in light intensity (Smith et al., 1993).

The spectral quality of light controls seed dormancy in many plant species (Grime, 1979; Silvertown, 1980; Fenner, 1985), as well as regulating growth and asexual reproduction in grasses (Fenner, 1978; Deregibus et al., 1985). Phytochrome, a pigment found in plant and seed tissues, is responsible for this phenomenon (Vleeshouwers et al., 1995). It can exist in two forms, each of which can convert to the other by absorbing light of particular wavelengths. One form absorbs red light, and the other far-red light. Germination and growth in many species is regulated by the ratio of red to far-red forms of phytochrome. Since leaves alter the ratio of red to far-red light, mainly through selective absorption by chlorophyll, the presence of a canopy can affect germination or growth in a wide range of plant species (Aphalo and Ballaré, 1995; Hofstede et al., 1995).

1.2.3 Water

Deep-rooted perennial plants may access soil moisture from depth during periods when the upper soil layers are dry (Mooney et al., 1980). Under certain circumstances some species continue to lift water nocturnally (Richards and Caldwell, 1987). This process, known as hydraulic lift, occurs during periods of low transpiration when the water potential of the upper soil layers is lower than the root xylem water potential, and if the internal flow resistance of the root system is sufficiently low (Caldwell et al., 1998). Although conclusively demonstrating this process in the field is difficult (Caldwell and Richards, 1989; Dawson, 1993), hydraulic lift has been identified in a surprisingly broad range of plant lifeforms (Caldwell et al., 1998). Furthermore, the transfer of water by roots from damp to dry soil layers can occur in other directions; movement of water from topsoil to drier parts of the soil profile has also been demonstrated (Burgess et al., 1998).

Substantial amounts of water can be moved by hydraulic lift. It is estimated that a large sugar maple (*Acer saccharum*) can lift 40-80 l of water a night (Dawson, 1996). The water moved by hydraulic lift is utilised the following day, permitting transpiration to exceed the rate at which water can be supplied by the roots from deep soil layers (Richards and Caldwell, 1987; Caldwell and Richards, 1989; Dawson, 1993). Other plants growing in the vicinity may also utilise this water (Caldwell and Richards, 1989; Dawson, 1993). Nutrient acquisition is also coupled with water availability (Cowling, 1978; Goldberg and Novoplansky, 1997), so hydraulic lift is potentially an important way that plants modify their local environments.

Plants can also affect access to water by redirecting precipitation with their canopies (Pressland, 1973; Aston, 1979; Loustau et al., 1992). There are three ways that canopies affect the passage of rainfall: interception, where precipitation is captured by the canopy and lost through evaporation; throughfall, where precipitation passes through the canopy to the ground below; and stemflow, where the flow of precipitation is diverted by the canopy along the branches and down the trunk.

Many arid-zone trees and shrubs divert a substantial portion of rainfall towards their trunks as stemflow (Tromble, 1983; Navar and Bryan, 1990; Mauchamp and Janeau, 1993; De Soyza et al., 1997). This water flows through narrow crevices and pores in the bark, following the root-soil interface to deeper soil where it is inaccessible to the roots of most other plants (Nulsen et al., 1986; Joffre and Rambal, 1988; Martinez-Meza and Whitford, 1996). Thus stemflow appears to be an important means by which desert plants can efficiently harvest and store rainfall. It can increase the effective rainfall to the plant several-fold compared with ambient levels (Tromble, 1983; Weltzin and Coughenour, 1990; Vetaas, 1992; Ko and Reich, 1993; Haworth and McPherson, 1995).

The relative magnitude of stemflow and intercept depend on both the size and intensity of the rainfall event (Mauchamp and Janeau, 1993; Haworth and McPherson, 1995; Martinez-Meza and Whitford, 1996). Dense canopies or hot conditions may result in little or no precipitation penetrating canopies during small rainfall events. Nor does stemflow commence until the branches and trunk of the tree or shrub are wetted. The relative importance of stemflow usually increases up to rainfall of about 10-15 mm, and then declines (Pressland, 1973; Haworth and McPherson, 1995). In the case of heavy or prolonged rain most of the precipitation penetrates the canopy, and intercept and stemflow become an insignificant in comparison to throughfall.

Canopy structure affects the way that the canopy redistributes precipitation. Differences in rainfall redistribution have been reported between species (Aston, 1979; Thurow et al., 1987; Navar and Bryan, 1990; Martinez-Meza and Whitford, 1996) and between different canopy morphologies within a species (De Soyza et al., 1997). To date there is limited understanding of the relationship between canopy morphology and precipitation redistribution, although evidence suggests that canopy size, leaf area, and branch angle and length are important (Mauchamp and Janeau, 1993; Haworth and McPherson, 1995; Martinez-Meza and Whitford, 1996).

1.2.4 Soil nutrients

Nutrient levels are generally higher in under-canopy soils than in soils found outside the canopy. This trend has been found in a wide variety of habitats and vegetation communities, but is most pronounced in arid and semi-arid systems where background nutrient levels tend to be low (Charley and West, 1975; Cowling, 1978; Bernhard-Reversat, 1982; Garner and Steinberger, 1989).

The higher nutrient levels in soils under tree and shrub canopies may be a consequence of plant recruitment rates being greater in high nutrient sites. That is, soils under canopies are more fertile because trees and shrubs are more likely to grow in fertile sites. Alternatively the higher nutrient levels may be the result of physical or biological processes associated with the presence of woody perennial plants that result in the accumulation of soil resources.

Several lines of evidence support the latter hypothesis over the former. Firstly, a number of studies have shown a correlation between size or age of the plant and the degree of soil enrichment (Callaway et al., 1991; Isichei and Muoghalu, 1992; Pugnaire et al., 1996a; Facelli and Brock, 2000). This is consistent with a cumulative process dependent on the presence of a woody perennial, although it could be argued that the plant may be able to grow larger because the soil is more fertile. Secondly, several studies have found that soil nutrient levels decline after the death of the plant (Barnes and Archer, 1996; Kelly and Burke, 1997; Facelli and Brock, 2000). This is consistent with higher levels of soil nutrients being the result of biological activity, but not consistent with the pre-existing difference hypothesis.

Even stronger evidence was provided by the results of a removal experiment with *Prosopis* trees in an arid grassland in Arizona (Klemmedson and Tiedemann, 1986; Tiedemann and Klemmedson, 1986). The trees were cut at the base of the trunk, and the stumps were swabbed with diesel oil to suppress regrowth. The site was revisited after 13 years and soil sampling was conducted. During the intervening period, about half of the removed *Prosopis* trees had resprouted. Soil collected from under removed canopies had lower nutrient levels than soil from under control trees, but was still higher than soil from inter-canopy spaces. Soil from canopies that had resprouted showed intermediate nutrient levels. Soil nitrogen levels showed the greatest response to the treatments, whereas sulfur and phosphorus showed little difference. These results show that the soil nutrient enrichment effects are dependent on tree presence. Furthermore, they demonstrate that the influence of the tree on soil nutrients slowly declines over a period of many years.

One model explaining the association between perennial plant canopies and nutrient levels is the "fertile islands" hypothesis (Garner and Steinberger, 1989). This proposes that the distribution of nitrogen in ecosystems is determined by both biotic and abiotic processes. The abiotic processes are dispersive, tending to redistribute nitrogen down gradients until equilibrium is reached. Conversely, biotic processes tend to concentrate nitrogen. According to Garner and Steinberger (1989), the availability of moisture accelerates both types of processes, but abiotic processes are more sensitive to moisture than biotic processes. Consequently biotic processes become more important in terms of nitrogen transport as aridity increases. Because trees and shrubs are centres of biological activity in arid regions, nutrient cycling by biotic agencies results in higher nitrogen levels in soils around trees and shrubs.

Plant canopies may also trap and accumulate wind-borne nutrients (Callaway and Nadkarni, 1991; Schauffler et al., 1996; De Soyza et al., 1997) or provide a substrate for nitrogen-fixing lichens (Knops et al., 1996). Considerable quantities of nutrients can be acquired in these ways. The combination of these processes with stemflow has been proposed as an alternative mechanism for the creation of fertile islands (Whitford et al., 1997).

1.3 Non-resource interactions

Two other important non-resource kinds of plant canopy interactions with the environment can be identified. Both occur widely, and in many environments can have substantial effects on plant growth and survival.

1.3.1 Temperature

Plant leaves may be heated well above ambient air temperatures when they are exposed to full sunlight (Sinclair and Thomas, 1970), leading to increased transpiration rates (Drake et al., 1970). Leaf heating can also lead to tissue destruction and leaf death if the temperature becomes too high. Shoot and root temperature, rather than water stress, is the primary cause of seedling mortality among cacti (Turner et al., 1966; Nobel, 1989), and the distribution of adult plants is determined by the availability of shaded micro-habitats where the mortality rate of seedlings is lower.

Plant canopies moderate the diurnal extremes of air temperature, and provide some protection from radiative heating. During daylight hours air temperatures under canopies in semi-arid and arid environments are generally lower than in open areas (Franco and Nobel, 1989; Callaway et al., 1991; Kellman and Kading, 1992; Ko and Reich, 1993; Belsky et al., 1993; Fulbright et al., 1995; Barnes and Archer, 1996), while the rate of temperature loss during the night is reduced (Parker and Muller, 1982; Georgiadis, 1989). Thus under-canopy vegetation generally experiences a more moderate temperature regime than vegetation in the inter-canopy spaces.

Soil temperature has several important effects on seed germination. Seeds display species-specific dormancy responses to temperature; whereas some seeds will not germinate below a given temperature, others require a period of cold before dormancy can be broken (Probert, 1992; Vleeshouwers et al., 1995). Similar species-specific responses to high temperatures have also been found. Furthermore, the diurnal amplitude of temperature fluctuations is an important dormancy-breaking cue for some species (Fenner, 1985; Probert, 1992). Consequently any factor that alters the magnitude or variability of soil temperatures (such as shading) has the potential to affect the germination probabilities of the soil seed bank, and this effect is likely to differ between species. Seedling survivorship may also be affected if soil temperature changes alters the timing of germination, for seedlings emerging early in the growing season tend to suffer lower mortality rates than seedlings emerging later in the growing season (Miller, 1987).

1.3.2 Leaf litter

Leaf litter has diverse and sometimes profound effects that are often difficult to predict (Tilman and Wedin, 1991; Molofsky et al., 2000; Hastwell and Facelli, 2000). It is also a means by which trees can extend their zone of influence. For example, autumn leaf fall in temperate deciduous woodlands and forest can result in a windblown carpet of leaf litter extending many tens of metres from its source (Facelli and Carson, 1991). More importantly, leaf litter creates spatial and temporal heterogeneity in germination microsites (Facelli and Pickett, 1991b; Molofsky et al., 2000).

Leaf litter has been shown to have stage-specific effects on woody seedlings. Germination rates in some species are increased while other species may be unaffected (Facelli and Kerrigan, 1996; Facelli and Ladd, 1996; Hastwell and Facelli, 2000). Species requiring light to break seed dormancy may be inhibited from germinating by the presence of litter (Peterson and Facelli, 1992). Emergence in small-seeded species can also be inhibited if the litter layer is so thick that seed embryo reserves are exhausted before the hypocotyl reaches light (Myster, 1994; Peterson and Facelli, 1992). Litter may delay emergence and reduce seedling robustness, impairing the chances of a seedling successfully competing and establishing (Miller, 1987). On the other hand establishment may be indirectly facilitated by litter suppressing the emergence of small-seeded herbaceous competitors (Facelli, 1994; Facelli and Pickett, 1991a). Conversely the association of arthropod herbivores with leaf litter can indirectly lead to reduced seedling biomass and increased seedling mortality (Facelli, 1994).

1.4 Local-scale interactions

1.4.1 Plant-plant interactions - the balance between positive and negative effects

The net effect of one plant on another can be positive, negative or neutral (Callaway and Walker, 1997; Brooker and Callaghan, 1998). The magnitude of such a net effect exists along a continuum, with mortality or recruitment failure at the negative extreme and the attainment of maximum fitness at the positive extreme. This net effect is comprised of the balance of all the interactions between the two plants, any one of which may be positive, negative or neutral (Bertness and Callaway, 1994; Holmgren et al., 1997; Holzapfel and Mahall, 1999). However, it should be kept in mind that any effect resulting in recruitment failure or mortality before reproduction would negate all other interactive effects. On the other hand, the maximisation of fitness would require that all effects be neutral or positive.

Interactions may take two forms, one being the mediation of resource availability, the other being the control of factors that may be hazardous. Hazards are entities or events such as herbivores, disease, salinity and wind damage that cause loss of biomass or that reduce fitness (Andrewartha and Birch, 1954).

The magnitude and direction of net effects may change in time. Seasonal variation can see a change in the direction of the net effect of one plant on another (Holzapfel and Mahall, 1999; Tielborger and Kadmon, 2000). For example, the shade provided by a tree to a shrub in arid systems may result in the tree having a net positive effect on the shrub during the hotter months of the year by reducing temperatures and evapotranspiration rates. However, when compared to a shrub growing in the open, the net effect may become negative during cooler months when there is little water stress but the shrub's photosynthetic production is reduced by low light levels.

Ontogenetic change may also affect the direction of net effects when canopy structure changes, altering light penetration, litter retention and under-canopy temperatures (De Soyza et al., 1997). Root growth may also alter the balance of plant-plant interactions by changing the spatial patterns of nutrient and water acquisition (Callaway et al., 1991). Differences in under-storey grass productivity in oaks was correlated with the density of near-surface rootlets. This in turn was correlated with soil moisture levels, leading to speculation that trees that had sent roots into deep soil aquifers possessed few surface rootlets, permitting higher under-storey productivity (Callaway et al., 1991).

Evidence suggests that positive interactions become of greater significance as environments become more stressful for plants (Bertness and Leonard, 1997; Callaway and Walker, 1997; Holmgren et al., 1997). Two hypotheses have been proposed to explain this. One is that the positive effects of amelioration of hazards exceeds the negative effects of competition in stressful environments (Brooker and Callaghan, 1998). The other is that competition for resources under stressful conditions will be negligible because growth rates are low, so positive interactions become relatively more important (Callaway and Walker, 1997; Goldberg and Novoplansky, 1997).

1.4.2 Interactions and temporal variance in resource availability

Generally speaking, soil resource availability is variable and may even be discontinuous, particularly in arid systems (Goldberg and Novoplansky, 1997). As environments become more arid the amplitude of soil moisture availability through time increases. Soils are very dry for long periods, interrupted only by brief pulses of moisture following heavy rain. Since nutrient uptake is dependent on soil moisture, soil resources show two distinct phases of availability (Goldberg and Novoplansky, 1997). Evidence suggests that competition is less intense during periods of low resource availability, and other processes (such as tolerance and facilitation) become more important. During the long periods of low soil resource availability plant growth is low or negative; survival becomes of primary importance. At times of high soil resource availability processes of growth and recruitment dominate, and competition for resources becomes important.

1.5 From local interactions to larger-scale consequences

Clearly, a great deal of biotic and abiotic heterogeneity is associated with the presence of plant canopies, and evidence suggests that much of this heterogeneity is directly or indirectly generated by the plants themselves. This has implications for the temporal dynamics of systems at both local and larger scales. Furthermore, heterogeneity at local scales can alter productivity across larger scales (Noy-Meir, 1981). This section shall discuss these issues in the context of arid and semi-arid systems where heterogeneity is associated with isolated shrubs and trees, and where resources for plant growth are often at low levels.

1.5.1 Patch dynamics and isolated trees

Savanna systems have been likened to forests, in that both systems comprise a matrix of structurally homogeneous vegetation (a continuous layer of grasses *vs.* a forest canopy) interrupted by breaks (trees or shrubs *vs.* canopy gaps) (Belsky and Canham, 1994). In effect, savanna systems are the structural inverse of forests.

The patch dynamics model provides a framework for understanding the processes of growth, death and replacement in systems possessing relatively discrete areas with differing environmental qualities. As a spatially-explicit elaboration of the Intermediate Disturbance Hypothesis (Connell, 1978) and the Dynamic Equilibrium Model (Huston, 1979), the patch dynamics model stresses the importance of disturbance in creating relatively small-scale resource rich gaps that provide recruitment opportunities (Brokaw, 1985; Pickett and White, 1985; Runkle, 1985). Belsky and Canham (1994) proposed that the patch dynamic model could also be applied to savanna systems, but whereas structural change in forests is triggered by canopy loss, change in savannas is initiated by tree seedling recruitment. The other substantial difference is in the time scales involved: gap closure in forests occurs in a matter of a few decades, whereas many savanna trees are thought to live well in excess of 100 years (Crisp and Lange, 1976; Crisp, 1978; Facelli and Brock, 2000). Furthermore, the differences between canopy and gap areas in forests are at their maximum at the time the gaps are created, and the differences steadily decline. On the other hand, the differences between canopy and open areas in savannas may at first be indistinguishable, and gradually increase until the trees senesces and dies (Facelli and Brock, 2000), resulting in a sequence of changes in the species composition of the vegetation below trees. But, as with forest gaps, seedling recruitment in savannas creates heterogeneity in light intensity and spectral quality, air and soil temperature, and soil moisture and nutrient concentrations (Vetaas, 1992; Belsky and Canham, 1994). The main difference in resource availability between savannas and forests is that soil nutrient and moisture levels tend to be higher in forest gaps than under canopies, whereas the converse is the case in savannas.

1.5.2 Zones of influence

The influence of an individual tree or shrub on its surroundings may be conceptualised as a series of concentric zones centred on the main axis of the plant (Zinke, 1962; Belsky and Canham, 1994). The degree of soil enrichment, the extent of rainfall diversion and the amount of shading at any given point can all be expressed as functions of the distance from the main axis. Each zone possesses its own particular combination of light, nutrient, water and temperature levels (Belsky and Canham, 1994), creating a set of distinct micro-environments. Consequently, each zone also tends to possess its own particular vegetation community (Belsky and Canham, 1994; Facelli and Brock, 2000).

1.5.3 Biodiversity

Although perennial plants clearly possess the capacity to modify their local environments, they may not necessarily create the types or magnitudes of differences necessary to permit new species to exist within the system. However some studies have identified plant species that are only found below the canopies of perennial plants (Muller, 1953; Parker and Muller, 1982; Whitford and Whitford, 1978; Vetaas, 1992; Facelli and Brock, 2000). Furthermore, other species have been shown to be highly dependent on nurse plants for establishment (Turner et al., 1966; Fuentes et al., 1984; Franco and Nobel, 1989; Aguiar et al., 1992; Flores-Martinez et al., 1994). The importance of canopy habitats in increasing biodiversity has been further emphasised by reciprocal transplant experiments demonstrating that some understorey species cannot survive outside the canopy micro-environment (Maranon and Bartolome, 1993).

Hacker and Gaines (1997) presented a model predicting increased community species diversity as a result of facilitatory interactions in stressful environments. In this model an increase in environmental stress disproportionately affects the dominant species within a community. The consequent reduction in competition permits previously excluded species to coexist. If one of these new species facilitates others by ameliorating stress or by providing protection, then further species may enter the community.

A cellular automata modelling sessile organisms competing for space found that local interactions were responsible for defining larger-scale species boundaries (Wilson and Nisbet, 1997). Habitat amelioration may create sharp boundaries in population densities along smooth environmental gradients. Where a trade-off between colonisation ability and habitat amelioration occurred, the boundaries between species distributions tended to be sharp. However, if the presence of one species increased recruitment of another species, boundaries in species composition were less distinct.

1.5.4 Patchiness, productivity and scarce resources

The accumulation of soil resources around trees and shrubs may affect productivity at larger scales *via* two related mechanisms. Firstly, plants have minimum resource thresholds below which they show very little or no growth (Noy-Meir, 1981), and other thresholds below which they may not survive. Higher resource levels around trees may allow growth and production to continue at times when levels in the surrounding landscape fall below the minima required for growth. Similarly, areas under trees may act as refugia during times when resource levels fall below the survival threshold in the surrounding landscape. So the variability in resource levels induced by trees may increase system-level productivity.

Most plant growth responses to resource levels are non-linear, or are linear over only part of their range (Noy-Meir, 1981; Ruel and Ayres, 1999). Due to the mathematical property of non-linear functions described by Jensen's inequality (Ruel and Ayres, 1999), variability in resource availability means that landscape-level productivity will differ from what it would be if resources were evenly distributed (Ruel and

Ayres, 1999). The direction of change depends on the shape of the curve that describes the relationship between resource levels and plant growth rates. If the growth function is decelerating over the range of resource levels across the landscape, overall productivity will be lower than it would be if resources were evenly distributed. Conversely, where the growth function is accelerating, overall productivity will increase (Ruel and Ayres, 1999). Thus, if trees do in fact create heterogeneity by redistributing soil nutrients or changing soil moisture levels, they are almost certainly affecting ecosystem functioning.

1.6 Conclusions

Much of our understanding of plant ecology can be summarised in two simple statements. Firstly, plants respond to their environments. Secondly, plants can locally modify their environments. Thus plants that locally modify their environments may affect other plants growing within the region of modification.

A substantial body of literature associates the presence of perennial plants with environmental heterogeneity. Some of this heterogeneity is directly attributable to the physiological activities of plants, or to the size and shape of their aboveground parts. Rainfall redistribution, soil and air temperature, and light quality and intensity are all affected by plant canopies. Soil moisture may be affected by both plant canopies and plant root systems.

Soil nutrient levels under canopies frequently differ from levels in open spaces, but the source of this heterogeneity may be due to pre-existing patchiness or to processes directly or indirectly associated with trees. Although causation has rarely been demonstrated, there is growing evidence that increased soil resource availability is due to biological activity rather than pre-existing heterogeneity.

These local modifications may have larger consequences. Ecosystem functioning, nutrient cycling and biodiversity may all be affected if local modifications are of sufficient magnitude to alter productivity or to permit the coexistence of extra species within the broader landscape. Numerous studies provide evidence that this can be the case. Some studies report several-fold changes in productivity associated with canopies, while others demonstrate species-specific dependency on under-canopy sites for coexistence or for recruitment. Local positive interactions are able to increase larger-scale biodiversity.

The current re-evaluation of plant-plant interactions by ecologists has demonstrated that positive interactions are important, and that they deserve more attention. The net direction of plant interactions is now thought to be contextual - the degree of environmental stress is likely to determine whether competitive or facilitative interactions dominate. Furthermore the direction may change seasonally or with ontogenetic change.

The structure, size, shape and persistence of plant canopies appear to be important in many of the processes of local modification by plants. Further research in the area of the effects of canopy attributes has the potential to produce a predictive schema for determining the effects of plants on their surroundings.

1.6.1 Research objectives

The aims of this research are to quantify the heterogeneity in soil resources and plant communities associated with trees, to identify processes by which tree canopies generate heterogeneity, to measure differences in heterogeneity associated with variation in canopy morphology, and to examine the effects of canopy morphology on emergence and growth of selected understorey species. I use a combination of observational and experimental approaches to address these questions.

Soil resource levels and understorey communities are surveyed to determine whether they differ with canopy shape and size (Chapters 2 and 3). The data from these surveys are also used to determine whether or not fertile islands are associated with the clonal tree *Alectryon oleifolius*, and to see if soil resources accumulate as trees grow.

I develop an experimental methodology utilising artificial canopies to permit tests of the effects of shading and rainfall redirection independently of the effects of nutrient accumulation (Chapter 4) . This methodology is applied to test canopy effects on emergence of two herbaceous species with contrasting seed coat characteristics, *Carrichtera annua* and *Danthonia caespitosa* (Chapter 5). Artificial canopies are also used to investigate the effects of shading in facilitating growth and survivorship in the chenopod shrub *Enchylaena tomentosa* (Chapter 6). This experiment tests whether or not facilitation becomes stronger as environmental stress increases, and whether or not facilitation of survivorship differs from facilitation of growth.

The results of this experiment were not entirely consistent with current models of the relationship between facilitation and environmental gradients. I test the assumptions of current models by developing an alternative model that explicitly incorporates both local modification by plants and neighbour responses to those modifications (Chapter 7). In the final chapter I summarise the major findings of my research and frame them within the context of current knowledge.

Chapter 2

Are fertility islands associated with *Alectryon oleifolius*?

2.1 Introduction

In many ecosystems mature woody plants are associated with spatial heterogeneity in soil resources. Reports of elevated soil nutrient levels below plant canopies come from temperate deciduous (Callaway et al., 1991) and evergreen (Zinke, 1962) forests and woodlands, tropical woodlands (Dunham, 1991) and savannas (Kellman, 1979; Belsky et al., 1989, 1993), and arid shrublands (De Soyza et al., 1997) and savannas (Bernhard-Reversat, 1982; Dean et al., 1999). The few reports from Australian ecosystems are consistent with these findings (Tongway and Ludwig, 1990; Jackson and Ash, 1998; Cheal, 1999; Facelli and Brock, 2000).

Debate continues over whether fertile islands are created by biotic processes or whether they represent pre-existing heterogeneity favouring the establishment of woody perennials. However, a body of evidence implicating biotic processes is accumulating. Correlations between plant size or age and the degree of soil enrichment (Everett et al., 1983; Isichei and Muoghalu, 1992; Pugnaire et al., 1996a; Facelli and Brock, 2000) suggest that cumulative processes dependent on plant presence are responsible for the creation of fertile islands. Although the elevated nutrient levels may persist for decades after the death of the plant (Barnes and Archer, 1996), reductions in soil fertility as trees senesce and die further indicate that the processes are associated with biological activity (Facelli and Brock, 2000), rather than being solely due to physical capture of material transported by wind or water (Ludwig and Tongway, 1995). Other evidence can be found in the spatial distributions of soil resources in arid grasslands. Comparisons between grasslands that have been invaded by shrubs in recent decades and adjacent uninvaded areas showed differences in the scale of variability in soil resources (Schlesinger et al., 1996). The scale of spatial autocorrelation in shrub-invaded areas closely matched the canopy diameter of the shrubs, while uninvaded grasslands showed spatial autocorrelation at considerably larger scales. This suggests that the heterogeneity in the shrub-invaded areas is the result of processes associated with shrubs.

Controlled experimental removal of *Prosopis* tree canopies provide some of the strongest evidence to date that fertility islands are generated by biological activity (Klemmedson and Tiedemann, 1986; Tiedemann and Klemmedson, 1986). Thirteen years after canopy removal, soil from under control canopies had higher nutrient levels than soil from under removed canopies, while both had higher levels than soils from inter-canopy spaces. Some individuals had resprouted after removal; soils from under these regrown canopies had nutrient levels that were intermediate between control canopies and removed canopies. Maintenance of elevated nutrient levels depended on the presence of tree canopies, and the degree of enhancement was a function of either canopy size or the duration of canopy presence.

It is not yet clear which biotic processes are important in generating fertility islands. Several mechanisms have been proposed, but they are difficult to test and require very long-term experiments. One plausible explanation is nutrient pumping (Kellman, 1979; Scholes and Archer, 1997), whereby plants redistribute nutrients by acquiring nutrients through their roots from one location, such as deep soil layers or from soil beyond the canopy edge, and depositing them under the canopy as plant litter. This process is mediated by selective scavenging of nutrients prior to leaf abscission (Nilsen and Schlesinger, 1981), with nutrient retranslocation showing considerable interspecific variation (Chapin and Kedrowski, 1983). Hydraulic lift, the nocturnal translocation of water between soil layers across a soil water potential via plant roots, might also redistribute some solutes, and could potentially accelerate biogeochemical nutrient cycling processes (Caldwell et al., 1998).

It has also been suggested that the aerodynamics of canopy shape plays a role in fertility island formation (De Soyza et al., 1997). Some canopy shapes create localised vortices that increase the likelihood of litter being removed by wind, while other canopy shapes direct airflow in a manner that increases leaf litter retention. Within-species comparisons of canopies that do and do not retain litter show higher concentrations of nutrients in the soils below canopies that retain litter (De Soyza et al., 1997).

Micro-environmental differences associated with plant canopies may also affect nutrient accumulation. The rate of decomposition of organic matter is affected by both temperature and moisture levels (Aerts, 1997), which are in turn affected by the presence and structure of plant canopies (Vetaas, 1992; Haworth and McPherson, 1995; Breshears et al., 1998).

Nutrient accumulation can also occur as a result of animal activity. Vertebrates make use of canopies as perching or resting sites (McDonnell and Stiles, 1983), as refugia from more severe external conditions (Dean et al., 1999), and as foraging areas (Halligan, 1974), transporting nutrients from the intercanopy spaces into the canopy zones.

Garner and Steinberger (1989) proposed that the creation of fertile islands was the result of the actions of two counteracting forces. Physical mechanisms, such as diffusion, leaching and wind transport, tend to be dispersive, whereas biological mechanisms associated with growth tend to concentrate nutrients. Using nitrogen transport as an example, Garner and Steinberger (1989) claimed that physical transport mechanisms were accelerated by moisture to a greater extent than biological transport mechanisms. At some point the rate of physical dispersion of nitrogen will begin to exceed the rate of biological concentration. However, the presence of the fertile island phenomenon in both mesic and xeric environments is inconsistent with the predictions of this hypothesis.

Facilitation of understorey species by woody perennials may potentially affect nutrient accumulation *via* increased plant productivity in the understorey community. Many studies have demonstrated differences in productivity between canopies and open areas (Frost and McDougald, 1989; Georgiadis, 1989; Grouzis and Akpo, 1997), but the responses appear to be conditional. Comparisons across sites have found large changes in the magnitude, and sometimes in the direction, of the response to canopy presence (Ratliff et al., 1991). These site-related differences have been associated with differences in rainfall or in below-canopy soil moisture (Callaway et al., 1991; Belsky et al., 1993; Belsky, 1994). Furthermore, elevated nutrient levels were associated with higher understorey biomass in some studies (Pugnaire et al., 1996a,b) but not others (Ko and Reich, 1993). Thus productivity may be affected by shifts in the balance between negative and positive interactions between trees and their understorey occupants (Holmgren et al., 1997). So where positive interactions outweigh negative interactions overall, understorey productivity may contribute to the creation of fertile islands.

The spatial distribution of habitats in savannas is more complex than a simple dichotomy of tree and open patches. Belsky and Canham (1994) drew an analogy between patch dynamics in forest gaps and the dynamics of isolated trees in savannas. They proposed a spatially explicit model in which trees exerted concentric zones of influence centred around the tree's trunk. The zones differ from each other in the levels of light, temperature, soil moisture and soil nutrients, providing a set of microhabitats quite distinct from the areas between trees. The Belsky and Canham (1994) model emphasises that the zonation is the result of differing combinations of processes that change with the distance from the tree trunk.

I conducted a pilot survey of soil nutrient levels and leaf litter densities associated with the clonal tree *Alectryon oleifolius*, which is widely distributed through arid southern Australia (Jessop and Toelken, 1986). This species was selected for two main reasons. Firstly, it would provide a comparison with the larger and possibly longer-lived *Acacia papyrocarpa*, which has been studied by Facelli and Brock (2000). Secondly, *A. oleifolius* has a variable habit, making it a useful subject for studying the effects of canopy morphology on local environmental modification (see Chapter 3).

The primary objective of the pilot study was to determine whether or not fertility islands are associated with *A. oleifolius*. I also used the data to refine the design for a more detailed survey of soil resources and canopy morphology (Chapter 3). Finally, I conducted exploratory analyses into the relationships between leaf litter loads, soil enrichment and grazing intensity.

2.2 Methods

2.2.1 Site selection

The study was conducted at Middleback Station (32° 57'S, 137° 24'E, altitude 75 m) 21 km north west of Whyalla, South Australia, and at Koonamore Station (32° 07'S, 139° 22'E, altitude 200 m) approximately 60 km north-west of Yunta, South Australia. Both sites have comparable climates, with similar mean annual rainfall (*c.* 200 mm) and temperature ranges (Carrodus et al., 1965; Andrew, 1978). Calcareous red-brown earths are the most common soil types at both sites; these soils may also be overlaid by low sand dunes at Koonamore.

2.2.2 Tree selection

Alectryon trees were selected for sampling in locations subjected to different levels of sheep grazing intensity. I wished to avoid the effects of any close neighbours, so larger, isolated trees were chosen. At Koonamore Station, four trees were selected inside the T.G.B. Osborn Vegetation Reserve (KVR), where they are protected from grazing by sheep and rabbits but not kangaroos, and four within 200 metres of the Reserve fence in Mustering Paddock 3 (KG), which is used as a holding paddock during shearing and subjected to intermittently high grazing levels (Figure 2.1). Within each location litter samples were collected from under two trees, and soil samples from under the other two. At Middleback Station two trees were selected at two locations, one in Depot Paddock (FB) and the other approximately 5 km south in Overland Paddock (ML) (Figure 2.2). As the ML site was more distant from the nearest watering point than was the FB site, this provided sites with low and high sheep grazing intensity respectively (Stafford Smith, 1984; Andrew and Lange, 1986).

Sampling was conducted at Koonamore on 22-25 August 1997, and at Middleback on 25 October 1997. The sampling regime was refined during the course of this work so that soil nutrients could be linked with litter densities. So whereas litter samples and soil samples were collected from different trees at Koonamore, both soil and litter samples were collected from under the same trees at Middleback.

2.2.3 Sampling methods

Canopy size

The height of each tree was measured with a 5 m surveyor's staff. Trees that exceeded 5 m in height were recorded as '> 5.0 m'. The maximum northward radius and the circumference of the trunk at 50 cm above ground level were also recorded. For trees with multiple trunks, I recorded the sum of the individual circumferences. Canopy data were not recorded for the KVR-2 soil sampling tree, and I was subsequently

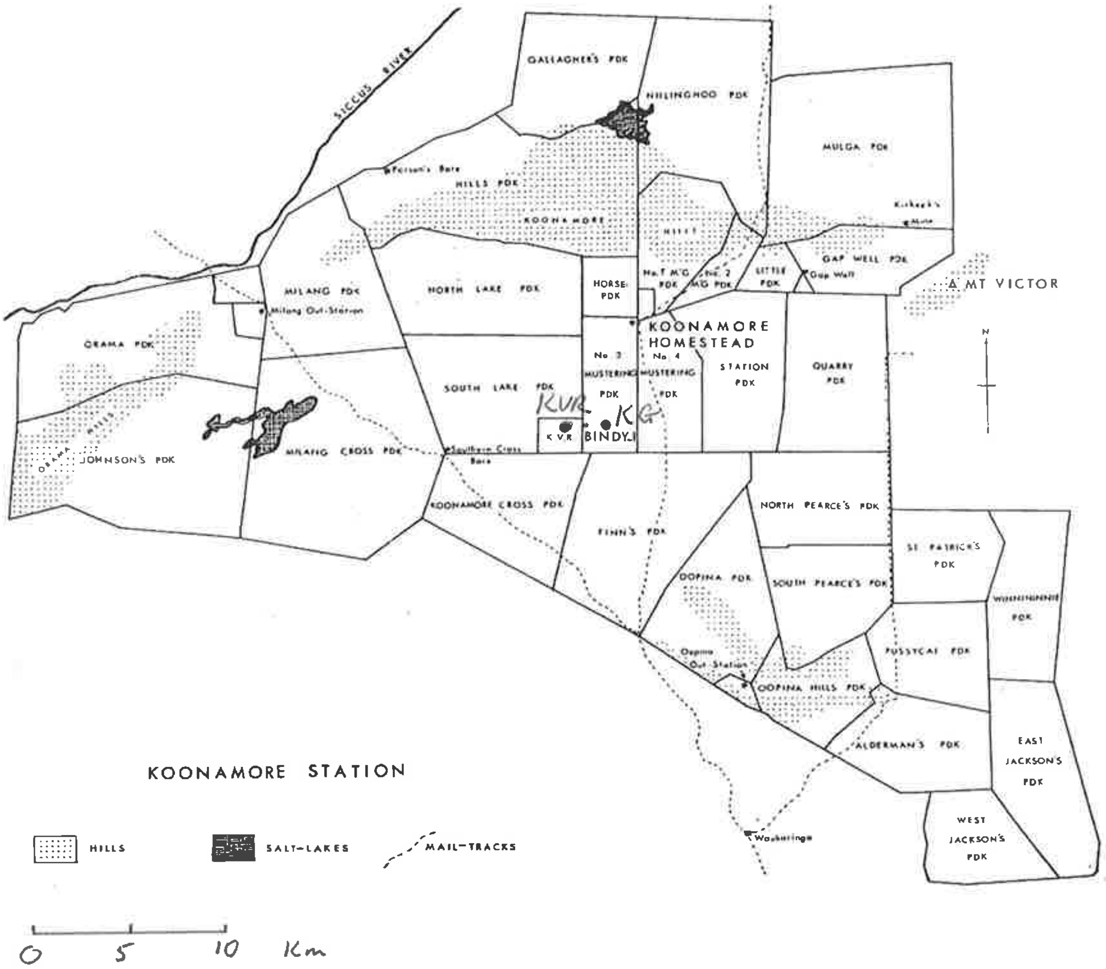


Figure 2.1: Approximate locations (in red) of *Alectryon oleifolius* trees selected for sampling at Koonamore Station. (Map adopted from Carrodus et al. (1965).)

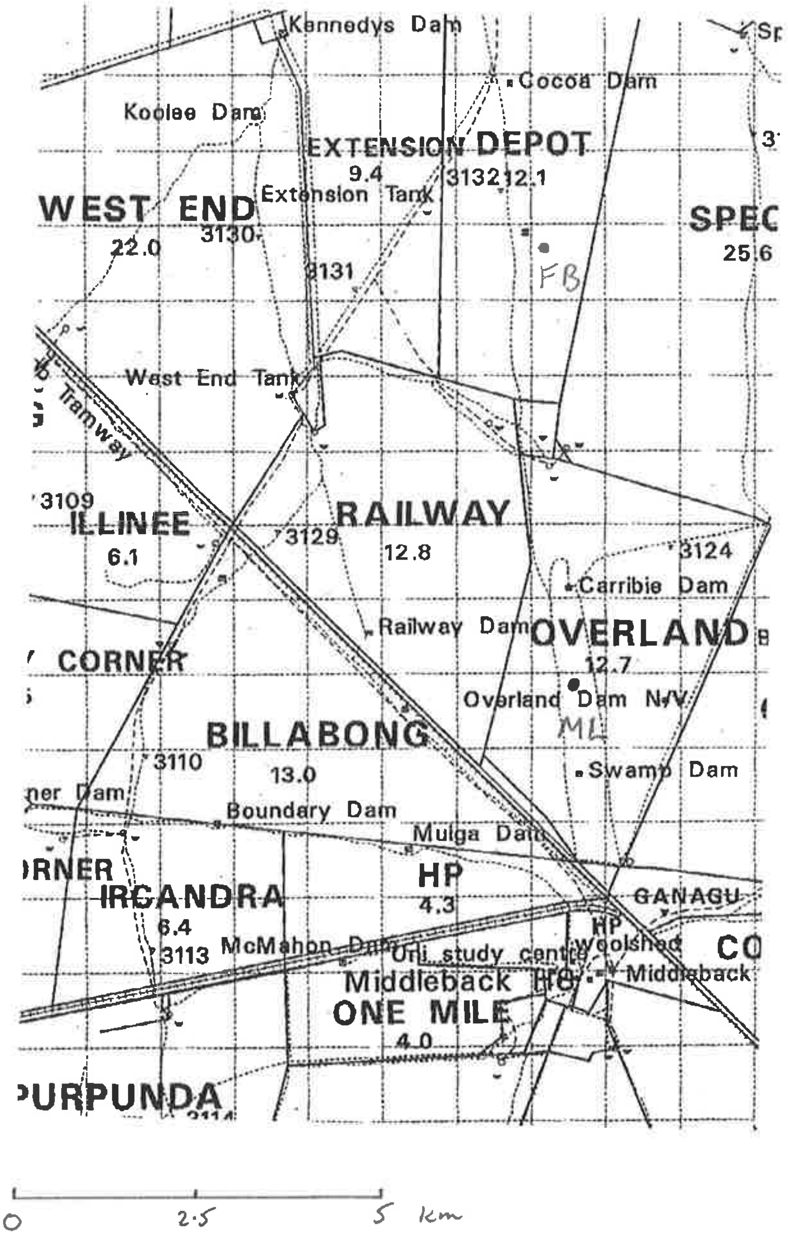


Figure 2.2: Approximate locations (in red) of *Alectryon oleifolius* trees selected for sampling at Middleback Station. (Map adopted from Roopena 1:50 000 sheet, Pastoral Management Branch, Department of Environment and Natural Resources (1996)).

unable to positively relocate the tree.

Leaf litter

Leaf litter was collected from within a 20 × 20 cm area from 8 randomly selected points under each canopy. I defined litter as all unattached plant-derived material. The random points were generated in advance using Skalski (1987) algorithm, assuming a maximum canopy radius of 2.5 m. Excess random points were generated so that any that fell outside the canopy could be discarded. Litter was not collected from one tree that had large numbers of aggressive ants in its canopy (ML 2; Middleback Station, low grazing intensity).

Litter samples were sieved through a 1.67 × 1.43 mm mesh to remove soil particles. The retained material was then sorted into 3 categories - sticks (greater than 3 mm diameter), leaf material and vertebrate faeces - and air-dried for 48 hours at 85° C before weighing.

Soil

I collected 43 mm diameter soil cores to a depth of 4 cm. I chose this volume and depth as the majority of soil resources in arid soils are concentrated in the upper few centimetres (Schlesinger and Pilmanis, 1998), and because it approximates the volume of soil a seed or small seedling is likely to experience. The soil core size also provided measures of small-scale soil heterogeneity, which many soil studies overlook.

I used a stratified random sampling scheme designed to provide the most intense coverage near the trunk, where I anticipated that stemflow and a longer history of tree influence might produce greater spatial variability in soil resources. I collected fewer samples outside the canopy where I expected nutrient levels to be less variable. Three zones were delineated - Trunk (0-25 cm from the trunk), Under canopy (25 cm -3 m from the trunk) and Open (0-5 m outside canopy edge). Four sectors were defined - East (45-135°), South (135-225°), West (225-315°) and North (315-45°).

The combination of zones and sectors gave twelve sampling segments. Three samples were collected from random locations in each segment below the canopy, and two from each segment outside the canopy, giving a total of 32 samples for each tree. The algorithm used to determine random locations (Skalski, 1987) provides each point within a segment a uniform chance of being chosen. Since most of the area within a segment is at it's farthest extent from the trunk, sampling points tend to be concentrated near the segment edge farthest from the trunk.

Soil samples were sieved through a 1 mm square mesh prior to nutrient analysis. The samples were analysed for pH, electrical conductivity (EC), organic carbon (organic C), total nitrogen (N), and available phosphorus (P).

pH Soil pH was measured with a Hanna Instruments HI 8424 pHmeter. Eight g of dry soil were placed in a tube and mixed with 40 ml of deionised water at 20°C by inverting the tube four times. The samples were then allowed to settle and equilibrate for one hour before measurement took place. The meter was recalibrated with a known solution after every 20 measurements.

Electrical Conductivity Electrical conductivity was measured with a Radiometer CDM2e Conductivity Meter. Eight g of dry soil were placed in a tube and mixed with 40 ml of deionised water at 20°C by inverting the tube four times. The samples were then allowed to settle and equilibrate for one hour before measurement took place. The electrode was rinsed with deionised water after each measurement, and the meter was zero calibrated at the start of each batch of measurements.

Soil Nutrients The organic carbon content of samples was determined using Walkley and Black's titration procedure (Allison, 1965). The Kjeldahl method was used to determine the total nitrogen content of soil samples (Bradstreet, 1965), and available phosphorus was measured using the bicarbonate-extractable method (Watanabe and Olsen, 1965).

2.2.4 Data Analyses

I checked for differences in canopy dimensions between sites and between grazing levels, so that I could verify the validity of making comparisons between locations. As the level of replication was very low ($n = 2$), I used two-way factorial randomisation tests of canopy height, canopy radius and trunk circumference (NPFact 1.0 (May et al., 1993a)), with site and grazing level as the factors. The software does not accommodate missing data, so only the litter sampling trees could be tested. Trees with heights greater than 5 m were treated as 5.01 m high.

I wanted to see if there were consistent relationships between the canopy dimensions that I could use to reduce the number of canopy parameters to be measured in the comprehensive survey (Chapter 3). I calculated non-parametric correlations between canopy height, canopy radius and trunk circumference (Spearman ρ, JMP 3.1.4 (SAS Institute, 1997)). Canopy heights greater than 5 m were excluded from the analysis, but correlations of canopy radius and trunk circumference were made on the full data set.

The degree of correlation between the different litter components was assessed using the Spearman measure of association, ρ (JMP 3.1.4 (SAS Institute, 1997)). I also tested for the effects of distance and direction of the sampling point from the trunk on litter weight using a nested MANCOVA (JMP 3.1.4 (SAS Institute, 1997)). The factor 'sector' modelled location, using the same angular criteria as used in the stratification of the soil sampling. The dependent variables were $\log_e(\text{stick} + 1)$ and $\sqrt{(\text{leaf} + 1)}$. The faeces data, having a high proportion of zeroes, could not be satisfactorily transformed to meet the assumptions of MANOVA, and so were not used in this analysis. The model consisted of site, location nested within site, tree nested within location, and sector nested within tree, with distance from the trunk as the covariate.

Soil EC data contained many extreme values. Only the pH data were normally distributed; data for the other soil variables were $\log_e$ transformed to satisfy the assumptions of parametric methods. Correlations between all soil variables were measured with Pearson's r (JMP 3.1.4 (SAS Institute, 1997)). Correlations were assessed for the entire data set, for data grouped by zone and data grouped by site. Data was also grouped by site with zone, but the lower number of points (n=16 in the Open zone, n=24 in the Trunk and Under zones) resulted in many correlations being non-significant. Consequently these latter results are not presented.

I tested the relationships between canopy dimensions and soil and litter variables. Canopy radius and trunk circumference were regressed against pH, $\log_e$ organic carbon, $\log_e$ total nitrogen, $\log_e$ available phosphorus and $\log_e$ electrical conductivity. As three of the seven measured canopies used for soil sampling had heights greater than 5 m, I did not investigate the relationship between height and soil nutrient concentrations. Canopy height, canopy radius and trunk circumference were regressed against $\log_e(\text{stick} + 1)$ and $\sqrt{(\text{leaf} + 1)}$. I carried out non-parametric correlations on faeces weight and the three canopy measures, as the faeces data contained many zeroes (Spearman ρ, JMP 3.1.4 (SAS Institute, 1997)). Two of seven canopies used for litter sampling had heights greater than 5 m; data from these two canopies was excluded from the analysis of the relationship between height and litter.

Soil nutrient data were also subjected to inferential statistical analysis to verify the presence of fertile islands under *A. oleifolius*. I conducted a nested MANOVA to investigate whether soil variables changed between zones or with direction relative to the trunk. The model consisted of site, location nested within site, tree nested within location and zone nested within tree, sector nested within tree, and the interaction of zone and sector nested within tree. The dependent variables were pH, $\log_e$ organic C, $\log_e$ N and $\log_e$ P. The other soil variable, EC, was excluded from the analysis as it's distribution violated the assumptions of MANOVA. *Post hoc* comparisons were made between zones. Comparisons were also made between the north and south sectors, and between the east and west sectors within each zone.

I also examined the relationship between leaf litter weights and soil nutrient levels.

Site	Location	Canopy height (m)	Canopy radius (m)	Trunk circ. (m)
Koonamore	**KG 1 soil**	> 5.0	2.7	1.70
	KG 1 litter	> 5.0	3.6	1.40
	KG 2 soil	> 5.0	3.0	2.80[a]
	KG 2 litter	4.5	1.75	0.75
	KVR 1 soil	4.3	1.1	1.0
	KVR 1 litter	3.4	2.45	1.0[b]
	KVR 2 litter	4.3	0.5	0.7
Middleback	**FB 1**	4.5	3.7	2.1[b]
	FB 2	>5.0	5.0	2.59[b]
	ML 1	3.5	2.7	0.7
	ML 2	3.2	2.7	1.45

Table 2.1: Canopy dimensions of the *Alectryon oleifolius* trees used for soil and litter sampling. Canopy radius is the maximum northward radius of the canopy. Trunk circumference was measured at 50 cm above ground level; the sum of circumferences is given for multi-stemmed trees. a = three trunks at 50 cm above ground level, b = two trunks at 50 cm above ground level.

Both soil and litter samples were collected from three trees at Middleback Station. The soil data from the Trunk and Under zones were pooled and the Open data was excluded as litter had only been collected from under the canopies. Their relationship was explored graphically with plots constructed from the means and standard errors of soil and litter measurements from each tree (MathSoft, 1999).

2.3 Results

2.3.1 Canopy Size

Although there were no differences in the canopy radii or the trunk circumferences between sites or between grazing levels, canopy height was greater in the high grazing sites than in the low grazing sites (Table 2.1, $P = 0.0270$). There was a strong correlation between canopy radius and trunk circumference (Spearman $\rho = 0.7265$, $P = 0.0066$), but the correlations with canopy height were not significant.

2.3.2 Leaf Litter

Litter weights varied considerably between trees (Figure 2.3). The distributions of stick litter weights within trees tended to be strongly right-skewed, while faeces weight data contained many zeroes.

The litter variables were strongly correlated across all sites (Table 2.2) but the correlations were not significant within some locations. Only the high grazing intensity sites (KG and FB) showed significant relationships. However, the trees sampled in the high grazing locations were taller than those from the low grazing locations.

Leaf litter and faeces weights were correlated with some canopy dimensions, but stick weight was not (Table 2.3). All canopy measures were significantly correlated with faeces weight, while only canopy radius was significantly correlated with leaf weight.

Leaf and stick litter weights differed between Middleback and Koonamore, between levels of grazing intensity, between trees and with distance from the tree trunks (Table 2.4, Figure 2.4). However, litter did not differ between sectors.

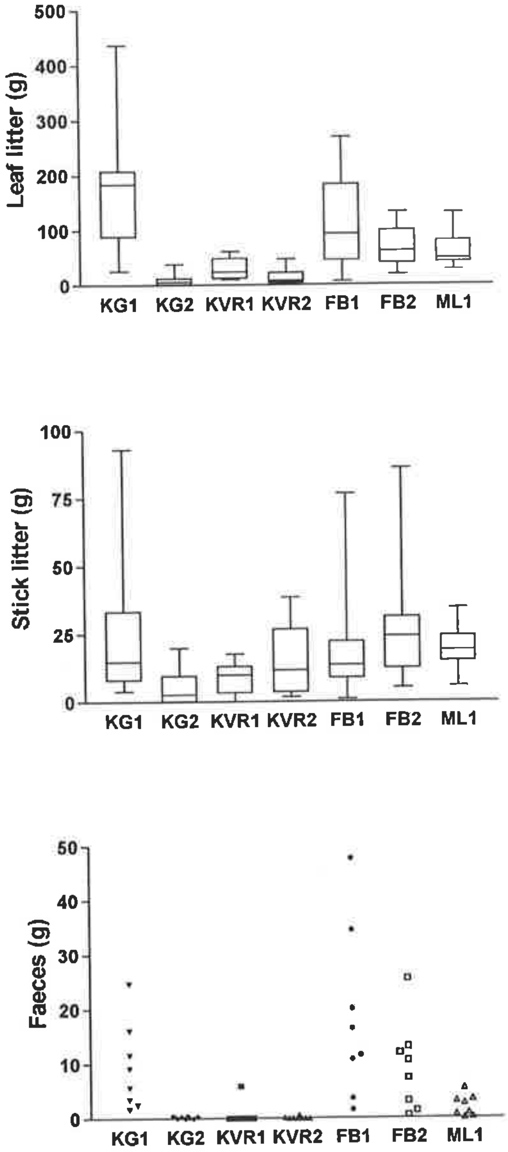


Figure 2.3: Dry weight of plant litter collected from 20 × 20 cm areas under *Alectryon oleifolius* canopies. KG = Mustering Paddock 3, Koonamore Station, KVR = T.G.B. Osborn Vegetation Reserve, Koonamore Station, FB = Depot Paddock, Middleback Station, ML = Overland Paddock, Middleback Station. Note that only one tree was sampled at the ML site.

Site	Variables	Spearman ρ	prob > $\mid \rho \mid$
All	**Stick and Leaf**	0.6268	<0.0001
	Faeces and Leaf	0.7431	<0.0001
	Faeces and Stick	0.4277	0.0010
KG	**Stick and Leaf**	0.7447	0.0009
	Faeces and Leaf	0.8147	0.0001
	Faeces and Stick	0.5180	0.0398
KVR	**Stick and Leaf**	0.2706	0.3108
	Faeces and Leaf	0.4598	0.0731
	Faeces and Stick	0.3420	0.1948
FB	**Stick and Leaf**	0.7206	0.0016
	Faeces and Leaf	0.7294	0.0013
	Faeces and Stick	0.4000	0.1248
ML	**Stick and Leaf**	0.3810	0.3518
	Faeces and Leaf	-0.3333	0.4198
	Faeces and Stick	0.4762	0.2329

Table 2.2: Correlations of leaf litter components from preliminary survey. All - pooled data, KG - Mustering Paddock 3, Koonamore Station, KVR - T.G.B. Osborn Vegetation Reserve, Koonamore Station, FB - Depot Paddock, Middleback Station, ML - Overland Paddock Middleback Station. Data are from sampling conducted under two *Alectryon oleifolius* trees at each site, except for ML where one tree was sampled.

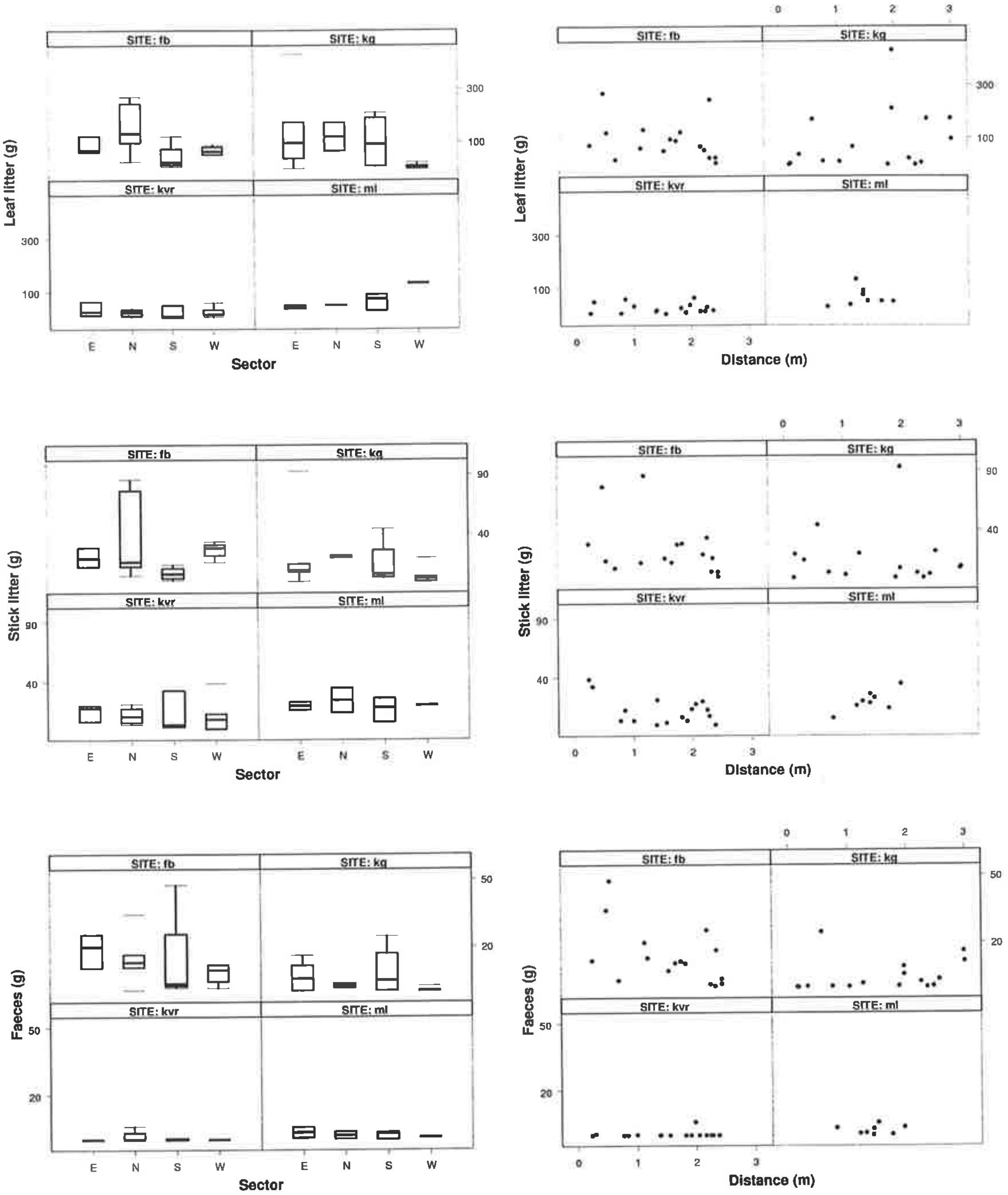


Figure 2.4: Plant litter weights by direction from *Alectryon oleifolius* trunks (left hand graphs) and by distance from trunk (right hand graphs). E = 45-135°, S = 135-225°, W = 225-315°, N = 315-45°.

		Canopy height	Canopy radius	Trunk circumference
Stick	r^2	0.0185	0.0406	0.0157
Leaf	r^2	0.0092	0.1881***	0.0001
Faeces	ρ	0.2921**	0.7538***	0.3068*

Table 2.3: Canopy dimensions as predictors of leaf litter weights. Linear regression of canopy dimensions was conducted on $\log_e$ Stick weight+1 and square root Leaf weight+1. Nonparametric correlations were conducted on canopy dimensions and Faeces weight. * - significant at $P < 0.05$, ** - significant at $P < 0.01$, *** - significant at $P < 0.001$.

	Value	F	DF Num	DF Den	Prob>F
Whole Model	1.3291	2.2098	52	58	0.0018
Intercept	0.8167	62.3955	2	28	0.0000
Site	0.2542	4.7721	2	28	0.0165
Location(Site)	0.3131	2.6915	4	58	0.0397
Tree(Location)	0.6988	5.1914	6	58	0.0002
Sector(Tree)	0.8454	1.1177	38	58	0.3457
Distance	0.3199	6.5853	2	28	0.0045

Table 2.4: MANCOVA on leaf litter ($\log_e$ Stick weight+1 and square root Leaf weight+1) collected from under *Alectryon oleifolius* canopies. Distance is a covariate in the model.

2.3.3 Soil

Organic carbon, total nitrogen, available phosphorus and electrical conductivity levels tended to be higher and more variable under tree canopies than in the open zone (Figs 2.5 and 2.6). Data tended to be strongly right skewed, especially for electrical conductivity. Soil pH did not follow these patterns (Figure 2.7); variance and skew were lower and differences between zones were less pronounced.

There were strong positive correlations between $\log_e$ organic C, $\log_e$ N, $\log_e$ P and $\log_e$ EC across all sites (Table 2.5). There were also negative correlations between pH and $\log_e$ organic C, $\log_e$ N and $\log_e$ P, but no relationship between pH and $\log_e$ EC.

These patterns changed when correlations within zones were examined. Although the Under zone showed the same pattern of correlations as the data across all sites, the Trunk and Open zones differed. There was no correlation between $\log_e$ organic C and $\log_e$ P in the Trunk zone. In the Open zone the correlation between $\log_e$ P and $\log_e$ EC was negative, while the correlation between pH and $\log_e$ EC became positive and significant. There was no correlation between $\log_e$ EC and $\log_e$ P.

Correlations within sites followed the patterns found across all sites, with several exceptions at the FB site. Here the correlation between pH and $\log_e$ EC was positive and significant, but there were no correlations between pH and $\log_e$ organic C, $\log_e$ N or $\log_e$ P.

Canopy radius and especially trunk circumference were significantly correlated with soil variables, but the strength of the correlations varied between zones (Table 2.6). Correlations for $\log_e$ organic C and $\log_e$ P were stronger in the trunk zone than in the other zones for both canopy radius and trunk circumference. A similar pattern was found for $\log_e$ N in the correlations with trunk circumference, but the correlations with canopy radius were not significant. Both canopy radius and trunk circumference were correlated with pH in the open zone, but not under the canopy. Likewise, $\log_e$ EC was correlated with trunk circumference only in the open, but not with canopy

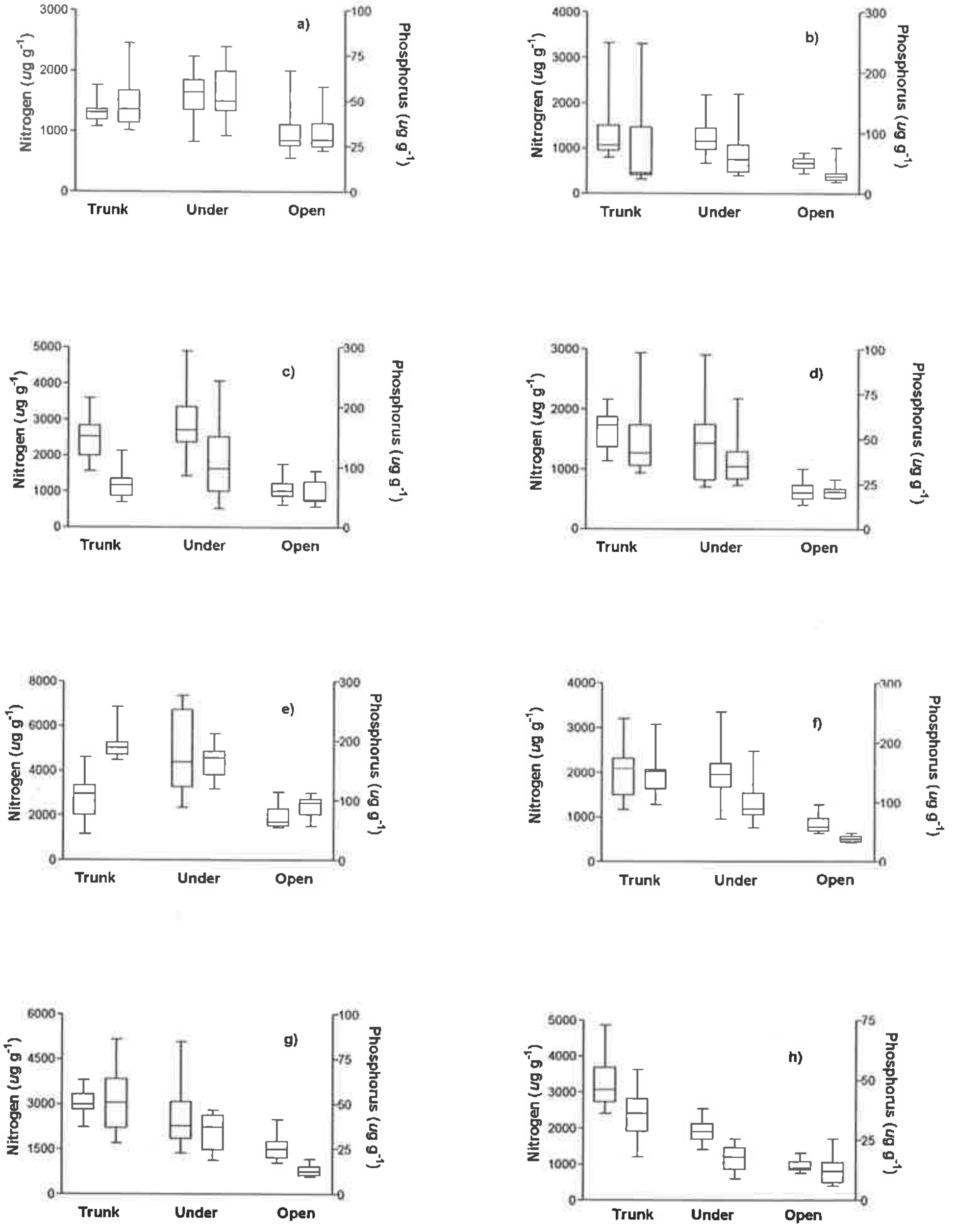


Figure 2.5: Total nitrogen (left) and available phosphorus (right) concentrations in soil under *Alectryon oleifolius*. Samples were collected to a depth of 4 cm. a) KG1, b) KG2, c) KVR1, d) KVR2, e) FB1, f) FB2, g) ML1, h) ML2.

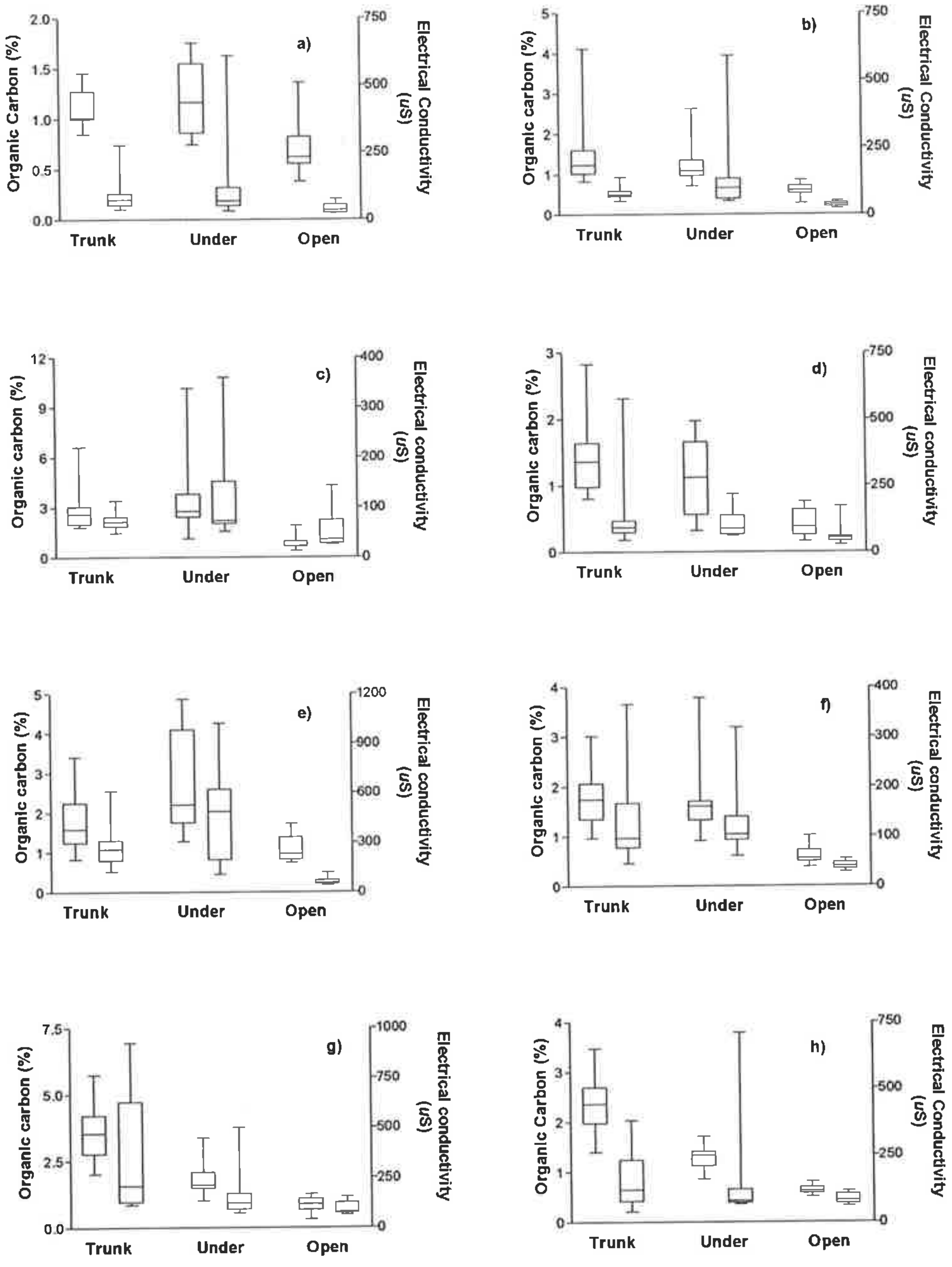


Figure 2.6: Organic carbon (left) and electrical conductivity (right) concentrations in soil under *Alectryon oleifolius*. Samples were collected to a depth of 4 cm. a) KG1, b) KG2, c) KVR1, d) KVR2, e) FB1, f) FB2, g) ML1, h) ML2.

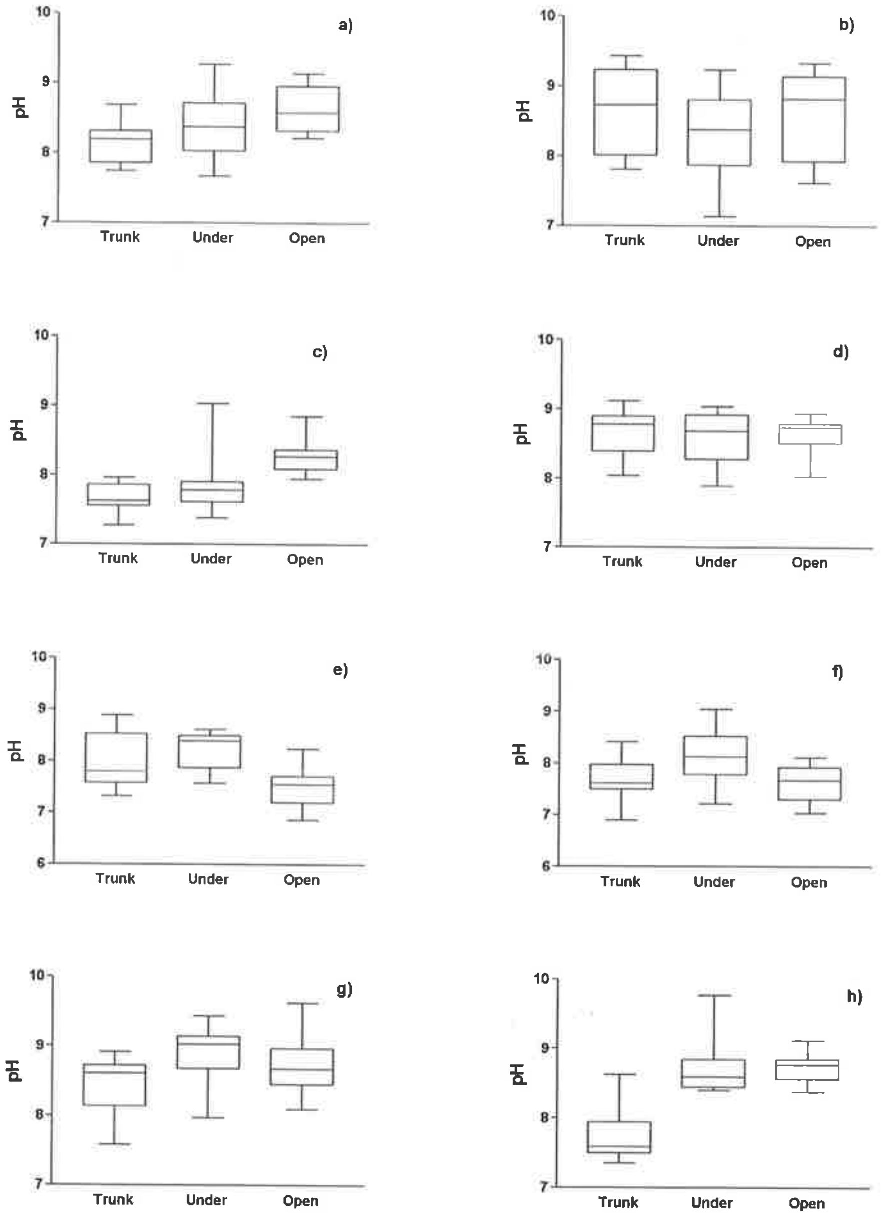


Figure 2.7: pH of soil under *Alectryon oleifolius*. Samples were collected to a depth of 4 cm. a) KG1, b) KG2, c) KVR1, d) KVR2, e) FB1, f) FB2, g) ML1, h) ML2.

radius. Trunk circumference was a better predictor of all soil variables except $\log_e$ P than was canopy radius.

Soil nutrient levels ($\log_e$ organic C, $\log_e$ N, $\log_e$ P) and pH (Figures 2.8, 2.9 and 2.10) differed between Middleback and Koonamore, between high and low grazing locations within these sites, between trees within locations, between zones within trees, and between sectors within trees, with the effects of zone and sector not being independent (Table 2.7). Each of the zones differed from the others (all $P=$ 0.0000). In the open zone there were no differences between the north and south sectors, or between the east and west sectors (P=0.6179 and 0.7288 respectively). However, in the under zone soil nutrients differed between the north and south sectors ($P=$ 0.0000), and between the east and west sectors ($P=$ 0.0059). Likewise north and south differed in the trunk zone ($P=$ 0.0000) but not between east and west (P=0.0675).

With one exception there was no evidence of any relationships between litter weights and soil nutrient levels from three trees sampled at Middleback Station (Figures 2.11, 2.12 and 2.13). However, there was a suggestion of a relationship between faeces weight and P (Figure 2.13), although it is difficult to infer much from only three points.

Group:	**All**	**Zone**			**Location**			
level:	All	Trunk	Under	Open	KG	KVR	FB	ML
ln N ln C								
r	0.9014	0.8252	0.8824	0.8693	0.8779	0.9694	0.9168	0.8959
P	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
ln P ln C								
r	0.5197	0.1262	0.5439	0.3864	0.6596	0.7861	0.6759	0.8489
P	0.0000	0.2205	0.0000	0.0018	0.0000	0.0000	0.0000	0.0000
ln P ln N								
r	0.5096	0.2443	0.4961	0.3261	0.6464	0.7949	0.6857	0.7984
P	0.0000	0.0164	0.0000	0.0091	0.0000	0.0000	0.0000	0.0000
ln EC ln C								
r	0.5967	0.3943	0.5431	0.3582	0.6618	0.5111	0.6785	0.5631
P	0.0000	0.0001	0.0000	0.0037	0.0000	0.0000	0.0000	0.0000
ln EC ln N								
r	0.6568	0.4937	0.6273	0.4599	0.6235	0.5252	0.7174	0.4916
P	0.0000	0.0000	0.0000	0.0001	0.0000	0.0000	0.0000	0.0000
ln EC ln P								
r	0.3914	0.3240	0.4167	-0.2634	0.4923	0.4246	0.7164	0.4980
P	0.0000	0.0013	0.0000	0.0370	0.0000	0.0005	0.0000	0.0000
pH ln C								
r	-0.3383	-0.3350	-0.4776	-0.2212	-0.3664	-0.6324	0.0239	-0.3528
P	0.0000	0.0008	0.0000	0.0790	0.0029	0.0000	0.8511	0.0042
pH ln N								
r	-0.3188	-0.4340	-0.3119	-0.2666	-0.4000	-0.6375	0.1194	-0.3837
P	0.0000	0.0000	0.0020	0.0332	0.0011	0.0000	0.3474	0.0017
pH ln P								
r	-0.4503	-0.3258	-0.4790	-0.5986	-0.3521	-0.6020	0.1682	-0.2912
P	0.0000	0.0012	0.0000	0.0000	0.0043	0.0000	0.1840	0.0196
pH ln EC								
r	-0.0144	-0.0996	-0.0405	0.3570	-0.0441	-0.0622	0.2860	-0.0801
P	0.8184	0.3342	0.6950	0.0038	0.7296	0.6252	0.0219	0.5294

Table 2.5: Correlations (Pearson r) between soil resources under and around *Alectryon oleifolius* canopies. Correlations are given for: All = pooled survey data, Zone = data pooled from each sampling zone, Location = data pooled from each location. KG = Mustering Paddock 3, Koonamore Station, KVR = T.G.B. Osborn Vegetation Reserve, Koonamore Station, FB = Depot Paddock, Middleback Station, ML = Overland Paddock, Middleback Station. Data were $\log_e$ transformed where necessary.

		pH	**Organic carbon**	**Total nitrogen**	**Available phosphorus**	**Electrical conductivity**
Radius	r^2					
Zone	**trunk**	0.0011	0.0755*	0.0116	0.2546***	0.0448
	under	0.0017	0.0417	0.0011	0.0501*	0.0356
	open	0.2172***	0.0049	0.0006	0.0278	0.0094
Girth	r^2					
Zone	**trunk**	0.0071	0.3105***	0.2419***	0.1457***	0.0376
	under	0.0417	0.0718*	0.0786**	0.1099**	0.0028
	open	0.1251**	0.0375	0.1500**	0.1431**	0.2112***

Table 2.6: Canopy radius and trunk circumference ('Girth') as predictors of soil resources. Linear regression of canopy dimensions was conducted on pH, $\log_e$ organic carbon, $\log_e$ total nitrogen, $\log_e$ available phosphorus and $\log_e$ electrical conductivity. Data were grouped by zone of sampling; trunk = 0-0.25 m from tree trunk, under = 0.25-3 m from tree trunk, open = 0-5 m from canopy edge. * - significant at $P < 0.05$, ** - significant at $P < 0.01$, *** - significant at $P < 0.001$.

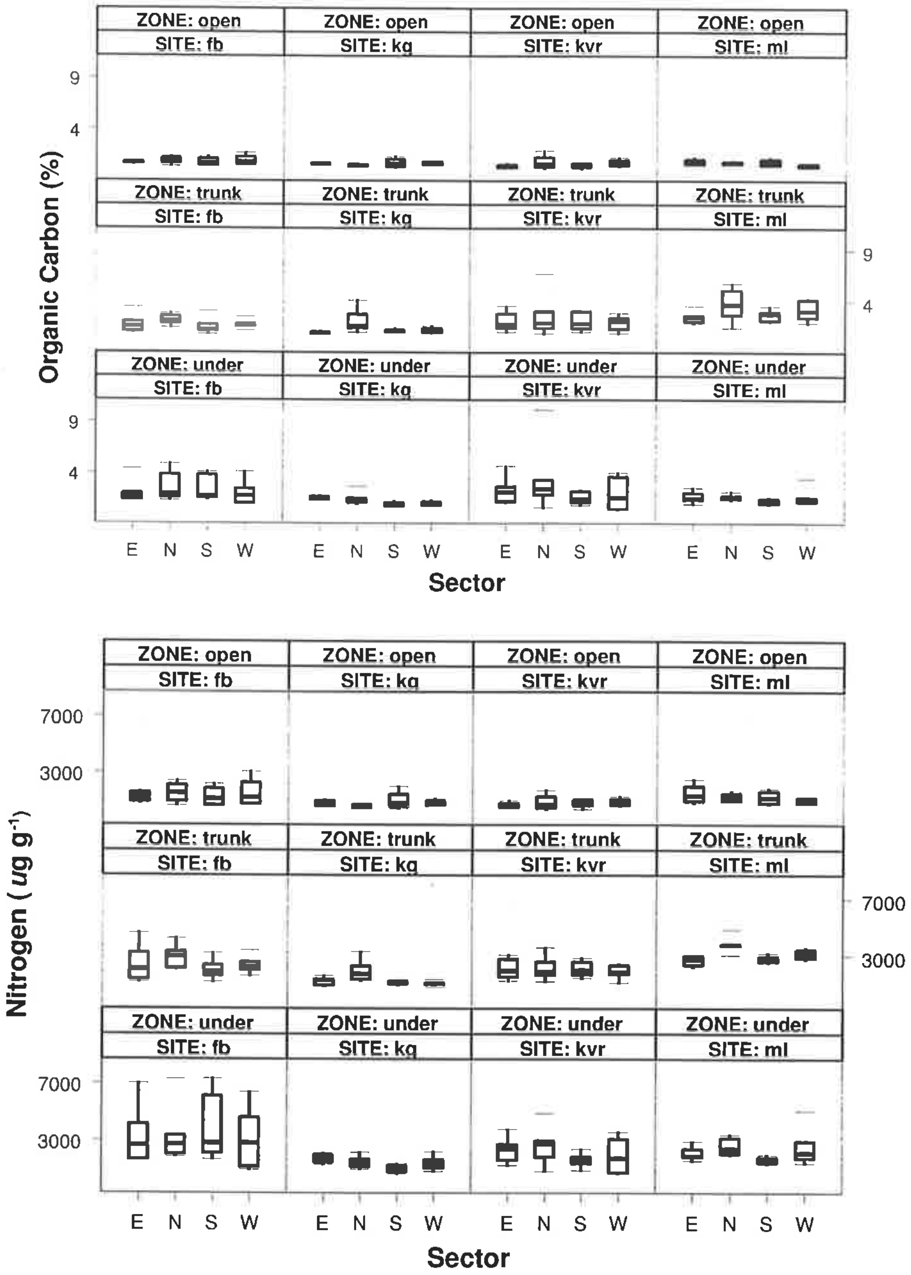


Figure 2.8: Organic carbon and total nitrogen contents of soil collected at different distances (zone) and angles (sector) from *Alectryon oleifolius* trunks. Soil samples were collected to a depth of 4 cm. E = 45-135°, S = 135-225°, W = 225-315°, N = 315-45°.

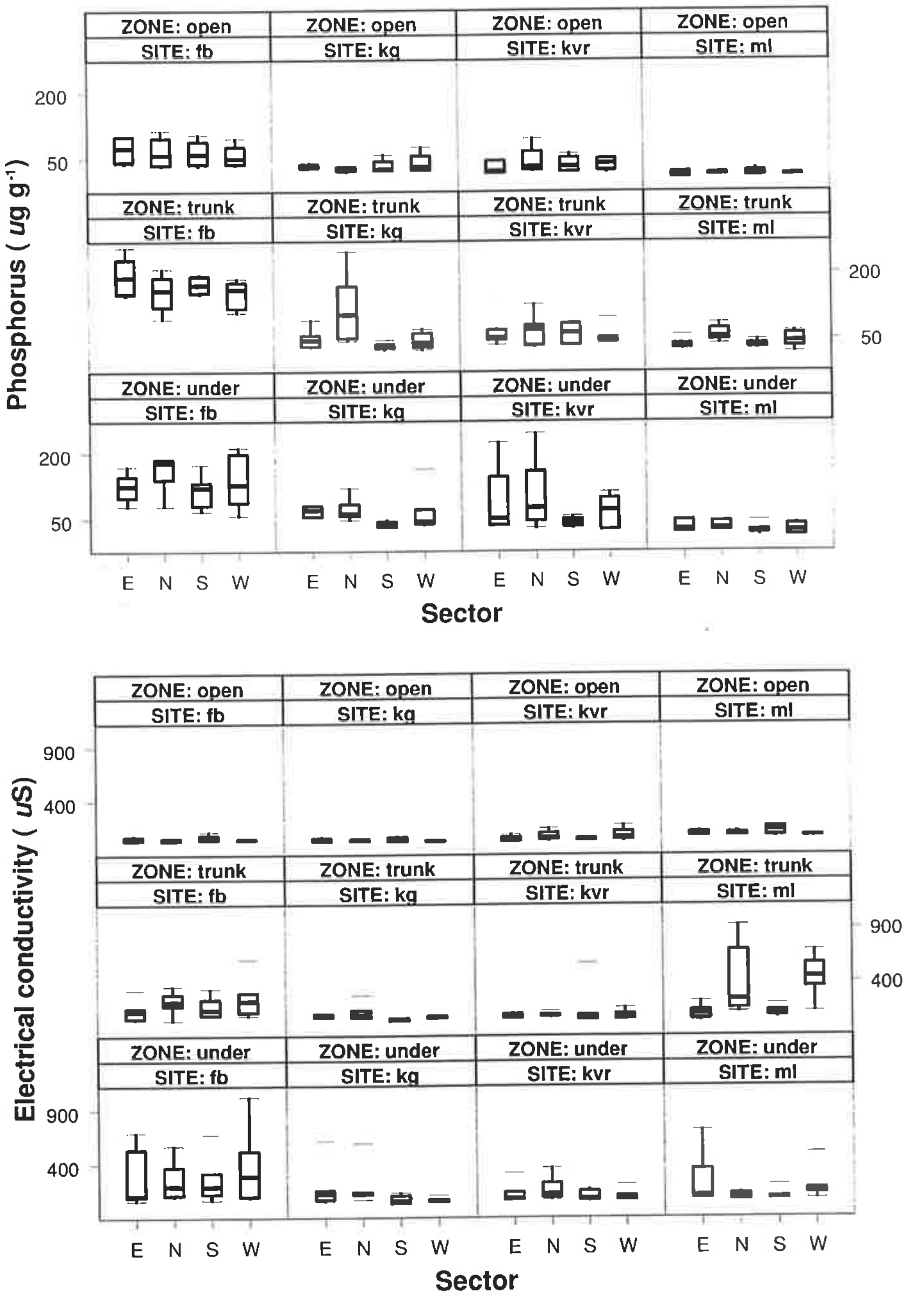


Figure 2.9: Available phosphorus content and electrical conductivity of soil collected at different distances (zone) and angles (sector) from *Alectryon oleifolius* trunks. Soil samples were collected to a depth of 4 cm. E = 45-135°, S = 135-225°, W = 225-315°, N = 315-45°.

	Value	F	DF Num	DF Den	Prob>F
Whole Model	3.1309	6.0298	380	636	0.0000
Intercept	0.9998	205175.72	4	156	0.0000
Site	0.6637	76.9739	4	156	0.0000
Location(Site)	1.0381	42.3609	8	314	0.0000
Tree(Location)	1.2944	19.0177	16	636	0.0000
Zone(Tree)	1.8056	8.1765	64	636	0.0000
Sector(Tree)	0.7799	1.6045	96	636	0.0005
Zone*Sector(Tree)	1.3114	1.6158	192	636	0.0000

Table 2.7: MANOVA on $\log_e$ organic carbon, $\log_e$ nitrogen, $\log_e$ phosphorus and pH from soil under *A. oleifolius* (Pillai's Trace, identity matrix). Each zone differed from the other two (contrasts, $P = 0.0000$, Pillai's Trace), while the north sectors differed from the south but east did not differ from west ($P=$ 0.0005 and 0.1438 respectively). Within the open zone neither north-south nor east-west comparisons differed ($P=$ 0.6179 and 0.7288), but both differed in the under zone ($P=$ 0.0000 and 0.0059). The north sectors differed from the south in the trunk zone but east did not differ from west ($P=$ 0.0000 and 0.0675).

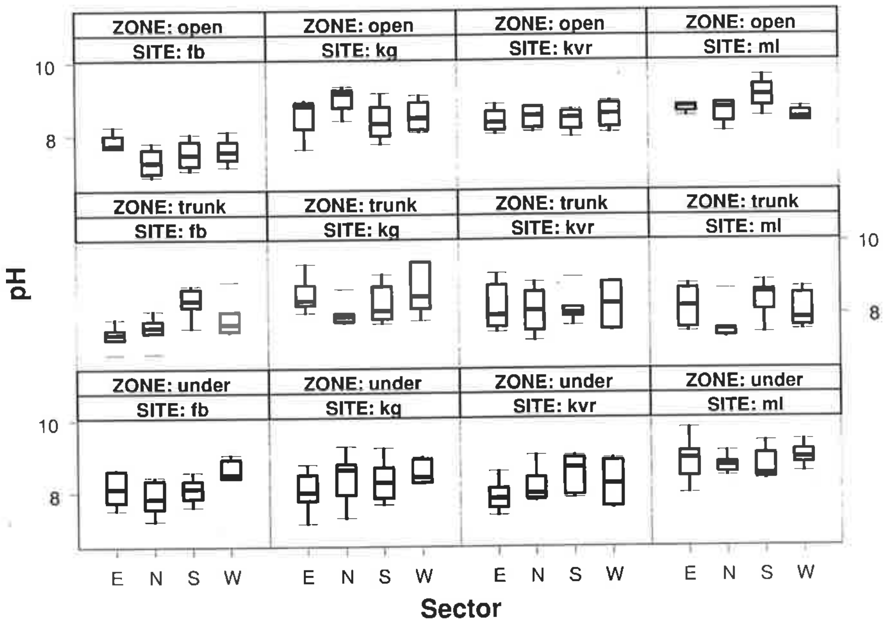


Figure 2.10: pH of soil collected at different distances (zone) and angles (sector) from *Alectryon oleifolius* trunks. Soil samples were collected to a depth of 4 cm. E = 45-135°, S = 135-225°, W = 225-315°, N = 315-45°.

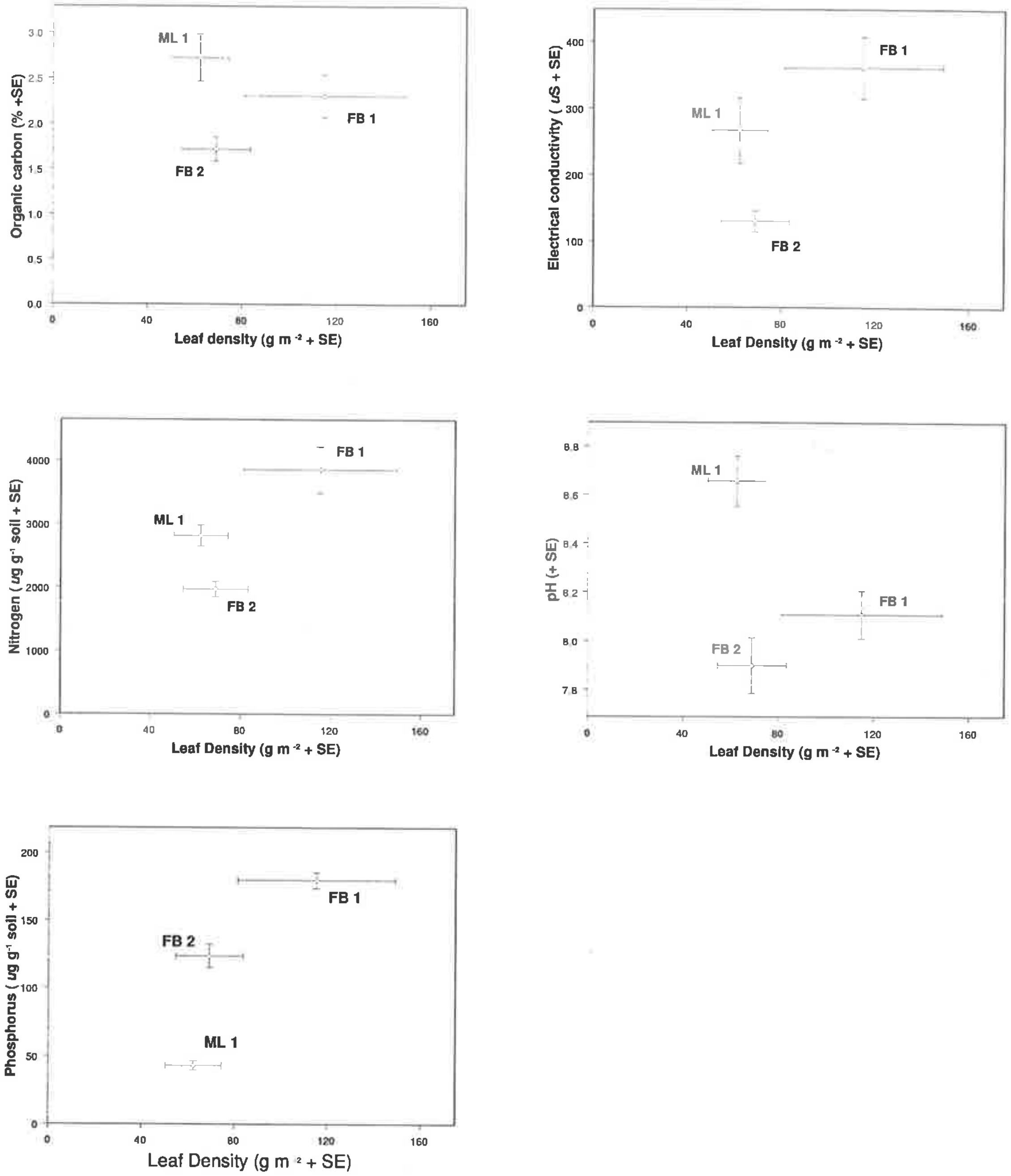


Figure 2.11: Leaf litter and soil resource levels under *Alectryon oleifolius* canopies at Middleback Station.

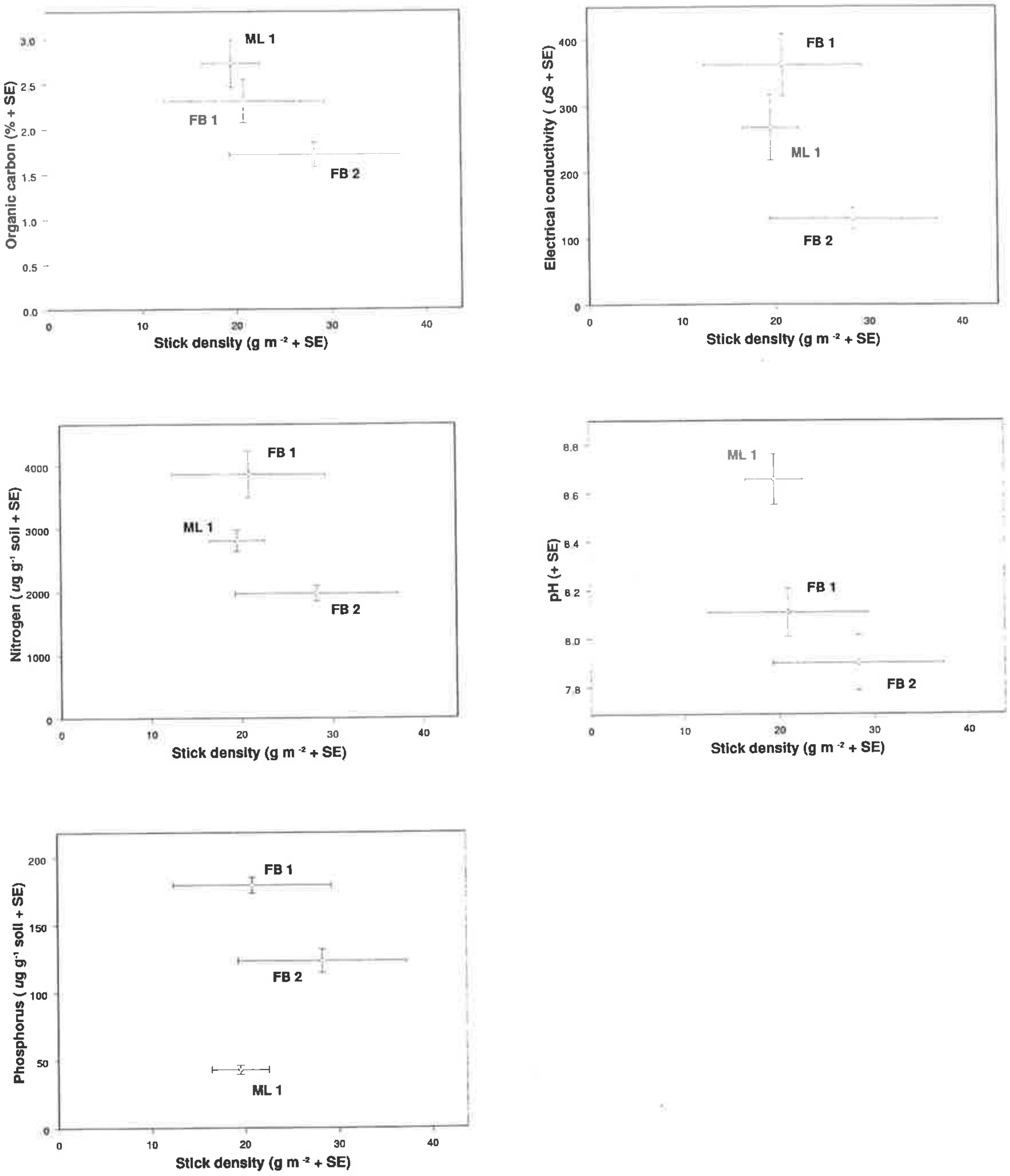


Figure 2.12: Stick litter and soil resource levels under *Alectryon oleifolius* canopies at Middleback Station.

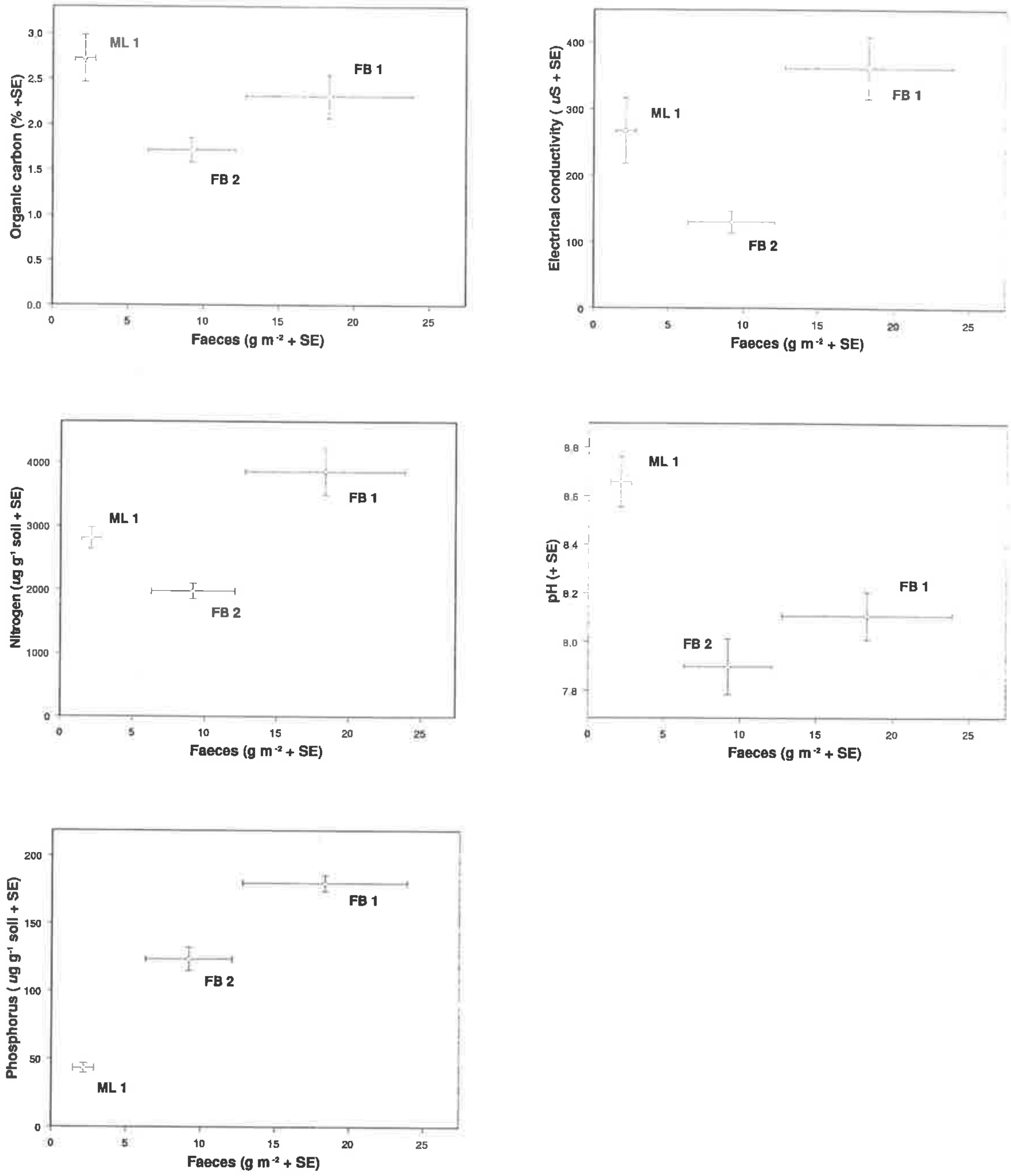


Figure 2.13: Soil resource levels and mammal faeces weights in leaf litter under *Alectryon oleifolius* canopies at Middleback Station.

2.4 Discussion

This survey provided unambiguous evidence of an association of elevated soil nutrient levels with the presence of *A. oleifolius* canopies. These results establish that, as with many other woody perennials, fertility islands are associated with large *A.oleifolius*. Furthermore, the results add to the body of evidence indicating the ubiquity of the fertile island phenomenon.

Despite the fact that the survey only covered the upper end of the size range of this species, there were indications that soil nutrient levels under tree canopies are related to tree size. This is consistent with observations in the same region of soil nutrient levels under *Acacia papyrocarpa* (Facelli and Brock, 2000), where nutrient levels increase with estimated age until the tree begins to senesce. Likewise, increases in below-canopy soil nutrient levels with tree age have been reported from a semi-arid Spanish shrubland (Pugnaire et al., 1996a), from a Nigerian savanna (Isichei and Muoghalu, 1992) in a study that confounded size and species, and from a South African savanna in a study that confounded tree size with tree density (Roos and Allsopp, 1997).

These data do not indicate whether the fertile island phenomenon is the product of preexisting heterogeneity in soil resources, or the result of biotic processes associated with trees. The correlations between canopy dimensions and soil resources may merely indicate that *A. oleifolius* can attain a greater size under higher nutrient conditions. Nevertheless, it is also consistent with time- or size-dependent processes associated with trees resulting in the accumulation of soil resources.

The survey provides further evidence supporting this latter view. The correlations between soil resources changed between sampling zones, suggesting that the processes of decomposition, mineralisation and leaching vary with distance from the tree trunk. Further evidence comes from the directional differences in soil resource levels within zones. Whereas there were no differences between north and south, or between east and west outside the canopy, such differences could be found under the canopy, suggesting that shading may affect nutrient dynamics. Moreover, although the levels of replication in the open zone were lower, the variances in soil resources were also lower, indicating that the scales at which nutrient cycling processes operate differ between canopy and open spaces.

Since the biogeochemical processes involved in nutrient cycling are affected by temperature and moisture levels (Aerts, 1997; Caldwell et al., 1998), the changes in correlations and the differences between tree sides indicate that canopies may exert substantial influence on soils through their effects on soil temperature and moisture. The differences may also reflect accumulated historical effects. As a tree grows, its zone of influence expands outwards; points closer to the trunk are subjected to canopy microenvironments and litter deposition for a longer time than more distant points. As the dynamics of accumulation and loss differs between nutrients (Facelli and Brock, 2000), their correlations may be expected to change with the period of accumulation. Tannins or other leachates contained within stemflow water might also affect decomposition processes, giving rise to the patterns I observed.

Alternatively, the directional differences in soil nutrient levels may reflect differences in litter deposition. Strong prevailing winds could remove most litter from the upwind sides of trees, with litter accumulating on the downwind sides. However the data from the litter survey do not support this hypothesis. While litter weight declined with distance from the trunk, there were no differences in density between sampling sectors.

Litter density appears to be a complex function of canopy size. Relationships between canopy dimensions and litter weights were far weaker than those between canopy dimensions and soil nutrient levels. Of the directly plant-derived items only leaf weight was significantly correlated with any canopy measures. However, the changes in the correlations between litter components across locations, and therefore between tree height, suggest differential changes in the production, decomposition and loss of litter items with tree size. Clearly, this area warrants closer investigation for it has implications for nutrient cycling and litter-mediated habitat modification (Facelli and Pickett, 1991a,b).

Faeces weight was correlated with all canopy measures, particularly those that would be most strongly linked with the size and intensity of the shadow cast by the tree. This is consistent with mammals spending more time under the largest and shadiest trees. The litter and nutrient data suggest that this may affect the available P levels in below canopy soils. The pattern is also consistent with canopy size affecting decomposition rates. Regrettably time and financial constraints prevented me from pursuing this any further.

2.4.1 Summary

Although this survey was primarily intended as a pilot study it provided some valuable information. It clearly established the association of fertile islands with *A. oleifolius* canopies, and indicated that both litter weights and soil nutrient levels were related to canopy size. It also showed differential changes in nutrient levels with distance and direction from the trunk, which suggests that canopy-related influences affect nutrient cycling processes. Finally, it provided some evidence that grazing by domestic stock may affect the processes of nutrient accumulation.

Chapter 3

Canopy Morphology, Fertile Islands and Plant Community Composition.

3.1 Introduction

The association between woody perennials and fertile islands has led to proposals that plants are in some way responsible for the accumulation of soil resources. These proposals invoke either physical or biotic mechanisms of accumulation. The physical mechanisms involve capture of airborne nutrients (Whitford et al., 1997) or water-transported debris (Ludwig and Tongway, 1995) by above-ground plant structures, while the biotic mechanisms involve *in situ* litter production and decomposition (Zinke, 1962; Facelli and Brock, 2000), or other aspects of nutrient cycling and transport (Garner and Steinberger, 1989).

Several published studies indicate the potential for canopy structure to either modify environments in such ways as to induce concentrations of nutrients in the soils under canopies, or for canopy size to act as a surrogate measure of the duration of cumulative processes of nutrient concentration (De Soyza et al., 1997; Dean et al., 1999; Facelli and Brock, 2000). Canopy shape was surmised to influence the extent of nutrient concentration under *Larrea tridentata* shrubs in the Chihuahuan Desert (De Soyza et al., 1997). Cone-shaped *Larrea* canopies accumulated less plant litter than hemispherical canopies, apparently due to differences in ground-level wind flow under the shrubs. Fertile islands were associated with the shrubs that accumulated higher litter loads, whereas the nutrient levels of soils under shrubs that retained little litter did not differ from those of soils from inter-canopy spaces.

The degree of nutrient accumulation in fertile islands also appears to be correlated with the length of time that the site has been occupied by a shrub or tree. Facelli and Brock (2000) examined the nutrient dynamics of soils under the canopies of the long-lived tree *A. papyrocarpa*. Estimating tree age class using a set of canopy characteristics based primarily on canopy size and shape (Lange and Purdie, 1976), Facelli and Brock (2000) reported that nutrient concentrations in the soils under the canopies increased until the trees reached maturity. When the trees senesced, and as their canopies began to disintegrate, nutrient concentrations began to decline. This process of nutrient loss accelerated following the death of the tree.

There are a number of processes that may be responsible for the gradual accumulation of nutrients during the lifetime of a woody plant. The retention and accumulation of plant litter, and subsequent nutrient cycling *via* decomposition, has been identified as one process (De Soyza et al., 1997). The fixation of nitrogen by bacterial symbionts in legumes is another: it is interesting to note that many of the reported observation of fertile islands involve Leguminosae. Soil nutrients might also accumulate when habitat amelioration increases understorey productivity, thereby increasing plant litter production. Subsequent litter decomposition would result in greater localisation of soil nutrients. Alternatively, habitat amelioration may change the physical structure of the understorey community. If the perennial shrub cover increases, not only may overall productivity increase but the associated changes to airflow may increase the proportion of litter that is retained under the canopy. This could be of particular importance to nutrient cycling and fertile island formation in windy regions.

Herbivory is likely to interact with some of these putative processes. Although herbivores and other animals transport nutrients to large isolated trees in some systems (Dean et al., 1999), animal activity below canopies may have other effects that can affect site productivity and nutrient cycling. Reduction in understorey biomass through grazing can reduce site productivity, and may also impair the ability of understorey shrubs to retain litter. Frequent disturbance by animals may reduce seedling establishment, although such disturbance may also be important in creating microsites conducive to germination and establishment (Gutterman and Herr, 1981; Dean and Milton, 1991). The costs and benefits of such disturbance may depend on the thickness of the litter layer (Facelli and Pickett, 1991b) and the seed sizes of the plant species that are affected. Thus the introduction of new herbivores into ecosystems has the potential to profoundly alter soil nutrient dynamics.

Plant community composition under tree canopies frequently differs from that found in the inter-canopy spaces (Parker and Muller, 1982; Maranon and Bartolome, 1993; Belsky and Canham, 1994; Facelli and Brock, 2000). This may be due to pre-existing or biologically-generated soil heterogeneity favouring the recruitment of a different suite of plant species, or it may be due to facilitation of those species by the host plant through changes to the local micro-environment. Alternatively, it may be due to differential propagule dispersal between habitat types (Tester et al., 1987). If plants are indeed either directly or indirectly the causative agents in these processes of soil and vegetation change, we might expect that variation in plant characters (such as size, canopy shape, species and age) may be associated with variation in the degree of soil nutrient enrichment in the fertile islands.

Zones of reduced plant cover around trees and shrubs have been described in several studies (Johnson, 1978; Andrew, 1978; Brock, 1993). This phenomenon may be attributable to depletion of soil resources by the trees' surface root systems, which may extend many metres beyond canopy edges (Belsky et al., 1989; Vetaas, 1992). Allelopathy (Muller, 1969; Johnson, 1978) and vertebrate activity (Bartholomew, 1970; Halligan, 1974) have also been implicated. At Middleback Station, near Whyalla in South Australia, *Acacia papyrocarpa* trees are accompanied by distinct halo zones with reduced abundances of the common grasses *Stipa nitida* and *Danthonia caespitosa* (Andrew, 1978; Brock, 1993). However, cover of the common chenopod shrubs *Atriplex vesicaria* and *Maireana sedifolia* does not differ.

The possible effects of trees and shrubs on soil resources can be conceptualised in terms of the changes in soil resource levels with distance from the tree trunk (Figure 3.1). If trees have no effect on soil resources, levels near the trunk will not differ from levels at more distant locations (Figure 3.1a). If nutrients accumulate under trees, resource levels will decrease with distance (Figure 3.1b). Conversely, resource levels will increase with distance from the trunk if trees deplete soil nutrients (Figure 3.1c). Processes of soil resource depletion by tree roots may operate over larger distances than canopy-related processes of accumulation where tree roots extend appreciably beyond the canopy edge. This would result in a more complex pattern of soil resources, where levels near the trunk are greater than in areas distant from trees, while levels in the region immediately beyond the canopy edge are lower than in more distant locations (Figure 3.1d).

I conducted a survey of the plants, plant litter and soils associated with the canopies of the small clonal tree *Alectryon oleifolius*. I characterised canopy sizes and shapes to see how they were correlated with changes in soil nutrient levels, litter densities and understorey plant community composition. I also sampled sites with differing vertebrate herbivore communities to investigate the potential for herbivores to alter nutrient cycling and nutrient redistribution processes.

This survey had several objectives. The first was to describe the differences in plant litter densities, plant species composition and soil organic carbon concentrations associated with the presence of *A. oleifolius* canopies. My intent was to gain some

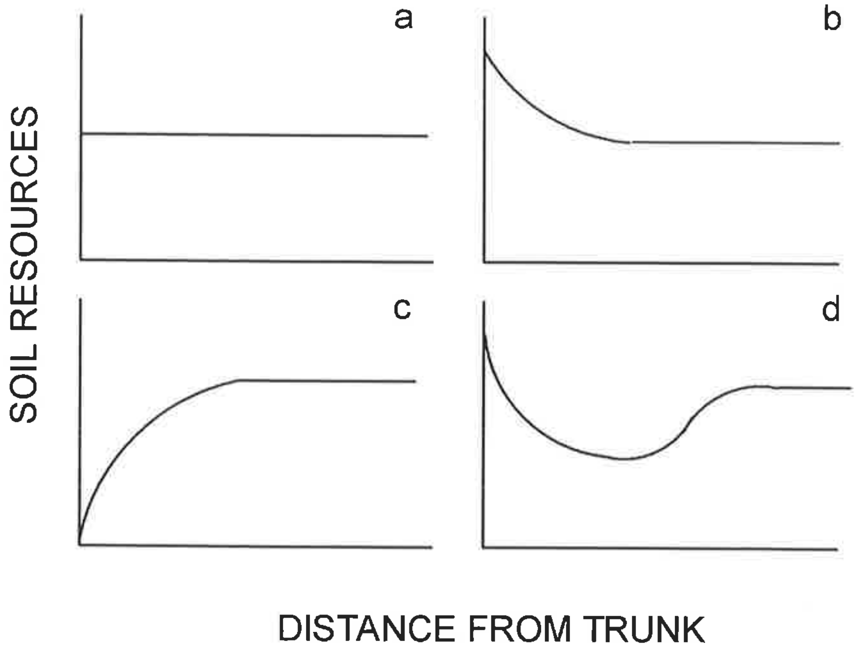


Figure 3.1: Changes in soil resource levels with distance from tree trunks assuming a) no effect of trees on soil resources, b) net increase, c) net decrease, and d) net increase below canopy and net decrease in extra-canopy root zone ('halo' effect).

insight into the consequences of the environmental heterogeneity associated with trees for co-occurring species, and to quantify the extent and intensity of elevated soil resource levels. The second objective was to identify which, if any, aspects of canopy morphology could be used to predict the patterns of difference that I observed, in order to evaluate which canopy processes might be responsible for creating those patterns. For example, I investigated the relationships between litter density and canopy shape, and between canopy size and plant species composition, to assess the role of canopy aerodynamics and canopy shading in determining patterns of litter distribution and plant species diversity. Finally, I examined the data to see if they were consistent with any of several hypothetical sequences of events that might generate fertile islands. In particular, I tested the hypothesis that soil resources accumulate in the presence of trees by examining the relationship between soil organic carbon concentrations and canopy size.

The use of *Alectryon oleifolius* had several advantages. It has a relatively variable habit, making it a good subject for examining the effects of canopy morphology. Furthermore, because of its clonal habit, within-patch comparisons are less likely to be obscured by genetic variation between individuals. The clonal habit also generates a variety of canopy aggregations, which permitted testing the effects of continuity between canopies.

3.2 Survey methods

3.2.1 Site

I established four sites in and near the T.G.B. Osborn Vegetation Reserve on Koonamore Station, South Australia (Figure 3.2). The sites were chosen so that they encompassed a range of vertebrate grazing intensities. Domestic stock have been excluded from the reserve since 1925, and active rabbit control since 1975 has reduced rabbit numbers to very low levels (R. Sinclair *pers. comm.*). Consequently sites within the Reserve have been subjected to grazing by kangaroos alone since 1975. The sites in South Lake and Koonamore Cross paddocks are also grazed by sheep and rabbits. In the South Australian arid zone sheep tend to occupy the upwind parts of paddocks, and the observed grazing intensities within paddocks increase towards the fenceline in the direction of the prevailing wind (Noble, 1975; Stafford Smith, 1984). The prevailing winds at Koonamore are southerly (Noble, 1975), so the South Lake site, being near the southern fenceline of the paddock, is more intensely grazed by sheep than the Koonamore Cross site, which is close to that paddock's northern fenceline.

Three of the sites (Reserve A, South Lake and Koonamore Cross) were located on calcareous red-brown earths on flat areas, while the fourth site (Reserve B) was on a low sand ridge.

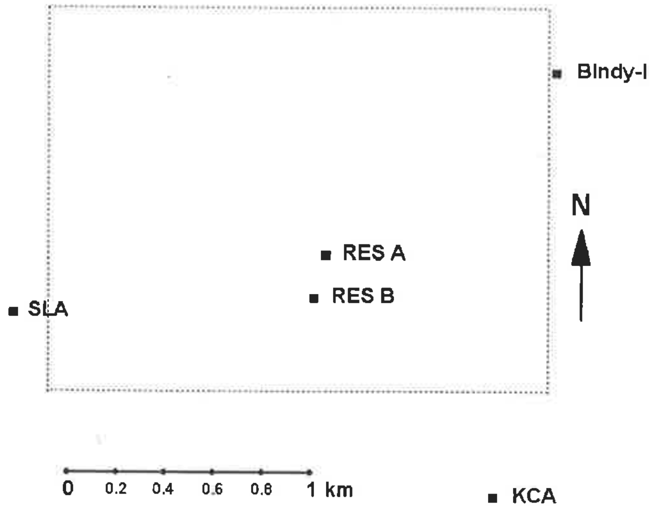


Figure 3.2: Locations of survey sites relative to Bindy-i (32° 06'S 139° 21'E). The broken line indicates the fenceline around the T.G.B. Osborn Vegetation Reserve. RES A = Reserve A, RES B = Reserve B, KCA = Koonamore Cross, SLA = South Lake.

3.2.2 Survey Protocols

At each site I marked out a 50 m by 50 m area containing *A. oleifolius*, and selected 5 or 6 trees for sampling. I attempted to sample across the range of tree sizes at each site while minimizing any overlap in the sampling area around each tree.

Canopy morphology

I wished to characterise canopy parameters that were likely to affect the undercanopy microenvironment. Light intensity, soil temperatures and evaporation rates are most affected by the position of the canopy's shadow during the middle of the day (Breshears et al., 1997, 1998). In the southern hemisphere this is primarily determined, relative to the position of the trunk, by the size and shape of the canopy as seen from the north. Consequently, I measured the maximum canopy radius to the north, and the height above ground at which the maximum occurred (Figure 3.3). I also measured the northward radius of the base of the canopy, and the height of the canopy base. Maximum canopy height was measured with a 5 m surveyor's staff, and

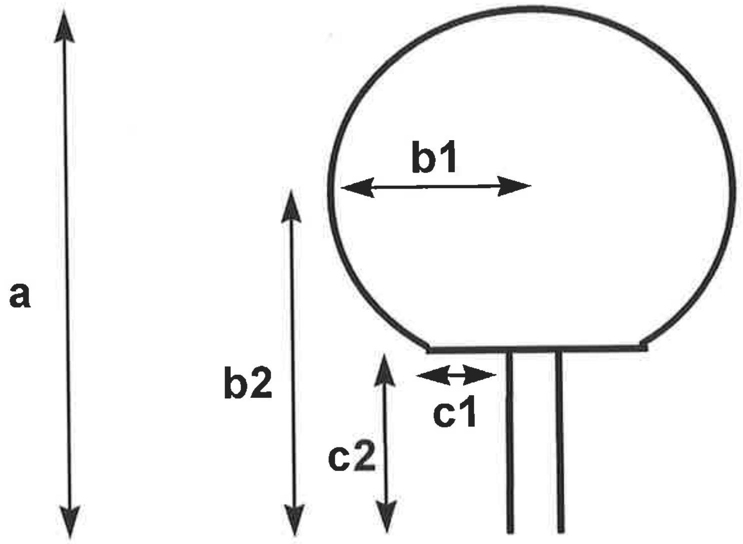


Figure 3.3: Measures of canopy dimensions used in the *Alectryon oleifolius* survey: a= canopy height, b1= maximum canopy radius, b= height of maximum radius, c1= radius of canopy base, c2= height of canopy base.

the shape of the canopy as seen from the north was visually classed as one of seven possible categories (Figure 3.4). Where tree height exceeded the maximum height of the staff, the height was recorded as > 5 m.

During the pilot survey I had observed the trunks of dead trees under some *A. oleifolius* canopies. I also found one long-dead *A. oleifolius* that had new shoots emerging from below ground. These observations suggest the possibility that *A. oleifolius* may cyclically occupy the same position over very long time spans by re-sprouting from rootstock. If this is occurring, it may affect the degree of soil nutrient enrichment and the composition of the understorey community. Consequently I recorded the number of dead trunks under each canopy.

Soil and plant characters may also be affected by other trees in the vicinity of the target tree, as well as by animal activity under the tree. Soil disturbance by kangaroos was recorded. I also measured the number of trees over 1.5 m high (as 'conspecifics'

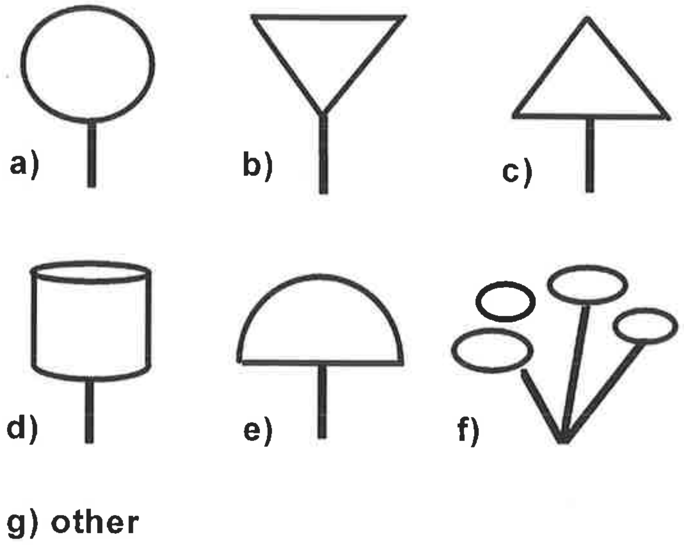


Figure 3.4: Measures of canopy morphology used in *Alectryon oleifolius* survey at Koonamore Station. Canopy shape classes: a= spherical, b= inverted cone, c= cone, d= cylindrical, e= hemispherical, f= fragmented and g= other.

or 'other species') within a 15 m radius of the target tree, and recorded the bearing and distance of the nearest tree from the target tree's trunk. I also recorded which quadrants were occupied by neighbours within 15 m. Where the target tree's canopy was continuous with its neighbour's canopies, I measured the extent of the cluster's canopy to the north, east and west. The southerly extent was not measured as it would be expected to have less effect on light levels and soil temperatures within the sampling area.

Soil, vegetation and leaf litter sampling

Six transects were established at random angles from the trunk of each tree. A stratified random sampling scheme was taken along each transect, the zones being 0 - 1.2 m, 1.2 m - 2.5 m, 2.5 m - 7.5 m and 7.5 m - 15 m from the tree trunk. One 7 × 7 cm soil sample was collected to a depth of 10 cm at a random distance within each zone on each transect. This provided 24 soil samples per tree. I elected to collect a larger volume of soil than in the pilot study to reduce the variance while still approximating the rhizosphere of a seedling. I also collected soil to a greater distance from the trunk than previously in an attempt to resolve whether *A. oleifolius* depletes surface soil nutrients in the zone around the canopy edge.

Vegetation was sampled similarly, using a different set of random distances along the same transects. The presence or absence of 18 plant species was scored for each of 36 squares within a 40 × 40 cm quadrat. Twentyfour samples were scored for each tree. I chose some species that are primarily found either under or outside canopy areas of *A. papyrocarpa* (Facelli and Brock, 2000), and others that are ubiquitous. All were likely to be observable throughout the year. The species were *Atriplex stipitata, A. vesicaria, Carrichtera annua, Chenopodium gaudichaudiana, Enchylaena tomentosa, Eriochiton sclerolaenoides, Exocarpus aphyllus, Exocarpus sparteus, Maireana appressa, M. erioclada, M. pyramidata, M. sedifolia, Rhagodia parabolica, R. spinescens, R. ulicina, Sisymbrium sp. and Tetragonia tetragonoides.* Grasses were grouped due to the difficulty in identifying non-flowering plants. To reduce the possibility of overlap between adjacent transects, one corner of the quadrat was placed at the random distance, while the diagonally opposite corner was placed along the transect on the side farthest from the trunk.

I initially sampled leaf litter within all zones, but found litter was sparse beyond the canopy edge and was usually derived from nearby shrubs rather than the target tree (Figure 3.5). Visual inspection of other trees confirmed that this pattern of leaf litter distribution was widespread. Consequently I limited sampling to the two innermost zones along each transect, giving a total of 12 samples per tree. I collected all unattached material within a 20 × 20 cm quadrat.

Plant litter and vertebrate faeces were sorted into six categories: leaf, stick, detritus, and kangaroo, sheep and rabbit faeces. Samples were first sieved through a 1.67 × 1.43 mm mesh. All material passing through the mesh was discarded, as were stones and larger soil particles. Any lignified material, such as bark, twigs and *A. oleifolius* fruits, with some portion having a diameter greater than 2.5 mm

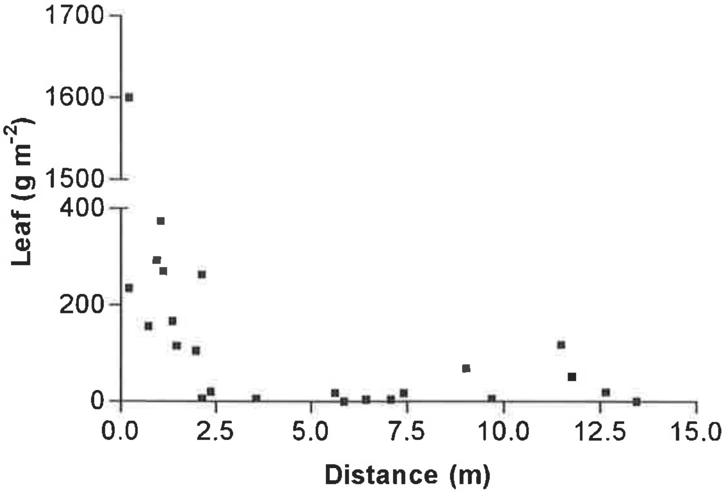


Figure 3.5: Density of the leaf component of plant litter under an *A. oleifolius* canopy at the Reserve A site at different distances from the tree trunk. Note interrupted y-axis.

was classed as 'stick'. Samples were then sieved through a colander with 4 mm diameter holes. Material retained in the colander was classed as 'leaf' (this being the predominant constituent of this size class in most samples), while material passing through the colander but retained by the sieve was classed as 'detritus'. Animal faeces were identified using Morrison (1981) and Triggs (1996).

In order to avoid disturbing materials before they were sampled, vegetation was sampled first, then litter and finally soil.

3.2.3 Data treatment and analyses

These data were subjected to a series of analyses designed to identify patterns in the distribution of plant species and soil nutrients in relation to *A. oleifolius* trees, and to identify canopy characteristics that may influence the patterns of distribution. I also examined the distributions of plant litter and animal faeces in relation to *A. oleifolius* canopies. I then used the information from these analyses to select characters for regression analyses.

The data were examined and checked prior to analyses. The organic carbon data were examined for outliers. Soil analyses were repeated on any samples that were more than 1.5 times the interquartile distance away from the first and third quartiles. I then substituted each anomalous measurement with the mean of its original and repeated measurements. Plant species that occurred fewer than 5 times out of the 484 vegetation samples were excluded from the analyses, reducing the number of species from 18 to 9. Surprisingly *Maireana sedifolia*, which is found both in the open and under tree canopies at Middleback Station (Facelli and Brock, 2000), was not encountered in any samples. The species tested were *Atriplex stipitata, A. vesicaria, Enchylaena tomentosa, Eriochiton sclerolaenoides*, grasses, *Maireana appressa, M. pyramidata, Rhagodia spinescens, and Sisymbrium sp.*. Nearly a quarter of the samples did not include any of these species. To avoid having to exclude so many samples from the analyses, I generated a new categorical vegetation measure that denoted the absence of all of the nine species. This measure is referred to as the "bare" species category. Note that many of these "bare" samples had evidence of occupation by annual and ephemeral species that were not scored in the survey.

Tree heights that were recorded as > 5 m were treated as having a height of 5.2 m for the purposes of analyses. This figure was chosen as being the smallest increment beyond 5 m that I would not have extrapolated in the field.

One sampling point was completely devoid of litter items. I elected to exclude it from the analyses, rather than create a new category for just one sample.

Cluster analyses and ordinations

I conducted cluster analyses using Ward's Group Linkage Method with the Relative Euclidean distance measure (McCune and Mefford, 1999). As the data did not fulfil the assumptions of multivariate normality, I chose to use Non-metric Multidimensional Scaling (NMS) with the Relative Sorensen distance measure for ordinations, as this method is particularly robust. Iterative trials were conducted prior to final analyses

	Factors	Species Frequency	Litter Density
Quantitative	Species sample distance	●	
	Species sample angle	●	
	Litter sample distance		●
	Litter sample angle		●
	Soil organic carbon content	●	●
	Canopy height	●	●
	Maximum canopy radius	●	●
	Height of max. canopy radius	●	●
	Basal canopy radius	●	●
	Height of basal canopy radius	●	●
	# dead trunks under canopy	●	●
	# conspecifics within 15 m	●	●
	# other tree spp within 15 m	●	●
	Distance to nearest tree	●	●
	Angle of nearest tree	●	●
	Extent of canopy cluster N	●	●
	Extent of canopy cluster E	●	●
	Extent of canopy cluster W	●	●
Categorical	Site	●	●
	Canopy shape	●	●
	Kangaroo dig under canopy	●	●
	Canopy part of a cluster	●	●
	Trees in quadrant 1	●	●
	Trees in quadrant 2	●	●
	Trees in quadrant 3	●	●
	Trees in quadrant 4	●	●

Table 3.1: Factors in the environmental matrices used for ordinations on species frequency and litter density.

to determine the appropriate number of ordination axes. I used Kendall's τ as the measure of correlation between physical parameters and ordination axes because it is more robust to outliers than least-squares measures.

Firstly, I wished to establish whether or not the distribution of canopy sizes differed between sites. This was important because it would facilitate the interpretation of site-related differences between data. I tested the null hypothesis that canopy sizes did not differ between sites with Multi-Response Permutation Procedures (MRPP) (McCune and Mefford, 1999) using the Relative Sorensen distance measure.

Cluster analyses were followed by ordinations with environmental characteristics, using three axes for the species-environment ordination and two axes for the litter-environment ordination (see Table 3.1 for factors in the environmental matrices). I then conducted Indicator Species analyses (Dufrene and Legendre, 1997; McCune and Mefford, 1999), grouping the response variables by those environmental variables that were most strongly correlated with the ordination axes. I arbitrarily set a lower limit of $|\tau| = 0.15$ in choosing grouping variables. The implementation of this procedure in McCune and Mefford (1999) creates groupings from continuous variables by rounding down to the nearest integer.

Indicator Species analysis uses the relative mean species abundances within each group and the relative within-group frequency of species occurrence to derive an indicator value.[1] Monte Carlo simulations are then used to test whether species presence can be used to predict a group. I also conducted Indicator Species analyses using categorical environmental variables, such as site and canopy shape.

---

[1] Here relative mean abundance refers to the mean number of individuals of a given species per sample as a proportion of the mean total number of individuals of all species per sample, while relative frequency refers to the mean number of samples per group that contain a given species as a proportion of the number of samples per group.

Linear regressions

The organic carbon data, consisting of a single dependent variable and a large number of independent variables, were subjected to multiple regression analysis. To reduce the likelihood of collinearity among independent variables, I selected a smaller number of canopy variables on the basis of the degree of correlation between them, using Spearman's ρ as the measure of correlation. I started by choosing the variable that had the greatest range of correlations (*i.e.* highly correlated with one variable and poorly correlated with others), and then iteratively selecting variables that were not significantly correlated with the initial variable or with each other. This reduced the initial set of canopy variables to three approximately orthogonal measures: radius of the canopy base, height of the canopy base, and number of trunks at 50 cm. These variables were incorporated into a linear regression model that also included the categorical canopy measures. The objective of this analysis was to assess linear relationships between $\log_e$ organic carbon and measures of canopy dimensions. Non-significant terms were iteratively removed from the model, using the Robust Linear Regression routine in the RobLib library in S-Plus 2000, which provides MM estimates (MathSoft 2000).

I also used the Robust Linear Regression routine to conduct ANOVA-style analysis on a larger data set that including data on site and neighbourhood (*i.e.* the number and location of neighbouring trees). The initial model included all canopy measures, as well as relevant interaction terms (*e.g.* sample distance$*$tree height). This permitted an assessment of how much more of the variability in the data could be explained using information about the surroundings of the sampled trees. Non-significant terms were again iteratively removed from the model.

Linear regressions

The organic carbon data, consisting of a single dependent variable and a large number of independent variables, were subjected to multiple regression analysis. To reduce the likelihood of collinearity among independent variables, I selected a smaller number of canopy variables on the basis of the degree of correlation between them, using Spearman's ρ as the measure of correlation. I started by choosing the variable that had the greatest range of correlations (*i.e.* highly correlated with one variable and poorly correlated with others), and then iteratively selecting variables that were not significantly correlated with the initial variable or with each other. This reduced the initial set of canopy variables to three approximately orthogonal measures: radius of the canopy base, height of the canopy base, and number of trunks at 50 cm. These variables were incorporated into a linear regression model that also included the categorical canopy measures. The objective of this analysis was to assess linear relationships between $\log_e$ organic carbon and measures of canopy dimensions. Non-significant terms were iteratively removed from the model, using the Robust Linear Regression routine in the RobLib library in S-Plus 2000, which provides MM estimates (MathSoft 2000).

I also used the Robust Linear Regression routine to conduct ANOVA-style analysis on a larger data set that including data on site and neighbourhood (*i.e.* the number and location of neighbouring trees). The initial model included all canopy measures, as well as relevant interaction terms (*e.g.* sample distance$*$tree height). This permitted an assessment of how much more of the variability in the data could be explained using information about the surroundings of the sampled trees. Non-significant terms were again iteratively removed from the model.

	Height	Max. radius	Radius height	Radius of base	Height of base
Max. radius	0.6532*				
Radius height	0.6343*	0.1833			
Radius of base	0.4651	0.9279*	-0.0150		
Height of base	0.5717*	0.1350	0.6562*	-0.0271	
# trunks	-0.3949	-0.2972	-0.2321	-0.1868	-0.0620

Table 3.2: Rank correlations between canopy measures (Spearman's ρ (SAS Institute, 1997)). Canopy radii were measured to the northward side of the canopy. * denotes correlations that are significant at $P = 0.05$.

3.3 Survey results

3.3.1 Canopy dimensions

Canopy height was significantly correlated with maximum canopy radius, height of maximum radius and height of canopy base (Table 3.2). Maximum canopy radius was correlated with radius of canopy base, and height of maximum radius was correlated with height of canopy base. The number of trunks was not significantly correlated with any of the other canopy dimensions.

Neither the number of dead trunks below canopies nor any of the canopy dimensions differed between sites (Table 3.3, Figure 3.6). However, small differences between sites may not have been detected as sample sizes were small. The non-parametric multivariate distribution of canopy characteristics (canopy dimensions plus neighbourhood data) did not vary between sites ($P = 0.5711$, Multi-response Permutation Procedure, (McCune and Mefford, 1999)), confirming the univariate results.

Shape	n	**Height**	**Radius**	**Radius height**	**Base height**	**Base radius**
Sphere	4	3.3 (3.1, $\geq$5.0)	1.565 (0.75, 2.35)	2.5 (1.7, 3.9)	1.23 (0.6, 2.01)	1.35 (1.0, 1.55)
Inverted cone	6	3.9 (1.95, $\geq$5.0)	1.83 (0.72, 3.3)	1.925 (1.1, $\geq$5.0)	1.525 (0, 3.06)	1.5 (1.0, 1.9)
Cone	1	4.4	2.9	1.7	2.64	1.2
Cylinder	1	4.1	1.72	3.5	1.07	1.4
Hemisphere	4	4.75 (3.9, $\geq$5.0)	2.25 (1.55, 4.2)	2.6 (1.5, 3.1)	1.65 (1.0, 4.2)	1.6 (0.55, 1.9)
Other	5	3.9 (0.4, 4.7)	1.7 (0, 2.3)	2.7 (0.4, 2.9)	1.08 (0, 1.9)	1.5 (0.4, 1.7)

Table 3.3: Canopy shapes and dimensions (m) of *A. oleifolius* trees sampled in the survey. Medians are given in the upper row within each canopy shape, minima and maxima are provided in parentheses where $n > 1$. Sphere: 1 at Reserve A and Koonamore Cross, 2 at South Lake. Inverted cone: 1 at Reserve A, South Lake and Koonamore Cross, 3 at Reserve B. Cone: 1 at Koonamore Cross. Cylinder: 1 at Koonamore Cross. Hemisphere: 1 at Reserve B, 3 at Reserve A. Other: 1 at Reserve A, Reserve B and Koonamore Cross, 2 at South Lake.

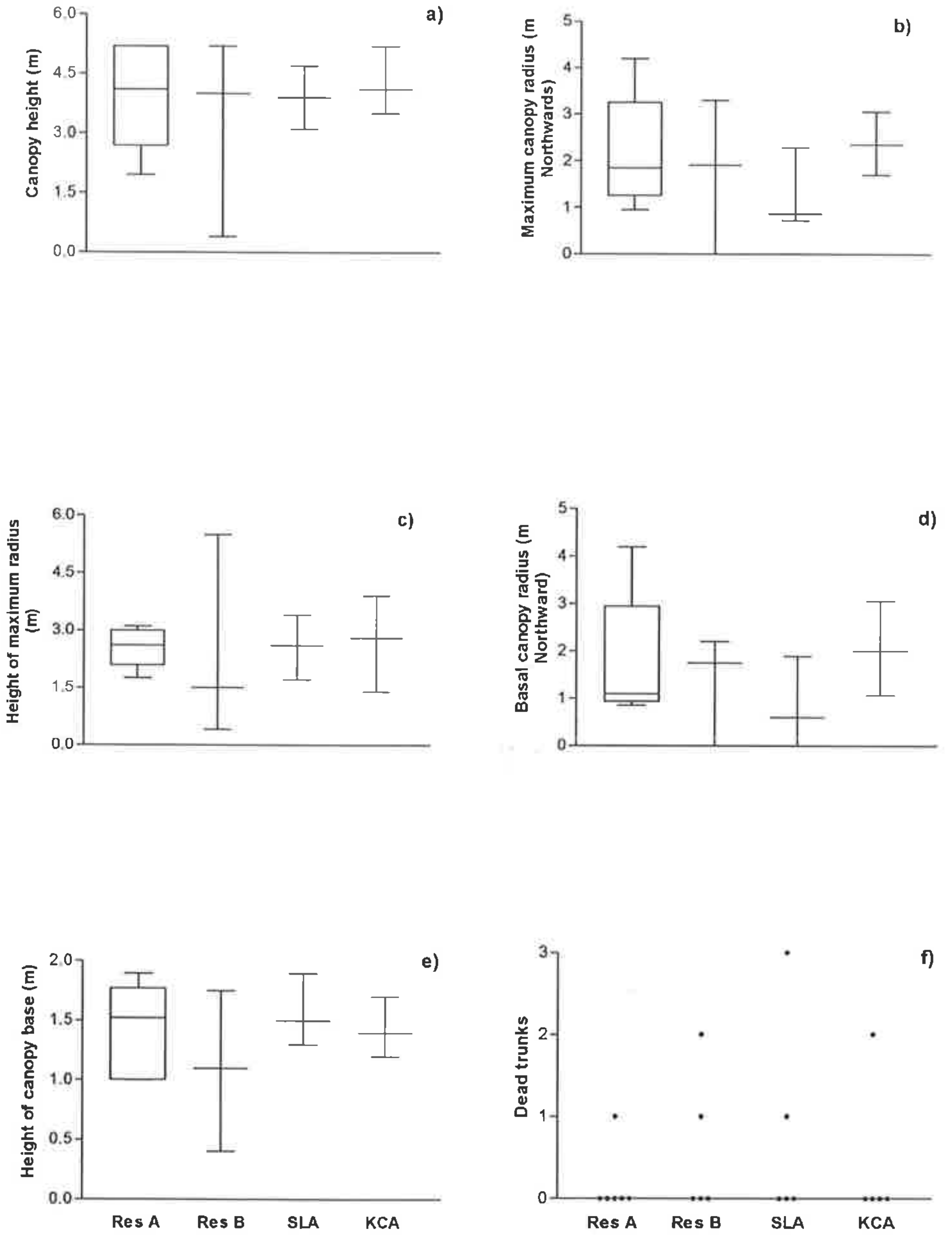


Figure 3.6: Distributions of canopy dimensions by site. None of the measures differed between sites (P = 0.7963, 0.2989, 0.8994, 0.3393, 0.3543 and 0.7458 for a) canopy height, b) maximum canopy radius, c) height of maximum radius, d) radius of canopy base, e) height of canopy base and f) # dead trunks respectively. Permutation test (May et al., 1993a). Reserve A $n = 6$, Reserve B, South Lake and Koonamore Cross n=5). Whiskers indicate minima and maxima, bars indicate medians, and boxes indicate 1st and 3rd quartiles where $n \geq 6$.

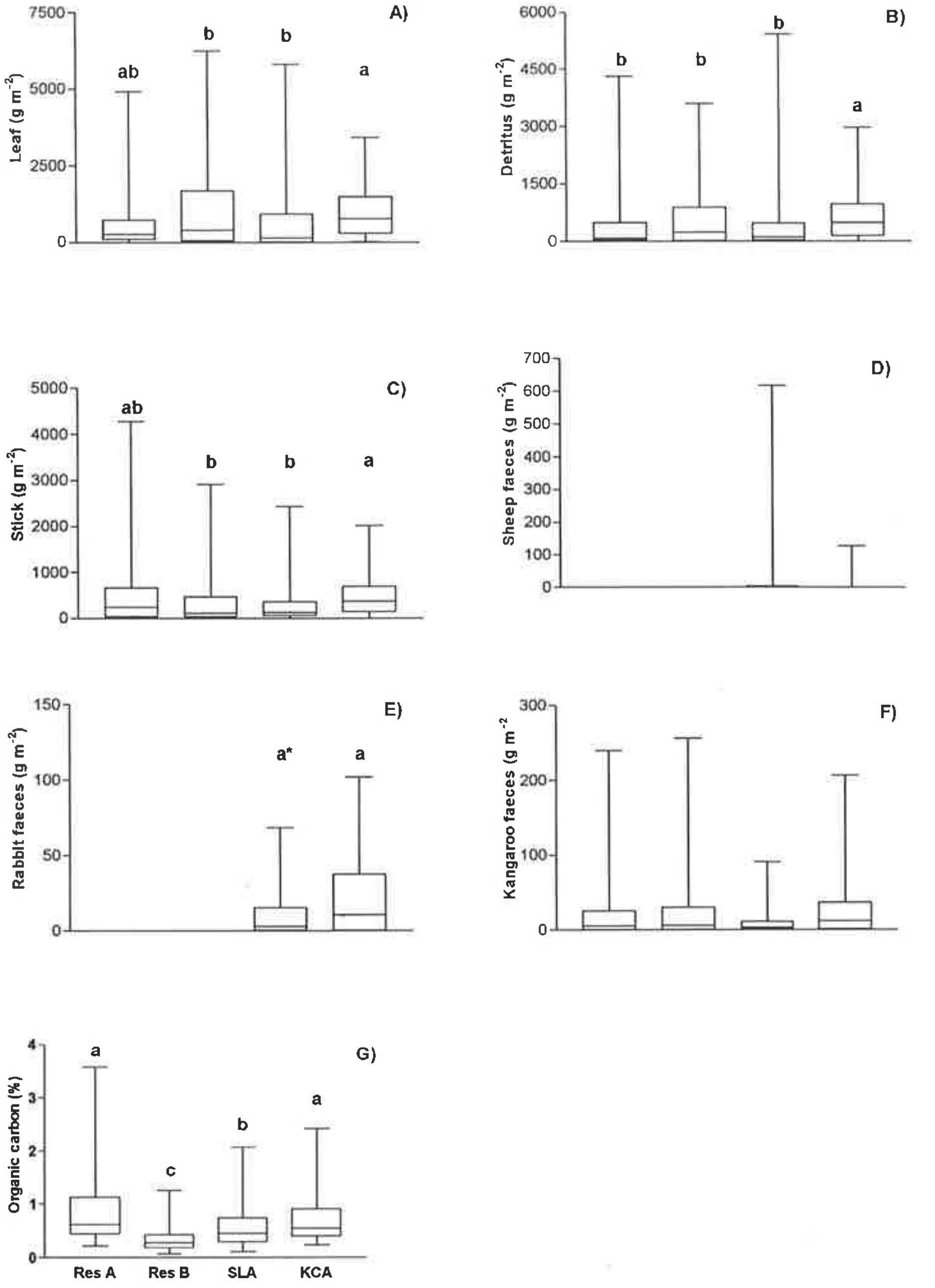


Figure 3.7: Distributions of litter components and soil organic carbon concentrations by site. Shared lowercase letters indicate that sites do not differ (Dunn's Multiple Comparisons (GraphPad, 1999)). * indicates marginal difference between sites ($P = 0.0509$). For litter samples (A-F), $n = 60$ except for Reserve A where $n = 84$. For organic carbon samples (G) $n = 120$ except for Reserve A where $n = 144$. Whiskers indicate minima and maxima, bars indicate medians, and boxes indicate 1st and 3rd quartiles.

3.3.2 Leaf litter

There were site-related differences in several litter components. Leaf, detritus and stick densities all differed between sites ($P = 0.0010$, 0.0005 and 0.0023 respectively, Kruskal-Wallis, GraphPad (1999)). Leaf and stick densities were highest at the Koonamore Cross site and lowest at the Reserve B and South Lake sites (Figure 3.7), with levels at the Reserve A site not differing from any of the others. Detritus densities were higher at the Koonamore Cross site than at the other three sites (Figure 3.7). As expected, sheep and rabbit faeces were not found in the litter at either of the Reserve sites (Figure 3.7). While there were no differences in the densities of sheep faeces between the South Lake and Koonamore Cross sites ($P = 0.3116$, Mann-Whitney U-test (GraphPad, 1999)), rabbit faeces densities were marginally higher at Koonamore Cross ($P = 0.0509$, Mann-Whitney U-test (GraphPad, 1999)). Kangaroo faeces densities did not differ between sites ($P = 0.1078$, Kruskal-Wallis (GraphPad, 1999)).

3.3.3 Ordinations

Plant species frequencies

In terms of the 18 plant species scored in this survey, the communities around *A. oleifolius* trees were more diverse at the Reserve A and Koonamore Cross sites than were those at the Reserve B and South Lake sites. The species composition of each vegetation sample fell into one of four major groupings (Plate 3.1). Group 1 comprised those samples in which none of the target species were found (*i.e.* the "bare" category). Most of the Group 1 samples were from the Reserve B site. This group of samples was more homogeneous than the other groups. This is not surprising, as it consisted of a dichotomous variable derived from the absence of the entities measured in the samples in the other three groups. Group 2 contained samples with perennial grasses with or without other species. Most of these samples

Variable	Axis1	Axis 2	Axis 3
Sample distance	0.046	-0.160	-0.079
Sample angle	-0.001	-0.038	0.041
Organic carbon	0.230	-0.165	-0.160
Canopy height	0.214	-0.041	-0.090
Max. canopy radius	0.106	-0.090	-0.098
Height of max. radius	0.234	-0.050	-0.092
Radius of canopy base	0.070	-0.045	-0.086
Height of canopy base	0.174	-0.070	-0.053
# dead trunks	-0.032	-0.052	0.100
# conspecifics within 15 m	-0.024	-0.004	0.098
# other tree spp. within 15 m	-0.090	-0.160	0.205
Nearest tree (m)	-0.125	0.117	-0.007
Nearest tree (°)	-0.010	0.032	-0.140
N cluster extent (m)	0.052	-0.068	-0.053
E cluster extent (m)	0.128	-0.034	-0.014
W cluster extent (m)	0.013	-0.050	-0.021

Table 3.4: Correlations between ordination axes and environmental variables in the ordination of species frequencies (Kendall's τ (McCune and Mefford, 1999)).

Species	**Axis1**	**Axis 2**	**Axis 3**
Atriplex stipitata	0.028	0.072	-0.393
Atriplex vesicaria	0.274	-0.006	0.225
Enchylaena tomentosa	0.593	-0.373	-0.442
Eriochiton sclerolaenoides	-0.235	0.104	-0.294
Maireana appressa	0.115	0.087	0.313
Maireana pyramidata	0.026	-0.103	-0.164
Grass	0.000	0.671	-0.049
Rhagodia spinescens	0.145	-0.012	-0.006
Sisymbrium **sp.**	0.026	0.041	-0.147

Table 3.5: Correlations between ordination axes and species in the ordination of species frequencies (Kendall's τ (McCune and Mefford, 1999)). Note that the 'bare' category is absent as it is a categorical measure.

were from the South Lake site; very few were from the Reserve A site. Only 11 of the 120 samples in Group 2 contained target species other than grasses. Group 3 contained samples with *E. tomentosa* with or without other species. This was a more heterogenous group than Groups 1 and 2, as it contained a higher proportion of samples with more than one species. Relatively few Group 3 samples were from the Reserve B site. Group 4 contained the remaining samples, which fell into seven sub-groups dominated by each of the remaining seven target species. Most of these samples were from the Reserve A and Koonamore Cross sites; none were from South Lake.

Samples did not form discrete groupings in the ordination of species frequency and environment (Plate 3.2). The distribution of samples in three-dimensional space aggregated more by site (Plate 3.2) than by canopy shape (Plate 3.3), conjoined canopies, kangaroo activity, or occupation of quadrants by other trees (Appendix 3).

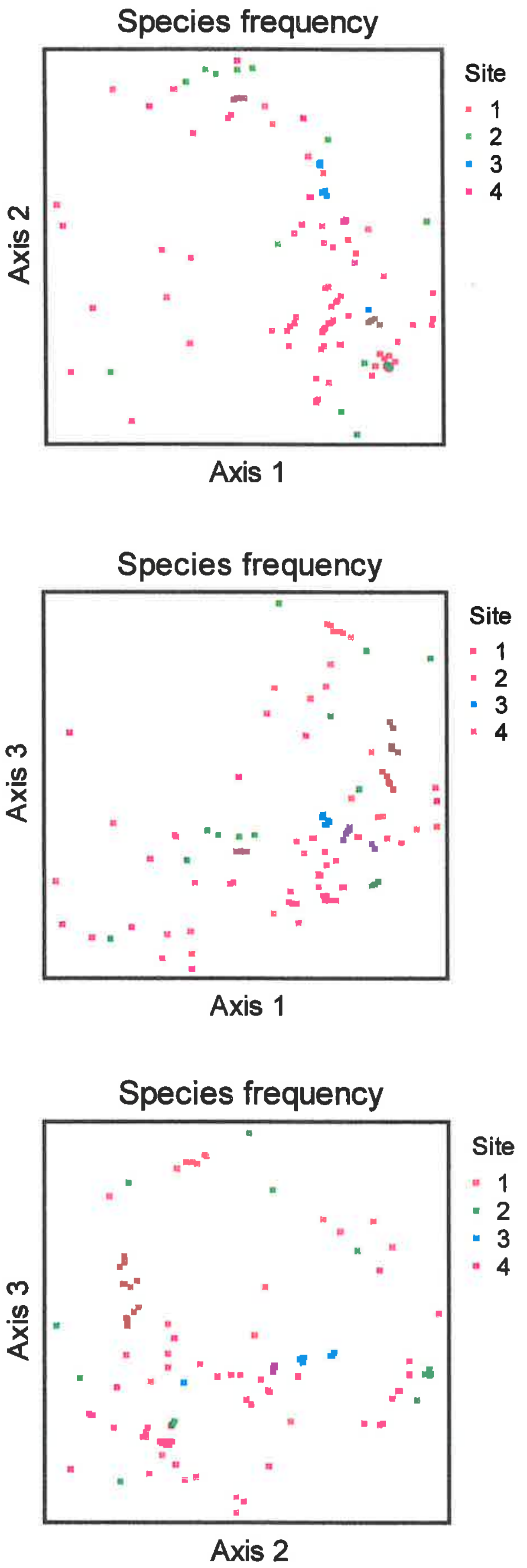


Plate 3.2 - Ordination of survey species frequencies around *Alectryon oleifolius* against environmental measures on three axes. Site 1 = Reserve A, 2 = Reserve B, 3 = South Lake, 4 = Koonamore Cross. Final stress = 13.94 %.

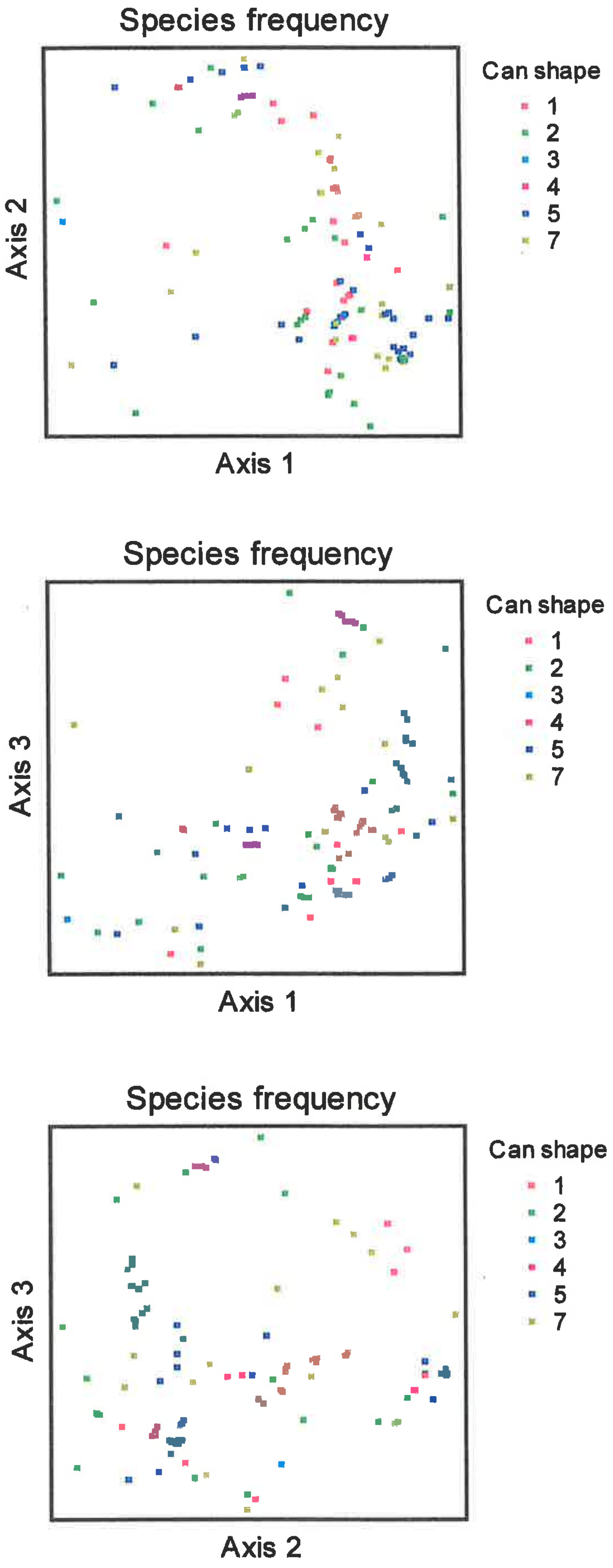


Plate 3.3 - Ordination of plant species frequencies with samples classed by canopy shape. Canopy shape 1 = spherical, 2 = upright cone, 3 = inverted cone, 4 = cylindrical, 5 = hemisperical, 6 = fragmented and 7 = other.

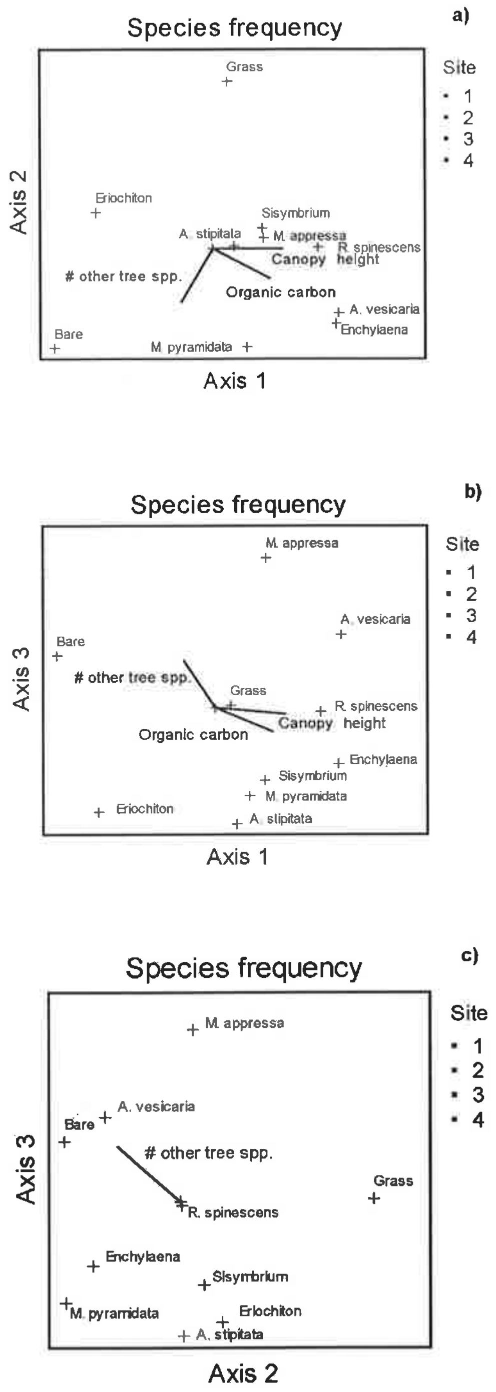


Figure 3.8: Directions of the environmental vectors in the ordination of species frequencies on axes a) 1 and 2, b) 1 and 3, c) 2 and 3. Only vectors with $r^2 \geq 0.08$ are shown; vector scaling = 500%. Site 1 = Reserve A, 2 = Reserve B, 3 = South Lake, 4 = Koonamore Cross.

Canopy height, soil organic carbon content and the number of trees other than *A. oleifolius* within 15 m were the strongest components of the ordination axes, whereas the sample angle and the number of conspecifics within 15 m provided the lowest explanation of the variation along the axes (Figure 3.8, Table 3.4). *Atriplex vesicaria, R. spinescens* and *E. tomentosa* were associated with taller canopies and higher organic carbon levels, whereas bare ground was associated with shorter canopies, lower organic carbon levels and large numbers of neighbouring trees other than *A. oleifolius* (Figure 3.8). *Sisymbrium* and *M. appressa* were associated with moderate organic carbon levels and modest canopy heights, and *Eriochiton sclerolaenoides* was found on soils with low levels of organic carbon near trees with low canopy heights and few non-*Alectryon* neighbours.

Indicator species analyses showed that species frequency and abundance differed between sites for all target species except *Rhagodia spinescens* (Table 3.6a). Neither *Sisymbrium* nor *M. appressa* were found in either of the grazed sites; in fact only three 'species' (*E. tomentosa*, grass and bare) were found at South Lake. *Atriplex vesicaria, E. tomentosa* and *M. appressa* were most frequent at Reserve A, bare and grass at Reserve B, grass at South Lake, and *A. stipitata, E. tomentosa* and grass at Koonamore Cross.

Some aspects of canopy morphology were associated with larger differences in species composition than others. Canopy shape (Table 3.6b), canopy height (Table 3.8a) and height of maximum canopy radius (Table 3.8b) were associated with considerable changes in species composition, while vegetation changes associated with the height of canopy base (Table 3.7b) were less systematic. *Eriochiton sclerolaenoides* was mostly found around inverted cone canopies, while *M. appressa* was predominantly associated with spherical and hemispherical canopies (Table 3.6b). *Atriplex vesicaria* occurred with most canopy shapes, but was more frequent and most abundant around hemispherical and 'other' canopies. *Maireana pyramidata* occurred infrequently, but was abundant in the samples in which it did occur. This may be

a) Site	**Res. A**	**Res. B**	**SLA**	**KCA**	*P*
Bare	13 (13)	56 (54)	15 (14)	16 (16)	$*$
A. stipitata	26 (9)	3 (3)	0 (0)	70 (28)	$*$
A. vesicaria	76 (26)	23 (8)	0 (0)	1 (2)	$*$
E. tomentosa	24 (35)	6 (15)	21 (30)	49 (46)	$*$
Eriochiton	73 (15)	0 (0)	0 (0)	27 (11)	$*$
M. appressa	99 (30)	1 (1)	0 (0)	0 (0)	$*$
M. pyramidata	0 (0)	1 (1)	0 (0)	99 (8)	$*$
Grass	3 (11)	11 (22)	70 (67)	17 (36)	$*$
R. spinescens	65 (4)	15 (3)	0 (0)	20 (1)	
Sisymbrium sp.	36 (2)	64 (8)	0 (0)	0 (0)	$*$

b) Canopy shape	**A**	**B**	**C**	**D**	**E**	**G**	*P*
Bare	12 (15)	27 (35)	7 (8)	20 (25)	16 (20)	19 (24)	
A. stipitata	14 (13)	8 (6)	49 (21)	8 (13)	16 (13)	5 (6)	$*$
A. vesicaria	8 (8)	18 (8)	0 (0)	0 (0)	48 (19)	26 (9)	$*$
E. tomentosa	14 (23)	8 (26)	28 (42)	20 (42)	16 (44)	13 (32)	
Eriochiton	11 (4)	84 (18)	5 (4)	0 (0)	0 (0)	0 (0)	$*$
M. appressa	65 (17)	2 (3)	0 (0)	0 (0)	29 (14)	4 (5)	$*$
M. pyramidata	21 (2)	77 (6)	0 (0)	0 (0)	2 (1)	0 (0)	
Grass	22 (46)	9 (21)	(25) 38	9 (46)	4 (19)	31 (47)	$*$
R. spinescens	20 (1)	9 (2)	0 (0)	0 (0)	71 (6)	0 (0)	
Sisymbrium sp.	0 (0)	3 (1)	0 (0)	0 (0)	67 (8)	30 (2)	

Table 3.6: The relative abundances and frequencies (in parentheses) of plant species by a) site and b) canopy shape. Reserve A $n=$ 124, Reserve B, South Lake and Koonamore Cross $n=$ 120. A = spherical ($n=$ 92), B = inverted cone ($n=$ 144), C = cone ($n=$ 24), D = cylindrical ($n=$ 24), E = hemispherical ($n=$ 84), G = other ($n=$ 116). $*$ indicates that the probability of the species frequency and abundance varying between groups is significant at $P = 0.05$ (Indicator Species analysis, McCune and Mefford (1999)).

a)	True	False	P	b)	0-1 m	1-2 m	P
Bare	51 (25)	49 (24)			69 (48)	31 (22)	$*$
A. stipitata	37 (9)	63 (11)			17 (4)	83 (10)	
A. vesicaria	69 (11)	31 (7)			51 (8)	49 (9)	
E. tomentosa	56 (38)	44 (25)	$*$		18 (13)	82 (34)	$*$
Eriochiton	0 (0)	100 (13)	$*$		0 (0)	100 (7)	
M. appressa	32 (8)	68 (8)			0 (0)	100 (9)	
M. pyramidata	1 (0)	99 (4)	$*$		12 (2)	88 (2)	
Grass	35 (31)	65 (36)	$*$		33 (29)	67 (34)	
R. spinescens	79 (3)	21 (0)			0 (0)	100 (2)	
Sisymbrium sp.	100 (4)	0 (0)	$*$		93 (15)	7 (1)	$*$

Table 3.7: a) The relative abundances and frequencies (in parentheses) of plant species by a) the continuity of the *A.oleifolius* canopy with adjacent canopies, and b) height of the canopy base. a) $n=$ 248 for true, $n=$ 236 for false. b) $n=$ 48 for 0-1 m, n=436 for 1-2 m. $*$ indicates that the probability of the species frequency and abundance varying between groups is significant at $P = 0.05$ (Indicator Species analysis, McCune and Mefford (1999)).

due to the larger size of *M. pyramidata* shrubs, or it may indicate a contagious distribution. It was mainly found in association with inverted cone canopies. Grasses were found near all canopy types, most abundantly around 'other' canopies and less frequently around inverted cone and hemispherical canopies. Likewise *A. stipitata* occurred around all canopy types, being most abundant near the only cone-shaped canopy in the survey and least frequent around inverted cone and 'other' canopies.

Both the relative frequency and abundance of *E. tomentosa* increased with canopy height (Table 3.8a). *Rhagodia spinescens* also showed a strong relationship to canopy height, with all but one of the samples containing this species coming from canopies 5 m or more high. Almost all the samples containing *Eriochiton sclerolaenoides* came from a single tree in the 1-2 m size class; given the lack of replication this distribution pattern may be attributable to factors other than canopy height. Grass frequency and abundance varied between canopy heights in an unpredictable manner. Few species varied with the height of the canopy base (Table 3.7b). *Sisymbrium* was almost always found associated with canopies whose base was less than 1 m above the ground. Bare ground showed a similar, though less pronounced, pattern. Conversely, *E. tomentosa* was most often associated with canopies with more elevated bases. Half of the species varied with the height at which the maximum canopy radius occurred (Table 3.8b), though *Eriochiton sclerolaenoides, M. appressa* and bare ground did so in an unpredictable fashion. The frequency and abundance of *R. spinescens* increased with height of maximum radius, while *E. tomentosa* showed a unimodal response with a peak at 3-4 m.

The frequency and abundance of about half of the species also varied with whether or not *A. oleifolius* canopies were contiguous with neighbouring canopies (Table 3.7a), even though this variable was not a large contributor to the ordination axes (Table 3.4). *Sisymbrium* was only found around trees with contiguous canopies, while *Eriochiton sclerolaenoides* and *M. pyramidata* were almost exclusively found around solitary trees. *E. tomentosa* was more common where *A. oleifolius* canopies were contiguous, while grasses were less frequent and disproportionately less abundant.

Community composition also changed with the number of trees other than *A. oleifolius* within 15 m (Table 3.9a). The relative frequency and abundance of grasses decreased sharply as the number of non-congeneric neighbours increased. Bare ground, *Eriochiton sclerolaenoides, M. appressa* and *M. pyramidata* also changed, but there is no apparent pattern of increase or decrease.

Neither the frequency nor the abundance of any of the target species varied with organic carbon levels (Table 3.9b), and only *E. tomentosa* varied with sample distance (Table 3.10). This species was most frequent and more abundant between 6 and 8 m from the tree trunk.

Litter density

Litter samples did not form discrete groupings in the ordination of litter component densities and environment (Plate 3.4). Nor were samples aggregated in accor-

a) Canopy height	**0-1 m**	**1-2 m**	**2-3 m**	**3-4 m**	**4-5 m**	**$\geq$ 5 m**	P
Bare	32 (71)	4 (8)	38 (83)	8 (18)	9 (20)	9 (20)	$*$
A. stipitata	0 (0)	22 (4)	0 (0)	19 (11)	17 (7)	43 (20)	
A. vesicaria	19 (13)	30 (17)	8 (8)	4 (7)	9 (5)	29 (18)	
E. tomentosa	0 (0)	1 (4)	3 (13)	23 (30)	28 (37)	45 (47)	$*$
Eriochiton	0 (0)	94 (75)	0 (0)	3 (5)	0 (1)	3 (5)	$*$
M. appressa	0 (0)	11 (13)	0 (0)	61 (13)	4 (4)	24 (10)	
M. pyramidata	0 (0)	0 (0)	0 (0)	75 (5)	1 (1)	24 (2)	
Grass	11 (21)	3 (8)	0 (0)	41 (45)	39 (43)	6 (15)	$*$
R. spinescens	0 (0)	0 (0)	0 (0)	19 (1)	0 (0)	81 (9)	$*$
Sisymbrium sp.	0 (0)	0 (0)	0 (0)	0 (0)	92 (5)	8 (2)	

b) Max. radius height	**0-1 m**	**1-2 m**	**2-3 m**	**3-4 m**	**$\geq$ 5 m**	P
Bare	42 (71)	15 (25)	13 (22)	7 (12)	22 (38)	$*$
A. stipitata	0 (0)	31 (9)	15 (8)	49 (18)	5 (4)	
A. vesicaria	25 (13)	8 (5)	19 (13)	17 (8)	30 (17)	
E. tomentosa	0 (0)	13 (22)	24 (33)	48 (54)	15 (33)	$*$
Eriochiton	0 (0)	87 (16)	0 (0)	13 (4)	0 (0)	$*$
M. appressa	0 (0)	2 (2)	72 (16)	18 (7)	8 (4)	$*$
M. pyramidata	0 (0)	76 (5)	0 (0)	24 (2)	0 (0)	
Grass	10 (21)	34 (39)	30 (34)	20 (34)	5 (8)	
R. spinescens	0 (0)	0 (0)	12 (1)	43 (5)	45 (13)	$*$
Sisymbrium sp.	0 (0)	47 (4)	28 (1)	0 (0)	25 (8)	

Table 3.8: The relative abundances and frequencies (in parentheses) of plant species by a) canopy height and b) height of the maximum canopy radius. a) $n=$ 24 for 0-1, 1-2, 2-3 m, $n=$ 160 for 3-4 m, $n=$ 164 for 4-5 m, $n=$ 88 for $\geq$ 5 m. b) $n=$ 24 for 0-1, $\geq$ 5 m, $n=$ 168 for 1-2 m, $n=$ 176 for 2-3 m, $n=$ 92 for 3-4 m. $*$ indicates that the probability of the species frequency and abundance varying between groups is significant at $P =$ 0.05 (Indicator Species analysis, McCune and Mefford (1999)).

a) # other trees	**0**	**1**	**2**	**3**	**4**	**7**	*P*
Bare	4 (6)	12 (21)	11 (20)	21 (38)	6 (10)	47 (83)	*
A. stipitata	0 (0)	23 (11)	52 (17)	25 (7)	0 (0)	0 (0)	
A. vesicaria	0 (0)	16 (9)	14 (8)	33 (13)	26 (30)	11 (8)	
E. tomentosa	18 (29)	28 (37)	27 (33)	23 (31)	0 (0)	3 (13)	
Eriochiton	0 (0)	5 (2)	95 (23)	0 (0)	0 (0)	0 (0)	*
M. appressa	0 (0)	3 (6)	1 (3)	5 (9)	92 (80)	0 (0)	*
M. pyramidata	0 (0)	10 (1)	90 (7)	0 (0)	0 (0)	0 (0)	*
Grass	66 (81)	17 (37)	9 (23)	6 (28)	2 (10)	0 (0)	*
R. spinescens	0 (0)	27 (1)	14 (3)	59 (6)	0 (0)	0 (0)	
Sisymbrium sp.	0 (0)	93 (4)	7 (2)	0 (0)	0 (0)	0 (0)	

b) Organic carbon	**0-1%**	**1-2%**	**2-3%**	**3-4%**	*P*
Bare	17 (16)	29 (26)	0 (0)	54 (50)	
A. stipitata	52 (11)	35 (10)	12 (8)	0 (0)	
A. vesicaria	56 (14)	44 (9)	0 (0)	0 (0)	
E. tomentosa	31(63)	10 (25)	30 (77)	29 (50)	
Eriochiton	44 (2)	56 (7)	0 (0)	0 (0)	
M. appressa	46 (6)	54 (8)	0 (0)	0 (0)	
M. pyramidata	40 (2)	60 (2)	0 (0)	0 (0)	
Grass	14 (17)	40 (37)	11 (15)	35 (50)	
R. spinescens	22 (6)	5 (1)	73 (8)	0 (0)	
Sisymbrium sp.	78 (3)	22 (2)	0 (0)	0 (0)	

Table 3.9: The relative abundances and frequencies (in parentheses) of plant species by a) the number of trees within 15 m that were not congeneric with *A. oleifolius*, and b) soil organic carbon content 0-10 cm depth. a) $n=$ 48 for 0 neighbours, $n=$ 204 for 1, $n=$ 120 for 2, $n=$ 68 for 3, 4 n= 20, 7 n= 24. b) $n=$ 405 for 0-1%, $n=$ 64 for 1-2%, $n=$ 13 for 2-3%,$n=$ 2 for 3-4%. $*$ indicates that the probability of the species frequency and abundance varying between groups is significant at $P = 0.05$ (Indicator Species analysis, McCune and Mefford (1999)).

	0-1m	**1-2m**	**2-3m**	**3-4m**	**4-5m**	**5-6m**	**6-7m**	**7-8m**
Bare	5 (21)	5 (21)	7 (27)	13 (50)	7 (26)	5 (18)	6 (23)	7 (25)
A. stipitata	5 (9)	7 (9)	9 (16)	2 (6)	18 (11)	1 (4)	8 (13)	5 (7)
A. vesicaria	16 (11)	8 (9)	16 (14)	0 (0)	15 (11)	5 (7)	6 (7)	15 (14)
E. tomentosa	3 (23)	3 (18)	4 (21)	5 (31)	8 (47)	8 (43)	11 (67)	9 (50)
Eriochiton	16 (10)	4 (7)	1 (2)	10 (13)	10 (11)	11 (7)	1 (3)	0 (0)
M. appressa	8 (11)	16 (14)	7 (7)	0 (0)	0 (0)	6 (7)	1 (3)	17 (7)
M. pyramidata	0 (0)	0 (2)	0 (0)	2 (6)	9 (5)	17 (7)	9 (3)	4 (4)
Grass	9 (46)	12 (43)	14 (39)	3 (19)	2 (21)	5 (29)	5 (13)	2 (18)
R. spinescens	1 (1)	2 (2)	0 (0)	0 (0)	1 (5)	15 (4)	0 (0)	7 (4)
Sisymbrium sp.	1 (2)	1 (1)	0 (0)	0 (0)	0 (0)	0 (0)	32 (10)	8 (4)

(contd.)	**8-9m**	**9-10m**	**10-11m**	**11-12m**	**12-13m**	**13-14m**	**14-15m**	*P*
Bare	3 (11)	4 (17)	9 (33)	6 (22)	5 (18)	11 (43)	7 (25)	
A. stipitata	24 (33)	0 (0)	1 (7)	2 (11)	10 (12)	6 (9)	3 (5)	
A. vesicaria	0 (0)	3 (8)	5 (7)	2 (6)	0 (0)	7 (13)	2 (5)	
E. tomentosa	18 (67)	7 (33)	4 (33)	3 (33)	6 (35)	2 (22)	7 (50)	$*$
Eriochiton	0 (0)	3 (8)	1 (7)	3 (6)	16 (12)	11 (4)	13 (5)	
M. appressa	10 (11)	0 (0)	12 (7)	17 (11)	8 (6)	0 (0)	0 (0)	
M. pyramidata	28 (11)	0 (0)	0 (0)	0 (0)	31 (12)	0 (0)	0 (0)	
Grass	2 (11)	13 (50)	5 (13)	10 (33)	9 (35)	2 (26)	5 (20)	
R. spinescens	0 (0)	0 (0)	32 (7)	36 (6)	0 (0)	0 (0)	5 (5)	
Sisymbrium sp.	0 (0)	0 (0)	23 (7)	0 (0)	7 (6)	27 (9)	0 (0)	

Table 3.10: The relative abundances and frequencies (in parentheses) of plant species by distance from *A. oleifolius* trunks. $n=$ 91 for 0-1 m, $n=$ 102 for 1-2 m, $n=$ 56 for 2-3 m, $n=$ 16 for 3-4 m, $n=$ 19 for 4-5 m, $n=$ 28 for 5-6, 7-8 m, $n=$ 30 for 6-7 m, $n=$ 9 for 8-9 m, $n=$ 12 for 9-10 m, $n=$ 15 for 10-11 m, $n=$ 18 for 11-12 m, $n=$ 17 for 12-13 m, $n=$ 23 for 13-14 m, $n=$ 20 for 14-15 m. $*$ indicates that the probability of the species frequency and abundance varying between groups is significant at $P = 0.05$ (Indicator Species analysis, McCune and Mefford (1999)).

Litter component	Axis 1	Axis 2
Stick	0.132	-0.106
Leaf	0.386	0.137
Detritus	0.466	-0.011
Kangaroo faeces	0.237	-0.028
Sheep faeces	0.147	-0.045
Rabbit faeces	0.219	-0.042

Table 3.11: Correlations between ordination axes and litter components in the ordination of litter densities (Kendall's τ, McCune and Mefford (1999)).

dance consistent with any of the categorical measures (site, canopy shape, conjoined canopies, kangaroo activity and quadrat occupation) (Plate 3.4, Appendix 3). The relative strengths of the correlations between environmental variables and ordination axes differed somewhat between the measures, Kendall's τ and Pearson's r. According to Kendall's τ, height of maximum radius and northerly and westward cluster extent were the strongest positive components of the first ordination axis, while distance to the nearest tree was strongly negatively correlated (Table 3.12). Correlations with the second axis were less strong, with the negatively correlated canopy height, height of maximum radius and height of canopy base being the most prominent (Table 3.12). Sample angle and the number of dead trunks were the least important variables. In contrast, canopy height and northerly cluster extent were the strongest positive components of the first ordination axis as measured by Pearson's r, while distance to the nearest tree was even more strongly negatively correlated (Figure 3.9). Correlations with the second axis were weaker and below the vector r^2 cutoff value for Figure 3.9. Sample distance was positively correlated with the second axis (r= 0.130), and easterly cluster extent was negatively correlated (r= -0.133). Detritus and leaf litter densities increased with canopy height and the northerly cluster extent, but leaf litter

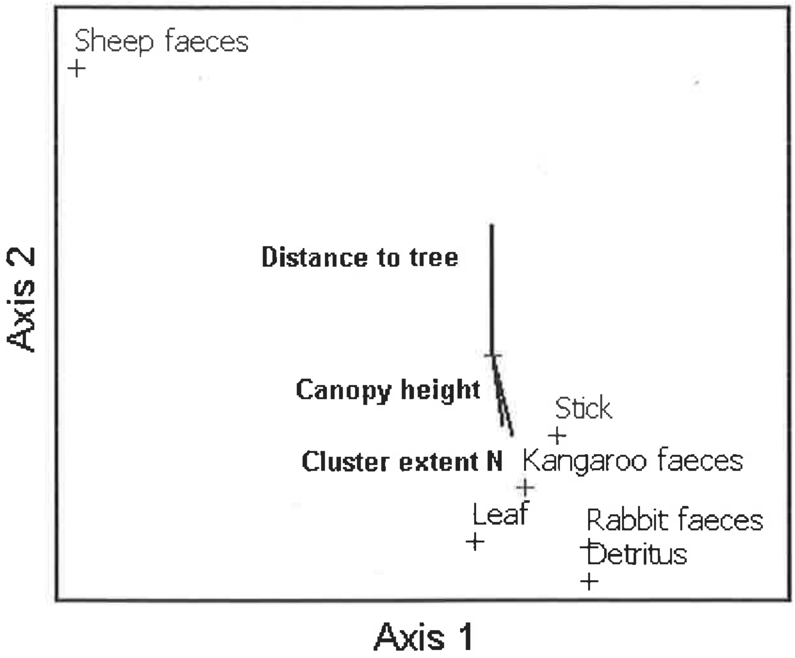


Figure 3.9: Directions of the environmental vectors (bold) in the ordination of litter densities. Only vectors with $r^2 \geq 0.052$ are shown, vector scaling = 500%. Final stress = 6.986

densities also increased when the canopy base was closer to the ground. Sheep faeces were most strongly associated with larger, more isolated trees (Figure 3.9).

The frequency and abundance of litter items varied with canopy shape and dimensions. While there was little change in the relative frequency of plant-derived litter items, their relative abundances varied between canopy shapes, as did both the frequencies and abundances of animal faeces (Table 3.14a). The relative abundances of leaf, detritus and stick components were highest under hemispherical canopies and lowest under spherical canopies. Kangaroo faeces also showed the same pattern of relative abundance, but the relative frequency was highest under conical canopies and lowest under inverted conical canopies. Rabbit faeces were most abundant under the sole cylindrical canopy, and absent from hemispherical canopies, all of which were inside the Reserve. The lowest levels of rabbit faeces below canopies accessible to rabbits were under spherical and inverted conical canopies.

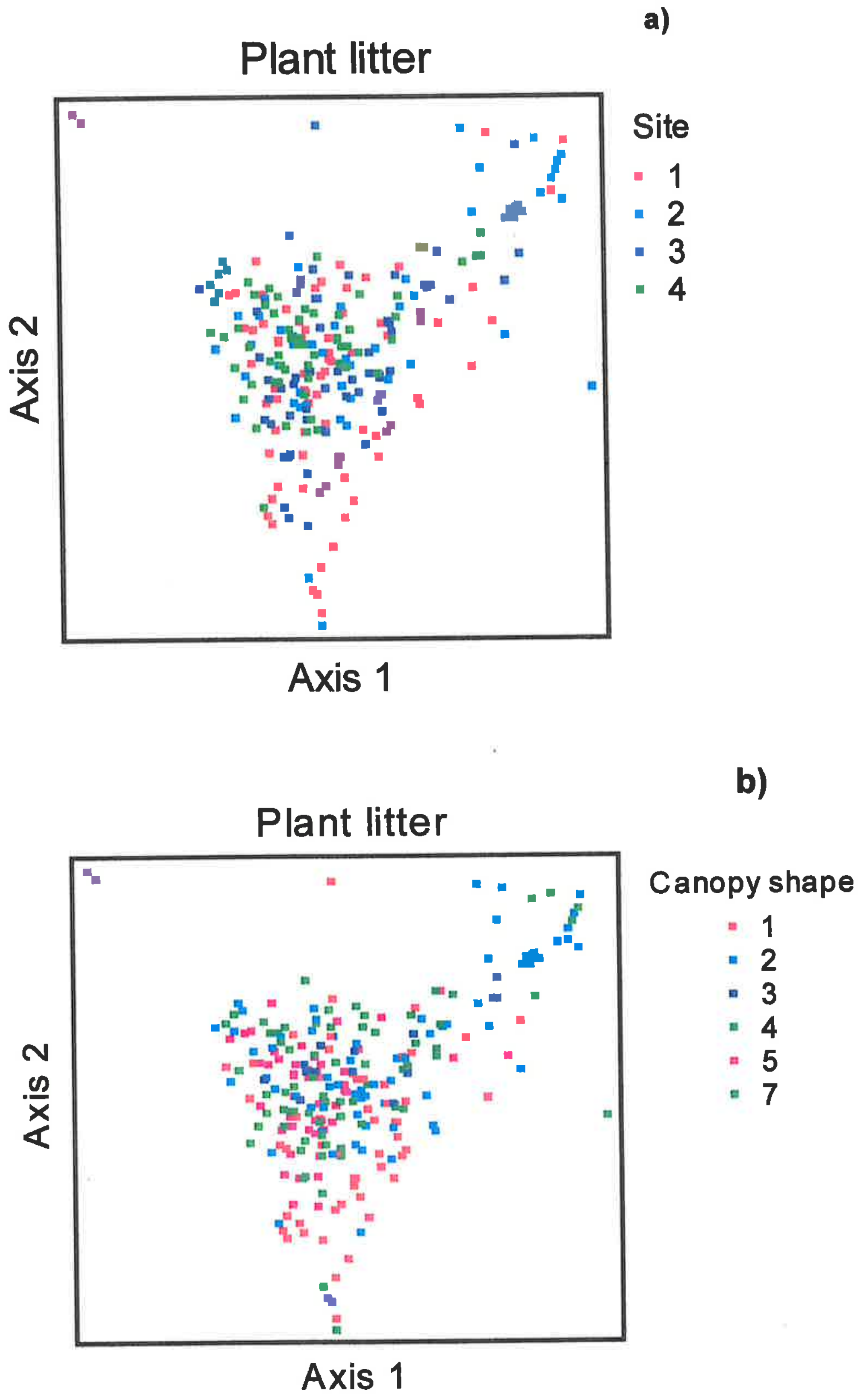


Plate 3.4 - Ordination of litter samples classed by a) site and b) canopy shape. Site 1 = Reserve A, 2 = Reserve B, 3 = South Lake, 4 = Koonamore Cross. Canopy shape 1 = spherical, 2 = upright cone, 3 = inverted cone, 4 = cylindrical, 5 = hemispherical, 6 = fragmented and 7 = other. Final stress = 6.91%.

Variable	Axis 1	Axis 2
Sample distance	-0.024	0.036
Sample angle	-0.040	0.004
Canopy height	0.179	-0.141
Max. canopy radius	0.072	-0.090
Height of max. radius	0.185	-0.102
Radius of canopy base	0.014	-0.057
Height of canopy base	0.174	-0.112
# dead trunks	-0.008	-0.054
# conspecifics within 15 m	0.110	0.063
# other tree spp. within 15 m	-0.071	0.011
Nearest tree (m)	-0.248	-0.004
Nearest tree (°)	0.146	0.064
N cluster extent	0.256	0.004
E cluster extent	0.165	-0.088
W cluster extent	0.195	-0.061

Table 3.12: Correlations between ordination axes and environmental variables in the ordination of litter densities (Kendall's τ, McCune and Mefford (1999)).

Height of canopy base	**0-1 m**	**1-2 m**	P
Stick	52 (87)	48 (96)	
Leaf	60 (91)	40 (98)	
Detritus	58 (96)	42 (99)	
Kangaroo faeces	64 (65)	36 (69)	
Sheep faeces	0 (0)	100 (13)	
Rabbit faeces	0 (0)	100 (33)	$*$

Table 3.13: The relative abundances and frequencies (in parentheses) of litter items by the height of the canopy base. n= 23 for 0-1 m, 240 for 1-2 m. $*$ indicates that the probability of the frequency and abundance of each type of litter item varying between groups is significant at $P = 0.05$ (Indicator Species analysis, McCune and Mefford (1999)).

Three canopy dimensions, canopy height, height of maximum radius and height of canopy base, were associated with changes in the frequency and abundances of litter items (Tables 3.14b, c and 3.13). Each of the types of plant-derived litter items were present in almost all samples, so there was little variation in the relative frequency. However, the relative frequencies of animal faeces varied considerably. The relative abundances of leaf, detritus and stick components all increased with canopy height, as did kangaroo faeces (Table 3.14b). Both sheep and rabbit faeces were never found under trees less than 3 m high, and were most abundant under trees 3-4 m (sheep) and 4-5 m (rabbit) high. Leaf and detritus abundances varied with the height of the maximum radius, showing unimodal responses peaking at 3-4 m. Rabbit faeces showed a similar, though more erratic, response. Sheep and rabbit faeces also varied with the height of the canopy base, both being absent from under canopies with bases less than 1 m above the ground (Table 3.13).

Litter abundance varied with the distance to the nearest tree (Table 3.15). Leaf, detritus and kangaroo faeces were all most abundant under canopies with a neighbour

a) Canopy shape	**A**	**B**	**C**	**D**	**E**	**G**	*P*
Stick	7 (90)	10 (96)	25 (100)	21 (100)	28 (100)	10 (95)	$*$
Leaf	7 (97)	9 (96)	22 (100)	22 (100)	32 (100)	9 (97)	$*$
Detritus	6 (100)	10 (97)	22 (100)	21 (100)	32 (100)	9 (98)	$*$
Kangaroo faeces	4 (57)	11 (51)	13 (92)	34 (83)	30 (85)	9 (81)	$*$
Sheep faeces	40 (13)	9 (11)	3 (17)	40 (25)	0 (0)	8 (17)	
Rabbit faeces	4 (28)	4 (18)	37 (67)	43 (92)	0 (0)	12 (51)	$*$

b) Canopy height	**0-1 m**	**1-2 m**	**2-3 m**	**3-4 m**	**4-5 m**	**$\geq$ 5 m**	*P*
Stick	2 (73)	3 (92)	5 (100)	14 (93)	32 (99)	46 (100)	$*$
Leaf	1 (82)	2 (92)	5 (92)	17 (98)	33 (99)	43 (100)	$*$
Detritus	1 (91)	0 (83)	3 (100)	12 (100)	35 (100)	48 (100)	$*$
Kangaroo faeces	5 (36)	3 (25)	15 (33)	13 (63)	28 (81)	36 (88)	$*$
Sheep faeces	0 (0)	0 (0)	0 (0)	63 (15)	31 (15)	7 (8)	
Rabbit faeces	0 (0)	0 (0)	0 (0)	27 (32)	62 (46)	11 (19)	$*$

c) Radius height	**0-1 m**	**1-2 m**	**2-3 m**	**3-4 m**	**$\geq$ 5 m**	*P*
Stick	1 (73)	16 (98)	20 (94)	33 (98)	29 (100)	
Leaf	1 (82)	20 (98)	21 (98)	33 (98)	25 (100)	$*$
Detritus	1 (91)	16 (98)	18 (100)	40 (100)	24 (100)	$*$
Kangaroo faeces	4 (36)	14 (61)	16 (69)	33 (85)	33 (83)	
Sheep faeces	0 (0)	3 (7)	48 (10)	49 (29)	0 (0)	
Rabbit faeces	0 (0)	24 (29)	18 (22)	58 (65)	0 (0)	$*$

Table 3.14: The relative abundances and frequencies (in parentheses) of litter items by a) canopy shape, b) canopy height and c) height of maximum radius. Canopy shape A = spherical (n= 59), B = inverted cone (n= 72), C = cone (n= 12), D = cylindrical (n= 12), E = hemispherical (n= 48), and G = other (n= 60). Canopy height n= 11 for 0-1 m, n= 12 for 1-2 and 2-3 m, n= 96 for 3-4 m, n= 84 for 4-5 m, n= 48 for ≥ 5 m. Height of maximum radius n= 11 for 0-1 m, n= 84 for 1-2 m, n= 108 for 2-3 m, n= 48 for 3-4 m and n= 12 for ≥ 5 m. $*$ indicates that the probability of the frequency and abundance of each type of litter item varying between groups is significant at $P = 0.05$ (Indicator Species analysis, McCune and Mefford (1999)).

	0-1 m	1-2 m	2-3 m	3-4 m	4-5 m	6-7 m	7-8 m	8-9 m	9-10 m	12-13 m	*P*
Stick	17 (96)	16 (100)	9 (100)	12 (96)	5 (88)	9 (87)	3 (100)	18 (100)	9 (100)	1 (92)	
Leaf	21 (96)	17 (100)	9 (100)	12 (100)	5 (96)	7 (91)	3 (96)	16 (100)	9 (100)	1 (92)	*
Detritus	25 (100)	16 (100)	10 (100)	13 (100)	4 (100)	8 (96)	3 (100)	16 (100)	5 (100)	0 (83)	*
Kangaroo faeces	23 (83)	15 (69)	17 (85)	15 (67)	4 (52)	5 (65)	6 (58)	10 (92)	4 (92)	1 (25)	*
Sheep faeces	20 (29)	0 (0)	47 (17)	1 (4)	1 (4)	5 (17)	2 (4)	2 (17)	23 (50)	0 (0)	
Rabbit faeces	11 (46)	0 (0)	20 (54)	1 (8)	1 (10)	6 (39)	7 (38)	37 (67)	16 (75)	0 (0)	*

Table 3.15: The relative abundances and frequencies (in parentheses) of litter items by the distance from the *A. oleifolius* trunk to the nearest tree. $n=$ 24 for 0-1, 3-4 and 7-8 m, $n=$ 36 for 1-2 m, $n=$ 48 for 2-3 and 4-5 m, $n=$ 23 for 6-7 m, $n=$ 12 for 8-9, 9-10 and 12-13 m. $*$ indicates that the probability of the frequency and abundance of each type of litter item varying between groups is significant at $P = 0.05$ (Indicator Species analysis, McCune and Mefford (1999)).

less than 4 m away, showing bimodal patterns with maxima at 0-1m and 8-9 m. Levels were lowest at 7-8 m and at 12-13 m. Sheep and rabbit faeces also varied, but the patterns are obscure.

The extent of contiguous canopies was associated with differences in litter abundance and frequency (Table 3.16). The relative abundance of sticks increased with the northward extent up to 5-6 m, though the pattern of increase is not smooth (Table 3.16a). Sheep and rabbit faeces were absent under canopies with northward extents of 2-6 m, but were found under canopies with little northward extent ($<$ 2 m) and under a single canopy that had a northward extent of 6-7 m. Leaf litter and animal faeces varied with eastward extent in an erratic manner (Table 3.16b). Kangaroo faeces and leaf litter were most abundant under trees with an eastward extent of 5-6 m, while sheep and rabbit faeces were most abundant under trees with an eastward extent of 8-9 and 2-3 m respectively. Both sheep and rabbit faeces were least abundant at 4-5 m and 10-11 m, and leaf litter at 4-5 m only. Kangaroo faeces were least abundant at both 0-1 m and 10-11 m. Leaf, detritus and rabbit faeces all showed a bimodal pattern with westward canopy extent (Table 3.16c), with the two maxima at 0-1 m and either 3-4 m (leaf and detritus) or 4-5 m (rabbit faeces). Minima were usually at 2-3 m, except for detritus where the minima occurred under canopies with a westward extent of 1-2 m.

3.3.4 Soils and canopy dimensions

Organic carbon concentrations decreased with distance from the tree trunk (Figure 3.10) ($\log_e$ organic carbon = -0.4070 - 0.0664 Sample distance, $r^2 = 0.1587$, P(slope = 0) = 0.0000, Robust Linear Regression (MathSoft, 2000)), while there was a very small but significant change with angle ($\log_e$ organic carbon = -0.6134 - 0.0007 Sample angle, $r^2 = 0.0087$, P(slope = 0) = 0.0448, Robust Linear Regression (MathSoft, 2000)). Much more of the sample variance was explained by including more of the canopy measures in the linear regression model (Table 3.17). The most parsimonious

a) North	0-1 m	1-2 m	2-3 m	3-4 m	4-5 m	5-6 m	6-7 m	P
Stick	8 (94)	10 (100)	4 (100)	14 (100)	20 (100)	29 (100)	15 (92)	$*$
Leaf	6 (97)	10 (100)	2 (100)	18 (100)	24 (100)	25 (100)	13 (92)	
Detritus	6 (98)	11 (100)	2 (100)	13 (100)	22 (100)	26 (100)	21 (100)	
Roo	6 (64)	19 (92)	6 (50)	14 (75)	27 (92)	16 (83)	12 (75)	
Sheep	17 (10)	27 (25)	0 (0)	0 (0)	0 (0)	0 (0)	56 (58)	$*$
Rabbit	9 (25)	57 (96)	0 (0)	0 (0)	0 (0)	0 (0)	34 (92)	$*$

b) East	0-1 m	2-3 m	4-5 m	5-6 m	8-9 m	10-11 m	P
Stick	13 (94)	8 (100)	7 (100)	26 (100)	23 (92)	24 (100)	
Leaf	13 (97)	11 (100)	4 (100)	30 (100)	22 (92)	19 (100)	$*$
Detritus	10 (98)	12 (100)	3 (100)	27 (100)	33 (100)	16 (100)	
Kangaroo faeces	8 (62)	23 (100)	9 (50)	35 (89)	17 (75)	8 (92)	$*$
Sheep faeces	18 (10)	10 (25)	0 (0)	15 (8)	57 (58)	0 (0)	$*$
Rabbit faeces	8 (25)	42 (100)	0 (0)	20 (31)	30 (92)	0 (0)	$*$

c) West	0-1 m	1-2 m	2-3 m	3-4 m	4-5 m	P
Stick	22 (94)	5 (100)	10 (100)	30 (97)	33 (100)	
Leaf	20 (97)	10 (100)	6 (100)	35 (97)	29 (100)	$*$
Detritus	19 (98)	4 (100)	5 (100)	43 (100)	29 (100)	$*$
Kangaroo faeces	13 (65)	2 (58)	12 (50)	35 (89)	38 (83)	
Sheep faeces	27 (9)	4 (17)	0 (0)	34 (28)	34 (13)	
Rabbit faeces	12 (22)	5 (42)	0 (0)	37 (64)	46 (46)	$*$

Table 3.16: The relative abundances and frequencies (in parentheses) of litter items by the extent of contiguous canopies a) northwards, b) eastwards and c) westwards. a) northwards $n=$ 179 for 0-1 m, $n=$ 24 for 1-2 m, $n=$ 12 for 2-3, 3-4, 4-5, 5-6 and 6-7 m. b) eastwards $n=$ 179 0-1 m, $n=$ 12 2-3, 4-5, 8-9 and 10-11 m, $n=$ 36 for 5-6 m. c) westwards $n=$ 179 for 0-1 m, $n=$ 12 for 1-2 and 2-3 m, $n=$ 36 for 3-4 m, $n=$ 24 for 4-5 m. $*$ indicates that the probability of the frequency and abundance of each type of litter item varying between groups is significant at $P = 0.05$ (Indicator Species analysis, McCune and Mefford (1999)).

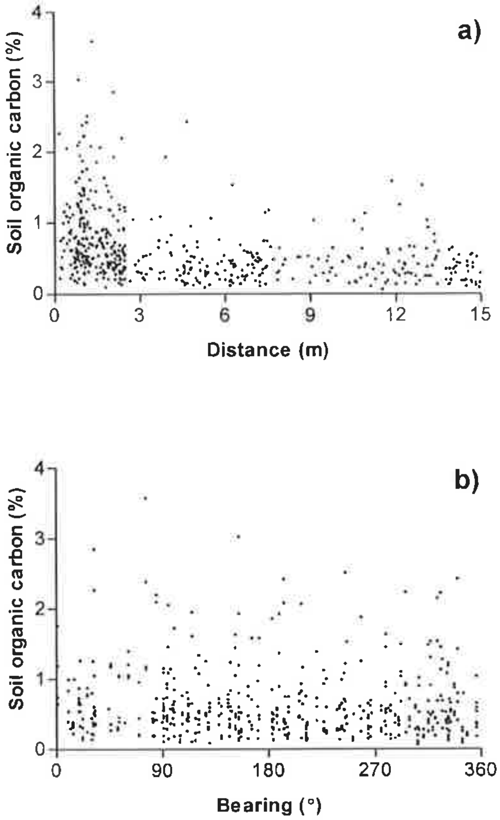


Figure 3.10: Change in soil organic carbon content at 0-10 cm depth with a) distance and b) angle from *A. oleifolius* trunk.

models including canopy measures and canopy with neighbourhood measures accounted for 41.24% and 44.33% of the sample variance respectively. Thus differences in canopy dimensions accounted for much more variation than differences between sites and between neighbourhoods. The factors in the most parsimonious model incorporating neighbourhood measures differed from the canopy measures model only in that site replaced height of canopy base.

Although the so-called "halo" zone of soil nutrient depletion by lateral roots is widely discussed in arid zone literature, I found no evidence of its existence. If *A. oleifolius* were depleting surface soils in the areas beyond the edges of their canopies, then soil resources should be lower a short distance outside the canopy edge than at greater distances from the canopy edge (Figure 3.1), assuming the more distant points were not approaching other trees. Thus I would expect organic carbon levels in zone c (2.5-7.5 m) to be consistently lower than the levels in zone d (7.5-15 m).

This was not the case (Figure 3.10a, Plate 3.13). Although some higher levels were detected at 10-15 m from the trunk, this was usually attributable to the sampling point being close to a site of nutrient accumulation, such as another tree or large shrub. Some soil nutrients, such as calcium and potassium, may not be well correlated with organic carbon. However, the preliminary survey established that organic carbon and total nitrogen were strongly correlated ($r = 0.9014$), while organic carbon and available phosphorus were correlated ($r = 0.5197$) except in the immediate vicinity of the trunk (see Chapter 2.3.3).

3.4 Perennial shrub cover and fertile island development - methods

I wished to investigate the changes to soils, litter levels and understorey plant communities that occur as *A. oleifolius* grow. I used canopy height, basal canopy height and maximum canopy radius as the measures of tree growth and persistence. I calculated a measure of perennial shrub cover by summing the frequency scores for *A. stipitata, A. vesicaria, E. tomentosa, M. pyramidata* and *R. spinescens*. I then calculated the medians of perennial shrub cover, soil organic carbon content, and leaf litter densities from each tree for each sampling zone. Medians were used because I was unable to display variance in three-dimensional graphs and because some of the measures showed skewed distributions. Median shrub cover, median organic carbon and median leaf litter density were plotted against canopy height and canopy radius, or against basal canopy height and canopy radius. These graphical analyses were confirmed with a MANCOVA on $\log_e$ transformed data (shrub cover, organic carbon, stick, leaf and detritus) from zones a and b, with zone and tree nested within site as the factors and canopy height, canopy radius and height of canopy base as covariates. As I did not collect litter from the two outermost zones, shrub cover and organic carbon data from zones c and d were not included in this analysis. I

Source	χ^2 Df	Wald	P(>Wald)
a) $r^2 = 0.4124$			
Sample distance	1	156.2984	0.0000
Sample angle	1	7.9579	0.0048
Canopy shape	5	41.0193	0.0000
Radius of canopy base	1	11.4745	0.0007
Height of canopy base	1	5.0807	0.0242
b) $r^2 = 0.4433$			
Sample distance	1	169.7376	0.0000
Sample angle	1	5.5760	0.0182
Site	3	130.6826	0.0000
Canopy shape	5	11.2818	0.0008
Radius of canopy base	1	24.6369	0.0000

Table 3.17: a) Regression of soil organic carbon content by sample location and canopy characteristics. The line of best fit is given by *log_e organic carbon = -1.3057 - 0.0629 Sample distance - 0.0007 Sample angle + Canopy shape + 0.0777 Radius of canopy base + 0.7599 Height of canopy base* where the Canopy shape constants are: spherical = -0.2373, inverted cone = 0.1407, cone = 0.0691, cylindrical = 0.0387, hemispherical = -0.0314, other = 0. (S-Plus 2000 (MathSoft, 1999), Robust Linear MM Regression (MathSoft, 2000)). b) Regression of soil organic carbon content by sample location, canopy and site characteristics. The line of best fit is given by *log_e organic carbon = -0.3327 - 0.0638 Sample distance - 0.0006 Sample angle + Canopy shape + Site + 0.0312 Radius of canopy base* where the Site constants are: Reserve A = -0.4231, Reserve B = 0.0782, South Lake = 0.0958 and Koonamore Cross = 0; while the Canopy shape constants are: spherical = 0.0109, inverted cone = 0.0147, cone = 0.0231, cylindrical = 0.0731, hemispherical = -0.0279, other = 0. (S-Plus 2000 (MathSoft, 1999), Robust Linear MM Regression (MathSoft, 2000)).

tested for interactions between zone and each of the covariates, iteratively removing non-significant terms.

In order to more clearly visualise the changes associated with tree size, I plotted perennial shrub cover, organic soil content and leaf litter density against tree height for each site. I excluded trees that had neighbours within 3 metres of their trunks from one set of plots to determine whether or not these measures were affected by the proximity of other trees. I plotted untransformed data to better illustrate the trends: the error bars should be regarded cautiously as the data are not normally distributed.

3.4.1 Two-phase nutrient accumulation model - methods

The results of the above analyses suggested a new hypothesis regarding the creation of fertile islands by woody perennials, that I shall refer to as the two-phase model of nutrient accumulation. In the first phase, in which there are low levels of standing litter and little change in soil nutrients, tree canopies grow until they are large enough to increase the density of perennial shrubs through habitat amelioration. Then, during the second stage, the shrubs trap and retain plant litter, localising nutrient cycling processes and resulting in an overall increase in soil resource levels. To test this hypothesis, I conducted a series of ANOVAs in which I treated the data from all the trees within each site as having come from a single individual at each site over time. This space-for-time substitution was effectively a notional repeated measures experiment, so I used site as a random effect in each of the ANOVAs. I first tested the relationship between canopy height and $\log_e$ shrub cover. The initial model was site, canopy height nested within site, zone nested within site and height$*$zone. Non-significant terms were iteratively removed. I then tested whether canopy height and $\log_e$ shrub cover could explain the variation in $\log_e$ organic carbon and $\log_e$ leaf density. The initial models for these ANOVAs were site, canopy height nested within site, zone nested within site, $\log_e$ shrub cover nested within site, canopy radius nested within site, and the interactions between $\log_e$ shrub cover and canopy height, canopy radius and zone. Note that data from zones a and b only were used because I did not have litter data for zones c and d.

In these analyses I used canopy height as an analogue of duration of occupation by a single tree growing at each of four given sites. In order to examine the changes that occur during the life of a tree I conducted *post hoc* contrasts between canopy height within each site for each of the four response variables ($\log_e$ shrub cover, leaf density, detritus density and organic carbon). This necessitated treating canopy height as a categorical factor in the analyses rather than as a covariate. The $\log_e$ shrub cover contrasts were conducted following an ANOVA as described above. However, the remaining contrasts required slightly different models, as the number of degrees of freedom changed as a result of altering the way that canopy height was represented in the models. Thus, in the cases of $\log_e$ leaf density, $\log_e$ detritus density and $\log_e$ organic carbon, *post hoc* contrasts were made following an ANOVA with site, zone nested within site, canopy height nested within site, $\log_e$ shrub cover and canopy radius as the factors. Site was treated as a random effect, and canopy radius was a covariate.

3.5 Perennial shrub cover and fertile island development - results

Log_e shrub cover, organic carbon, leaf density, stick density and detritus densities varied with canopy height, canopy radius and height of canopy base (Table 3.18). They also differed between zones a and b. Median perennial shrub cover below canopies began to increase when the canopies reached a height of about 3.5 m (Plates 3.5 and 3.6). There were also indications that median shrub cover declines in the region closest to the tree trunk as height approaches 5 m. Median leaf litter density and soil organic carbon content below canopies also showed sudden increases once the 3.5 m height threshold was exceeded. These patterns decreased with distance

Source	Value	F	DF Num	DF Den	Prob>F
Whole Model	1.8299	6.0471	105	1100	0.0000
Intercept	0.1627	8.3915	5	216	0.0000
Tree[Site]	1.4740	5.4099	85	1100	0.0000
Zone	0.1699	8.8453	5	216	0.0000
Canopy height	0.1130	5.5061	5	216	0.0001
Canopy radius	0.1078	5.2213	5	216	0.0002
Height of canopy base	0.1246	6.1486	5	216	0.0000

Table 3.18: MANCOVA (SAS Institute, 1997) on $\log_e$ shrub cover, $\log_e$ organic carbon, $\log_e$ stick density, $\log_e$ leaf density and $\log_e$ detritus densities. F values are for Pillai's trace using an identity matrix. Canopy height, canopy radius and height of canopy base are covariates.

from the trunk. They are most pronounced in zones a (0-1.2 m) and b (1.2-2.5 m), less distinct in zone c (2.5-7.5 m) and barely detectable in zone d (7.5-15 m) (Plates 3.5, 3.6, 3.7 and 3.8).

Log_e shrub cover, organic carbon, leaf density, stick density and detritus densities also varied between trees within sites (Table 3.18). Shrub cover at the Reserve B and South Lake sites was lower than at the Reserve A and Koonamore Cross sites (Plates 3.9 and 3.10), and consistently low under trees less than 3.5 m high. Within 1.2 m of the trunk, shrub cover increased as canopy height increased beyond 3.5 m up to about 4.5 m, but then generally declined, whereas in zone b (1.2-2.5 m) it tended to continue increasing with canopy height. Further from the trunk in zones c and d (2.5-15 m), shrub cover showed less variability with canopy height with the exception of the largest trees at the Reserve A and Koonamore Cross sites. Shrub cover under trees with neighbours within 3 m was usually higher in zones a and b than under trees without near neighbours.

Leaf litter densities within 2.5 m of the trunk showed a general increase with

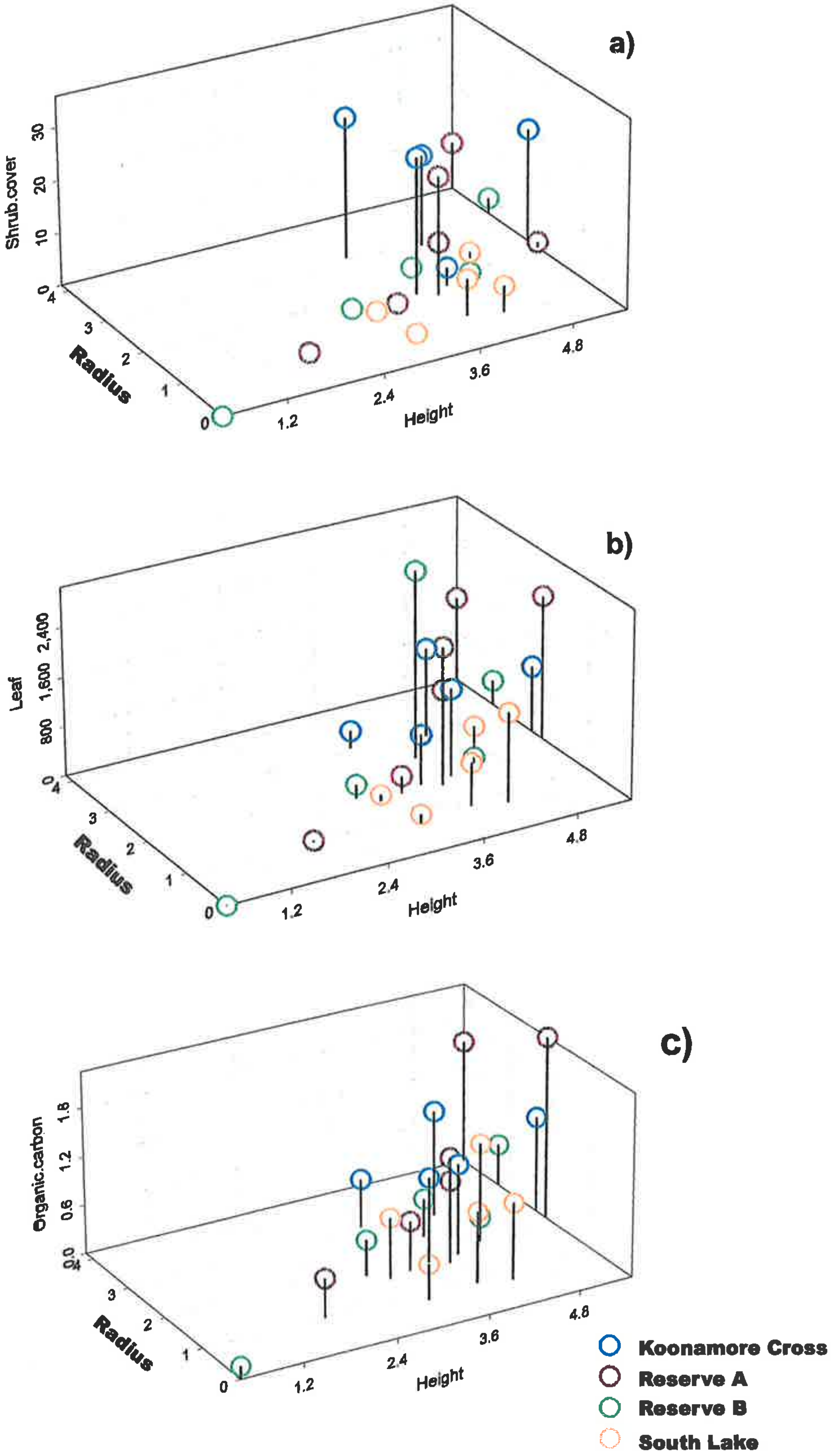


Plate 3.5 - Changes to median a) perennial shrub cover frequency, b) leaf litter density (g m^{-2}) and c) organic carbon concentration (%) under *A. oleifolius* canopies within 1.2 m of the trunk (zone a) with respect to canopy height and canopy radius.

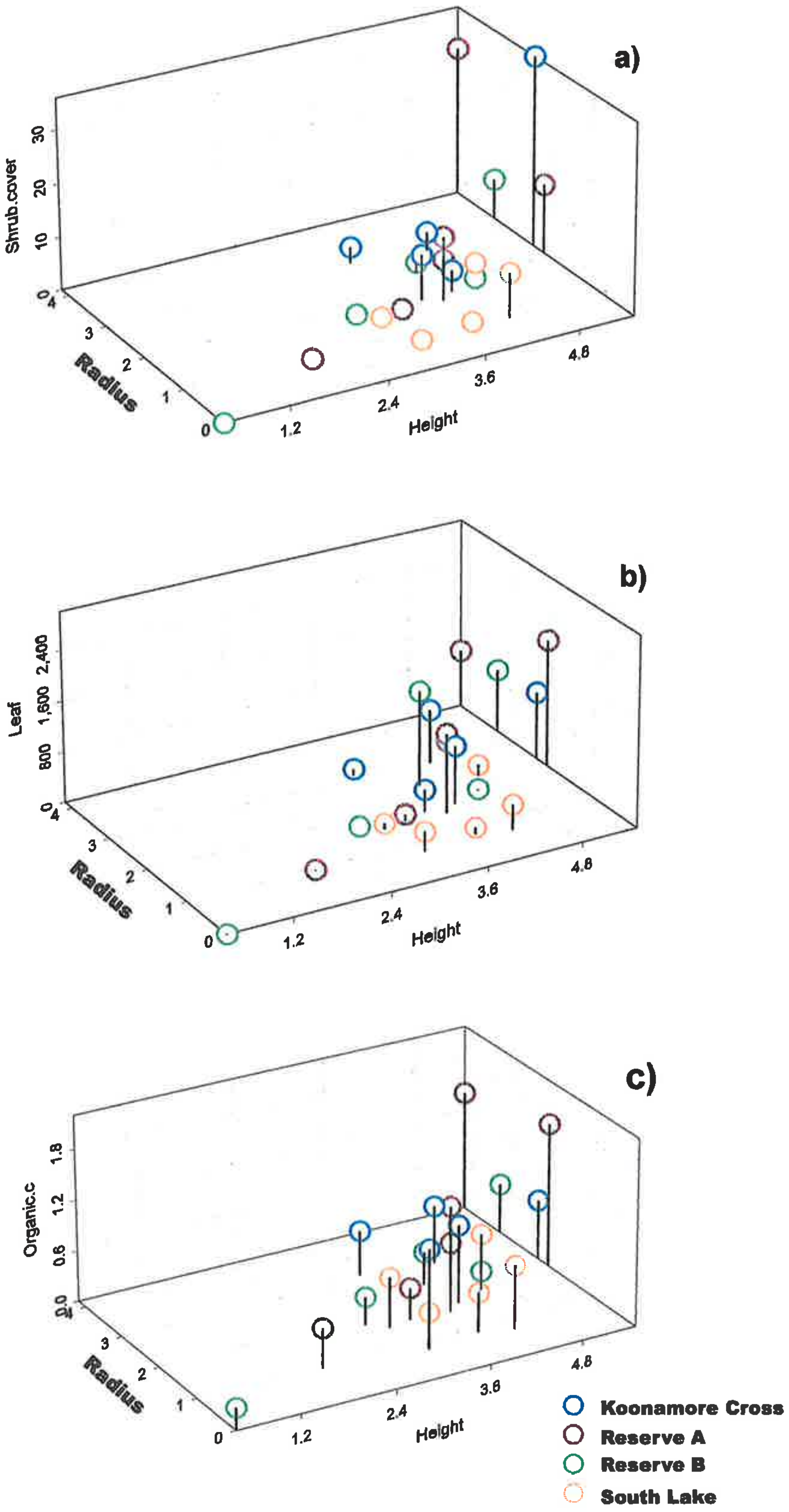


Plate 3.6 - Changes to median a) perennial shrub cover frequency, b) leaf litter density (g m^{-2}) and c) organic carbon concentration (%) under *A. oleifolius* canopies between 1.2 and 2.5 m of the trunk (zone b) with respect to canopy height and canopy radius.

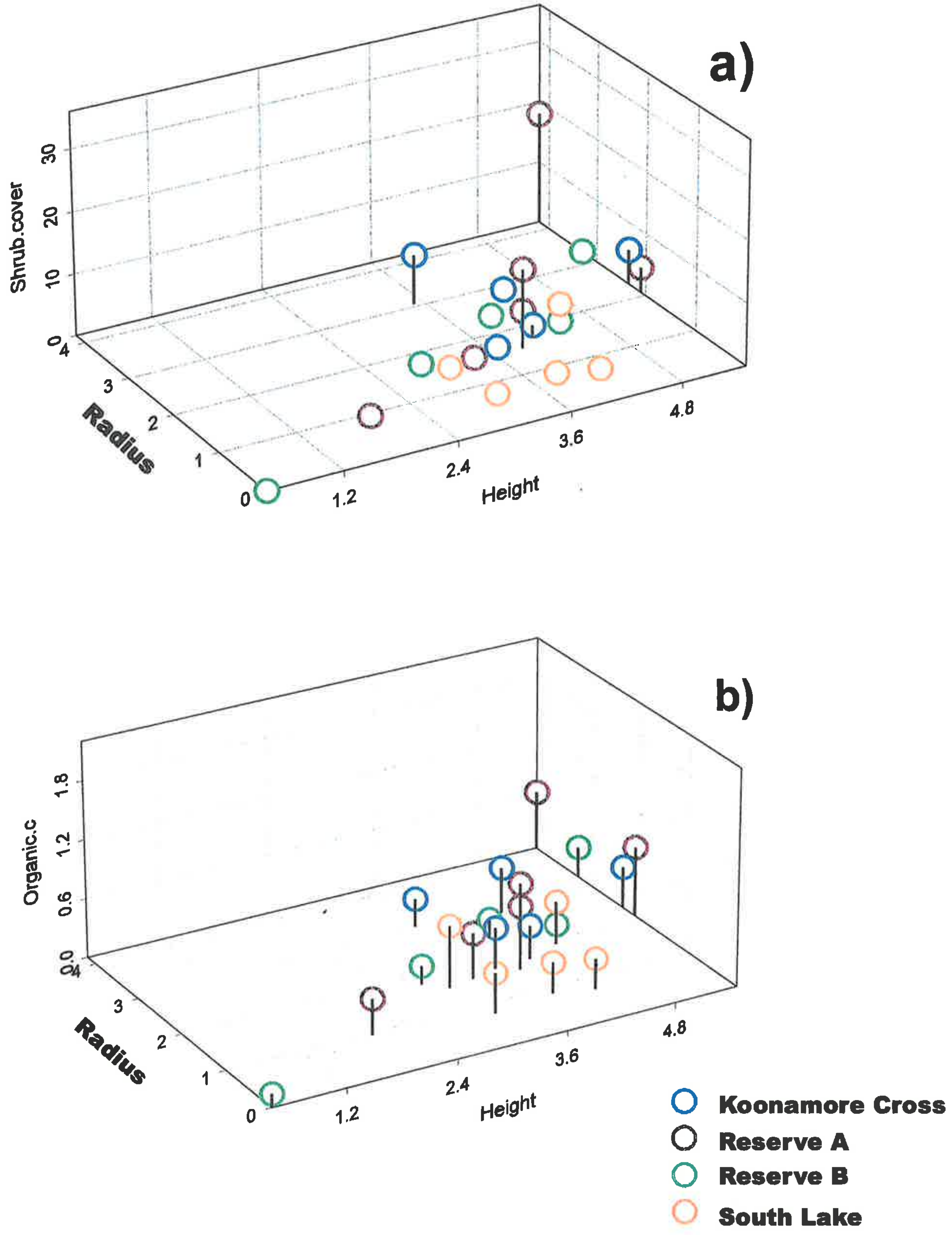


Plate 3.7 - Changes to median a) perennial shrub cover frequency and b) organic carbon concentration (%) under *A. oleifolius* canopies between 2.5 and 7.5 m of the trunk (zone c) with respect to canopy height and canopy radius.

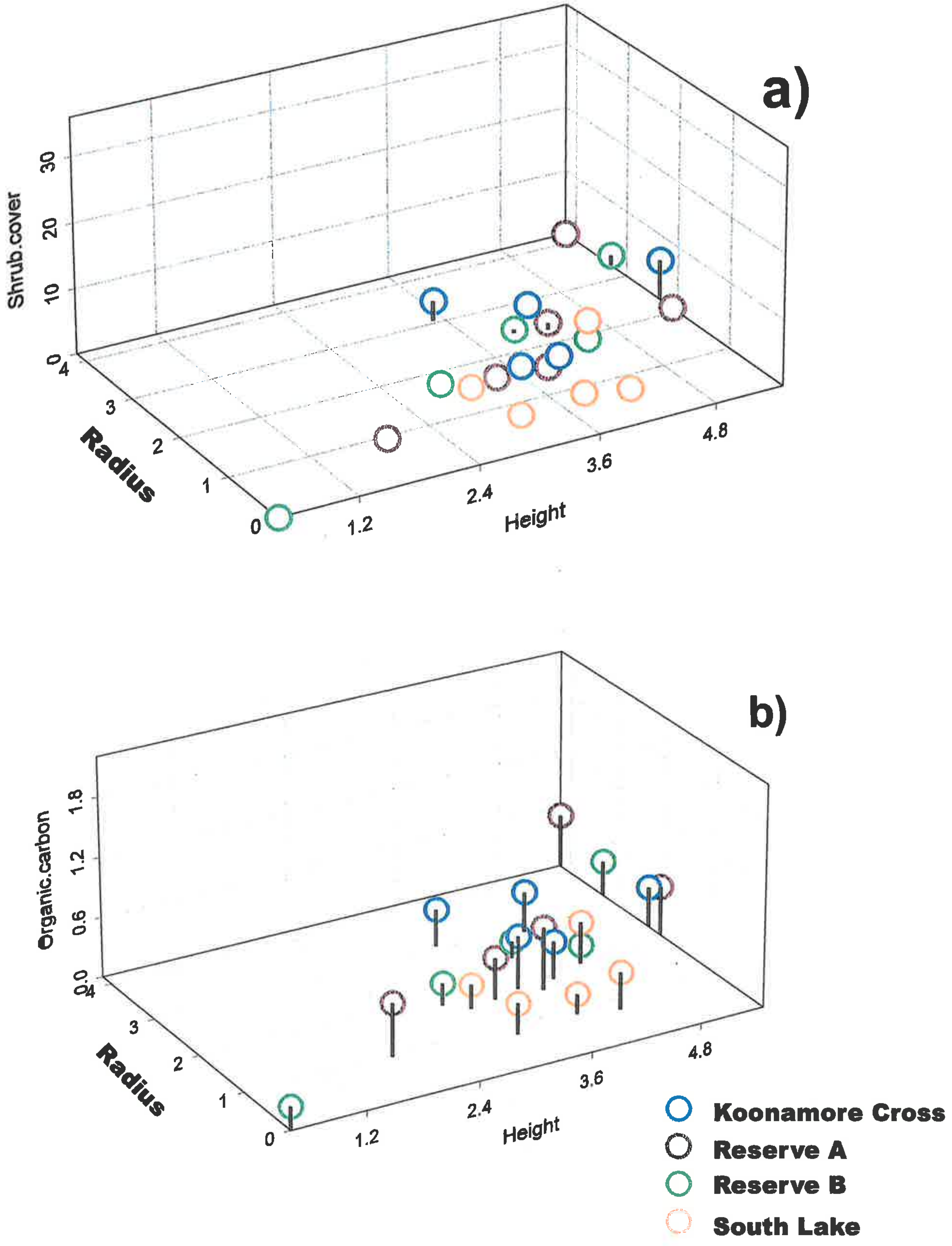


Plate 3.8 - Changes to median a) perennial shrub cover frequency and b) organic carbon concentration (%) under *A. oleifolius* canopies between 7.5 and 15 m of the trunk (zone d) with respect to canopy height and canopy radius.

Source	SS	DF	F	Prob > F
$\log_e$ Shrub cover	$r^2 = 0.3496$			
Site	109.951	3	30.0079	<0.0001
Zone[Site]	80.9263	12	5.5216	<0.0001
Canopy height[Site]	101.191	16	5.1782	<0.0001

Table 3.19: Repeated measures ANOVA (SAS Institute, 1997) of the effect of canopy height on $\log_e$ perennial shrub cover, using site as a random effect. Data from trees of differing height at each site were analysed as though they had been obtained from one tree per site at different times.

increasing canopy height, with some suggestion that they may be approaching an asymptotic limit as canopy height exceeds 4.5 m (Plates 3.11 and 3.12). Again, litter densities under trees with near neighbours appear to be higher than under trees of similar height without near neighbours. Organic carbon concentrations (Plates 3.13 and 3.14) show trends closely resembling those of leaf litter density, with little indication of any relationship between canopy height and organic carbon in the outer zones (2.5-15 m).

3.5.1 Two-phase nutrient accumulation model - results

Log_e shrub cover in zones a and b differed between canopy heights within sites (Table 3.19, Plates 3.15). The highest levels of shrub cover occurred under the tallest canopies, except at South Lake where the second tallest canopy had the highest shrub cover (Plate 3.15). The lowest levels of shrub cover were found under the lowest canopies, except at Reserve B.

Log_e shrub cover also differed between sites (Table 3.19). Cover was greatest at Koonamore Cross, followed by Reserve A while South Lake and Reserve B had the least shrub cover (Table 3.20).

	Reserve B	South Lake	Koonamore Cross
Reserve A	0.0000*	0.0000*	0.0075*
Reserve B		0.4612	0.0000*
South Lake			0.0000*

Table 3.20: *Post hoc* contrasts of $\log_e$ shrub cover by site. Asterisks denote significant comparisons at the critical alpha level $\alpha' = 0.0085$.

Log_e leaf density differed with canopy height and canopy radius (Table 3.21a, Plate 3.15). More importantly, it also changed with $\log_e$ shrub cover, indicating that site and canopy dimensions alone are insufficient to fully explain the variation in leaf litter density. Leaf density was lowest when canopy height was smallest, except at South Lake where there were no differences between canopy heights, and highest under the tallest canopies (Plate 3.15).

Log_e detritus density showed similar patterns of change with canopy dimension and shrub cover to $\log_e$ leaf density, but the changes with canopy height and shrub cover were not independent of each other (Table 3.21b, Plate 3.16). This suggests an interaction between the processes of litter production and retention, and the processes of litter decomposition. The order of differences in detritus density closely follows that of leaf density at all sites except South Lake (Plate 3.16). Detritus density was greatest when canopy height was greatest (Reserve A and B) or second greatest (South Lake and Koonamore Cross), and lowest under the shortest canopies (Plate 3.16).

Log_e organic carbon levels varied with canopy height and radius, but did not change with shrub cover (Table 3.21c, Plate 3.16). Organic carbon levels were greatest under the tallest canopies at each site except Koonamore Cross, where the highest levels occurred under the second tallest canopy (Plate 3.16). However, equally high levels were found under the shortest tree at South Lake, and relatively low levels were

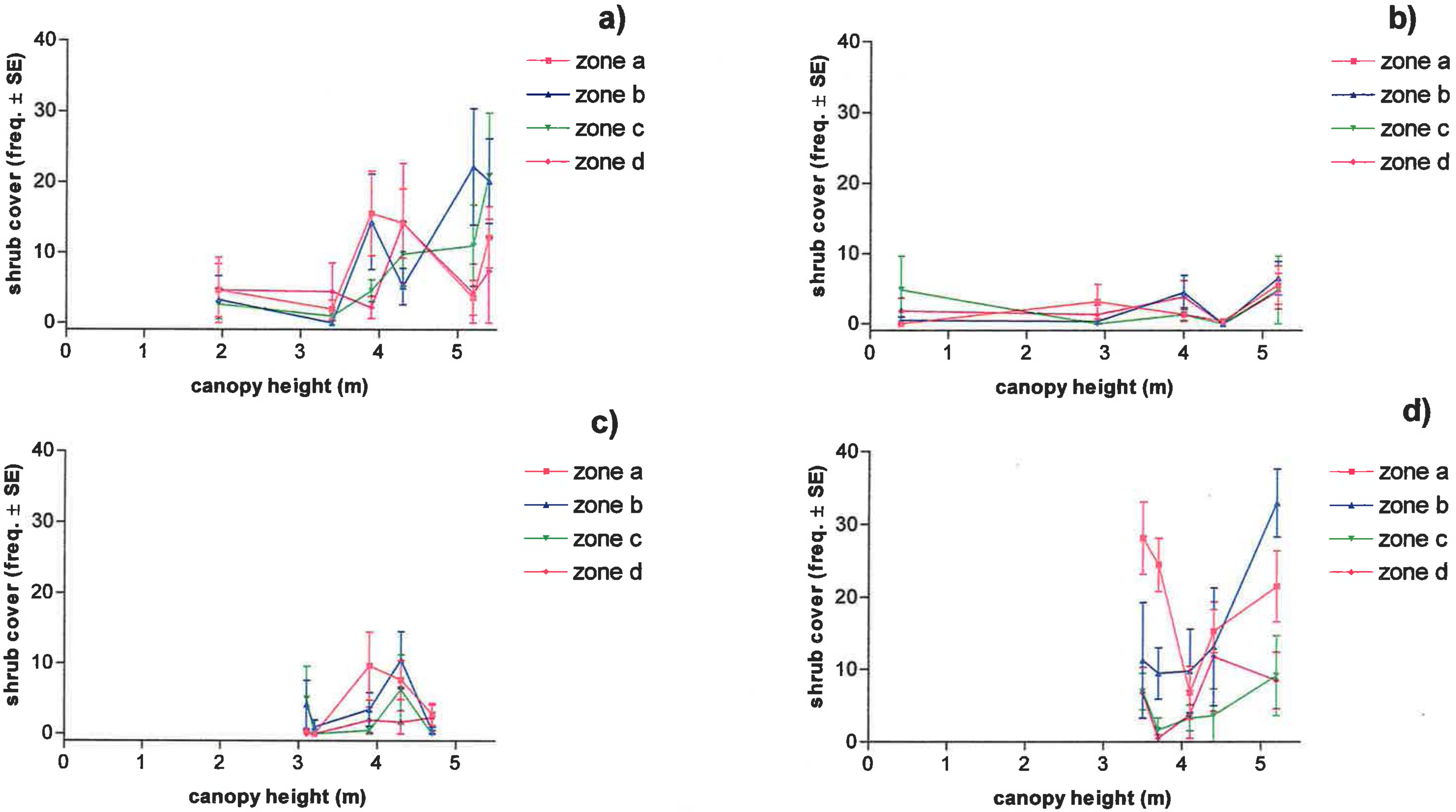


Plate 3.9 - Changes in shrub cover frequency with tree height at four distances from A. oleifolius tree trunks. a) Reserve A, b) Reserve B, c) South Lake and d) Koonamore Cross. Zone a = 0-1.2 m from trunk, zone b = 1.2-2.5 m, zone c = 2.5-7.5 m, zone d = 7.5-15 m. n = 6 at the Reserve B, South Lake and Koonamore Cross sites. n = 5 at the Reserve A site except for the 1.95 m tree, where n = 6.

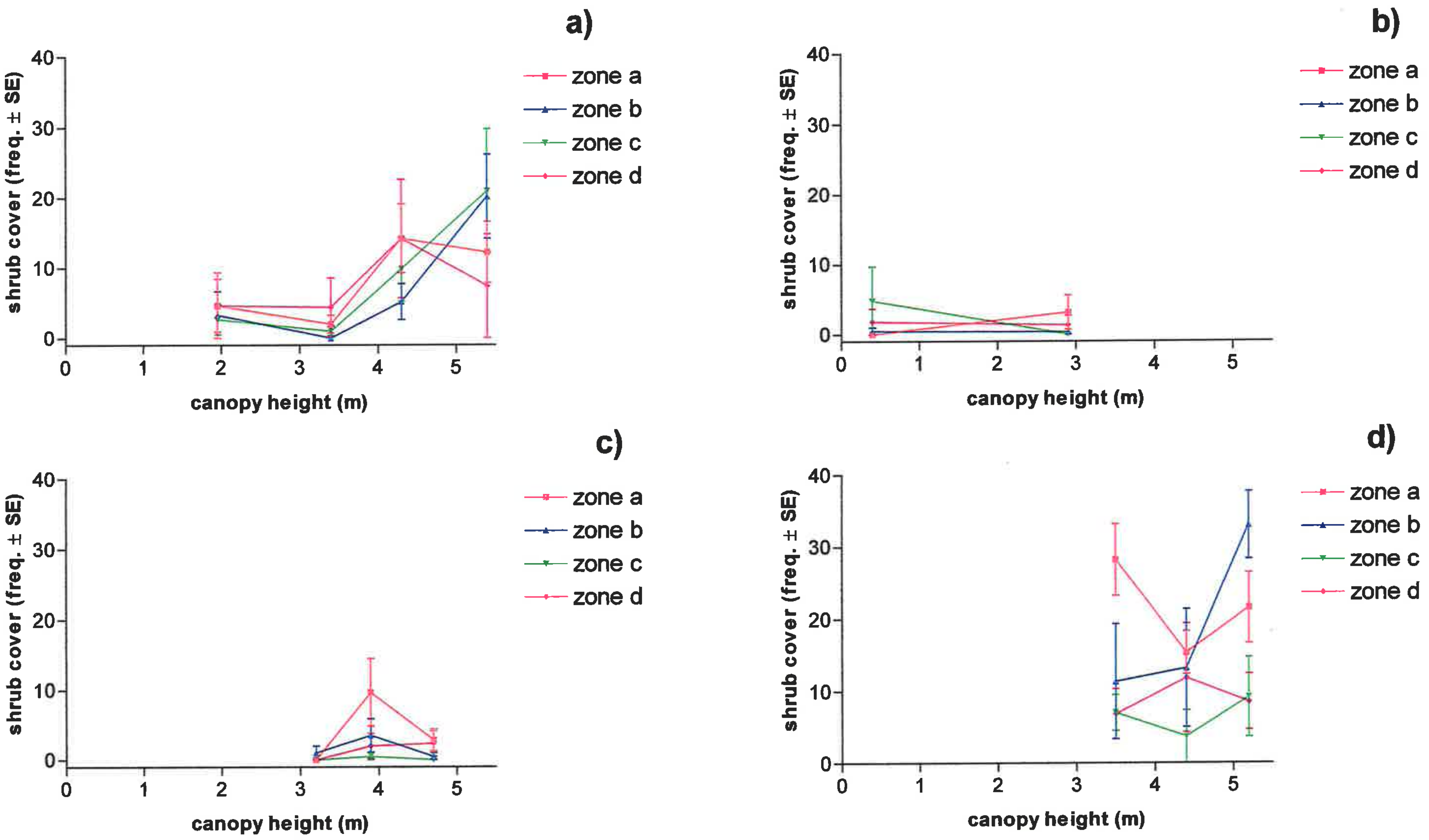


Plate 3.10 - Changes in shrub cover frequency with tree height at four distances from A. oleifolius tree trunks. Trees with neighbours less than 3 m from the trunk are excluded. a) Reserve A, b) Reserve B, c) South Lake and d) Koonamore Cross. Zone a = 0-1.2 m from trunk, zone b = 1.2-2.5 m, zone c = 2.5-7.5 m, zone d = 7.5-15 m. n = 6 at the Reserve B, South Lake and Koonamore Cross sites. n = 5 at the Reserve A site except for the 1.95 m tree, where n = 6.

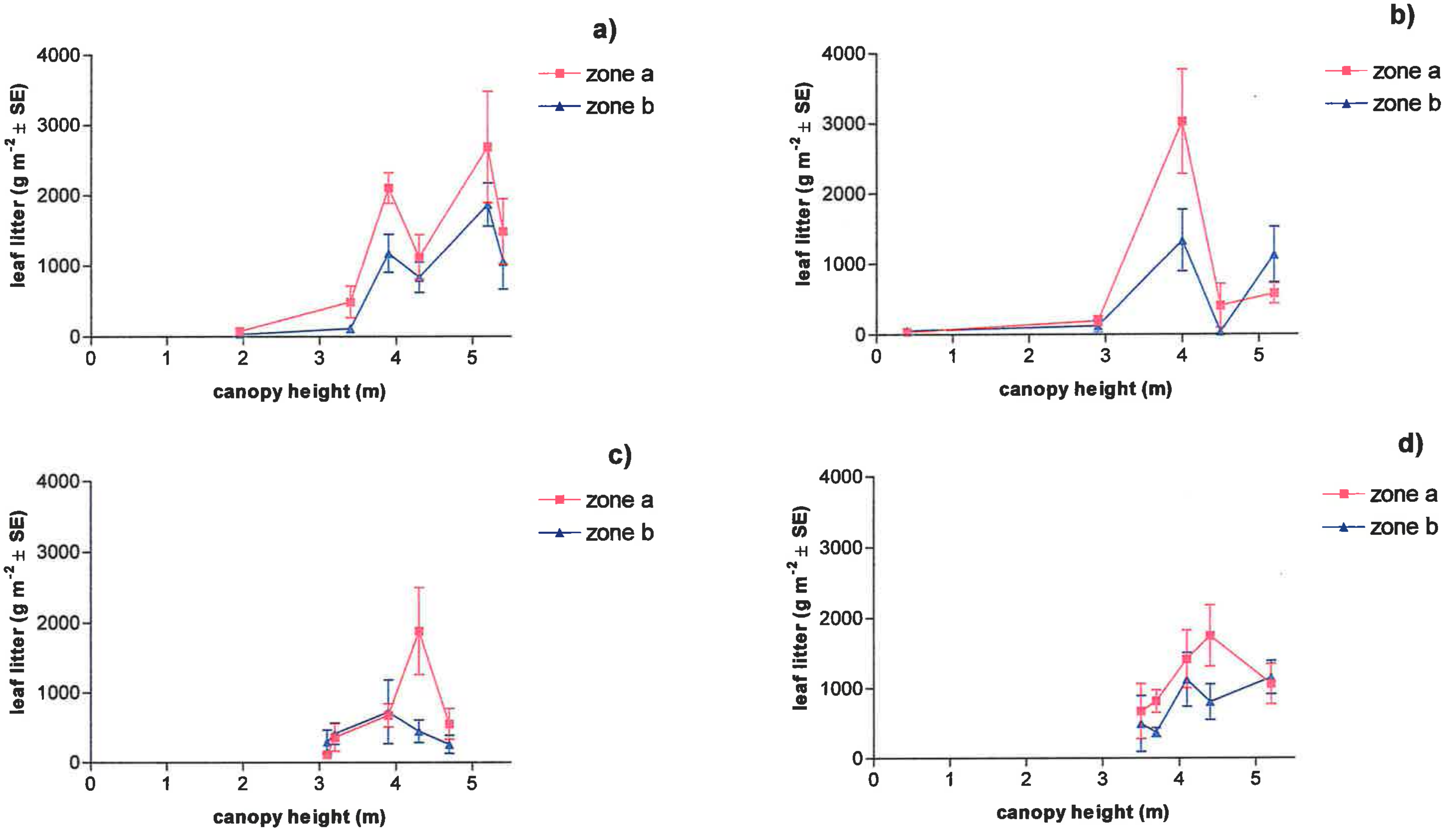


Plate 3.11 - Changes in the leaf component of plant litter with tree height at two distances from A. oleifolius tree trunks. a) Reserve A, b) Reserve B, c) South Lake and d) Koonamore Cross. Zone a = 0-1.2 m from trunk, zone b = 1.2-2.5 m. (n = 6).

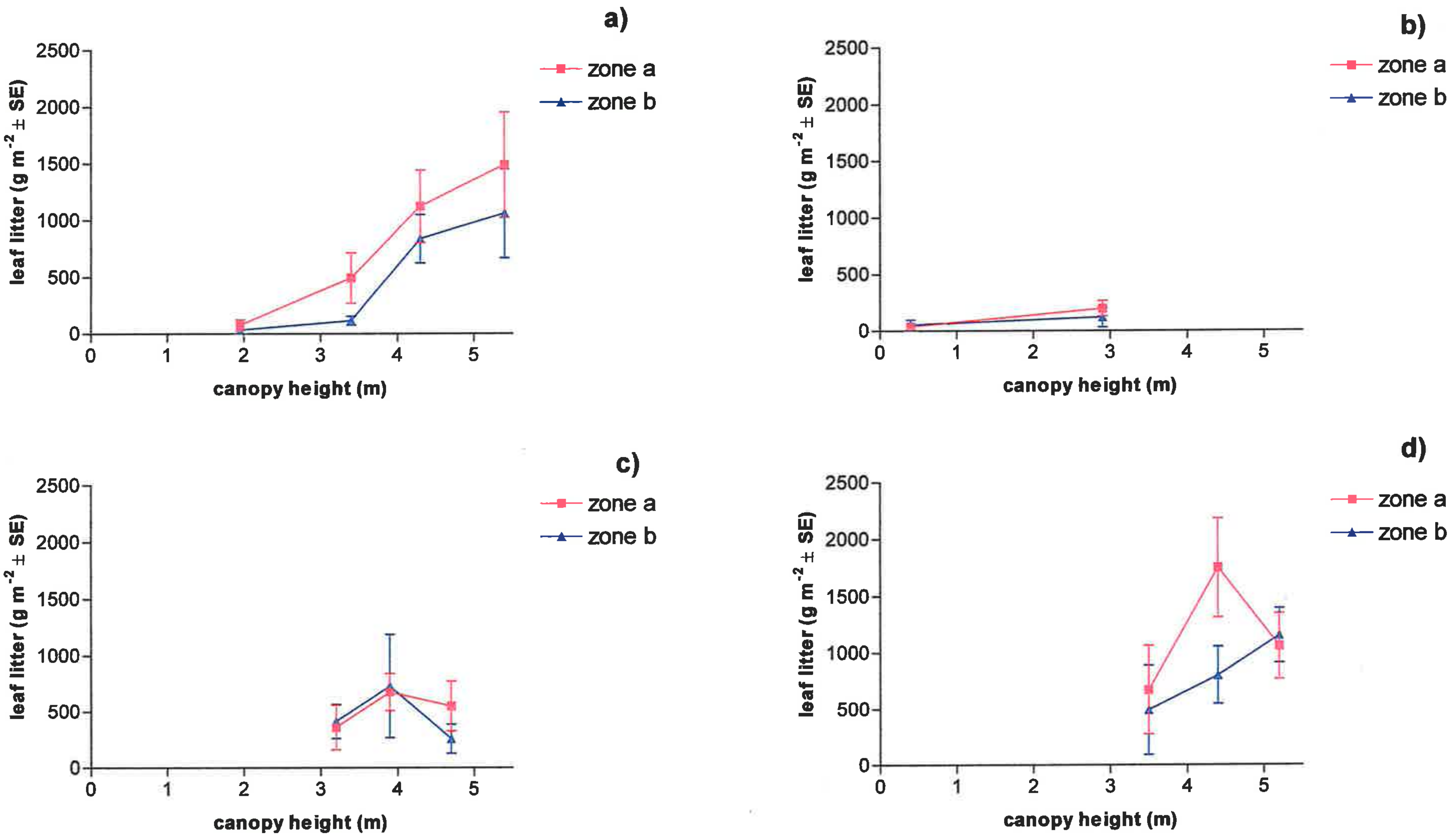


Plate 3.12 - Changes in the leaf component of plant litter with tree height at two distances from A. oleifolius tree trunks. Trees with neighbours less than 3 m from the trunk are excluded. a) Reserve A, b) Reserve B, c) South Lake and d) Koonamore Cross. Zone a = 0-1.2 m from trunk, zone b = 1.2-2.5 m. (n = 6).

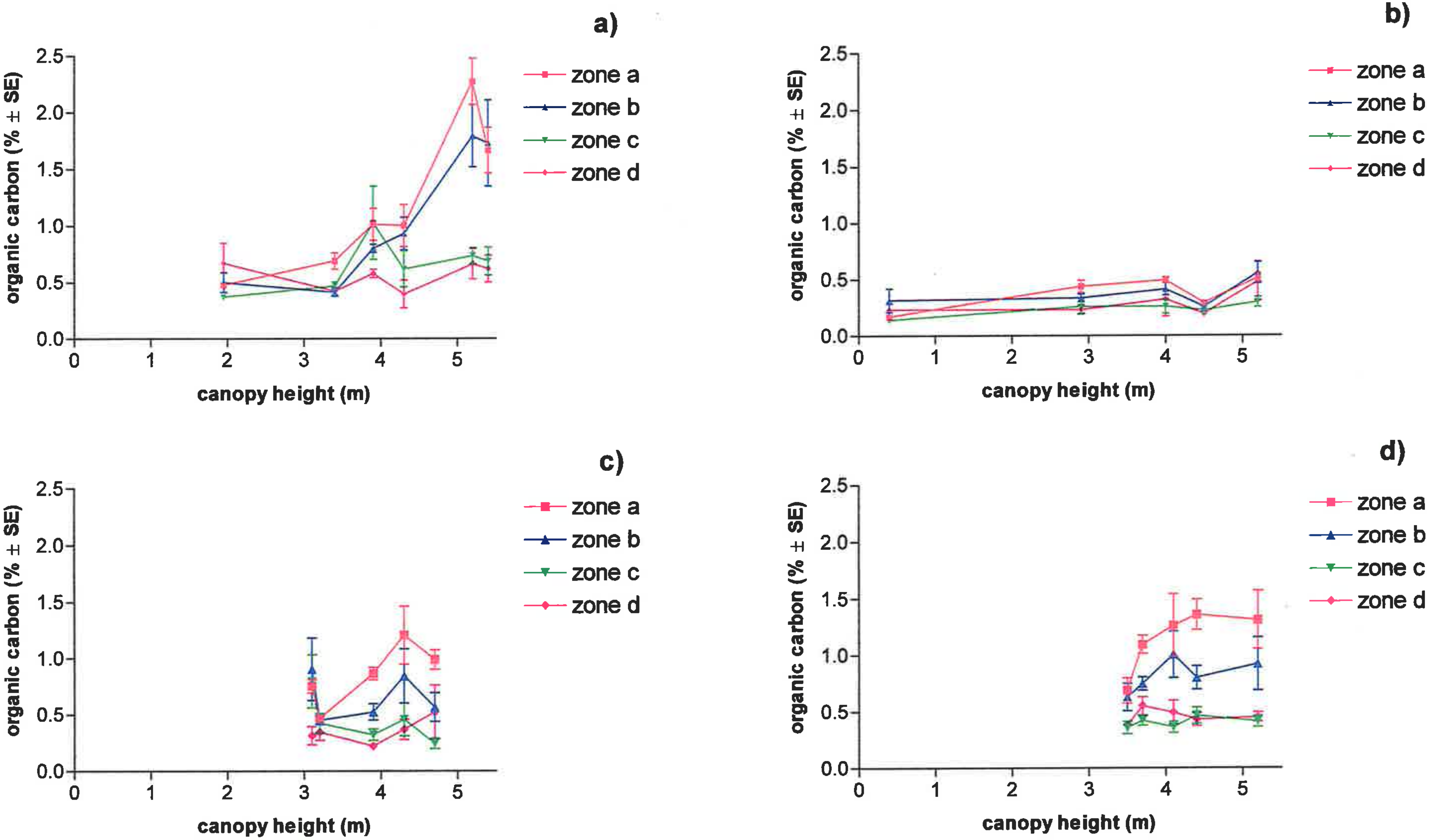


Plate 3.13 -Changes in organic carbon content with tree height at four distances from A. oleifolius tree trunks. a) Reserve A, b) Reserve B, c) South Lake and d) Koonamore Cross. Zone a = 0-1.2 m from trunk, zone b = 1.2-2.5 m, zone c = 2.5-7.5 m, zone d = 7.5-15 m. (n = 6).

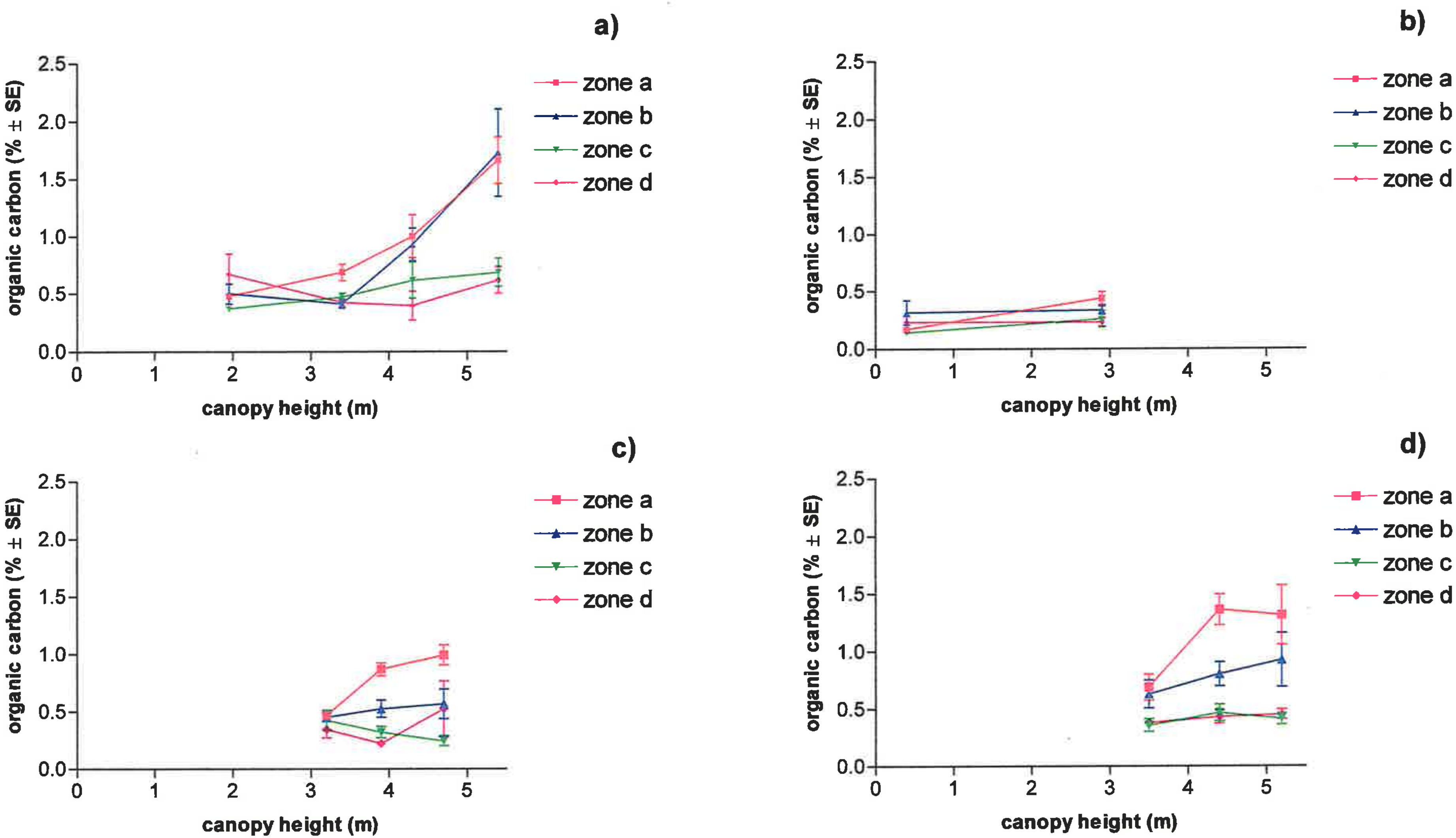


Plate 3.14 - Changes in soil organic carbon content with tree height at four distances from A. oleifolius tree trunks. Trees with neighbours less than 3 m from the trunk are excluded. a) Reserve A, b) Reserve B, c) South Lake and d) Koonamore Cross. Zone a = 0-1.2 m from trunk, zone b = 1.2-2.5 m, zone c = 2.5-7.5 m, zone d = 7.5-15 m. (n = 6).

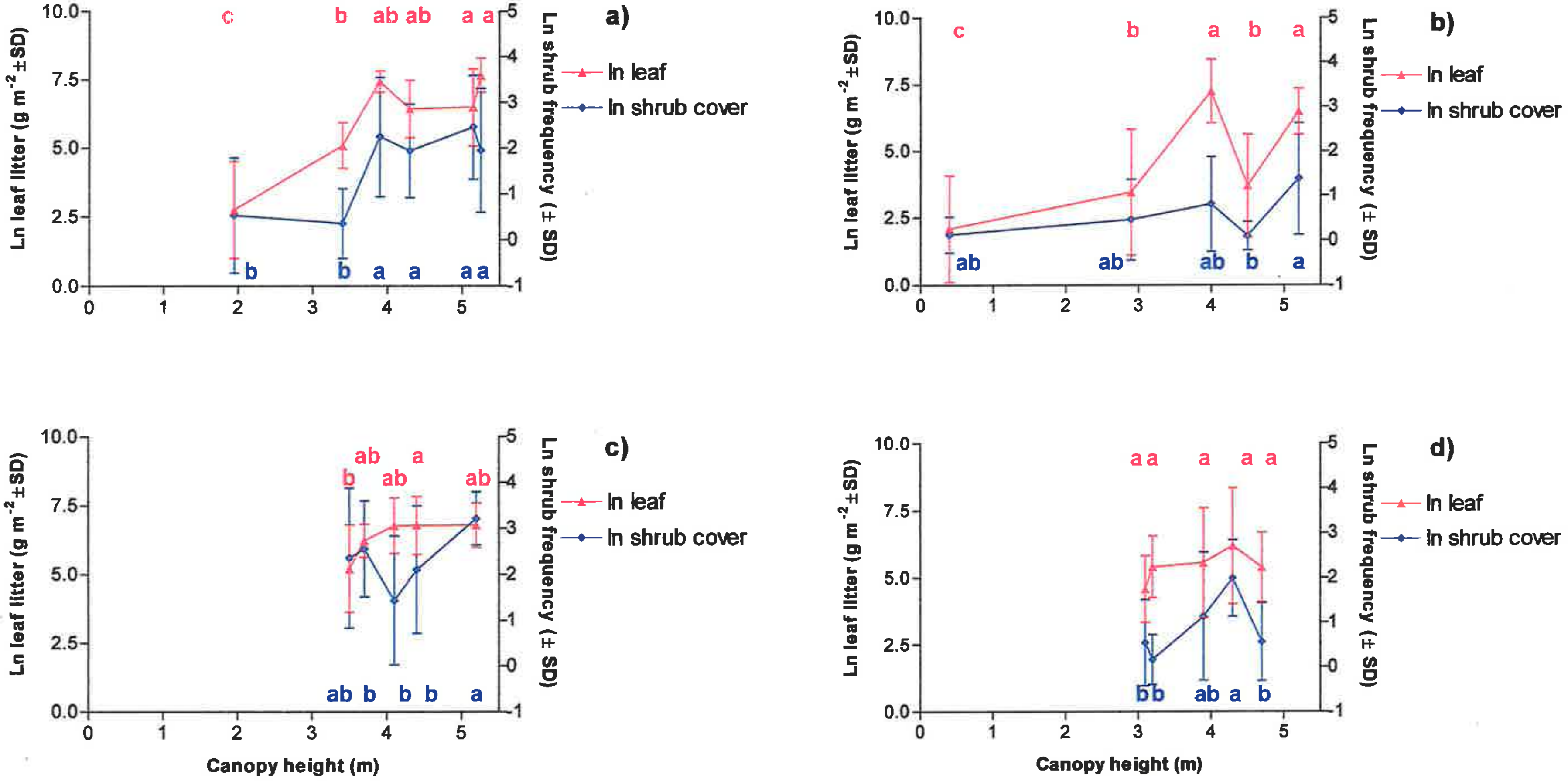


Plate 3.15 - Leaf litter density (red) and shrub cover (blue) 0-2.5 m from trunk under *A. oleifolius* canopies of differing heights. a) = Reserve A, b) = Reserve B, c) = Koonamore Cross and d) = South Lake. Shared lower case letters indicate that heights do not differ (Post hoc contrasts following repeated measures ANOVA, space-for-time substitution).

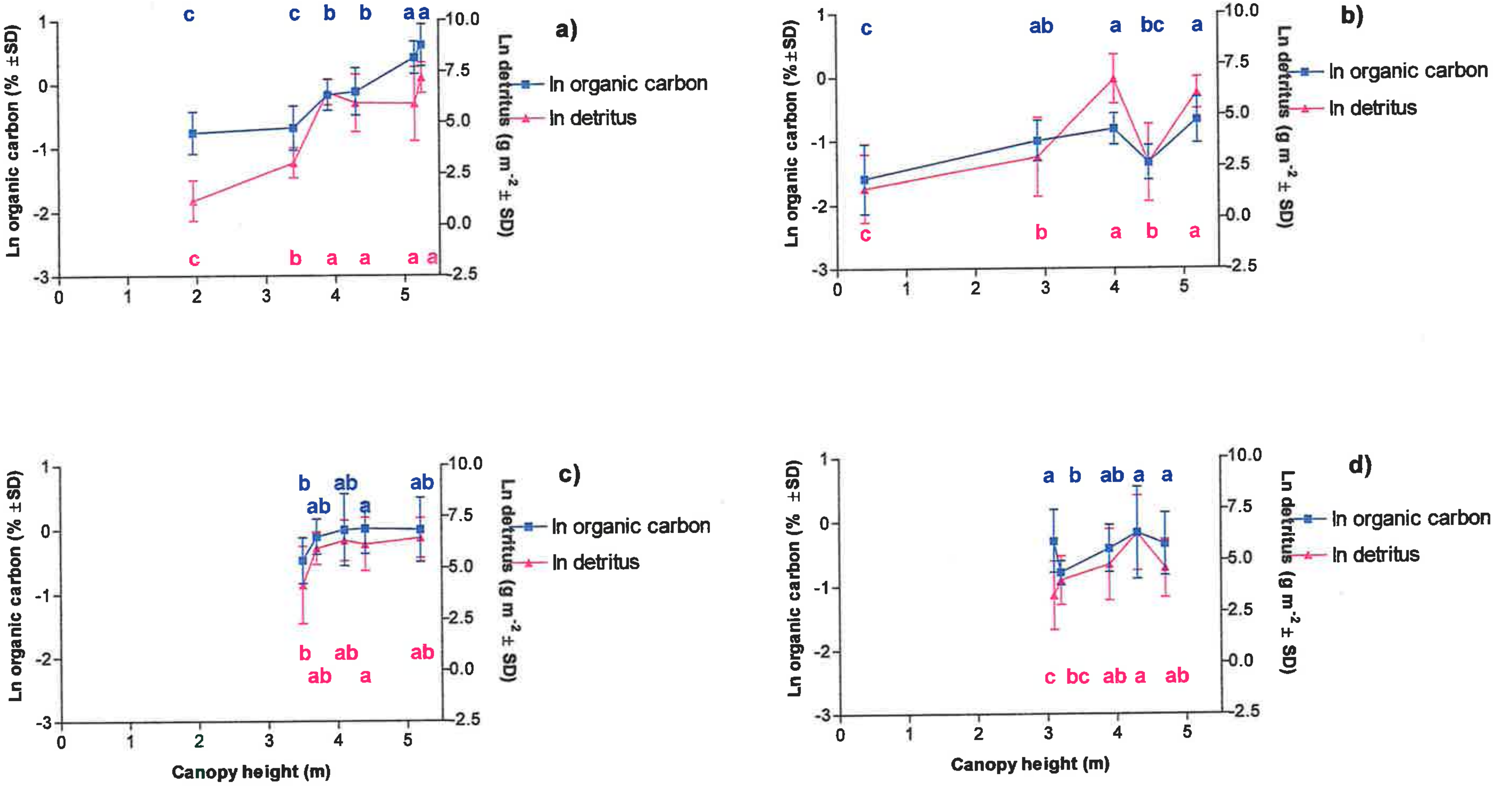


Plate 3.16 - Detritus density (magenta) and soil organic carbon (blue) 0-2.5 m from trunk under *A. oleifolius* canopies of differing heights. a) = Reserve A, b) = Reserve B, c) = Koonamore Cross and d) = South Lake. Shared lower case letters indicate that heights do not differ (Post hoc contrasts following repeated measures ANOVA, space-for-time substitution).

Source	**SS**	**DF**	**F**	**Prob > F**
a) $\log_e$ Leaf density	$r^2 = 0.5510$			
Site	24.5694	3	3.9700	0.0088
Zone[Site]	33.5602	4	4.0670	0.0034
Canopy height[Site]	112.922	4	13.6846	<0.0001
Radius[Site]	53.9124	4	6.5334	0.0001
$\log_e$ Shrub cover[Site]	33.8467	4	4.1018	0.0032
$\log_e$ Shrub cover*Zone[Site]	18.1558	4	2.2002	0.0700
b) $\log_c$ Detritus density	$r^2 = 0.6404$			
Site	38.021	3	6.4625	0.0003
Zone[Site]	25.4171	4	3.2401	0.0131
Canopy height[Site]	173.275	4	22.0889	<0.0001
Radius[Site]	103.505	4	13.1946	<0.0001
$\log_e$ Shrub cover[Site]	28.191	4	3.5937	0.0073
$\log_e$ Shrub cover* Canopy height[Site]	19.4366	4	2.4777	0.0451
c) $\log_e$ Organic carbon	$r^2 = 0.6442$			
Site	1.4748	3	3.0598	0.0291
Zone[Site]	3.96093	4	6.1635	0.0001
Canopy height[Site]	7.76596	4	12.0843	<0.0001
Radius[Site]	3.02818	4	4.7120	0.0011
$\log_e$ Shrub cover[Site]	0.93626	4	1.4569	0.2163

Table 3.21: Repeated measures ANCOVA (SAS Institute, 1997) of the effect of canopy height and perennial shrub cover on a) $\log_e$ leaf litter density, b) $\log_e$ litter detritus density and c) $\log_e$ soil organic carbon content. Site was declared a random effect. Data from trees of differing height at each site were analysed as though they had been obtained from one tree per site at different times.

found under the second tallest canopy at Reserve B.

3.6 Discussion

The results of this survey establish that *A. oleifolius* is associated with substantial spatial heterogeneity in leaf litter density, in the composition of the shrub and forb community, and in the soil organic carbon content. The results further suggest that this heterogeneity is most likely created, through direct and indirect effects, by the presence of *A. oleifolius*. *Enchylaena tomentosa, Rhagodia spinescens* and *Atriplex vesicaria* were much more abundant under trees than in the open, while *Eriochiton sclerolaenoides*, grass and bare ground were far more likely to be found outside canopy areas, indicating that canopy habitats may help maintain biodiversity at the paddock scale. Both litter densities and soil organic carbon content increase along the gradient from open space to *A. oleifolius* trunks, while perennial shrub cover rises.

The differences between canopy and open habitats that are described conform closely to those that have been reported elsewhere (Tester et al., 1987; Vetaas, 1992; Dean et al., 1999; Facelli and Brock, 2000). Perhaps the most surprising results were the complete absence of *M. sedifolia* from the vegetation samples, and the greater abundance of *Atriplex vesicaria* under trees. *Maireana sedifolia* sometimes occurred within tens of metres of my sites (*pers. obs.*), but was never in close proximity to *A. oleifolius*. This is in contrast to its distribution in a similar system at Middleback Station, where *M. sedifolia* and *A. vesicaria* are common in both open spaces and under the canopies of *Acacia papyrocarpa*, a tree somewhat larger than *A. oleifolius* (Facelli and Brock, 2000).

These results add to the body of evidence supporting the ubiquity of the habitat changes associated with the presence of woody perennials. Of greater interest, however, is that the data indicate that these changes are cumulative; as the trees grow, the differences between under-canopy locations and inter-canopy spaces increase. Such observations are inconsistent with the hypothesis that fertile islands are the consequence of pre-existing heterogeneity in soil resources. Instead, the data are consistent with the hypothesis that fertile islands are generated through biological activity associated with the presence of woody plants.

The results also illustrate the effects of some aspects of canopy structure on plant litter density, soil organic carbon content and plant species composition. In particular, canopy height is associated with these changes, although it is hard to determine whether these are direct effects or whether canopy height is an analogue of time-related cumulative processes. These observations correspond with other studies that have found evidence that woody perennial plants generate heterogeneity in soil resource levels by accumulating nutrients in the soils below their canopies (Pugnaire et al., 1996a; Cheal, 1999; Facelli and Brock, 2000).

Importantly, the difference between open soils and soil adjacent to the trunk also increases with canopy height, indicating that tree size is independent of ambient soil nutrient levels. This too supports the hypothesis that fertile islands are the result of cumulative processes associated with trees. Moreover, the highest levels of plant litter and soil organic carbon are found closest to the trunk. Assuming that canopy height is correlated to tree age, this is consistent with a model in which the tree's sphere of influence expands radially as the tree grows, for the areas that would have been subject to modification for longer periods show larger differences relative to open areas.

Other aspects of canopy morphology appeared to affect nutrient and litter accumulation, as well as influencing plant community composition. There were differences between canopies of differing shapes; unfortunately the lack of replication of some shapes and their confounding with site and canopy height create difficulties in interpreting these results. However, some results appear robust. The confounding factors provide no reason why, for instance, *M. appressa* should be so infrequently associated with inverted cone canopies. Nor do they provide a convincing explanation as to why litter densities tend to be lower under spherical, inverted cone and "other" canopy types than they are under the rest of the canopy types. The height at which the maximum northward canopy radius occurs also appears to be important, particularly for *E. tomentosa, M. appressa* and *R. spinescens.* Plant litter density also increases with the height of the maximum radius, although the close correlation between radius height and canopy height means it is difficult to separate the effects of one from the other.

One of the issues that this survey was intended to resolve was whether habitat modification by canopies directly contributes to the creation of fertile islands and their associated plant communities, or whether canopy size was simply correlated with other age-dependent processes of accumulation and change. The canopy shape-related differences provide some evidence that the former may be the case, but other stronger evidence emerged from the data. Some of the trees I sampled were members of clusters of trees with more or less continuous canopies. Consequently, the physical environment under these trees were determined more by the collective canopy than by the canopy of the tree being sampled. Furthermore, the size of the collective canopy will have little correlation with the age of the individuals that comprise it, especially in stands where the trees are of differing sizes.

The effects of the collective canopy are apparent when comparisons are made with more isolated trees. In general, trees belonging to a cluster tended to have higher leaf litter densities, higher soil organic carbon concentrations and more perennial shrub cover than similarly sized solitary trees. The under-canopy communities had greater abundances of *E. tomentosa* and *Sisymbrium*, and less *Eriochiton sclerolaenoides* and grasses. Plant litter densities showed a generally increasing trend with the size of the collective canopy, rather than with the size of the individual tree, and the below-canopy organic carbon levels were generally higher under trees in clusters than under more isolated canopies.

This could be attributable to two factors. If canopy size is responsible for creating conditions that foster shrub growth and facilitate nutrient accumulation, then adjoining canopies should supplement the effects of the individual canopy. In fact, each individual tree within the group would experience the benefits of habitat modification and amelioration of the larger canopy while only contributing the metabolic costs of generating and supporting a smaller canopy. Alternatively, higher soil resources and shrub cover may be due to the trees falling within the zones of influence of other larger trees within the cluster. If this was the case, the degree of enhancement in comparison to isolated trees would be proportional to the size of adjacent canopies, and inversely proportional to the distance between the trunks. The survey data cannot distinguish between these two possible causes, for although I measured the distance to the trunk of the nearest tree, I did not collect data on the sizes of neighbouring canopies.

One of the difficulties in determining the direct effects, if any, of canopies is that the current state of the below-canopy habitat will be strongly influenced by the history of the occupation of the site. So if canopy size and shape influence the processes that facilitate shrub recruitment and litter and nutrient accumulation, the state at any given time will depend on the effects of both the canopy size and shape at that time, and on the effects of all prior sizes and shapes. The difference between canopy and open habitats could be modelled as the product of the differences in inputs and outputs integrated over the time of occupation. The tractability of this problem may depend on the consistency of a species' growth trajectories.

3.6.1 Two-phase nutrient accumulation model

The survey data provide a provisional picture of the changes that occur through time following the establishment of an *A. oleifolius* sapling, and suggest a model analogous to that proposed by Archer et al. (1988). Initially, soil nutrient levels, leaf litter density and plant species diversity in the vicinity of the sapling are at background levels. Being a slow growing species, little changes for many years. When the tree reaches some 3.5 m, shrubs establish in the shade of the canopy, plant litter accumulates and soil nutrient levels begin to increase. It must be noted, however, that the precise sequence of events and the timescales involved are unclear at this stage. The tree continues to grow, its canopy expanding upwards and outwards, extending its shade zone over a greater area. For a time, shrub density continues to increase. Then the levels of accumulated litter and soil nutrients begin to asymptotically approach their maxima. This is presumably a result of the processes of litter decomposition rates and nutrient leaching equilibrating with litter production and nutrient inputs. There is also some evidence that shrub cover declines sharply. The highest litter densities recorded in this survey were found below large canopies with sparse shrub cover, where the remains of dead shrubs could be found buried under the litter layer. This could be the result of high litter densities preventing the recruitment of new cohorts of shrubs, reduced soil moisture attributable to increased rainfall intercept by the larger canopy or thicker litter layer, increased disturbance from mammals attracted to larger shade patches, or perhaps as a consequence of declining light levels as the canopy grows.

Others have suggested that the elevated nutrient levels found around perennial plants in arid systems are the consequence of passive processes of physical entrapment, such as the capture of airborne dust particles (Whitford et al., 1997) or organic debris transported by sheet water flow (Ludwig and Tongway, 1995). However, Facelli and Brock (2000) emphasised the importance of *in situ* production and retention of organic material, having found changes in soil nutrients associated with biological activity but no change in the concentrations of nutrients typically deposited as airborne dust. I propose a model explaining the creation of fertile islands by *A. oleifolius* in terms of both biological processes and physical capture, where fertile islands are indirectly generated by the tree facilitating the establishment of perennial shrubs. Following establishment, the *A. oleifolius* canopy grows large enough to appreciably modify the under-canopy environment, providing better establishment opportunities for several shrub species. Other factors, such as climatically-driven recruitment events or some modest level of litter accumulation, may also play a part, but adequate canopy size appears to be a pre-requisite. Once shrubs establish in the shade of the canopy, plant litter accumulates either through higher levels of litter retention or through higher site productivity, and soil nutrient levels increase, creating the fertile island. This continues until litter levels reach a point where they induce shrub recruitment failure. As the existing shrubs senesce and die, rates of litter retention or production fall. Ultimately litter density declines to levels that permit shrub recruitment to recommence, and the cycle of accumulation begins anew. Due to its longer retention time (Vinton and Burke, 1995; van Breeman and Finzi, 1998) and continued inputs from litter decay, soil organic carbon levels do not show pronounced oscillations.

This model, linking processes of shrub proliferation, litter accumulation and nutrient enrichment, is supported by the observed effects of grazing on plant communities and organic carbon levels. Trees at the heavily grazed South Lake site had lower shrub cover and lower litter densities than similarly-sized trees at sites where vertebrate grazing pressure was substantially lower (Reserve A and Koonamore Cross). The reduced shrub and litter densities were accompanied by lower soil organic carbon levels at the South Lake site. Although no small trees were sampled at Koonamore Cross, the distributions of canopy sizes between Reserve A and South Lake were similar, so this can be discounted as a causative factor. The sites also had similar clay loam soils; although it is possible that the nutrient differences are due to more subtle variation in the soils or to differences in erosion, the data are clearly consistent with the model of tree-facilitated shrub recruitment leading to increased litter retention and recycling.

The main area of disagreement between the model and the survey data lies in the absence of a relationship between shrub cover and organic carbon levels in the space-for-time substitution analyses. This may mean that the model is incorrect. It may also be due to the influence of longer-term historical effects. Shrub cover at South Lake is lower than at the other clay loam sites, consistent with the effects of higher levels of sheep grazing. Although organic carbon levels are also lower than at the other clay loam sites, they may still show some residual elevation as a consequence of nutrient accumulation that occurred before the introduction of sheep to the area. This is plausible, for observed changes in soil resources under *A. papyrocarpa* at Middleback Station show that accumulated nutrients, including organic carbon, persist for many decades after inputs cease (Facelli and Brock, 2000). Given the similarities between Koonamore and Middleback in soil types and climatic conditions, the decay rates in soil resource levels might be expected to be similar.

Conclusions

The results establish that considerable heterogeneity in soil organic carbon, plant litter density and plant community composition is associated with the presence of *A. oleifolius* canopies at Koonamore Station. The magnitude of the differences between canopy and open habitats increases with canopy height; the areas around small trees may be indistinguishable from open areas, while large trees are associated with distinct plant communities, much higher leaf litter densities and soil organic carbon concentrations that are several times higher than background levels. These data are interpreted as indicating that the heterogeneity is created during the life of the tree, and that the processes involved are cumulative. Further support to the view that trees directly or indirectly generate fertile islands is provided by the findings that differences in canopy shape were accompanied by differences in the species composition of under-canopy communities. Also, the finding that the processes of change appear to be accelerated when individual trees collectively form an extended canopy is consistent with the hypothesis.

I proposed a new two-phase process through which *A. oleifolius* creates fertile islands. In the first phase, the tree facilitates shrub establishment by providing shade. Then, during the second phase, soil nutrients accumulate because the shrubs entrap and retain more plant litter. Shrubs may also contribute to nutrient accumulation by increasing local plant productivity, or by producing more readily decomposable plant litter containing higher nutrient levels.

The results suggest that both the physical and the biological processes associated with woody perennials contribute to the creation of heterogeneity in arid landscapes. Furthermore, the physical processes of habitat modification and detritus capture by canopy structures and the biological processes of nutrient redistribution, plant productivity and litter decomposition are likely to create complex feedback loops that can potentially alter environments at the landscape level (Wilson and Agnew, 1992). The potential implications of plant-driven heterogeneity for plant productivity (Noy-Meir, 1981), nutrient cycling (Facelli and Brock, 2000) and plant biodiversity are clear, but are yet to be conclusively demonstrated.

Chapter 4

Artificial canopies emulate shading and rainfall redirection by trees

4.1 Introduction

Although soil and vegetation surveys can provide valuable information about the spatial distribution of plant species and soil resources relative to trees, confirmation of putative causative processes requires experimental evidence. However, depending on the hypothesis under test, there may be difficulties associated with establishing experiments in the vicinity of trees due to the confounding effects of higher soil resources levels below canopies. Differences in tree age and canopy morphology may also introduce variability in treatments that can reduce the power of experiments to detect effects.

Reciprocal transplants (Maranon and Bartolome, 1993), where slabs of soil are exchanged between canopy and open areas, can be used to circumvent the problem of systematic differences in soil nutrient levels. However, moving intact slabs large enough to accommodate the root system of target species is often difficult, and the problems associated with inter-canopy variability remain. The latter can be reduced by careful selection of trees, but where tree densities are low this may result in large spatial separation between subjects, with attendant problems of large-scale patterns of soil variability and even differences in precipitation and other weather events. Simultaneously resolving both sources of confounding or extraneous variability is not always feasible.

An alternative is to construct surrogates that model the processes of interest. This is closer to conventional approaches to experimental field ecology than may at first appear. Ecologists typically use individuals of a particular species as their experimental subjects to test ideas that they wish to generalise to much larger groupings of organisms. The experimental species is used as a surrogate for all members of the larger grouping; it models some characteristic common to all members of the larger group. Using surrogates is consistent with this approach while allowing greater flexibility in experimental design. More importantly, surrogates also offer the researcher a way of disentangling processes that may be irretrievably confounded in living organisms. Furthermore, it greatly reduces the variability between replicates attributable to natural variation, effectively increasing the experiment's statistical power to detect treatment effects.

Creating surrogates that impose the desired type of treatment is only the first step in the modelling process; it is also necessary to ensure that the treatment effects imposed by surrogates are biologically realistic, and that new confounding factors are not introduced. Researchers should verify that the surrogates behave as intended, and the treatments the surrogates impose should be validated by comparison with real systems (Jorgensen, 1986).

Numerous studies have quantified the differences in the plant communities between under canopy and open spaces, *e.g.* (Pugnaire et al., 1996b; Facelli and Brock, 2000). However, until relatively recently few field studies have tested the effects of shading on understorey species independently of the higher soil nutrient levels often found under tree canopies (Smith et al., 1987; Walker and Vitousek, 1991; Kellman and Kading, 1992). Cacti have received far more attention, and are known to be highly dependent on shade in their juvenile stages (Turner et al., 1966; Nobel, 1989; Franco and Nobel, 1989; Valiente-Banuet and Ezcurra, 1991; Flores-Martinez et al., 1994), being vulnerable to desiccation and to high temperatures. However, they tended to be viewed as a special case because of their high surface area to volume ratio and superficial root systems at the juvenile stage. More recently a number of workers have used artificial shading to examine canopy effects on plants other than cacti (Belsky, 1994; Davis et al., 1995; Greenlee and Callaway, 1996; Li and Wilson, 1998; Holzapfel and Mahall, 1999; Weltzin and McPherson, 1999; Kitzberger et al., 2000). Of these, some did not separate the effects of elevated soil nutrients from shading (Li and Wilson, 1998; Holzapfel and Mahall, 1999) while others provided levels of shading that may not be biologically realistic in terms of intensity or duration (Greenlee and Callaway, 1996; Weltzin and McPherson, 1999; Kitzberger et al., 2000).

Despite stemflow and canopy interception being widespread phenomena (Aston, 1979; Navar and Bryan, 1990; Martinez-Meza and Whitford, 1996), there appear to be no published studies on the effects of rainfall redistribution by canopies on understorey species, although Tielborger and Kadmon (2000) invoked canopy intercept to explain unexpected negative effects of shrubs on annuals in dry years. Given that stemflow may effectively amplify rainfall several-fold in areas near the trunk while reducing rainfall in the mid-parts of the canopy, rainfall redistribution could have profound consequences for understorey vegetation, particularly in semi-arid and arid communities.

I sought a means of experimentally testing the effects of shade independently of enhanced soil nutrient levels, and comparing the effects of shade alone with the effects of shade combined with rainfall redistribution. To this end, I designed and constructed artificial canopies and verified and validated the treatment effects. In this chapter I present details of the design and construction of the canopies. I also present data outlining the effects of each canopy type on rainfall distribution, soil temperature and light intensity, and provide some comparisons with the effects of *A. oleifolius* canopies on light intensity and soil temperature.

4.2 Methods

4.2.1 Site selection

Two 100 × 250 m quadrats were established on 8th March 1998. One was placed inside the north-western corner of the T.G.B. Osborn Vegetation Reserve. An 18 metre buffer was left between the quadrat and the northern fenceline to avoid any associated grazing or trampling effects. The other quadrat was placed in South Lake paddock outside the north-western corner of the Reserve. This quadrat was placed away from the corner to avoid excessive sheep traffic while being as close as practicable to the Reserve quadrat.

The site was chosen because it allowed cross fence comparisons between a long-grazed paddock and an area from which domestic stock had been excluded for over 70 years, and from which rabbits had been excluded for about 25 years. There were also few trees or large shrubs that might introduce extra soil or micro-climate variability into experiments.

Both quadrats had similar slopes and aspect, with solonized brown soils (Northcote Gc 1.12) (Carrodus et al., 1965). They had a sparse tree cover with widely scattered *Myoporum platycarpum* and *A. oleifolius*. *Atriplex vesicaria* and *Eremophila* spp.were the most common shrubs, and the herbaceous layer was primarily composed of *Sclerolaena* spp., *Danthonia caespitosa* and *Stipa* spp.

Canopy type	Dimensions (m)	Projected area (m^2)
Small Flat	1.7 x 1.7	2.89
Big Flat	3.6 x 3.6	12.96
Small V	0.91 (min. radius) x 1.06 (max. radius)	2.89
Big V	2.05 (min. radius) x 2.39 (max. radius)	14.64

Table 4.1: The dimensions of the artificial canopies, and the area of their shadows assuming the sun is directly overhead.

4.2.2 Materials

I constructed artificial canopies using the highest density neutral shadecloth available, black nylon 75/80% Weathashade^{TM}. I avoided other colours, especially green, because of the effects that the red:far red ratio of light has on seed dormancy (Pons, 1992; Murdoch and Ellis, 1992) and plant shoot extension (Aphalo and Ballaré, 1995). Although this means the artificial canopies differ from tree canopies with regard to the spectral quality of their shade, the species-specific differences in the spectral quality of light transmitted through tree canopies introduces a potentially confounding element that I wished to avoid. The optical density approximates the level of shading provided by at least two common arid zone trees, *A. oleifolius* (pers. obs.) and *Acacia papyrocarpa* (J. Prider pers. comm.).

I constructed four types of canopies; two square flat canopies, 'Small Flat' and 'Big Flat', made from single pieces of shadecloth, and two hexagonal V-shaped canopies, 'Small V' and 'Big V', made from 6 triangular pieces of shadecloth (Table 4.1). Polyester thread was used for all sewing. The flat canopies were designed to provide shading without redistributing rainfall, while the V-shaped canopies were designed to provide shade and also direct rainfall towards their central axes. It should be noted that these treatments do not permit testing the effects of rainfall redirection alone.

The canopies were pre-fabricated in Adelaide and erected at Koonamore between 9 March and 13 May 1998. Two replicates of each canopy type were erected at random positions in each quadrat. The canopies were oriented so that the most northerly edge of the shadecloth was aligned east-west, ensuring that their shadows progressed evenly across the ground and that the area covered was consistent between replicates. Untreated *Pinus radiata* posts were used for the vertical supports to avoid any effects of copper chrome arsenate leachate; 45 x 45 mm posts were used for the flat canopies and 70 x 70 mm posts were used for the V-shaped canopies. Lateral support in the V-shaped canopies was initially provided by six 50 mm plastic V-shaped angle extrusions. These were later replaced (January 1999) in the large V-shaped canopies by 38 mm diameter high tensile steel tubes after repeated wind damage. The shadecloth was attached to the lateral supports with nylon cable ties.

The flat canopies (Plate 4.0) were suspended from posts at a height of 1.2 metres. The posts were placed into holes dug to a depth of 0.5 m with a 87 mm Ø posthole digger. Soil removed was backfilled so that subsoil was placed at the bottom of the hole, with topsoil topping the refill. The soil was then lightly tamped to secure the post. The Small Flat canopies were suspended on ropes strung from posts placed on the corners of a 3.6 metre square, whereas the Big Flat canopies were directly attached to the posts. This permitted the use of one control treatment for both types of flat canopies. Each flat canopy was secured with a rope from the top of each post to metal stakes hammered into the ground.

The V-shaped shadecloth with attached angle extrusions was suspended from the central post at an angle of approximately 20° from the horizontal (Plate 4.0). The shadecloth was secured with wire to eyelets on the post 1 m above the ground. The post was placed into a hole dug to a depth of 0.75 m with a 105 mm Ø posthole digger. Soil was removed, backfilled and tamped as above. Excess sub-soil was stockpiled outside the experimental area so that it could be used to refill the postholes when the canopies were removed at the end of the study. Each canopy was secured with

Plate 4.0 - Artificial canopies used emulate shading and rainfall redirection by tree canopies. Flat canopies (top) provided shade while V-shaped canopies (below) provided a similar level of shading while redirecting rainfall towards the centre posts.

	Zone Radius (m)		
Canopy Type	**Centre**	**Mid**	**Outer**
Big V	0-0.3	0.65-1.0	1.3-1.6
Small V	0-0.3	0.4-1.0	1.4-1.7
Big Flat	0-0.3	0.65-0.85	0.85-1.05

Table 4.2: Radii of concentric zones used for measuring rainfall redirection under artificial canopies.

six ropes attached to the top of the post and the ends of the angle extrusions, and fixed to metal stakes hammered into the ground.

Soil and surface disturbance in the flat canopy treatments was controlled for by digging four 87 mm Ø holes on the corners of a 3.6 metre square to a depth of 0.5 m. The holes were then immediately refilled with the removed soil, making sure that subsoil was returned to depth and topsoil was used to fill the top of the hole, and then lightly tamped. The control treatment for the V-shaped canopies was similar, except that a single hole was dug to a depth of 0.75 m with a 105 mm Ø posthole digger. Each quadrat had two randomly placed replicates of each type of control.

4.2.3 Validating the models

In any modelling exercise it is important to verify that the models behave as intended, and to test the validity of the models by comparing them with data from natural systems (Jorgensen, 1986). Consequently I recorded rainfall, light and soil temperature data under the canopies. A limited amount of light and soil temperature data were also collected from under *A. oleifolius* canopies for comparison.

Rainfall redirection

Spatially explicit comparisons between artificial canopy types were made using arrays of raingauges. I constructed raingauges by connecting 750 ml glass bottles to 62 mm Ø plastic funnels with 10 mm internal Ø PVC tubing. The join between the bottle neck and the tubing was sealed with plastic insulation foam. The funnel rims were placed about 70 cm above ground level and affixed to wooden stakes. A small quantity of kerosene was added to each bottle to reduce evaporation, and was replaced after each reading.

Raingauges were placed under the canopies in three concentric zones; centre, mid and outer. The radii of these zones were varied between canopy types to accommodate the differences in canopy sizes (Table 4.2). Four raingauges were placed at random distances and angles from the canopy centre within each zone. Angles were restricted to the range between 90 and 270 degrees, minimizing sun exposure and thereby reducing error from evaporation. Three raingauges ('open') were placed a minimum of 5 metres from the nearest canopy as controls.

The number of raingauges that could be simultaneously deployed was limited by time constraints. Because it was more important to characterise the spatial patterns of rainfall redistribution under the canopies than to test the variability between replicates, I sampled under only one canopy of each type. Rainfall was measured under a Big V canopy and a Big Flat canopy between 7 January 1999 and 17 June 1999, and under a Big V canopy and a Small V canopy between 17 June 1999 and 24 November 1999. Rainfall was not measured under the Small Flat canopies as they were expected to have an effect on rainfall redistribution similar to the Big Flat canopies.

Rainfall was recorded as the raw quantity of rain in millilitres. Measurements were excluded if the raingauge bottle had fallen over, or if the funnel rim was not horizontal. During some periods many measurements had to be excluded, so data from some zones were absent or unreplicated. Consequently, some measurement periods were not included in the final analyses. Analysis of Big V-Big Flat rainfall redirection was

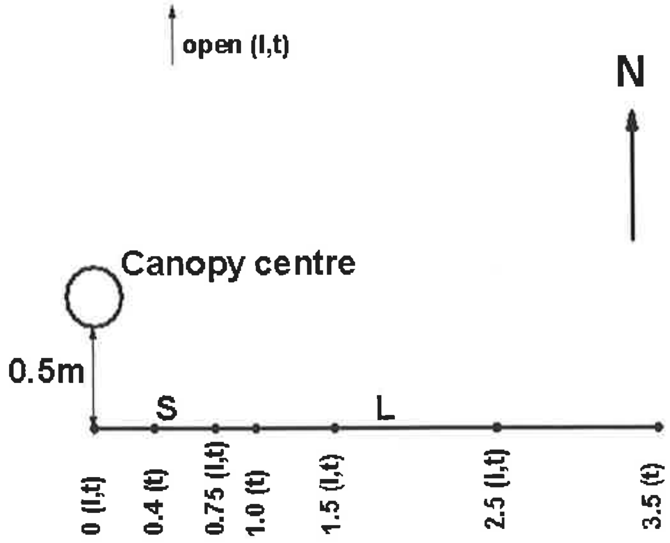


Figure 4.1: Arrangement of Li-cor PAR sensors and Type T thermocouples used for measuring and light intensity and soil temperature at 5.5 cm depth. "Open" sensors were placed between 5 and 10m to the north, clear of the influence of any canopies. l = Li-Cor sensor position, t = Type T thermocouple position. S indicates the location of the edges of Small canopies, L indicates the location of the edges of Big canopies. Numbers show the distance (in metres) along the transect from the canopy centre.

conducted on readings from four periods: 23 February, 24 February - 25 April, 8 May - 15 June and 15 - 17 June 1999. Analysis of Big V-Small V rainfall redirection was also conducted on readings from four periods: 17 - 30 June, 30 June - 24 July, 13 October and 14 October - 24 November. Data were log transformed to satisfy the assumptions of ANOVA. Since the raingauge positions were not re-randomised after each rainfall reading data were analysed as repeated-measures ANOVAs (SAS Institute, 1997). The ANOVA model used canopy type and time as fixed effects, zone was nested within canopy and raingauge was treated as a random effect nested in canopy and zone.

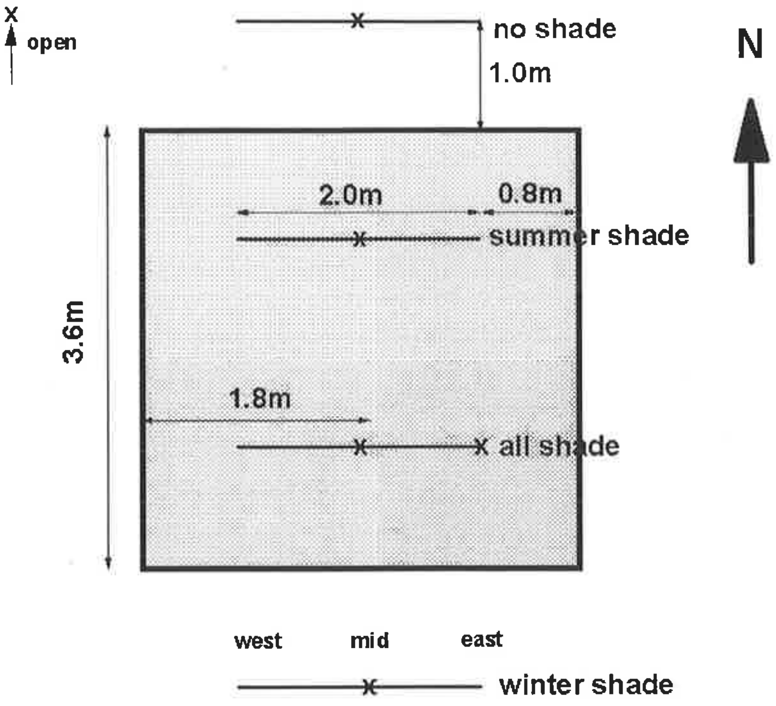


Figure 4.2: Arrangement of Li-cor sensors for measuring PAR under Big Flat canopy.

Light and soil temperature

Spatially explicit measurements of the effects of artificial canopies on incident photosynthetically active radiation (PAR) and soil temperature were conducted between February 1999 and February 2000. Prior to each set of measurements a set of thermocouples that provided temperature readings with a range not exceeding 0.3° C was selected. Light sensors (Li-Cor LI-190SZ Quantum sensors) and Type T thermocouples were arrayed along a transect running east from a point 0.5 m south of the canopy centre (Figure 4.1). The transect was offset southwards in an attempt to accommodate the southerly movement of the shadow patch during the winter months. In order to maximise the information that could be obtained from the limited number of sensors available, I assumed that the light and soil temperature gradients would be approximately symmetrical.

Light sensors were placed on the soil surface at 0, 0.75, 1.5 and 2.5 m east of the canopy centre, and thermocouples were inserted to a depth of 5.5 cm at 0, 0.4,

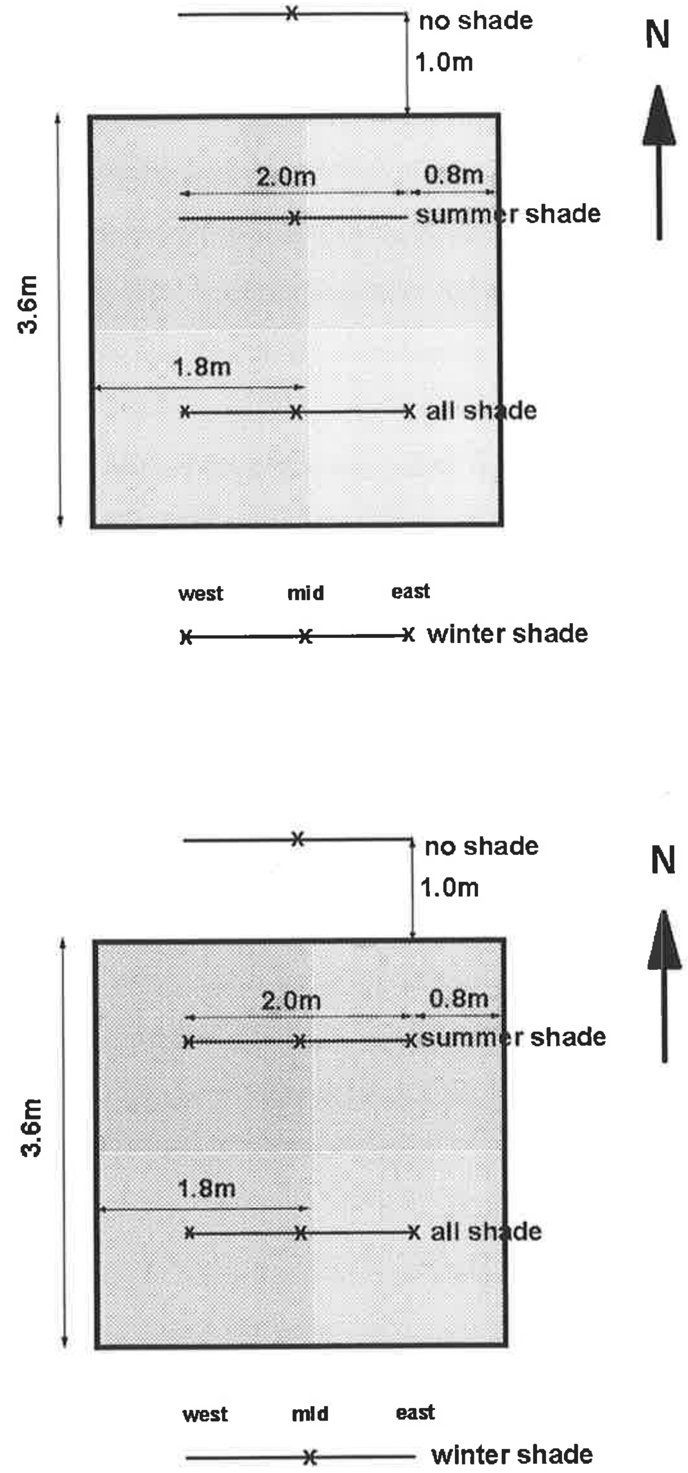


Figure 4.3: Arrangement of thermocouple probes for soil temperature measurements at 5.5 cm depth under Big Flat canopy during winter (above) and summer (below).

0.75, 1.0, 1.5, 2.5 and 3.5 m east of the canopy centre (Figure 4.1). A light sensor and a thermocouple were placed in the open between 5 and 10 m to the north as controls for canopy effects. Instantaneous PAR measurements were made every 15 seconds, and the mean of 4 consecutive measurements was logged every 1 minute by a Data Electronics Datataker 50. Soil temperatures, being less subject to short term fluctuation, were measured instantaneously and logged at 5 minute intervals by a Grant Instruments 1203 Squirrel logger.

There was some variability in PAR measurements caused by sensors not being perfectly level, and also from scattered light and sky light. These latter two sources of variation increase with proximity to the canopy edge. I tested the amount of shading provided by the shadecloth and the variation associated with measurement and light scatter. A subset of data, recorded between 12:58 hours and 14:53 hours on 24 February 1999 under a Small Flat canopy, was selected. During this period 3 sensors were in full sunlight, while two sensors were shaded. Percentage shading was calculated by dividing the shaded measurement by the sunlit measurement for all six possible shaded and sunlit combinations at each logging interval.

The Squirrel logger was unavailable for my January 2000 field trip, so a second Datataker 50 was used to log soil temperatures (at 5 minute intervals). However the Datataker 50 can accommodate only four Type T thermocouples. Consequently thermocouples were deployed at 0, 0.75 and 2.5 m along the transect, with the fourth thermocouple in the control position.

PAR and soil temperatures were also measured under *A. oleifolius* canopies that were similar in size to the Big V canopies, using the same arrangement of sensors. Measurements were logged under one *A. oleifolius* tree in the T.G.B. Osborn Vegetation Reserve and one *A. oleifolius* in the which HP paddock at Middleback Station in January and February 2000.

The PAR and soil temperature data sets are so large that inferential tests have the power to detect very small treatment differences. Typically, almost all pairwise comparisons between measurements along the transect are significant at the $P = 0.01$ level (results not presented). Many of these differences might not be biologically important, some may even be attributable to variation between the sensors. Although it is possible to test for a specified effect size, it is difficult to determine *a priori* at what point differences become biologically significant. Furthermore, the limited availability of equipment prevents valid inferential comparisons between canopies as the data were collected on different days. Cloud cover and air temperatures often differed, and I was sometimes unable to standardise the commencement and duration of data logging.

The objective of the sampling was to characterise the effects of the canopy treatments on the below canopy microenvironment. In view of this, and given the constraints discussed above, the data were summarised graphically and examined for patterns.

In order to prevent nocturnal measurements from biasing data sets, PAR data were censored to exclude any measurements where one or more sensors recorded less than 5 μmol m^{-2} sec^{-1}. This intensity was chosen as a cut-off point because it was below the compensation point of *Enchylaena tomentosa* (25 μmol m^{-2} sec^{-1} for shade adapted plants) (Jane Prider, pers. comm.), a common understorey species that was later used as an experimental subject. Soil temperature data were not censored except where there was reason to believe that a thermocouple gave erroneous measurements; nocturnal measurements were retained as I wanted to see whether canopies affected heat loss from the soil during the night.

Big Flat Canopy measurements

PAR and soil temperatures were also collected to another protocol later in my study. I had devised an experiment using the Big Flat canopies to test seasonal variations of the effects of shading on the growth and survival of an understorey shrub, *Enchylaena tomentosa* (Chapter 6). Seedling were planted in east-west rows under the Big Flat

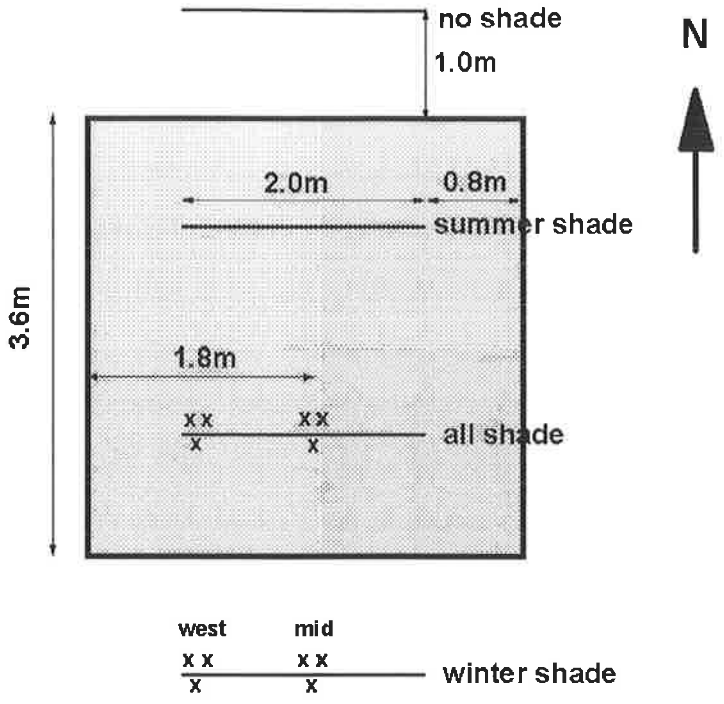


Figure 4.4: Arrangement of thermocouple probes for nocturnal soil temperature measurements at 5.5 cm depth under Big Flat canopy in June 2000.

canopies, the rows being arranged so that they were exposed to midday sun at different times of the year. These rows were labelled according to their exposure at noon; no shade, summer shade, all shade and winter shade. Since the sampling protocol described above provided no information about the northerly or the southerly parts of the undercanopy micro-environment, I designed a protocol that provided data that relates more directly to these experimental treatments.

A Li-Cor LI-190SZ Quantum sensor was placed in the centre of each of the four rows (Figure 4.2). The fifth sensor was placed at the eastern end of the all shade row to measure the effect of the greater exposure to morning sun.

Two sampling protocols were used for measuring soil temperatures at a depth of 5.5 cm (Figure 4.3). Both protocols had a Type T thermocouple in the centre of each of the four rows, and a thermocouple at the eastern and western ends of both of the shaded rows. Because of the seasonal movement of the shade patch, a different pair of rows were sampled with three thermocouples in winter and summer. Data logging equipment and sampling intervals were as described above.

It was necessary to modify this protocol for the January 2000 trip due to equipment unavailability. A Type T thermocouple was placed in the centre of the no shade, summer shade and all shade rows, and the fourth thermocouple was placed at the western end of the summer shade row.

The data collected during the study suggested that nocturnal soil heat loss may be lower under canopies than in the open during winter. In June 2000 I used a new soil temperature sampling protocol to further investigate nocturnal temperature changes (Figure 4.4). I used two Squirrel loggers and 14 Type T thermocouples. Thermocouples were placed at the apices of a 10 cm triangle at the centres and the western ends of the all shade and the winter shade rows, with two more thermocouples in the open. This arrangement permitted estimation of variability due to differences in the soils or the thermocouples. Unfortunately, one of the Squirrel loggers failed after the first night. I continued logging with the remaining logger, which had seven working channels, for another 24 hours. I then reconnected the thermocouples to the working logger so that I obtained triplicate measurements from the centres of the all shade and winter shade rows, with a single thermocouple in the open.

4.3 Results

4.3.1 Rainfall redirection

Whereas gaugings under the Big Flat canopy were normally distributed ($P > 0.05$), gaugings from the centre zones of the Big V and Small V canopies were strongly right skewed (Figures 4.5 and 4.6). Canopy type and zone within canopy affected $\log_e$(rainfall) when the Big V and Big Flat canopies were compared, but were not independent of measurement date (Table 4.3a). *Post hoc* comparisons showed that rainfall did not differ between zones under the Big Flat canopy during any measurement period, but that more rainfall was collected in the centre than in the mid or outer zones under the Big V canopy during some measurement periods, but not oth-

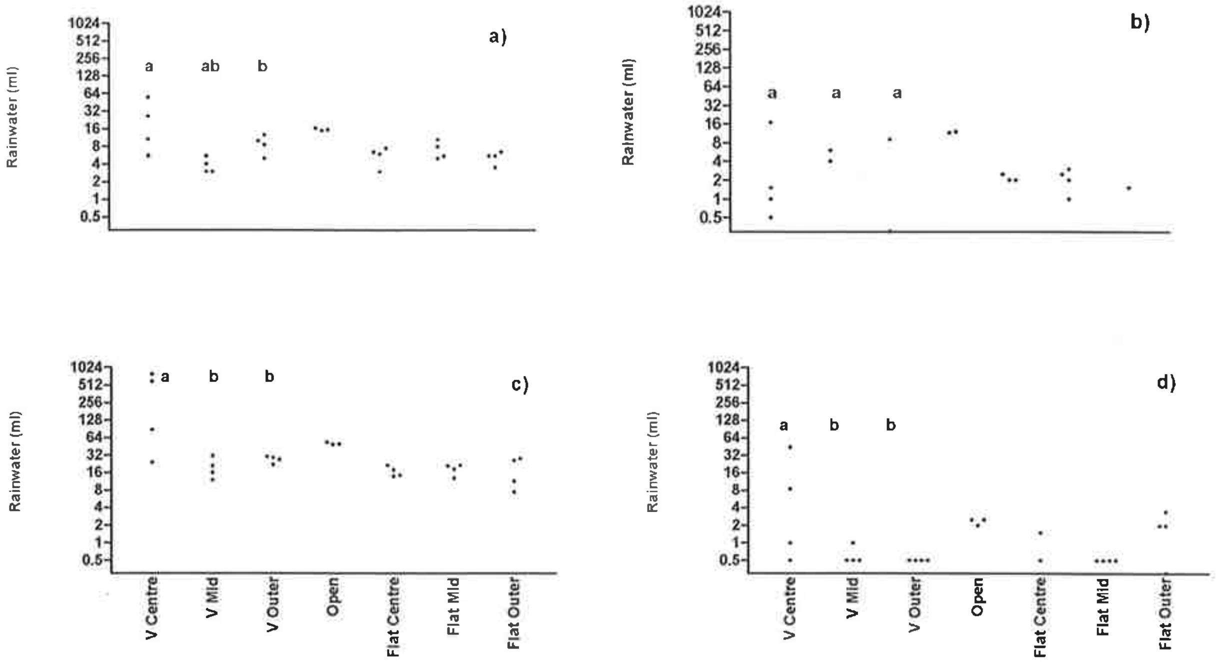


Figure 4.5: Amount of rainfall collected in raingauges under Big V and Big Flat canopies on a) 23 February, b) 24 February - 25 April, c) 8 May - 15 June, d) 15 -17 June 1999. Amounts less than 0.5 ml are shown as 0.3 ml for display purposes. Shared lower case letters indicate that rainfall did not differ between zones under Big V canopy (*Post hoc* contrasts, $\alpha' = 0.017$). There were no differences between zones under the Big Flat canopy during these recording periods. Note $\log_2$ scale on y axis.

ers (Figure 4.5). More rainfall was collected under the Big V canopy and in the open than under the Big Flat canopy. There were no differences between the Big V and the Small V canopies (Table 4.3b). *Post hoc* comparisons showed that whereas more rainfall was collected in the centre zone of the Big V canopy than in the other zones, there were no differences between zones under the Small V canopy. The inability of ANOVA to detect differences between the two V canopies may be due to the very high variability in the measurements in the centre zones (Figure 4.6).

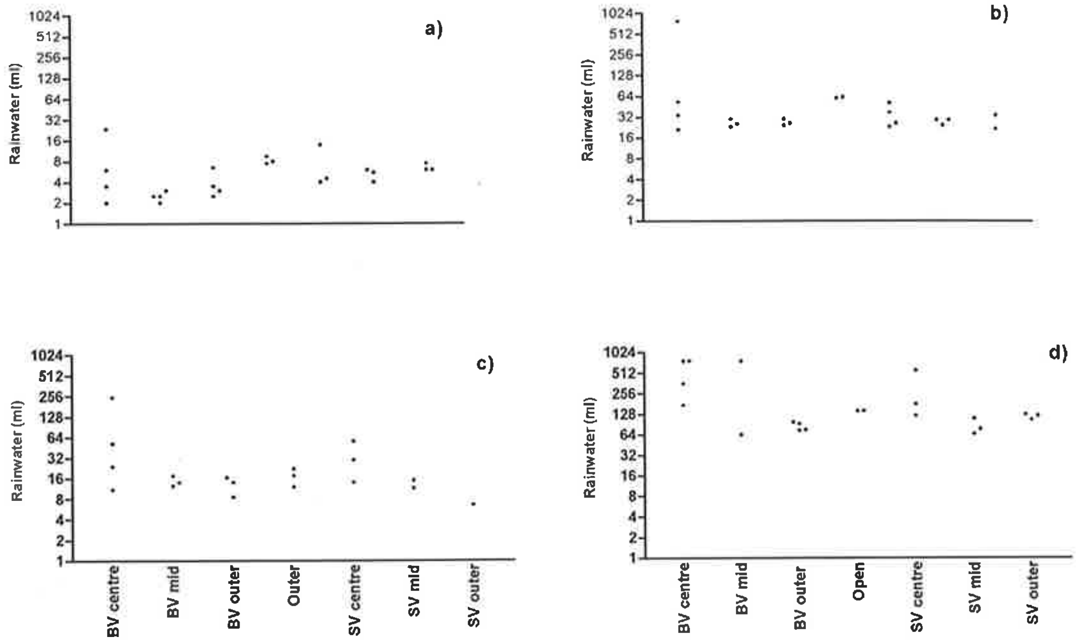


Figure 4.6: Amount of rainfall collected in raingauges under Big V and Small V canopies on a) 17 - 30 June, b) 30 June - 24 July, c) 13 October, d) 14 October - 24 November 1999. Amounts less than 0.5 ml are shown as 0.3 ml for display purposes. BV = Big V canopy, SV = Small V canopy. Amounts were higher in the centre zone than in the mid and outer zones under the Big V canopy, but did not differ between zones under the small V canopy (*Post hoc* contrasts, $\alpha' = 0.017$). Note $\log_2$ scale on y axis.

Source	**SS**	**DF**	**F**	**Prob > F**
a) $r^2 = 0.8357$				
Canopy	12.897	2	10.6408	0.0007
Position[Canopy]	7.548	4	3.1138	0.0382
Time	175.281	3	96.4078	< 0.0001
Time*Position[Canopy]	18.309	12	2.5175	0.0101
Subject[Position, Canopy]	4.928	20	0.4066	0.9855
b) $r^2 = 0.8614$				
Canopy	0.9169	2	1.0587	0.3539
Position[Canopy]	11.701	4	7.1657	0.0008
Time	129.963	3	92.4840	<0.0001
Subject[Position, Canopy]	8.1307	20	0.8679	0.6251

Table 4.3: Repeated measures ANOVA (SAS Institute, 1997) on the amount of rainfall collected under a) Big V and Big Flat canopies and b) Big V and Small V canopies. Subject[Position, Canopy] was used as a random effect.

4.3.2 Light

Mean shadecloth PAR transmission on 24 February 1999 was 25.05% (σ_{n-1} = 3.74%, n = 696). Median PAR levels under canopies were lower than in the open (Figure 4.7). Interquartile ranges and, to a lesser extent, maxima increased from under canopy centres to the open, with large increases in interquartile ranges at the canopy edges. Median PAR, interquartile ranges and maxima under an *A. oleifolius* canopy at Koonamore showed similar trends. Large canopies reduced interquartile ranges more than small canopies, and affected a greater length of the measuring transect. These trends were apparent at all times of year, and were most pronounced during summer.

The shadows cast by the canopies moved across the sensor array during the course of the day (Plate 4.1). The timing of shading was related to the sensors' position relative to the canopy centre; those closest to the canopy centre were shaded earlier in the morning than those towards the canopy edge. The time of day that shading starts affected the range and median values of daily PAR. The duration of shading was related to canopy size; sensors under large canopies were shaded longer than those under small canopies. Little or no shading was detected under the small canopies in May and July 1999, as their shadows were cast further south than the measuring transect.

One of the main differences between the artificial canopies and the *A. oleifolius* canopies was the small scale temporal fluctuations in PAR due to sunflecks passing through the tree canopies (Plate 4.1d). Whereas the sensor readings followed a predictable sigmoidal pattern until the tree's canopy shadow reached them, they subsequently showed large short term fluctuation until the shadow had passed.

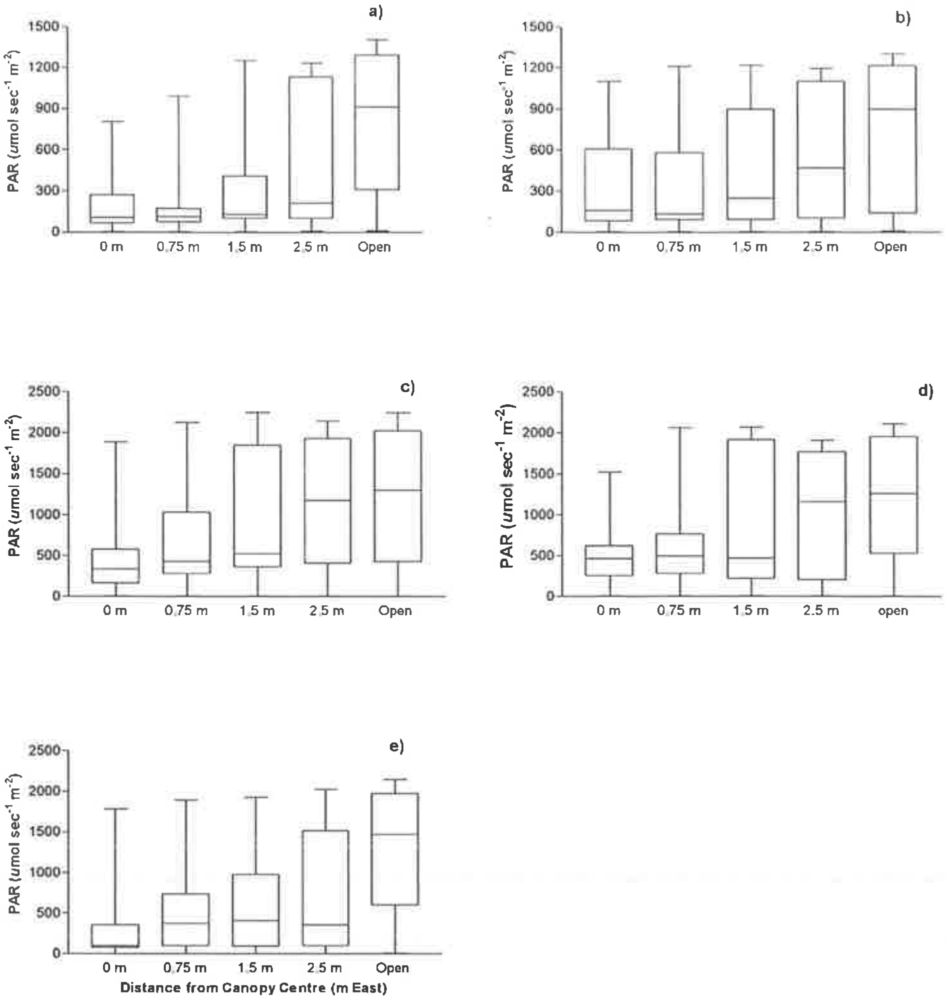


Figure 4.7: Photosynthetically active radiation (PAR) measured under a) Big Flat canopy, 6 May 1999, b) Big V canopy, 28 July 1999, c) Small V canopy, 24 November 1999, d) Small Flat canopy, 24 February 1999, and e) *A. oleifolius* canopy (radius 2.7 m east), T.G.B. Osborn Vegetation Reserve, Koonamore Station, 19 January 2000. Boxplot whiskers indicate minima and maxima, boxes and bars indicate first quartiles, medians and third quartiles. Note smaller range in y axis scale for a) and b).

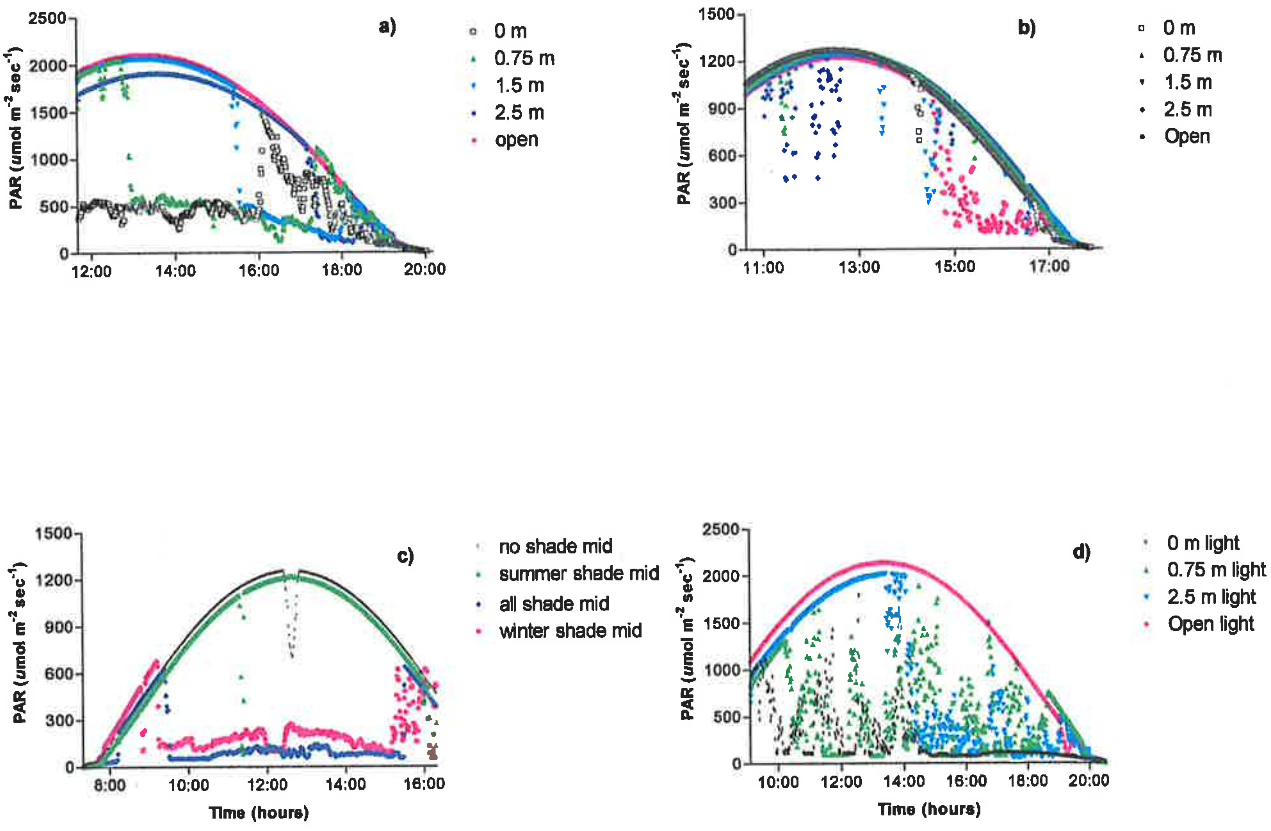


Plate 4.1 - Photosynthetically active radiation (PAR) measured under a-c) artificial canopies and d) *A. oleifoilus*. a) Small Flat canopy, 24 February 1999. b) Small Flat canopy, 25 July 1999. c) Big Flat canopy, 27 July 1999. d) *Alectryon oleifolius* at T.G.B. Osborn Vegetation Reserve, 19 January 2000. Canopy radius east = 2.7 m.

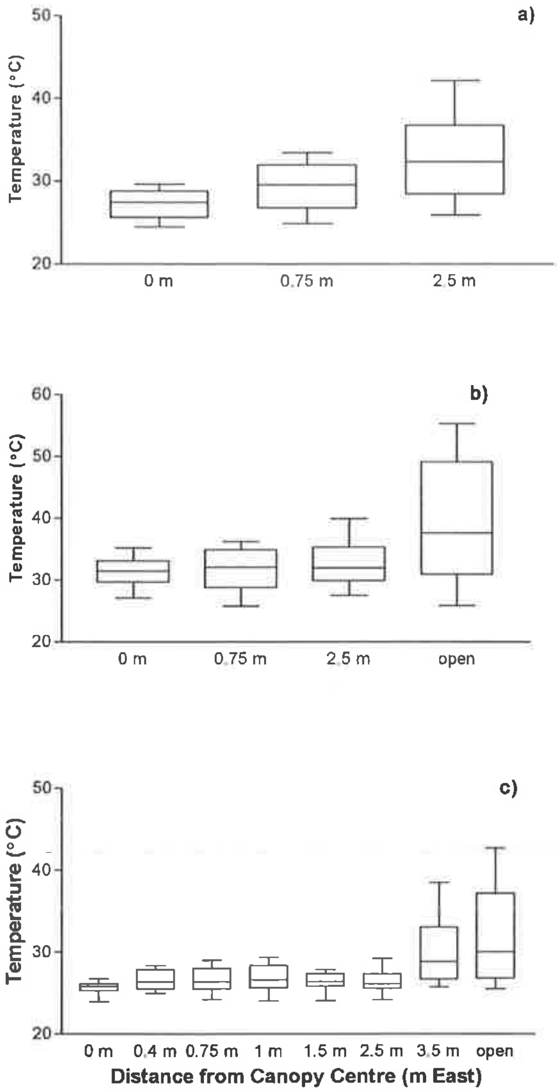


Figure 4.9: Soil temperatures at 5.5 cm depth under a) *A. oleifolius* (canopy radius east = 2.25 m) at HP Paddock, Middleback Station, 12-14 January 2000 b) *A. oleifolius* (canopy radius east = 2.7 m) at T.G.B. Osborn Vegetation Reserve, Koonamore Station, 19-20 January 2000 and c) *A. oleifolius* (canopy radius east = 2.7 m) at T.G.B. Osborn Vegetation Reserve, Koonamore Station, 24-25 February 2000. Open data absent from a) due to faulty thermocouple. Boxplot whiskers indicate minima and maxima, boxes and bars indicate first quartiles, medians and third quartiles.

canopies. This indicates that temperatures under canopies were less variable, and that the degree of variability is correlated with canopy size. The data also show abrupt changes in variability across the canopy edge. These trends in variability are also evident in the soil temperatures under *A. oleifolius* canopies at Koonamore Station and Middleback Station (Figure 4.9).

Data recorded along rows under the Big Flat canopies indicates that soil temperatures are not strictly symmetrical about the north-south axis. Soil temperatures at the western ends of the summer shade and all shade rows (Figure 4.10) were always more variable than at the eastern end, even though they should have received the same amount of insolation. Unfortunately there were too few quantum sensors available to verify this. Maxima were always higher at the western end, and interquartile ranges were usually larger.

There was a strong association between direct sunlight and soil heating. The timing of the start of soil heating closely corresponded to the arrival of direct illumination at sampling points (Plate 4.4). Likewise, soil temperatures dropped as soon as they fell into shadow.

Canopies reduced the rate of heat loss at night during winter (Plate 4.3). Soil temperatures in the centre of the all shade row of the Big Flat canopy were consistently warmer than open soils by midnight, despite tending to be cooler by day (Plate 4.3a and c). Data collected under other types of canopies during winter showed similar trends. Soil temperatures at the end of the all shade row showed a greater diurnal range than temperatures in the centre of the row (Plate 4.3b), although the differences were smaller than the comparisons between the centres of the all shade and the winter shade rows.

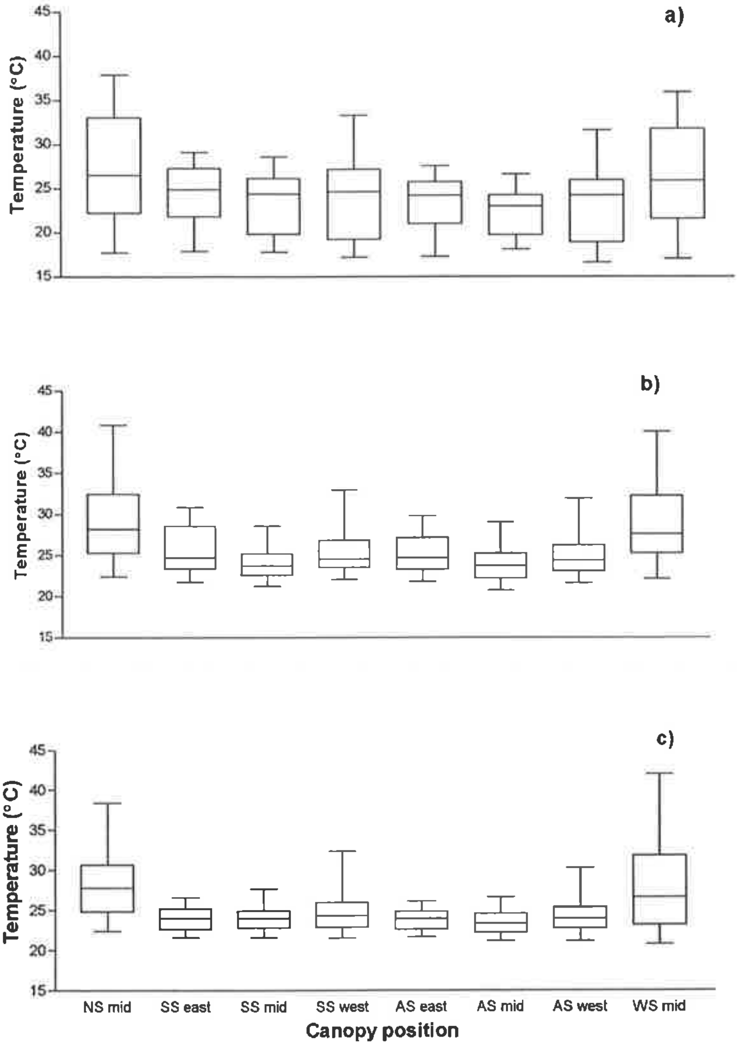


Figure 4.10: Soil temperatures at 5.5 cm depth under Big Flat canopies on a) 14-15 October 1999, b) 25-26 November 1999 and c) 22-24 February 2000. NS = no shade row, SS = summer shade row, AS = all shade row and WS = Winter Shade row. Boxplot whiskers indicate minima and maxima, boxes and bars indicate first quartiles, medians and third quartiles.

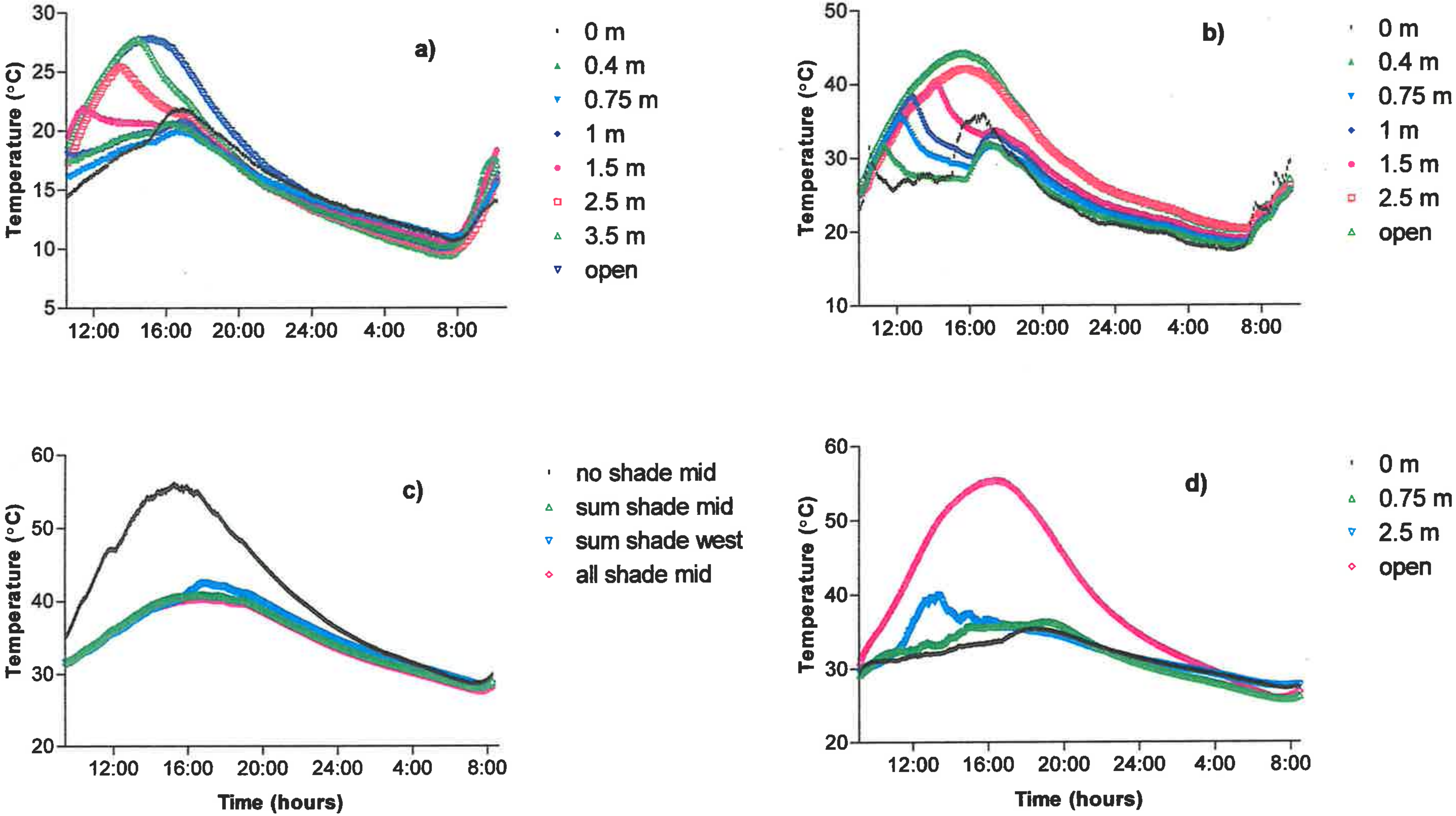


Plate 4.2 - Soil temperatures measured at 5.5 cm depth under canopies. a) Big Flat canopy, 6-7 May 1999. b) Small V canopy, 24-25 November 1999. c) Big Flat canopy, 18-19 January 2000. d) *Alectryon oleifolius* canopy, T.G.B. Osborn Vegetation Reserve, Koonamore Station, 19-20 January 2000. Canopy radius 2.7 m east.

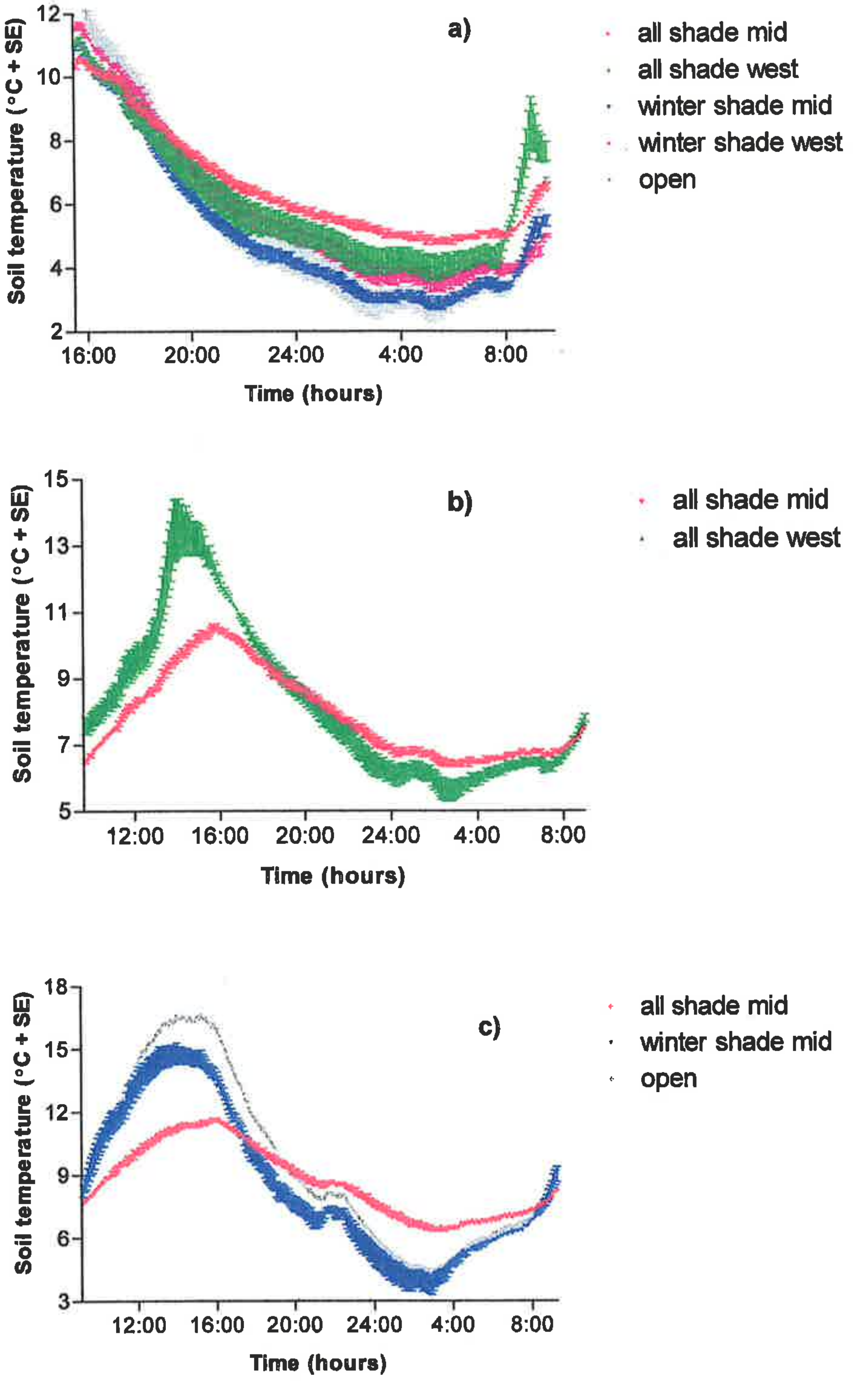


Plate 4.3 - Nocturnal soil temperatures at 5.5 cm depth under a Big Flat canopy on a) 28 - 29 June 2000 (*n* = 3, except *n* = 2 for open), b) 29 - 30 June 2000 (*n* = 3), and c) 30 June - 1 July 2000 (*n* = 3, except *n* = 1 for open).

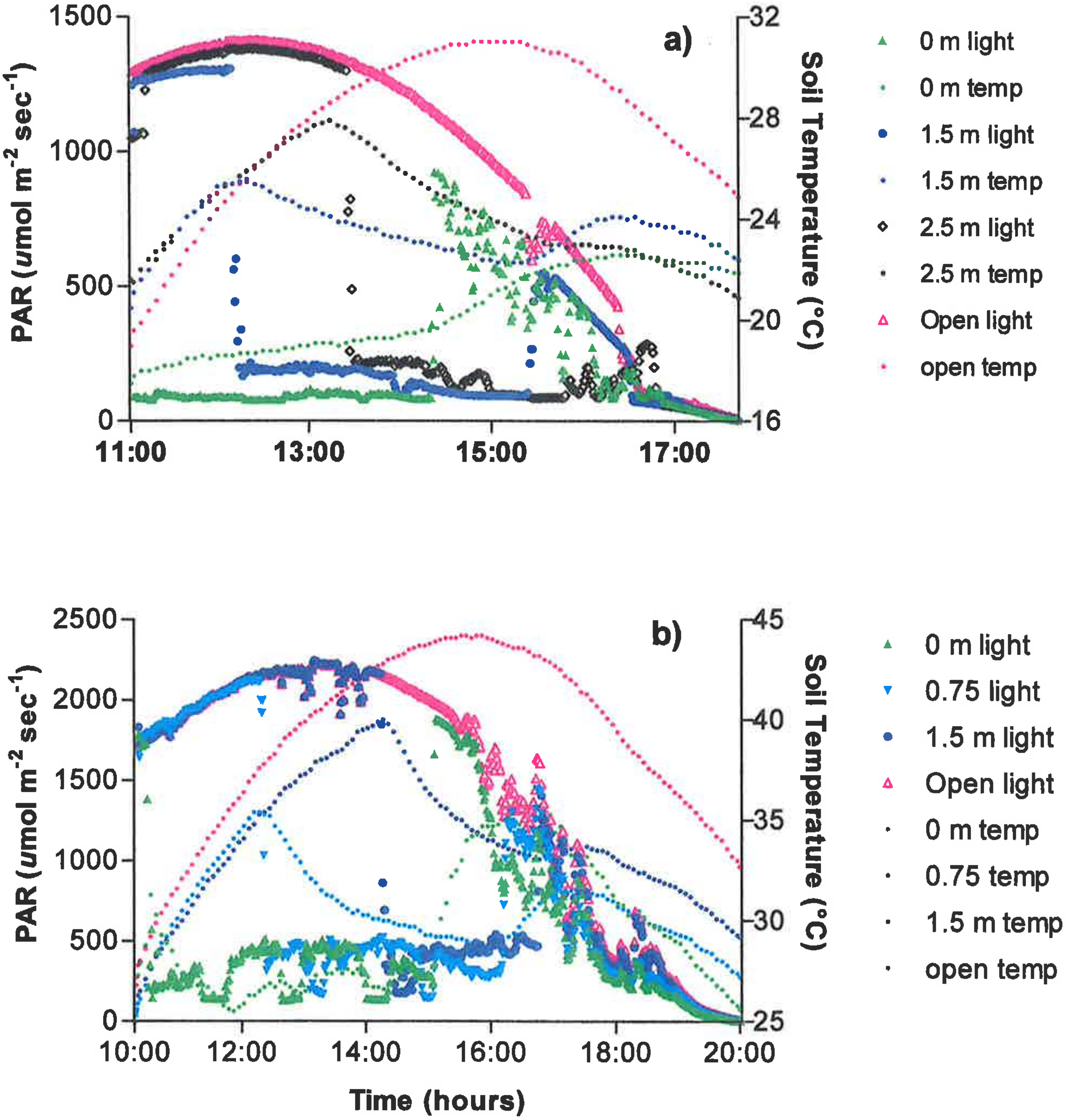


Plate 4.4 - Photosynthetically active radiation (PAR) and soil temperature at 5.5 cm soil depth measured under artificial canopies. a) Big V canopy, 5 May 1999. b) Small V canopy 24 November 1999.

4.4 Discussion

4.4.1 Comparing artificial canopies and trees

The artificial canopies successfully modelled the qualitative effects of tree canopies on PAR, soil temperatures and precipitation. Given that the measurements were consistent with measurements obtained from under *A. oleifolius* canopies, the effects of the artificial canopies can be deemed to be biologically realistic. They reduced light levels, moderated soil temperatures and intercepted and redirected rainfall. Large canopies had more effect on PAR and soil temperature than small canopies, while differences between Flat and V-shaped canopies within each size class were small and limited to the region near the canopy edges. The magnitude of these changes are also broadly comparable to other reports of the effects of tree canopies on microclimate (Table 4.4). Similar nocturnal moderation of soil temperatures has also been reported by Parker and Muller (1982), who found that *Quercus agrifolia* trees retained heat below their canopies overnight, creating differentials of 5 to 10° C between open and under canopy habitats. Aside from potential effects on seed dormancy (Probert, 1992; Vleeshouwers et al., 1995), higher nocturnal temperatures may increase survivorship in seedlings by reducing the effects of cold-induced photoinhibition (Ball et al., 1991; Holly et al., 1994; Skillman et al., 1996).

Differences in sampling techniques and measurement methods render quantitative comparisons of rainfall redirection with published data almost impossible. Furthermore, I did not measure rain flowing down the central axis of the canopies, as that would have interfered with experiments that were being conducted at the time of measurement. Studies show that interception and redirection of rainfall differs greatly between species (Aston, 1979; Navar and Bryan, 1990; Martinez-Meza and Whitford, 1996), and that it is affected by the duration and the intensity of the rainfall events as well as by the size and structure of the canopy (Pressland, 1973; Mauchamp and Janeau, 1993).

Community	**Species**	**Solar Radiation**	**Soil Temperature**
Semi-arid savanna[a]	*Acacia tortilis* *Adansonia digitata*	45-65%	12° C, 5 cm depth
Semi-arid woodland[b]	*Pinus edulis*	>50%	>10° C, 2 cm depth
Arid chenopod shrubland[c]	*Maireana pyramidata*	>90%	15° C, 1 cm depth
Mediterranean woodland[d]	*Acacia calamifolia* *Baeckea behrii*	50% 80%	5° C, 5 cm depth 5° C, 5 cm depth
Mediterranean woodland[e]	*Prosopis glandulosa*	no data	<12° C, 1 cm depth

Table 4.4: Reductions in light and soil temperatures under tree and shrub canopies. [a] Belsky et al. (1989, 1993), [b] Breshears et al. (1997, 1998), [c] Pound (1998), [d] Telfer (1998), [e] Fulbright et al. (1995).

The artificial canopies' main departure from biological realism was in the homogeneity of their shading. Most shrub and tree canopies impose heterogenous shade that is briefly interrupted by sun flecks. Although this difference does not appear to have much effect on daily mean PAR or soil temperature, it is known to affect the photosynthetic activity of some understorey plants. Many species perform a high proportion of their daily photosynthesis during the brief periods they are exposed to high intensity light in sun flecks (Curtis and Kincaid, 1984; Chazdon, 1988; Kursar and Coley, 1993). However, these reports have come from dense-canopied tropical and temperate forests, where photosynthesis is not seriously limited by water and where understorey PAR levels are often below 20 μmol m^{-2} sec^{-1}. This is much lower than the median intensities of 150 (winter) - 500 (summer) μmol m^{-2} sec^{-1} measured under the artificial canopies. These latter levels are in fact higher than sunfleck intensities in many tropical and deciduous forests (Chazdon, 1988). Furthermore, the saturation point of *Enchylaena tomentosa*, which was used as an experimental unit, is approximately 550 μmol m^{-2} sec^{-1} for shade adapted plants and approximately 1150 μmol m^{-2} sec^{-1} for sun adapted plants (J. Prider, pers. comm.). In other words, shaded *E. tomentosa* plants were not entirely dependent on direct early morning and late afternoon sunlight to maximise carbon assimilation. Consequently there is little reason to expect that the absence of sunflecks would greatly affect photosynthetic rates of plants growing under artificial canopies. Nevertheless, it must be acknowledged that sunfleck intensities under *A. oleifolius* could exceed 500 μmol m^{-2} sec^{-1} (Plate 4.1d).

4.4.2 Comparing artificial canopy types

The flat canopies withheld some precipitation without significantly redistributing rainfall, while the V-shaped canopies redirected rainfall towards their centres. Thus the canopies successfully modelled the interception and stemflow phenomena that have been reported from many tree and shrub species (Pressland, 1973; Aston, 1979; Navar and Bryan, 1990). The expected differences between Big and Small V canopies were not detected; this may be due to the small number of raingauges within each measuring zone coupled with very high variability between gauges.

Much of the variance in the centre zone of the V canopies was due to water running along the lateral supports and then dripping near the centre. I also observed water flowing down the central posts of the V canopies during rainfall and pooling at the base; the extent of this 'stemflow' was not quantified, but represented a visible amplification of ambient precipitation.

It would have been preferable to measure soil moisture content, rather than rely entirely on raingauge readings. Unfortunately, suitable equipment was not available at the time this work was conducted. Nor was the collection of soil samples for moisture determination by oven drying feasible, for that would have disturbed experiments that were running concurrently under the canopies.

The small east-west asymmetry in soil temperatures detected under the Big Flat canopies is probably a consequence of differences in the timing of solar irradiation. Soil directly illuminated in the morning when it is at its coldest is unlikely to become as hot as soil that is illuminated in the afternoon, having had hours of warming from the air, scattered radiation and radiant and transmitted radiation through the shadecloth. There may also be differences in the rates of temperature change. In the mornings, while light levels and air temperatures are low, the rate of heating will be reduced in comparison to the afternoons when light is more intense and air temperatures are higher. Likewise, the rate of cooling following shading in the mornings will be lower than in the afternoons, as the differential between air and soil temperatures at midday will usually be less than at dusk.

The canopies could be improved by increasing their durability. I found that I spent a substantial amount of time on canopy maintenance; the Big V canopies were particularly vulnerable to wind damage. They could be made more robust by sewing sleeves into the shadecloth, and attaching the canopy by inserting the lateral supports into the sleeves. Further support along the outer rim of the shadecloth would maintain tension and help prevent the shadecloth from sagging.

4.4.3 Summary

The artificial canopies proved to be a flexible and effective means of imposing light and rainfall redistribution treatments. At the same time they avoid the confounding effects of soil resources and eliminate variability in canopy structure. The basic design can be readily modified to impose differing levels of shading and rainfall redirection, as well as testing the effects of canopy size. This is a useful experimental technique that could be exploited to answer many questions of interest to ecologists and ecophysiologists.

Chapter 5

The effects of shade and rainfall redirection on emergence of *Carrichtera annua* and *Danthonia caespitosa*.

5.1 Introduction

Seed germination can be affected by a variety of environmental factors, including light quality, temperature and soil moisture (Fenner, 1985). As tree canopies may alter these and other environmental factors, the presence of trees has the potential to affect germination rates in the seedbank in the immediate vicinity.

The initiation of seed germination cannot occur until two sets of conditions are met. Firstly, the seed environment has to be suitable, with the appropriate temperature range and adequate levels of oxygen and moisture (Murdoch and Ellis, 1992). Secondly, the seed need to be in a receptive physiological state, *i.e.* dormancy must be broken (Murdoch and Ellis, 1992).

Environmental conditions can both trigger and terminate seed dormancy (Grime, 1979), and seed responses to these conditions show great variability both within (Gutterman, 1986) and between species (Murdoch and Ellis, 1992). The level and amplitude of ambient temperatures (Probert, 1992), the intensity, duration and spectral quality of light (Pons, 1992) and the chemical environment (Karssen and Hilhorst, 1992) may all affect seed dormancy. Furthermore, dormancy may be determined by interactions between environmental conditions. Seed dormancy responses to light have been found to vary with temperature in a number of species (Murdoch and Ellis, 1992; Pons, 1992), while responses to temperature vary with seed moisture levels (Probert, 1992).

Plant canopies modify light quality and intensity (Chazdon, 1988; Martens et al., 1997), soil temperature and moisture levels (Joffre and Rambal, 1993; Haworth and McPherson, 1995; Breshears et al., 1998) and soil chemistry (Charley and West, 1975; Romney et al., 1980). Consequently, given that germination responses tend to be species-specific, emergence from the germinable seedbank is likely to differ between canopy sites and open areas. In fact, due to the influence of the physical environment on seed dormancy, the composition of the germinable seedbank may also differ. Such differences have the potential to give rise to differences in the species composition of plant communities, although the ability to germinate in a given site does not necessarily ensure that seedlings will survive long enough to become part of the local community (Schupp, 1995).

While differences in the composition of emergent communities between canopy and open sites have been widely reported *e.g.* (Muller, 1953; Guttierrez et al., 1993; Pugnaire et al., 1996a), several non-exclusive processes may produce this pattern. Differences in dispersal shadows, spatial variability in the soil seedbank and in soil resources, differential seed predation, and post-emergence factors may all contribute to the creation of differences between canopy and open sites. To determine the effects of canopies on seedling emergence, field experiments that remove the confounding effects of the systematic spatial variability in soil resources and seedbank composition are required. The effects of canopy-induced differences in soil temperature and rainfall redirection on emergence can then be tested.

I conducted a field experiment to investigate which of these mechanisms are responsible for the effects that plant canopies have on emergence. In order to avoid the confounding influences of higher soil resource levels under trees, I used the artificial canopies described in Chapter 4. As these used black shadecloth to reduce light intensity, I was able to eliminate the effects of changes to the red:far red ratio on dormancy. The influence of soil moisture levels was tested by using flat and V-shaped canopies, allowing me to contrast the effects of shading with the effects of shading with rainfall redirection. I measured the emergence rates of two herbaceous species that are abundant in the T.G.B. Osborn Vegetation Reserve, the exotic annual forb *Carrichtera annua* and the native perennial grass *Danthonia caespitosa*. Both species are more abundant in open habitats than under canopies (Brock, 1993; Facelli and Brock, 2000; Barritt and Facelli, ress) (also see Chapter 3), although *C. annua* seedlings growing in the shade of fallen branches tend to be larger than seedlings fully exposed to direct sunlight.

5.2 Methods

I conducted two experiments on the effects of shade and rainfall redirection on emergence, one in 1998 and the other in 1999. Seeds of two species with contrasting seed coat characteristics were used; *C. annua* which possesses a hydrophilic mucilaginous outer coat, and *D. caespitosa*, whose lemmas are covered with numerous short hydrophobic hairs. *Carrichtera annua* seed becomes dormant at higher temperatures; germination rates in potted soil in a glasshouse approached zero when air temperatures exceeded 25° C (N. Wilczynski *pers. comm.*). The *C. annua* seed that I used was collected from Middleback Station, and the *D. caespitosa* seed came from the Flinders Ranges (supplier Blackwood Seeds, Murray Bridge, South Australia). Both collection locations are at similar latitudes and experience similar climatic conditions to Koonamore.

I tested the viability of both batches of seed prior to the field experiments. On 28 May 1998 I placed a sheet of Whatman No. 1 filter paper into each of twelve 55 mm Ø plastic petri dishes. I placed 20 *C. annua* seeds in each petri dish, and moistened the filter paper with reverse osmosis (RO) water. The seeds were incubated at room temperature at office lighting levels, and RO water was added as necessary to keep the filter papers moist. Emergence was counted every working day until 8 June 1998.

On 11 June 1998 I placed two sheets of Whatman No. 1 filter paper into each of fifteen 55 mm Ø plastic petri dishes. I placed ten *D. caespitosa* seeds in each petri dish, and moistened the filter paper with RO water. The seeds were incubated at room temperature at office lighting levels, and RO water was added as necessary to keep the filter papers moist. Emergence was counted every working day until 29 June 1998.

The viability of both seed batches was tested again in June 1999 to ensure that germination rates at room temperature had not fallen below 65%. This level was chosen as it provided a reasonable number of germinable seeds at the replication levels in the field experiments.

5.2.1 1998 experiment

On 11-14 July 1998 I defined two zones (inner and outer) around each of the artificial canopies in the T.G.B. Osborn Vegetation Reserve in which *C. annua* and *D. caespitosa* seed were planted. The inner zone was an annular band 0.1-0.2 m from the canopy centre, while the outer zone was 0.6-0.8 m from the centre (Figure 5.1). The inner zone under the Big V canopies receives more rainfall than the outer zone, whereas both zones under the flat canopies receive the same level of rainfall (see Chapter 4). The inner zone under the Small V canopies may also receive more rainfall than the outer zone, but the variability in the data was too great to detect

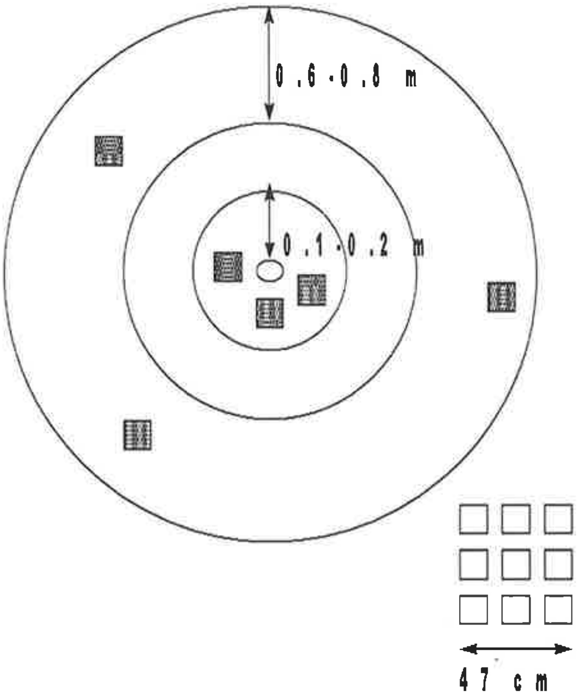


Figure 5.1: Schematic diagram of the arrangement of plots under artificial canopies in the 1998 emergence experiment. An inner (0.1-0.2 m) and an outer (0.6-0.8 m) zone were defined around the centre of each canopy, and three 47 × 47 cm plots were established in each zone. Each plot consisted of 9 subplots (see lower right), each of which were planted with either 32 *C. annua* seeds, 32 *D. caespitosa* seeds, 16 seeds of each species, or no seeds. Shaded squares represent randomly placed plots.

a statistical difference with the number of replicate raingauges that I used. Two replicates of each of the canopy types (Big V, Small V, Big Flat, Small Flat, Control V and Control Flat) were used in the experiment. In order to avoid the effects of direct sunlight slanting under the canopies during winter, I restricted seed planting to an area within each zone that fell between 60° and 300° from the central axis.

I established three 47 × 47 cm plots within each zone under each of the artificial canopies in the Reserve. The polar co-ordinates of each plot were randomly generated using the Skalski (1987) algorithm, with the proviso that the entire plot fell within the predetermined zone. All vegetation was removed from within each plot prior to planting seeds. The plots were divided into nine 9 × 9 cm subplots, with a 5 cm wide buffer strip between each subplot. A 5 cm wide buffer strip was also cleared around each plot. One of four seeding treatments were randomly allocated to each of the subplots. Hereafter I shall use the names of the genera planted as common names to denote each treatment, *i.e.* Carrichtera, Danthonia, Both and None. Thirty-two seeds were individually planted in each subplot at a depth of approximately 15 mm. After planting was completed the plots were given $1l$ of water from a watering can to help settle the soil. No further supplementary watering was provided. In the Both treatment, the species that was planted alternated between rows, so that a total of 16 seeds of each species was planted. No seeds were planted in the None treatment, but the soil was disturbed in the same manner as in the other treatments. There were two replicates of the Carrichtera, Danthonia and Both treatments within each plot, and three replicates of the None treatment. I chose to use a larger number of replicates for the None treatment to accommodate the larger variability in the soil seedbank. A total of 15,552 seeds were planted. Each subplot was marked with a colour-coded plastic golf tee to help identify the allocation of treatments. The plots were covered by 20 cm high 5 cm mesh wire cages to protect seedlings from vertebrate herbivores.

Seedling emergence was counted on 7-8 September and 27-28 October 1998. Seedlings that had emerged were marked with a toothpick; the toothpick was blackened with a felt-tip marker when the seedlings died.

Extremely high rates of *C. annua* emergence from the soil seedbank under one of the Small V canopies resulted in the October census taking much longer than expected. Due to time constraints I was unable to collect data from two of the three outer zone plots under this canopy.

5.2.2 1999 experiment

The design of this experiment was similar to the 1998 experiment, with modifications intended to eliminate the soil seedbank and to increase the germination rates of planted seed. The experiment was conducted under the artificial canopies in the

Reserve as *per* the 1998 experiment, except that I defined the inner zone as being 0.1-0.3 m from the canopy centre to make it consistent with size of the outer zone. I also restricted the angular locations to between 90° and 270° from the central axis of each canopy to further reduce the possibility of plots being fully exposed to direct sunlight during winter.

On 7 May 1999 I collected soil from South Lake paddock near the North-west corner of the Reserve to a depth of approximately 10 cm. The soil was transported to Adelaide, where it was pulverised and sieved through a 5 mm Ø colander before being pooled and thoroughly mixed. I then autoclaved the soil at 120° C for 35 minutes to kill any seeds it might contain.

The homogenised and sterilised soil was subsequently transported back to Koonamore, where it was placed into seedling punnets. I lined the bottom of the punnets (Masrac MK 8, 139 × 68 mm) with pieces of nylon gauze to prevent soil loss through the drainage holes while still allowing water exchange. I then placed approximately 260 ml of sieved, autoclaved soil into each punnet, before planting 21 seeds to a depth of about 2 mm. I chose the shallower depth of planting as I considered that one of the possible reasons for the low emergence rates in the 1998 experiment was that the seeds may have been planted too deeply. The seeding treatments were Carrichtera, Danthonia or None, and a total of 3,024 seeds were planted.

Three plots were randomly located within each zone under each canopy using the Skalski (1987) algorithm. I placed one punnet of each of the three seeding treatments in each plot, removing enough soil to allow the soil level within the punnets to be flush with the surrounding soil. The punnets were placed alongside one another, and any gaps between them were filled with loose soil. The order in which the different seeding treatments were placed within plots was randomly allocated.

The plots were not watered after planting as I deemed that the seeds were adequately covered with soil. However, the plots were caged as *per* the 1998 experiment.

Seedling emergence was counted on 12 October 1999 and 25 November 1999, and emergent seedlings were marked as previously described. A further emergence event followed heavy rain in late January and early February 2000, so a third count was made on 24 February 2000.

5.2.3 Data analyses

1998 experiment

The preponderance of zeroes in these data created many difficulties during analyses. Because there were so many zeroes in the data, I decided not to consider seedling survivorship, and to analyse only the cumulative emergence to 30 October 1998. Even so, the data could not be transformed to anything resembling a normal distribution; standard ANOVA methods were not a valid choice. Nor were any of the data a very good fit to the Poisson distribution. However, the negative binomial distribution provided a more satisfactory fit to the data, and has been successfully used with zero-inflated data in the past (Welsh et al., 1996) (W. Venables, *pers. comm.*). Consequently I used negative binomial Analysis of Deviance (ANODEV) to test for treatment effects. Nevertheless, the results of the analyses should be regarded conservatively, as the large number of zeroes may result in inflated deviances (W. Venables *pers. comm.*).

The use of conditional or mixed models is perhaps the best of current methods for analysing zero-inflated data (Welsh et al., 1996). Such models consist of two components, one that models the probability of a score being zero and the other modelling the non-zero data. I was unable to find any extra-zeroes routines that would allow me to use a full nested model, but the S-Plus function zipmixMenu (Yau, 2000) permitted the use of several covariates without nesting or interaction terms. This function uses zero-inflated Poisson regression modelling (ZIPS), fitting the zero data to a logistic distribution, and the non-zero data to a Poisson distribution (Lambert, 1992). The results of my ZIPS analyses should also be regarded conservatively, as the lack of nested terms means that the degrees of freedom and the error terms are calculated differently (Zar, 1999). Also note that zipmixMenu (Yau, 2000) provides P values to three decimal points rather than the customary four or more.

Given that both of the methods available had limitations or shortcomings, I verified the results of one method of analysis using the other. I chose to use negative binomial ANODEV (MathSoft (1999), function glm.nb (Venables and Ripley, 1999a)) for my primary analysis because it permitted the correct modelling of nested treatment effects, and I used the ZIPS model (which provided a better fit to the data) to verify significance in the main effects. The initial model used in the ANODEV was Canopy, Seeding nested within Canopy, Zone nested within Canopy, and the interaction between Seeding and Zone nested within Canopy. The highest order interaction terms were progressively dropped if they proved to be non-significant (Venables and Ripley, 1999b). The ZIPS model consisted of Canopy, Seeding and Zone, without any nested or interaction terms.

Pairwise comparisons were made between the levels of significant treatment effects by conducting ANODEVs on subsets of the data. The comparisons were designed to test the effects of the size of the shade patch (and rainfall harvesting area for V canopies) on emergence, and whether the combined effects of shade and rainfall redirection were different from the effects of shade alone. For these comparisons I used the S-Plus function glm (MathSoft, 1999) and fixed the negative binomial dispersion parameter θ at the value estimated by glm.nb (Venables and Ripley, 1999a) in the analysis of the complete data set. The critical α' was adjusted for the number of comparisons (Underwood, 1997).

1999 experiment

Similar problems with inflated zero counts were experienced with the data from the 1999 experiment. Consequently I used similar methods of analysis. I conducted analyses on emergence over three periods; cumulative emergence to November 1999 (spring emergence), new emergence in February 2000 (summer emergence) and their combined total (total emergence). Prior emergence was used as a covariate in the models for the summer emergence data to account for the reduction in the number of available seeds by spring germination. I was unable to conduct ANODEV on the summer Carrichtera and the spring Danthonia data as glm.nb failed to converge on an estimate of θ. This was possibly a consequence of the high proportion of zeroes.

I compared the spring emergence patterns with the summer patterns by introducing a Time factor into the analyses. If there were differences in the emergence responses to treatments between spring and summer, the interaction terms between Time and Canopy, Time and Seeding, or Time and Zone would be significant. Emergence data were converted to proportions of seed planted (spring) or proportion of seed remaining after spring emergence (summer). The $\arcsin\sqrt{p}$ transformation did not successfully transform the emergence proportion data to normality. Nor were attempts to analyse the data using ANODEV with Poisson or negative binomial distributions successful due to either an inability to converge on θ or because there was no response in some treatment levels. Instead, I analysed the data in two separate tests. I tested for qualitative differences between seasons by treating the data as a dichotomous response and analysing it using ANODEV with a binomial distribution. I tested for quantitative differences by conducting ANODEV with a Poisson distribution on all those data where emergence occurred, *i.e.* all counts greater than zero. The initial model for both types of analyses was Canopy, Time, the interaction between Canopy and Time, Seeding nested within Canopy, the interaction between Seeding and Time nested within Canopy, Zone nested within Canopy, the interaction between Zone and Time nested within Canopy, the interaction between Zone and Seeding nested within Canopy and the interaction between Zone, Seeding and Time nested within Canopy. The highest order interaction terms were progressively removed whenever they were not significant. I halted analysis whenever all of the interaction terms involving Time had been eliminated.

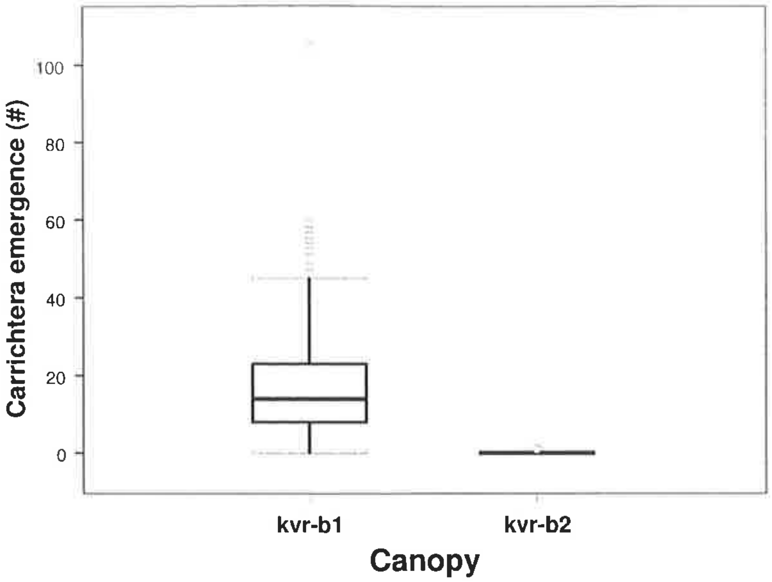


Figure 5.2: Total *Carrichtera annua* emergence per subplot under replicate Small V canopies in the 1998 experiment. Data were not collected from two of the six plots under kvr-b1 in October; the September data is used for those plots. Box spans 1st to 3rd quartiles, bar denotes median, whiskers denote minima and maxima, except for those points (open circles) more than 1.5 times the inter-quartile range from the median.

5.2.4 Data exclusions

1998 experiment

Data from the Small V canopies were excluded from the analyses for two reasons. Firstly, there were missing data from the October census. Secondly, and more importantly, *C. annua* emergence under one of the two Small V canopies was exceptionally high (Figure 5.2). The control subplots under this canopy, which were not planted with *C. annua* seed, also had high emergence rates, indicating that emergence from the *C. annua* soil seedbank was exceptionally high at this particular location. Consequently I decided to exclude the Small V data from the analyses.

1999 experiment

Some time between 29 June and 12 October 1999 the shadecloth on both of the Big V canopies slipped towards the centre poles, leaving most of the plots exposed to direct sunlight. The slippage also meant that the canopies would not have been funnelling rainfall towards the canopy centres. Since the treatment was inconsistently applied, I excluded the data from the Big V canopies from the analyses.

5.3 Results

5.3.1 Seed viability

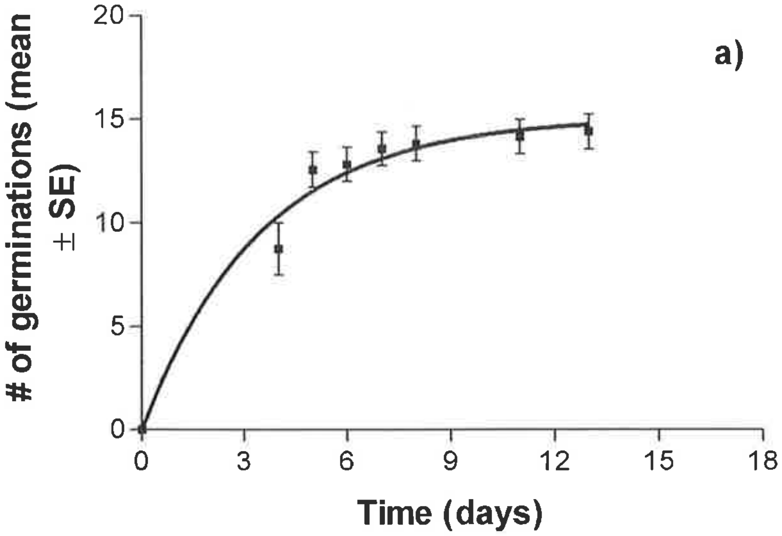
Both species readily germinated in petri dishes at room temperature, although *C. annua* germination was more variable than *D. caespitosa* (Figure 5.3). *C. annua* also germinated more rapidly than *D. caespitosa*, with a substantial proportion of the seeds germinating within four days. Mean germination rates were 72.1% of the total number of seeds (SD 14.5%, $n=$ 12) for *C. annua* and 77.3% (SD 12.2%, $n=$ 15) for *D. caespitosa*.

5.3.2 1998 emergence experiment

Danthonia caespitosa emergence tended to be higher than *C. annua* emergence, although overall emergence rates for both species were very low, with no emergence recorded from a high proportion of subplots. The data were also strongly skewed (Figure 5.4).

Carrichtera annua emergence varied between canopies and between seeding treatments (Table 5.1). ANODEV also indicated a difference in emergence between zones. This could be a spurious result as it was not verified by the ZIPS analysis, nor is apparent in the graph (Figure 5.4) . Emergence rates were higher under artificial canopies than in control (unshaded) treatments, but did not differ between canopy types or sizes (Figure 5.4).

Likewise, *D. caespitosa* emergence varied between canopies and between seeding treatments, but there was no suggestion of differences between zones (Table 5.2).



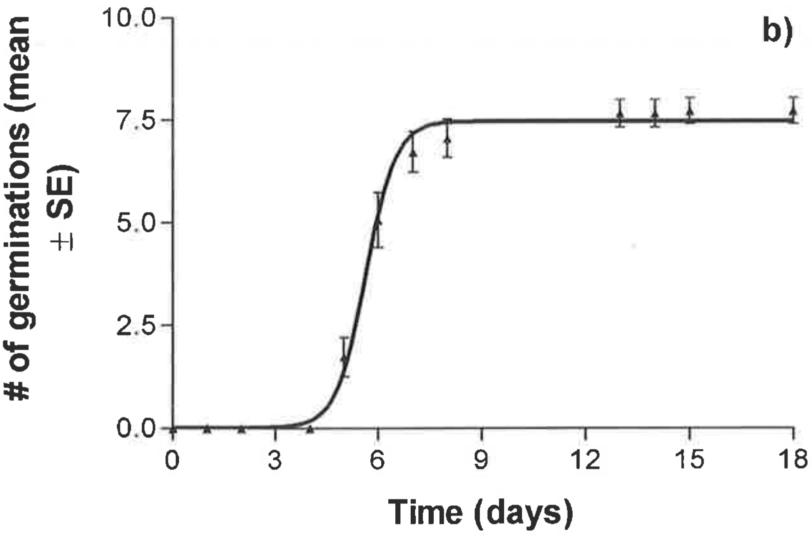


Figure 5.3: a) *Carrichtera annua* and b) *Danthonia caespitosa* viability as measured by germination in petri dishes at room temperature and lighting. Non-linear regressions were fitted, using the *F* test to select the model providing the best fit. a) Solid line indicates fitted one-phase exponential association model (R^2 = 0.7099), providing an estimated maximum germination rate of 75.55%of the total number of seeds, 95% CI (67.60, 83.55), n= 12. b) Solid line indicates fitted sigmoidal dose response model (R^2 = 0.8613), providing an estimated maximum germination rate of 74.9% of the total number of seeds, 95% CI (71.97, 77.82), n= 15. (GraphPad, 1999).

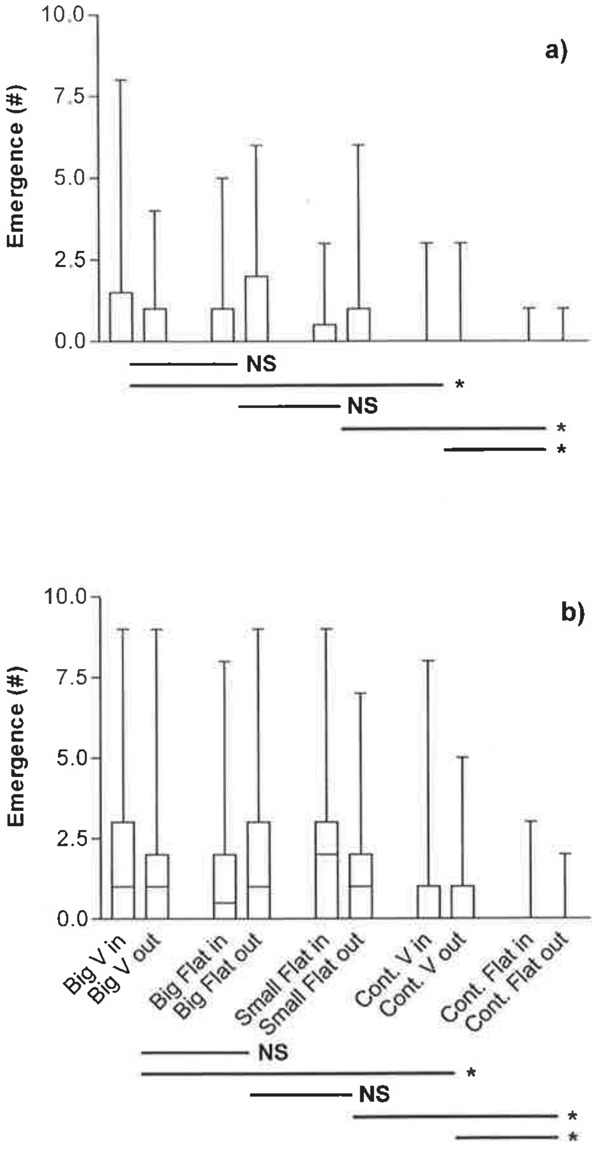


Figure 5.4: a) *Carrichtera annua* and b) *Danthonia caespitosa* emergence per subplot in 1998 experiment. Data from all seeding treatments are included within each zone-canopy level. Subplots were allocated four seeding treatments in which either 32 seeds of one species (Carrichtera and Danthonia, $n = 4$ each per canopy), 16 seeds of each species (Both, $n = 4$) or 0 seeds (None, $n = 6$) were planted. Lines below each graph indicate pairwise comparisons between canopy treatments (negative binomial ANODEV (Venables and Ripley, 1999a), MathSoft (1999)). in = inner zone, out = outer zone. $*$ indicates significant comparison at $\alpha' = 0.01$, **NS** indicates non-significant comparison. Whiskers mark maxima, boxes span 1st and 3rd quartiles, bars indicate medians.

a)	**Df**	**Deviance**	**Residual Df**	**Residual Deviance**	P (χ^2)
Null			539	694.7562	
Canopy	4	130.247	535	564.5092	<0.0001
Seeding[Canopy]	15	256.9217	520	307.5875	<0.0001
Zone[Canopy]	5	12.5732	515	295.0143	0.0277

b)		**Estimate**	**SD**	t	P
Logistic	**Intercept**	-1.438	0.585	-2.458	0.007
	Canopy	0.230	0.095	2.425	0.008
	Seeding	0.914	0.154	5.932	0.000
	Zone	-0.349	0.276	-1.263	0.103
Poisson	**Intercept**	1.267	0.318	3.985	0.000
	Canopy	-0.099	0.051	-1.937	0.026
	Seeding	-0.245	0.117	-2.096	0.018
	Zone	-0.002	0.153	-0.011	0.496

Table 5.1: a) Analysis of deviance on *Carrichtera annua* emergence in 1998. Data were fitted to a negative binomial distribution (MathSoft (1999), glm.nb (Venables and Ripley, 1999a)). b) Zero-inflated Poisson regression of *Carrichtera annua* emergence data in 1998. Pearson residual = 537.641, Deviance residual = 538.217, Log-likelihood = -425.895. (MathSoft (1999), function zipmixMenu (Yau, 2000)).

a)	Df	Deviance	Residual Df	Residual Deviance	P (χ^2)
Null			479	811.9693	
Canopy	4	131.3777	475	680.5916	<0.0001
Seeding[Canopy]	15	212.67	460	467.9216	<0.0001
Zone[Canopy]	5	9.4677	455	458.4538	0.0918

b)		Estimate	SD	t	P
Logistic	**Intercept**	-1.137	0.475	-2.393	0.008
	Canopy	0.025	0.073	0.339	0.367
	Seeding	0.329	0.101	3.258	0.001
	Zone	0.032	0.216	0.150	0.441
Poisson	**Intercept**	0.918	0.194	4.732	0.000
	Canopy	-0.063	0.029	-2.159	0.015
	Seeding	0.121	0.046	2.635	0.004
	Zone	-0.123	0.094	-1.304	0.096

Table 5.2: a) Analysis of deviance on *Danthonia caespitosa* emergence in 1998. Data were fitted to a negative binomial distribution (MathSoft (1999), glm.nb (Venables and Ripley, 1999a)). b) Zero-inflated Poisson regression of *Danthonia caespitosa* emergence data in 1998. Pearson residual = 631.161, Deviance residual = 902.879, Log-likelihood = -761.137. (MathSoft (1999), function zipmixMenu (Yau, 2000)).

ZIPS analysis indicated that there was no effect of canopy on whether any *D. caespitosa* emerged, but the magnitude of emergence differed between canopies whenever *D. caespitosa* emerged. Emergence rates were higher under artificial canopies than under control (unshaded) treatments, but did not differ between canopy types (Figure 5.4).

5.3.3 1999 emergence experiment

Overall emergence rates were again very low and strongly skewed, with no emergence recorded in many punnets. *Carrichtera annua* emergence rates were generally higher than *D. caespitosa* rates (Figures 5.5 and 5.6). Also, it appears that whereas summer *C. annua* emergence tended to occur in the punnets where spring emergence had occurred, this was not generally the case for *D. caespitosa*, with the exception of punnets in the inner zone under Small V canopies.

Emergence of *Carrichtera annua*

Carrichtera annua emergence in spring differed between canopies and between seeding treatments (Tables 5.3 and 5.4). The ZIPS analysis indicates that while zone did not affect the probability of punnets containing *C. annua* seedlings, the number of seedlings that emerged differed between zones. Conversely, canopy presence affected whether or not *C. annua* emerged, but did not affect the magnitude of emergence. During summer, zone and seeding had no effect, while both the occurrence and magnitude of emergence differed between canopies. The number of seedlings emerging in summer was not affected by the number that had emerged previously in spring, but prior emergence did affect whether or not emergence occurred in summer. Note that ANODEV was not conducted on the summer data as θ could not be estimated. Combined spring and summer emergence differed between canopies, between seeding treatments and between zones (Tables 5.3 and 5.4). The number of punnets in which there was no emergence did not differ between zones, but the magnitude of emergence did differ between zones (Table 5.3).

During spring and across both emergence periods, more *C. annua* seedlings emerged under the Big Flat canopies than under the Small Flat canopies (Figure 5.5). There were no differences between the Small Flat and the Small V canopies, but more emergence occurred under the small canopies than in the unshaded Control treatments. Total emergence under the Controls did not differ; statistical comparisons could not be made between the Controls for spring emergence as there was no treatment response. Comparisons between treatment levels in summer were not possible as θ could not be estimated. There was weak evidence that total *C. an-*

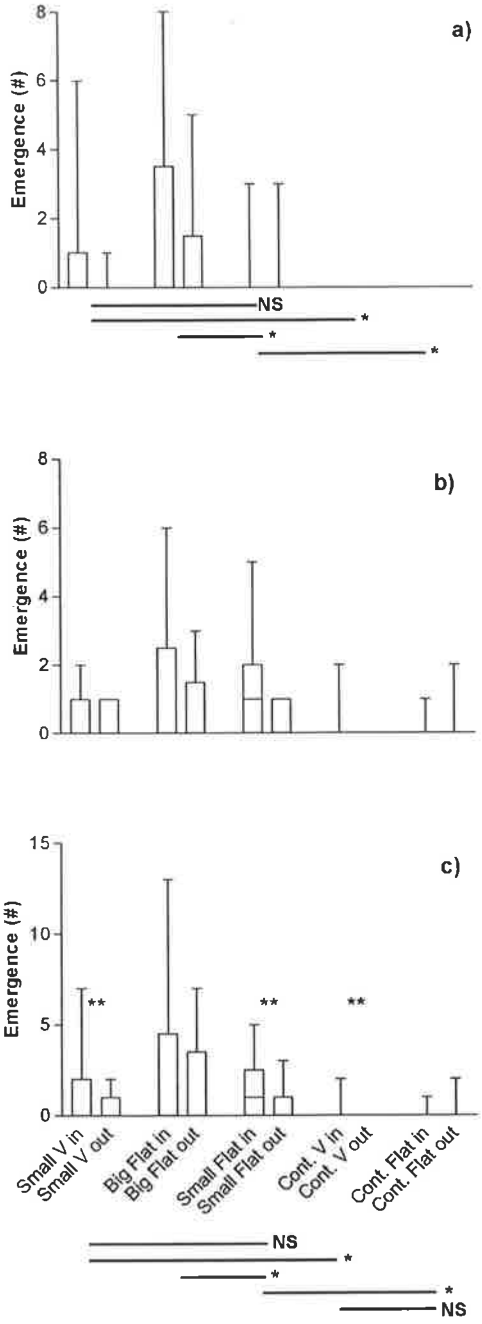


Figure 5.5: *Carrichtera annua* emergence in a) spring 1999, b) summer 1999-2000 and c) spring and summer combined. Data from all seeding treatments are shown for each zone-canopy level. Punnets filled with sterilised soil were planted with either 21 *C. annua* seeds, 21 *D. caespitosa* seeds, or 0 seeds. $**$ indicates comparisons between zones that were significant at $\alpha = 0.05$ but not at $\alpha' = 0.01$ (negative binomial ANODEV (Venables and Ripley, 1999a), MathSoft (1999)). Lines below graphs show pairwise comparisons between canopy treatments. $*$ indicates significant comparison at $\alpha' = 0.01$, **NS** indicates non-significant comparison. Whiskers mark maxima, boxes span 1st and 3rd quartiles, bars indicate medians.

nua emergence was higher in the inner zone of Small V, Small Flat and Control V canopies, with comparisons returning P values falling between $\alpha = 0.05$ and $\alpha' = 0.01$.

There were no indications that the treatment effects on the proportion of *C. annua* seed emerging differed between spring and summer (Table 5.5). While the number of punnets with no emergence was higher in spring, the magnitude of emergence in punnets with seedlings did not differ between seasons. Likewise, canopy and seeding affected whether or not emergence occurred, but not the size of the response.

Emergence of *Danthonia caespitosa*

Danthonia caespitosa emergence was very low in spring (Figure 5.6), and treatment effects could not be tested with ANODEV. The ZIPS analysis indicates that treatments had no effect on the number of punnets without *D. caespitosa* emergence, but that the magnitude of emergence in punnets with seedlings differed between canopies (Table 5.6). Given the very low levels of emergence, this result should be regarded cautiously. Summer emergence was higher, and differed between canopies and between seeding treatments, but not between zones (Tables 5.4 and 5.6). The number of punnets with no *D. caespitosa* emergence differed between canopies and seeding treatments, and was also affected by the number of seedlings that had emerged previously in spring (Table 5.6). However, the number of seedlings emerging in punnets did not differ between any of the treatments, nor was it affected by prior emergence. Total *D. caespitosa* emergence differed between seeding treatments, but not between zones (Tables 5.4 and 5.6). ANODEV and ZIPS differ over the effect of canopy, with ZIPS finding no difference and ANODEV returning a highly significant result. The reason for the discrepancy is unclear; visual inspection of the data suggests that *D. caespitosa* emergence is higher under the shade of artificial canopies than it is in the Control treatments (Figure 5.6).

Total *D. caespitosa* emergence and emergence during summer did not differ be-

Season	Component	Source	Estimate	SD	t	P
a) Spring	**Logistic**	**Intercept**	-4.03	3.076	-1.31	0.095
		Canopy	1.498	0.8	1.873	0.031
		Seeding	1.446	1.683	0.859	0.195
		Zone	-0.73	1.142	-0.64	0.261
	Poisson	**Intercept**	4.386	1.341	3.271	0.001
		Canopy	0.166	0.27	0.613	0.270
		Seeding	-2.435	0.987	-2.467	0.007
		Zone	-0.905	0.332	-2.726	0.003
b) Summer	**Logistic**	**Intercept**	0.748	1.291	0.580	0.281
		Canopy	-0.541	0.242	-2.236	0.013
		Seeding	0.366	0.444	0.825	0.205
		Zone	0.667	0.628	1.061	0.144
		Prior	-2.617	1.600	-1.636	0.051
	Poisson	**Intercept**	1.699	0.667	2.547	0.005
		Canopy	-0.180	0.090	-1.999	0.023
		Seeding	-0.332	0.274	-1.213	0.113
		Zone	-0.428	0.305	-1.403	0.080
		Prior	0.068	0.061	1.114	0.133
c) Total	**Logistic**	**Intercept**	-0.598	0.928	-0.645	0.260
		Canopy	-0.271	0.149	-1.821	0.034
		Seeding	0.661	0.337	1.960	0.025
		Zone	0.457	0.430	1.063	0.144
	Poisson	**Intercept**	3.399	0.390	8.716	0.000
		Canopy	-0.221	0.059	-3.753	0.000
		Seeding	-0.907	0.233	-3.893	0.000
		Zone	-0.457	0.207	-2.210	0.014

Table 5.3: Zero-inflated Poisson regression of *Carrichtera annua* emergence data for a) spring 1999, b) summer 2000 and c) spring and summer combined. Spring emergence is included as a covariate (Prior) in the summer analysis. Pearson residuals = a) 71.674, b) 167.6, c) 196.001. Deviance residuals = a) 88.338, b) 144.95, c) 216.099. Log-likelihood =a) -74.573, b) -126.773, c) -175.336. (MathSoft (1999), function zipmixMenu (Yau, 2000)).

	Source	Df	Deviance	Resid. Df	Residual Deviance	$P(\chi^2)$
a) Spring	**Null**			179	199.0643	
Carrichtera	**Canopy**	4	71.2393	175	127.825	<0.0001
	Seeding[Canopy]	10	78.27354	165	49.5515	<0.0001
b) Total	**Null**			179	365.2772	
Carrichtera	**Canopy**	4	105.3572	175	259.92	<0.0001
	Seeding[Canopy]	10	123.1192	165	136.8008	<0.0001
	Zone[Canopy]	5	16.1325	160	120.6683	0.0065
c) Summer	**Null**			179	212.3764	
Danthonia	**Canopy**	4	31.24339	175	181.133	<0.0001
	Seeding[Canopy]	10	89.00494	165	92.1281	<0.0001
d) Total	**Null**			179	221.4851	
Danthonia	**Canopy**	4	29.32444	175	192.1606	<0.0001
	Seeding[Canopy]	10	85.3197	165	106.8409	<0.0001

Table 5.4: ANODEVs on *Carrichtera annua* emergence from a) 27 July - 25 November 1999 and b) 27 July 1999 - 24 February 2000; and on *Danthonia caespitosa* emergence from c) 26 November 1999 - 24 February 2000 and d) 27 July 1999 - 24 February 2000. ANODEVs were not conducted on summer *C. annua* or spring *D. caespitosa* emergence because I was unable to obtain an estimate of the negative binomial dispersion parameter θ. (MathSoft (1999), function glm.nb (Venables and Ripley, 1999a)).

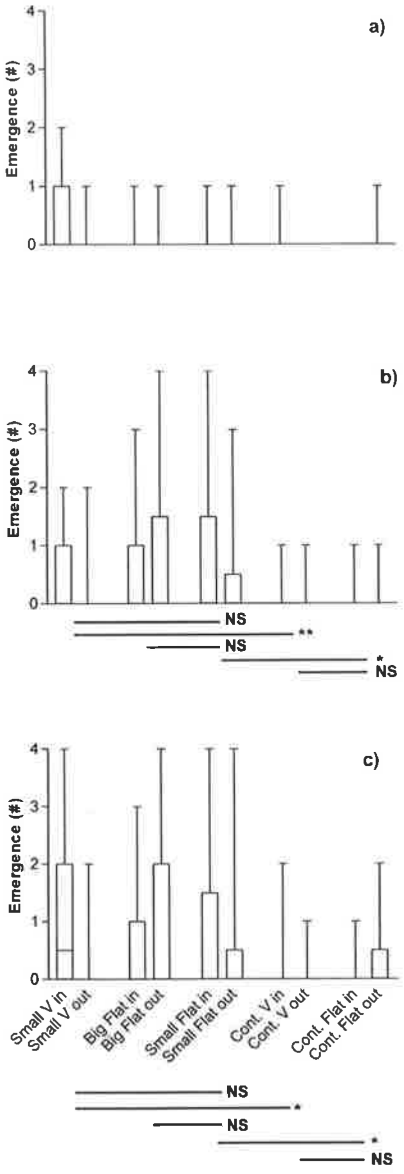


Figure 5.6: *Danthonia caespitosa* emergence in a) spring 1999, b) summer 1999-2000 and c) spring and summer combined. Data from all seeding treatments are shown for each zone-canopy level. Punnets filled with sterilised soil were planted with either 21 *C. annua* seeds, 21 *D. caespitosa* seeds, or 0 seeds. Lines below graphs show pairwise comparisons between canopy treatments. $*$ indicates significant comparison at $\alpha' = 0.01$, **NS** indicates non-significant comparison (negative binomial ANODEV (Venables and Ripley, 1999a), MathSoft (1999)). Whiskers mark maxima, boxes span 1st and 3rd quartiles, bars indicate medians.

Model	**Source**	**Df**	**Deviance**	**Residual Df**	**Residual Deviance**	$P(\chi^2)$
a) Binomial	**Null**			359	348.9176	
	Canopy	4	46.14002	355	302.7776	<0.0001
	Time	1	11.91857	354	290.859	0.0006
	Seeding[Canopy]	10	72.58628	340	212.4396	<0.0001
	Time*Canopy	4	5.8332	350	285.0258	0.2120
b) Poisson	**Null**			67	3.577907	
	Canopy	4	1.010525	63	2.567381	0.9082
	Time	1	0.179555	62	2.387826	0.6718
	Seeding[Canopy]	7	0.516525	55	1.871301	0.9994
	Time*Canopy	2	0.048518	53	1.822783	0.9760

Table 5.5: Comparisons between spring 1999 and summer 2000 *Carrichtera annua* emergence. a) Binomial ANODEV on occurrence of emergence. b) Poisson ANODEV on magnitude of response where emergence has occurred (MathSoft, 1999).

tween Big and Small Flat canopies, nor did it differ between Small V and Small Flat canopies or between the Controls (Figure 5.6). However, emergence was higher under the Small Flat canopies than under the Control Flat treatments. Similarly, total *D. caespitosa* emergence was higher under the Small V canopies than under the Control V canopies, with a non-significant difference in summer ($0.01 > P > 0.05$).

There were no indications that the treatment effects on the proportion of *D. caespitosa* seed emerging differed between spring and summer (Table 5.7). While the number of punnets with no *D. annua* emergence was higher in spring, the magnitude of emergence in punnets with seedlings did not differ between seasons. Likewise canopy, seeding and zone affected whether or not emergence occurred, but not the size of the response.

Season	Component	Source	Estimate	SD	t	P
a) Spring	**Logistic**	**Intercept**	-18.062	38.100	-0.474	0.318
		Canopy	0.631	0.542	1.164	0.122
		Seeding	-1.714	1.218	-1.407	0.080
		Zone	10.706	19.117	0.560	0.288
	Poisson	**Intercept**	-5.003	1.605	-3.117	0.001
		Canopy	0.538	0.214	2.512	0.006
		Seeding	0.194	0.340	0.571	0.284
		Zone	0.782	0.889	0.880	0.190
b) Summer	**Logistic**	**Intercept**	5.628	2.117	2.659	0.004
		Canopy	0.495	0.271	1.826	0.034
		Seeding	-2.416	0.668	-3.617	0.000
		Zone	-0.244	0.828	-0.295	0.384
		Prior	-4.624	2.469	-1.873	0.031
	Poisson	**Intercept**	-0.799	1.031	-0.775	0.219
		Canopy	0.045	0.113	0.394	0.347
		Seeding	0.301	0.343	0.877	0.190
		Zone	0.004	0.353	0.011	0.496
		Prior	-0.005	0.299	-0.016	0.494
c) Total	**Logistic**	**Intercept**	2.957	1.329	2.225	0.013
		Canopy	0.097	0.172	0.563	0.287
		Seeding	-1.444	0.373	-3.872	0.000
		Zone	0.394	0.557	0.707	0.240
	Poisson	**Intercept**	-0.543	0.866	-0.627	0.265
		Canopy	0.071	0.088	0.809	0.209
		Seeding	0.283	0.246	1.152	0.125
		Zone	-0.057	0.313	-0.182	0.428

Table 5.6: Zero-inflated Poisson regression of *Danthonia caespitosa* emergence data for a) spring 1999, b) summer 2000 and c) spring and summer combined. Spring emergence is included as a covariate (prior) in the summer analysis. Pearson residuals = a) 156.131, b) 123.291, c) 203.212. Deviance residuals = a) 72.635, b) 117.454, c) 164.096. Log-likelihood = a) -52.931, b) -103.659, c) -135.851. (MathSoft (1999), function zipmixMenu (Yau, 2000)).

Model	Source	Df	Deviance	Residual Df	Residual Deviance	$P(\chi^2)$
a) Binomial	**Null**			359	324.4041	
	Canopy	4	19.96356	355	304.4405	0.0005
	Time	1	17.11502	354	287.3255	<0.0001
	Time∗Canopy	4	3.61591	350	283.7096	0.4605
	Seeding[Canopy]	10	72.24733	340	211.4623	<0.0001
	Zone[Canopy]	5	18.64295	335	192.8193	0.0022
b) Poisson	**Null**			359	18.73581	
	Canopy	4	1.807389	355	16.92842	0.7711
	Time	1	2.208081	354	14.72034	0.1373
	Time∗Canopy	4	0.325076	340	9.1927	0.9881
	Seeding[Canopy]	10	5.202566	344	9.51778	0.8772
	Zone[Canopy]	5	0.961847	335	8.23086	0.9656

Table 5.7: Comparisons between spring 1999 and summer 2000 *Danthonia caespitosa* emergence. a) Binomial ANODEV on occurrence of emergence. b) Poisson ANODEV on magnitude of response where emergence has occurred. (MathSoft, 1999).

5.4 Discussion

Shading consistently increased the emergence rates of *C. annua* and *D. caespitosa* in both 1998 and 1999. The amount of shading also affected *C. annua* emergence, as 1999 rates were higher under large canopies than under small canopies. This is also evident in the marginally higher rates of emergence in the inner zones of the small canopies. That these patterns were absent from the 1998 data and the 1999 *D. caespitosa* data may be attributable to species-specific differences in germination requirements. Intra-specific differences in germination responses to temperature between local seed and the seed batches used in the experiments may also have contributed. Furthermore, the 1998 results may have been affected by spatial variability in the vertical distribution of the soil seedbank. In some locations the germinable soil seedbank may have been closer to the soil surface than in other locations, affecting both the ease of emergence and the soil temperature and moisture regimes. This may have had a particularly strong influence where the seedbank was closer to the surface than the experimentally planted seed.

5.4.1 Statistical issues

There was no evidence that emergence rates were affected by canopy rainfall redirection. However, two factors conspired against detecting the effect of this treatment. In both years data from one or other of the two sizes of V-shaped canopies had to be excluded, reducing the power of comparisons between those canopies that redirect rainfall and those that do not. The other factor was the very low response levels. There was no emergence at all in many experimental units. This, when coupled with high variability where emergence occurred, meant that only large treatment effects were detectable. Unfortunately I was unable to quantify the minimum detectable treatment effect. Most power analysis methods assume data to be normally distributed, a few accommodate binomial and Poisson data, and I know of none that are appropriate for negative binomial data. Nevertheless, I can conclude that while rainfall redirection may possibly have some effect on the emergence rates of *C. annua* and *D. caespitosa*, the effect of shading alone is much larger.

The differences between the logistic and Poisson parts of the ZIPS analyses are difficult to interpret. There is no obvious *a priori* reason why a treatment should have a significant effect on whether or not any emergence occurred without also affecting the magnitude of the response, or *vice versa*. However, such differences may be artifacts of the lack of discrimination between structural[1] and random zeroes in the analyses. Structural zeroes are difficult to identify in the 1998 experiment, because emergence from the soil seedbank was always possible. In the 1999 experiment, punnets that were not planted with seed of the target species should have produced structural zeroes. However, either the soil was not fully sterilised or seeds were dispersed into the punnets after the experiment was set up, for both species not infrequently emerged in punnets in which they were not planted. Nevertheless, the logistic part of the ZIPS analysis will contain a high proportion of structural zeroes, whereas there will be none in the Poisson part, which only considers non-zero data. Since the structural zeroes in the 1999 experiment are associated with the Seeding treatment, it follows that the Seeding term is likely to be significant in the logistic part of the analyses but not in the Poisson part. The *D. caespitosa* results follow this pattern, but the *C. annua* results do not. An examination of the raw data provided a plausible explanation for this difference. *Carrichtera annua* emerged in almost twice as many punnets in which its seeds were not planted as *D. caespitosa* (20 punnets *vs.* 11). Thus nearly twice as many *C. annua* control responses were in the Poisson part of the analysis. It is difficult to assess what effect this may have had on the significance testing of the other treatment effects.

There could also be argument about the classification of zeroes arising from treat-

---

[1] Structural zeroes are zeroes that arise when the response phenomenon cannot occur, whereas random zeroes are those that occur by chance (Welsh et al., 1996).

ment levels that enforce dormancy. By definition, these should be treated as structural zeroes, but on the other hand they represent a real response to a treatment and as such should be analysed with the rest of the data. Although removing structural zeroes from data is considered to be a statistically legitimate procedure (Welsh *pers. comm.*), I chose not to do so primarily because of the difficulties in identifying them with adequate confidence.

5.4.2 Biological effects

Attempting to disentangle the different effects of shade on emergence proved to be problematic. This was due to the complexity introduced by potential interactions between the effects of temperature and moisture. At first glance, it would appear that comparisons between patterns of emergence in spring and summer 1999 might be informative. If the effect of shading in reducing soil temperature determined emergence patterns, the difference between open and shaded sites should be larger in summer than in spring. However, closer consideration reveals potentially confounding factors and counterintuitive results. For instance, maximum soil temperatures in open areas in spring were similar to those in shaded areas in summer. Yet emergence rates under canopies in summer were much higher for both *C. annua* and *D. caespitosa* than in the open during spring. This may be attributable to the larger diurnal fluctuation in the open during winter and spring, where temperatures at a depth of 5.5 cm varied over a 15-20° C range compared with a range of 10-15° C under canopies during summer (see Chapter 4). However, increased temperature fluctuations are usually associated with breaking, rather than inducing dormancy (Probert, 1992). Essentially, the germination requirements of these two species are insufficiently understood to resolve this issue.

Although differences in day length between spring and summer may also have affected emergence (Pons, 1992), this too seems improbable given that the seed were buried to a depth of about 2 mm. It is unlikely that the light intensity at even this shallow depth would be sufficient to affect phytochrome responses. The most likely explanation for the seasonal patterns of seed emergence is that the dormancy responses of the seeds to temperature were affected by seed moisture levels (Probert, 1992). The unusually large rain events in January and February 2000 left the soil profile more deeply wetted than it had been during winter and spring (*pers. obs.*). Consequently, seeds may have been more fully imbibed, and they may have been at high moisture levels for longer periods than they were during the earlier stages of the experiment. This is consistent with the results of laboratory germination trials on *C. annua* in which less negative water potentials partially compensated for reductions in germination as temperatures increased (Facelli *unpublished data*).

The patterns of emergence of *C. annua* and *D. caespitosa* in these experiments were different from the actual plant distributions at Koonamore (see Chapter 3) or at Middleback Station (Brock, 1993; Facelli and Brock, 2000). Whereas emergence in the experiments was higher in shaded plots, both species are far more abundant in open sites than under tree canopies. This may be due to leaf litter under canopies inhibiting emergence (Facelli and Pickett, 1991b), or to canopy-induced changes to the red:far red ratio and their effects on seed dormancy (Pons, 1992). Alternatively, these species may be more abundant in open areas because the micro-environment below canopies may not be conducive to their growth and survival (Schupp, 1995), because they may not be able to compete successfully with in the under-canopy community in low light conditions (Schupp, 1995), or because of low seed availability due to an inability to disperse into these environments (Chambers and MacMahon, 1994; Schupp and Fuentes, 1995). Differences in the levels of exposure to pathogens or invertebrate herbivory between open and canopy sites could also lead to the discrepancy between emergence patterns and plant distributions.

Comparable effects of shading on the emergence of non-herbaceous plants have been reported for cacti (*Neobuxbaumia tetetzo*) in semi-arid matorral (Valiente-Banuet and Ezcurra, 1991), *Pinus* spp. in *Quercus* woodlands on sand dunes (Kellman and Kading, 1992), and woody shrubs (*Celtis pallida* and *Quercus humilis*) colonising temperate grasslands (Franco-Pizana et al., 1996; Rousset and Lepart, 2000). Three of these studies found that shade increased emergence rates independently of the soil differences associated with canopy presence (Valiente-Banuet and Ezcurra, 1991; Kellman and Kading, 1992; Rousset and Lepart, 2000). However, none of these studies were able to conclude whether the effects were attributable to shade-induced changes to soil moisture or soil temperature, although Valiente-Banuet and Ezcurra (1991) and Rousset and Lepart (2000) speculated in favour of soil moisture changes. Nor did any of these studies explicitly consider the consequences of the size of the shade patch.

5.4.3 Summary

Although the interpretation of the results of my experiments is clouded by more than the usual level of uncertainty, the value of shade in facilitating the germination and emergence of both *C. annua* and *D. caespitosa* is unequivocal. It is also clear that the size of the shade patch matters for at least *C. annua*. This underlines the importance of trees in generating microenvironmental heterogeneity in arid systems. It also provides evidence of an hierarchy of habitats based on the size of the shade patch cast by the canopy, in which germination responses differ between canopies of differing sizes. The results further suggest that shade patches may play a role in the persistence of populations of both species during periods of prolonged drought, when emergence rates in open areas approach zero.

Chapter 6

Effects of shading on growth and mortality of *Enchylaena tomentosa*.

6.1 Introduction

Recent theory regards interactions between plants as being a combination of positive and negative effects, and sees those effects as acting both simultaneously and bi-directionally (Callaway and Walker, 1997; Brooker and Callaghan, 1998). The net outcome, usually described as either 'competition' or 'facilitation', represents the consequences of the overall balance between positive and negative effects for plant growth or fitness. Unfortunately, the reduction of multiple interactions to a single label obscures the complexity of the dynamics of plant interactions. This simplification may also explain the tendency by ecologists to attribute either positive and negative effects to individual mechanisms when those mechanisms may be simultaneously exerting contrasting effects.

The outcomes of interactions between plants are not constant (Holzapfel and Mahall, 1999); the intensity and direction of interactions vary through time and depend on the abiotic context in which the plants are growing (Callaway and Walker, 1997; Goldberg and Novoplansky, 1997; Hacker and Gaines, 1997). Several authors have proposed that the balance between positive and negative interactions shifts towards the positive as conditions for plant growth become increasingly adverse (Bertness and Callaway, 1994; Callaway and Walker, 1997; Brooker and Callaghan, 1998). This prediction is partly based on an expectation of a decrease in the intensity of competition as resources become scarce (Goldberg and Novoplansky, 1997), and partly due to the fact that survival and growth for many plant species may not be possible without some amelioration of stressful conditions. Evidence from numerous field studies support this view (Callaway, 1995; Gerdol et al., 2000), although facilitation is not always detected in adverse environments (Olofsson et al., 1999). Furthermore, seasonality of stress factors (*e.g.* extreme cold or heat) or intermittent supply of scarce resources (*e.g.* rain in arid systems) can lead to cyclic or pulsed changes in the direction of plant interactions as stress or resource availability waxes and wanes (Greenlee and Callaway, 1996; Goldberg and Novoplansky, 1997).

Shading by shrubs and trees is one of the most commonly reported facilitative mechanisms in arid systems, usually manifesting as a reduction in mortality among seedlings and small plants (Callaway, 1995). Two factors appear to be involved: relief from water stress through reduced evaporation rates (Nobel, 1989; Valiente-Banuet and Ezcurra, 1991), and protection of plant tissues from lethal temperatures (Turner et al., 1966; Franco and Nobel, 1989; Valiente-Banuet and Ezcurra, 1991). Shading may also decrease seedling mortality by providing protection against cold-induced photoinhibition (Ball et al., 1991; Ball, 1994); although this phenomenon has not yet been reported from arid regions, the cold clear conditions that lead to such damage are common during winter mornings in many deserts. Reduced water stress may lead to increased productivity in shaded patches (Frost and McDougald, 1989; Weltzin and Coughenour, 1990; Callaway et al., 1991; Pugnaire et al., 1996a), though in many studies changes in the level of water stress are confounded with the higher soil nutrient levels found under the canopies of woody perennials (Belsky, 1994).

The consequences of reducing water stress through shading are complex and difficult to predict. The necessity for plants to open their stomata to photosynthesise may result in a trade-off between drought tolerance and shade tolerance (Smith and Huston, 1989). Lower light intensities below tree canopies mean that under-storey plants need to photosynthesise for longer periods to fix enough carbon to survive and reproduce. Therefore, plants open their stomata for extended periods, exposing them to greater water loss. Furthermore, plants respond to low light conditions by increasing the proportion of photosynthetic tissues relative to below-ground biomass. This means that the plant has a larger area of transpiring surfaces being serviced by a smaller water-acquiring system, leaving the plant more vulnerable to water stress (Holmgren et al., 1997). Consequently, the relationship between shading and growth is complex and multifactorial: it depends on shading intensity, soil moisture levels, atmospheric humidity and the physiological characteristics of the plant. Nevertheless, the advantages of lower thermal stress and reduced transpiration rates in shade can result in net gains under more xeric conditions, with losses more likely in mesic conditions (Holmgren et al., 1997). However, plants that are not as morphologically plastic may face fewer adverse outcomes when grown in the shade (Coomes and Grubb, 2000). In particular, deeper rooted species with low leaf area ratios and low specific leaf area appear better able to tolerate the combined effects of water stress and low light levels.

A recent test of the Smith and Huston (1989) photosynthetic trade-off model revealed a further level in complexity due to reductions in dark respiration rates at lower soil moisture levels (Holmgren, 2000). Furthermore, growth rates did not increase when plants grown at the lowest light levels (5% ambient PAR) were supplied with more water. Nor were growth rates higher when droughted plants were exposed to higher light levels. These results are not consistent with the Smith and Huston (1989) model, and may be at least partially attributable to reductions in the light compensation point under drier conditions (Holmgren, 2000). However, the maximum light level in this experiment was 25% ambient PAR, which is approximately the light intensity of the shade patches cast by trees in South Australian chenopod shrublands (see Chapter 4.3.2). Consequently there are difficulties in extrapolating Holmgren (2000) results to these systems, regardless of whatever differences in species-specific photosynthetic characteristics may exist.

It is clear that shading by tree canopies has multiple effects; it reduces plant and soil temperatures, decreases evaporation rates and thereby may increase soil moisture content, and has complex effects on plants through photosynthesis (Breshears et al., 1997, 1998). So this single mechanism of plant interaction can affect plants in a number of ways, and these effects may simultaneously act in opposite directions.

Further complexity arises from the spatially and temporally dynamic nature of shading. Shadows move in a shallow arc from west to east during the course of the day, and oscillate from north to south during the course of the year. Assuming the object casting the shadow is optically homogeneous, the daily movement creates an east-west PAR gradient. The lowest integrated daily PAR occurs at the location of the centre of the shadow at solar noon, with values rising outward along the daily path of the shadow. However, daily cycles in air temperature and plant water potentials mean that plants equidistant from the centre of the gradient may differ in their responses to light. The yearly movement creates seasonal differences in the spatial distribution of shading. Some areas may receive shading at one time of the year but not another, while other areas (depending on the size and elevation of the canopy) may receive shading throughout the year. Plants growing at different locations under isolated canopies will experience differences in the seasonality of shading, and differences in the daily level of shading within seasons. If the balance between positive and negative interactions depends on the severity of conditions, I predict that the differences in the timing and placement of shading will have positive, negative or neutral effects on understorey plants, depending upon prevailing conditions. I further predict that amelioration of high temperatures and evaporations rates will result in positive interactions being more important during summer when days are longer and light intensities are highest.

Enchylaena tomentosa is a small chenopod shrub commonly found throughout much of southern Australia (Jessop and Toelken, 1986). However, it occupies contrasting microhabitats across its range; it grows in the open on coastal foredunes but is almost exclusively restricted to under-canopy habitats in arid regions (Barker, 1972; Tester et al., 1987). In fact, there is a positive relationship between canopy density and *E. tomentosa* cover under *Acacia papyrocarpa* trees (Facelli and Brock, 2000). The pattern of distribution in the arid zone has been explained in terms of seed dispersal by birds (Tester et al., 1987) and higher emergence and growth rates in under-canopy soils (Facelli and Brock, 2000). However these hypotheses do not explain the differences in micro-habitat distribution between climatic zones, although a glasshouse experiment (Facelli and Brock, 2000) found some evidence that shading increased emergence rates.

In this chapter I report an experiment in which artificial canopies are used to model the interactions between tree canopies and understorey shrubs, and to examine the behaviour of interactions through time. I conducted a field experiment to test the hypothesis that the positive effects of shading on the growth and survival of *E. tomentosa* increased as seasonal conditions became more severe. I predicted that shaded plants would grow more slowly than unshaded plants during winter, but that shaded plants would grow more rapidly and survive longer during the summer months. Furthermore, I predicted that plants located on the edges of shade patches would show intermediate responses in comparison to fully shaded plants.

6.2 Methods

On 15-17 June 1999 I planted *Enchylaena tomentosa* seedlings (height 90.6± 19.1 mm, width 50.3±9.2 mm (mean±SD)), supplier Provenance Seeds, Exeter, South

Plate 6.0 - *Enchylaena tomentosa* seedlings growing under a Big Flat canopy. Seedlings were planted in rows that received noon shade at different times of the year. Here the northern edge of the shade patch is near its most southerly position, exposing the summer shade row (left) to noon sun. The all shade row (right) remains shaded at noon. *E. tomentosa* seedlings are protected from vertebrate herbivores by wire mesh cages.

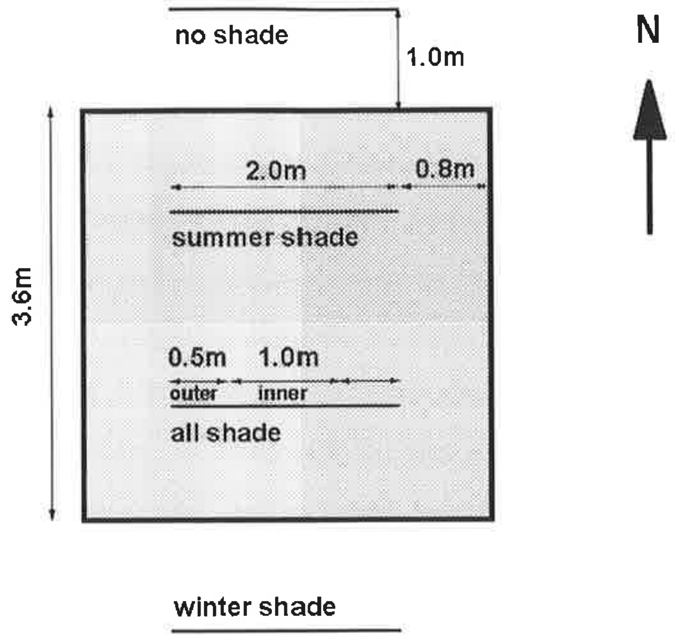


Figure 6.1: Plan view of *Enchylaena tomentosa* planting arrangement. Planting rows are denoted by horizontal bars, and are labelled according to season of noontime shading. For some analyses the position of each plant within each row was defined as "inner" or "outer". Stippled area denotes shadecloth.

Australia) under the Big Flat canopies at Koonamore Station. Canopies in both the Reserve and Grazed quadrats were used in this experiment, providing $n = 4$ replicates of the shading treatments. At each canopy five seedlings were planted at random distances along each of four east-west rows, with a minimum separation of 10 cm between each seedling to reduce the chance of seedlings overgrowing one another (Figure 6.1). The rows were 2 m long, and centred under the canopies so that the ends of the rows were 0.8 m inside the eastern and western edges of the canopies. This ensured that plants in shaded rows were not exposed to direct sunlight between mid-morning and mid-afternoon, and also created a shading gradient from the row centre to the row ends (see Chap 4.3.2).

The rows were placed 1 m on either side of the northern and southern edges of the canopies, so that the rows receiving direct sunlight at noon differed between seasons (Figure 6.1). The northernmost rows received direct noon sunlight throughout the year (no shade), whereas the rows 1 m south of the northern edges of the canopies received direct sunlight at noon in winter, but were shaded in summer (summer shade). The rows 1 m north of the southern edges of the canopies were shaded throughout the year at noon (all shade), while the southernmost rows received direct sunlight in summer but were shaded at noon in winter (winter shade). Note that all rows received direct early morning and late afternoon sunlight.

The seedlings were watered from a watering can at the time of planting, and were watered again on 30 June, 24 July and 29 July 1999 as conditions were unusually dry. No further supplementary watering was provided. The seedlings were protected from vertebrate herbivores with cones of 13 mm Ø wire mesh. I replaced the cones with larger wire mesh fences as the seedlings grew.

Seedling size was recorded as the maximum height and the maximum width of each seedling. Seedlings were measured and mortality recorded on 17 June, 24 July, 13 October, 24 November 1999, 18 January and 22 February 2000.

The positioning of the rows and the height of the shadecloth meant that the summer shade and winter shade rows passed into or out of shadow when the solar elevation moved through 50° above horizontal. As it was important to know which rows were shaded when constructing *post hoc* comparisons, I calculated the dates on which the transition occurred. This information would also have been useful for determining sampling dates, but unfortunately I did not find the formula until after the experiment had concluded. Dates were calculated by first determining the solar declination, and then finding the dates on which the solar elevation was 50° at noon. I used the following formula (Blair, 2000) to calculate solar declination (δ) -

$$\delta = -23.45 \cos \left[\frac{360(t_j+10)}{365}\right]$$

where t_j is the day of the year. I then derived the solar elevation (β) using the following identity (Blair, 2000) -

$$\sin(\beta) = (\sin\phi)(\sin\delta) + (\cos\phi)(\cos\delta)(\cos\hbar)$$

where ϕ is the latitude (southern latitudes are negative), and $\hbar$ is the hour angle. At solar noon $\hbar = 0$, and increases at the rate of 15° per hour before and after solar noon. From these calculations I determined that the summer shade row would be sunlit from 9 April until 3 September, and that the winter shade row would be shaded from 9 April until 3 September.

6.2.1 Data analyses

Excluded data

Thirteen *E. tomentosa* seedlings were found to have lost much of their above-ground tissue at the July 1999 census, apparently as a result of insect herbivory. Although five of these seedlings were among those that had died during the July-October period, most recovered and by October were similar in size to seedlings that had not been attacked. As a result, these seedlings showed very large negative growth during June-July, followed by very high positive growth during July-October. I decided to exclude data from all thirteen seedlings from analyses of plant size during July and October 1999 and from analyses of plant growth during June-July and July-October 1999, as there was evidence that their growth patterns were affected by herbivory during these periods. Data from surviving plants at later censuses were included in the analyses as there was no evidence of ongoing effects. The evidence that the plant damage affected rates or patterns of mortality was not strong enough to justify excluding these data from survival analyses. Mortality rates did not differ between affected and unaffected seedlings during July-October ($P = 0.0794$, Fisher Exact test, (May et al., 1993b)), nor did the two groups display differences in their survival responses to shading.

The corner of one of the canopies in the Reserve quadrat detached from its support pole, leaving the all shade row partially exposed to direct noon sun between the November 1999 and the January 2000 censuses. I excluded any data obtained from these seedlings after the November census from my analyses, as the treatment had not been consistently applied after this date.

Survivorship

The effects of the experimental treatments on *E. tomentosa* survival times were analysed by the Cox proportional hazards method (Venables and Ripley, 1999b), using distance from the centre of the row as a covariate. I iteratively reduced the model by removing the highest-order non-significant interaction terms as per Venables and Ripley (1999b). The test variable was the number of weeks that the seedling was known to survive; where a seedling was first recorded as dead, its survival duration was scored as the number of weeks to the previous census. Although this means that the survival times of plants that died are underestimated, I do not consider this to be a problem. The object of the analysis was to test for treatment effects on survival, rather than to obtain precise estimates of lifespan under different treatments. One disadvantage of Cox proportional hazards analysis is that *post hoc* comparisons are not available.

Because plant size may affect survival rates, I tested the effects of the last live height and width on *E. tomentosa* survival. Since plant size is confounded with both its age and with its position under the canopy, I nested the plant size terms within row and last live measurement time. Plant size remains confounded with distance from the centre of the row in this model, so I did not use distance as a covariate.

In order to further clarify the contributions of plant size and shading to mortality I compared the survival of plants in the sunlit rows with survival of similarly-sized plants from the shaded rows during the two periods of greatest mortality (July-October 1999 and January-February 2000). Due to the transition in the shading of the summer and winter shade rows during July-October, I restricted the comparison for this period to the no shade and all shade rows. Plant sizes did not differ between these rows (P = 0.0705 and 0.1796 for height and width respectively, randomisation test, (Manly, 1992)), so plant size could not confound the effects of shading at this time. I used the Fisher Exact Test (May et al., 1993b) to test the hypothesis that mortality rates did not differ between shading treatments. For the January-February 2000 period I determined the maximum heights and widths of plants in the no shade and winter shade rows (176 mm and 137 mm respectively) and then selected the subset of shaded plants that did not exceed these dimensions. This gave $n = 32$ (sunlit) and 19 (shaded) for comparisons by height, and $n = 32$ (sunlit) and 13 (shaded) for comparisons by width. Plant sizes did not differ between these sunlit and shaded groups ($P = 0.8694$ and 0.9114 for height and width respectively, randomisation test, (May et al., 1993a)). I used the Fisher Exact Test (May et al., 1993b) to test the one-tailed hypothesis that sunlit plants had higher rates of mortality than shaded plants of comparable size. In this instance I elected to use a one-tailed test because my working hypothesis was that shading would alleviate the adverse effects of stressful environmental conditions.

A major objective of this experiment was to determine whether the strength or direction of the effects of shading on mortality changed with seasonal conditions. Although the preceding analyses provide information about the effects of shading and plant size on survival times, they do not test for time-related changes in shading effects. To do so, I conducted a two-way factorial ANOVA on mortality rates, using time and shading treatment (Treatment) as factors. The Treatment factor had two levels, shaded and sunlit, so each level contains data from two rows. The summer shade and winter shade rows were excluded from the July-October data because of the transition in shading treatment in these rows during this period. To avoid bias arising from earlier deaths, I calculated mortality as

$$\text{Mortality Rate at t} = \frac{\text{number of deaths since } t_{-1}}{\text{number of plants alive at } t_{-1}}$$

The mortality rates were $\arcsin\sqrt{mortality}$ transformed. I used *post hoc* comparisons to determine whether mortality rates differed between shading treatments within each census period, and to find which census periods differed. The critical alpha levels were adjusted for multiple comparisons using the following equation (Underwood, 1997)

$$\alpha' = 1 - (1 - \alpha)^{1/r}$$

where r is the number of comparisons that were made.

Growth

The effects of shading on plant growth were analysed using repeated measures ANOVAs (SAS Institute, 1997), with the subject (*i.e.* the individual plant) treated as a random effect. Data were $\log_e$ transformed to fulfil the assumptions of ANOVA.

I originally intended to use the distance of each plant from the centre of its row as a covariate (Distance) in all of the analyses. Unfortunately, some data sets had insufficient degrees of freedom to allow me to do so. I circumvented this problem by converting the covariate Distance into a categorical factor with two levels, in which plants that were located in the central metre of the row were classed as "inner", and those within 0.5m of the ends of the rows were classed as "outer" (Figure 6.1). These distances were chosen to provide approximately equal numbers of replicates within each level. I then created a new factor (Location) by concatenating the new categorical factor with the Row factor. Thus, where necessary, plants were allocated shading treatments such as "winter shade inner" or "all shade outer" that were analysed as the Location factor. Preference was given to using Row and Distance as factors whenever the data had sufficient degrees of freedom.

The full ANOVA models for plant height and plant width included Canopy, Location nested within Canopy, Subject nested within Location and Canopy (and treated as the random effect), Time, Time crossed with Canopy, and Time crossed with Location. These models were iteratively reduced by removing the highest-order non-significant interaction terms until all the remaining highest-order terms were significant (Venables and Ripley, 1999b). I used $\log_e$ plant height, $\log_e$ plant width, and

$\log_e$ (height÷width) as the response variables. The latter variable was tested because *E. tomentosa* might respond to differences in shading regimes by altering the relative proportions of its shape. Such a response might not be detected by tests on height or width.

Following the main tests, contrasts were made comparing plant size between each successive census. There was no advantage in comparing sizes across longer intervals because size at any given time will be dependent on size at the previous measurement. Next, shaded rows were compared with unshaded rows at each census time to test the effect of seasonality of shading. I reconstituted the rows by selecting the appropriate levels of the factor Location. These comparisons were not conducted on data from the October census, as the shading treatment on the winter shade and summer shade rows changed on 3 September. Contrasts were not conducted on data from the June census, as there had been no time for the treatments to show any effect.

As the Time∗Location interaction was not significant it was dropped from the main test model on $\log_e$ (height÷width). Consequently, contrasts were made only between successive censuses, and not between shaded and unshaded rows at each census.

In order to test for changes in the direction of the net effect of shading, I also calculated the relative growth rates of every plant for each interval between censuses, and tested the data using repeated measures ANOVAs. The relative growth rates for plant width and plant height were calculated as

$$\text{relative } \Delta \text{ size} = \frac{\text{size at t - size at t}_{-1}}{\text{size at t}_{-1} \times \text{ number of weeks}}$$

Data were $\log_e(x + 1.2)$[1] transformed to satisfy the requirements of ANOVA. However, the transformed data for relative growth rate for height from the June-July 1999 period still departed from normality, so they were excluded from the analysis.

---

[1] I found that using a constant of 1.2 rather than the customary 1 provided a more normally distributed data set.

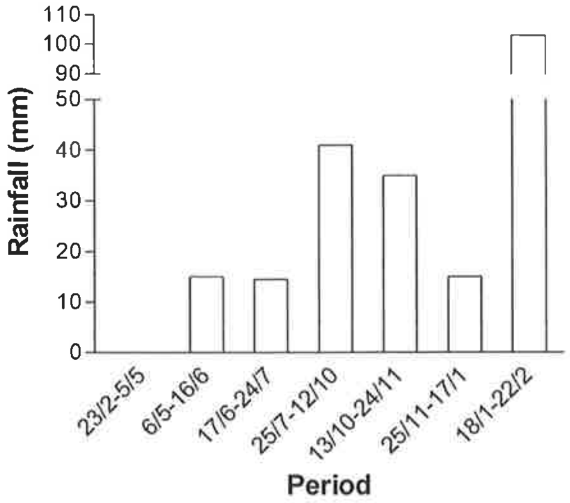


Figure 6.2: Rainfall recorded at Bindy-i, Koonamore Station, prior to and during the course of the experiment. The raingauge is approximately 2.4 km east of the experimental site.

Data from all census intervals was used in the analysis of the relative growth rates for width. The models followed those used for plant height and plant width data. However, restrictions on the number of available degrees of freedom in the relative Δ width data precluded use of the Location factor. There were sufficient degrees of freedom to accommodate the Row factor, but I could not include any terms that accounted for the position of plants along rows. In order to examine the changes in growth patterns *post hoc* comparisons were made between all census intervals, and between the predominantly shaded rows (summer shade and all shade) and the predominantly sunlit rows (winter shade and no shade). The effects of daily differences in the degree of shading were investigated by comparing the inner and outer zones of sunlit and shaded rows. However, because this demanded use of the Location factor rather than the Row factor in the main ANOVA model, I could only make these *post hoc* comparisons for the relative Δ height data, and not for the relative Δ width data.

Goldberg and Novoplansky (1997) postulated that plant growth and survival phases are temporally separated in systems where resources are strongly pulsed. In order to test this, I examined my data to see if periods of plant growth coincided with periods of high mortality. Because relative Δ size during the highest period of mortality (January-February 2000) was close to zero I chose to bootstrap the 95% confidence intervals of the mean to see whether or not growth was positive. I used 20,000 iterations to obtain the bias-corrected and adjusted (BCa) 95% percentiles (MathSoft, 1999) for mean relative Δ height and mean relative Δ width in the sunlit and shaded rows, using untransformed data.

6.3 Results

The period preceding the experiment was unusually dry, and there was little rain until July 1999 (Figure 6.2). Winter conditions were "the worst in 10 years" (Lachlan MacLachlan, Koonamore Station, *pers. comm*). Rainfall between August and November was above average, and this was followed by two major rainfall events during January-February 2000. However, the summer rain events were preceded by a period of extreme heat (daytime maxima > 45° C) during mid-late January.

6.3.1 Survivorship

Mortality was episodic, with most deaths occurring during July-October 1999 and January-February 2000 (Figure 6.3a). The high mortality rates between January and February 2000 followed a period of extreme heat in mid-late January.

Enchylaena tomentosa survival times differed between canopies and between rows, indicating that survival was affected by both the seasonal timing of shading and by random factors presumably associated with small-scale variability in soils (Table 6.1a, Figures 6.4, 6.5, 6.6 and 6.7). There was also an interaction between Distance and Row, indicating that survival in shaded rows was affected by the amount of daily light exposure. Over the duration of the experiment, more plants died in the no shade

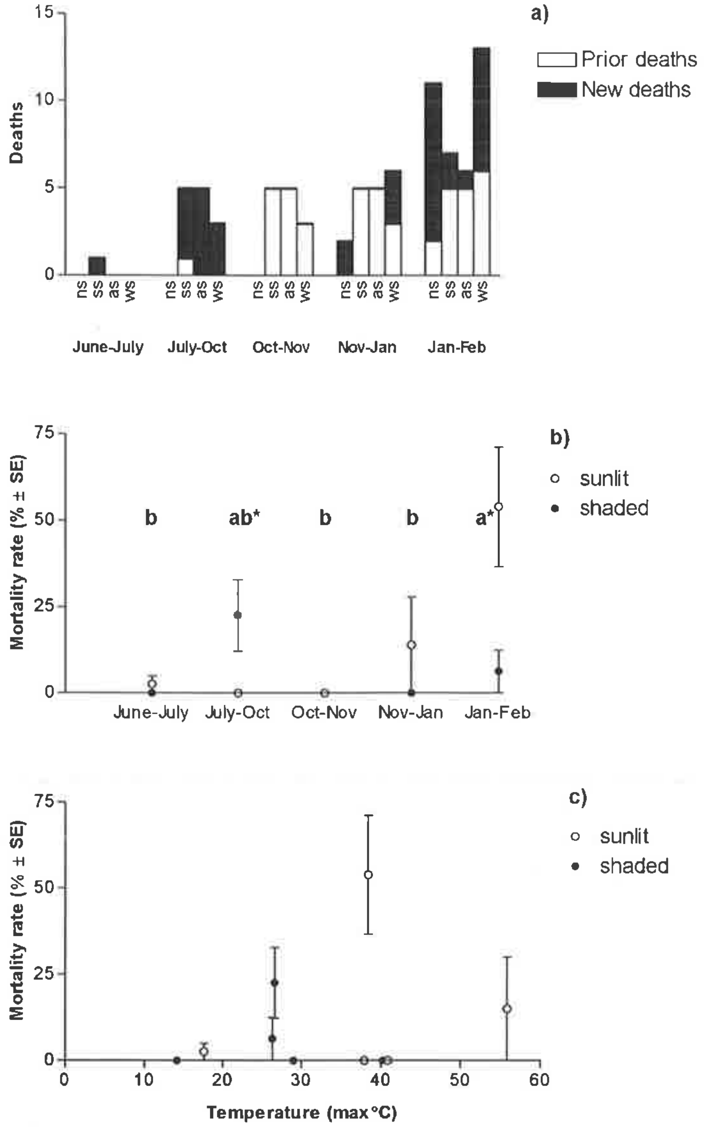


Figure 6.3: a) Cumulative mortality of *E. tomentosa* seedlings at differing shading levels. New deaths = deaths since the last census, Prior deaths = total deaths before the last census. ns = no shade, ss = summer shade, as = all shade and ws = winter shade. b) Mortality rates grouped by shading level for each census period. Mortality $= \frac{\text{number of deaths since } t_{-1}}{\text{number of plants alive at } t_{-1}} \times 100$. July-October summer shade and winter shade rows were excluded due to changed shading. Different letters indicate significant comparisons of overall mortality rates between census intervals ($\alpha' = 0.005$). Asterisks indicate significant effect of shading ($\alpha = 0.05$) ($n = 4$). c) Mortality rates and maximum daily soil temperatures at 5.5 cm depth recorded in centre of the no shade and all shade rows at the time of each census ($n = 4$).

	Source	DF	χ^2	Prob> χ^2
a)	**Whole Model**	31	57.1879	0.0029
	Canopy	3	9.8879	0.0195
	Row[Canopy]	12	30.4664	0.0024
	Distance	1	0.0001	0.9933
	Distance*Canopy	3	8.6934	0.0337
	Distance*Row[Canopy]	12	34.2542	0.0006
b)	**Whole Model**	35	113.2053	0.0000
	Canopy	3	0.0915	0.9928
	Row[Canopy]	12	6.7653	0.8727
	Height[Row, Time]	20	96.0623	0.0000
c)	**Whole Model**	35	114.9762	0.0000
	Canopy	3	1.7561	0.6245
	Row[Canopy]	12	9.4333	0.6655
	Width[Row, Time]	20	97.8333	0.0000

Table 6.1: Cox proportional hazards analysis (SAS Institute, 1997) of the survival of *E. tomentosa* seedlings. The season of shading is determined by the factor Row, and the daily duration of shading in shaded rows is determined by the distance from the centre of the row (the covariate Distance). a) tests the effect of season and duration of shading on survival times, b) and c) respectively test the effects of plant height and width on survival.

and winter shade rows than in the all shade and summer shade rows (P= 0.0413, permutation test, (May et al., 1993a)).

Survival times were also influenced by plant size after accounting for the confounding effects of time (Table 6.1b, c, Figures 6.4, 6.5, 6.6 and 6.7). This indicates that the positive effects of shading on growth could indirectly increase the probability

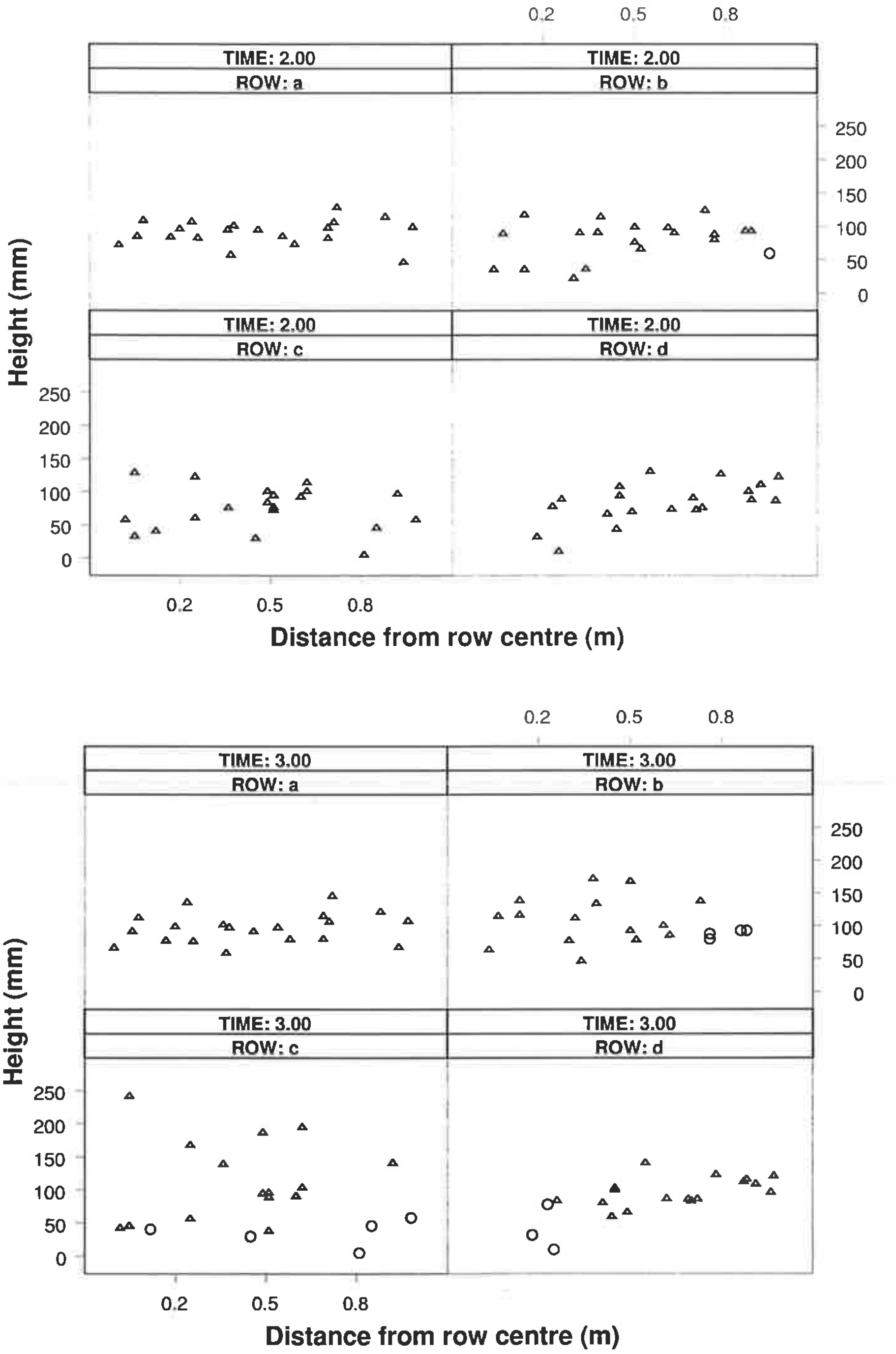
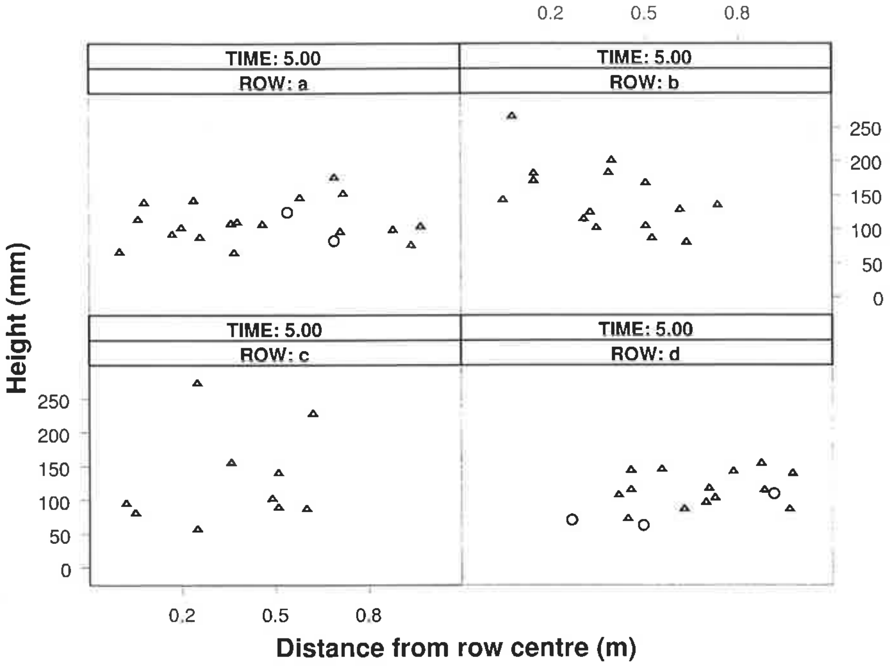


Figure 6.4: The relationship between plant height, plant position and mortality of *E. tomentosa* seedlings grown at differing levels of shading. Row a = no shade, row b = summer shade, row c = all shade and row d = winter shade. Time 2 = July 1999, Time 3 = October 1999. Triangles = live seedlings, circles = newly dead seedlings.



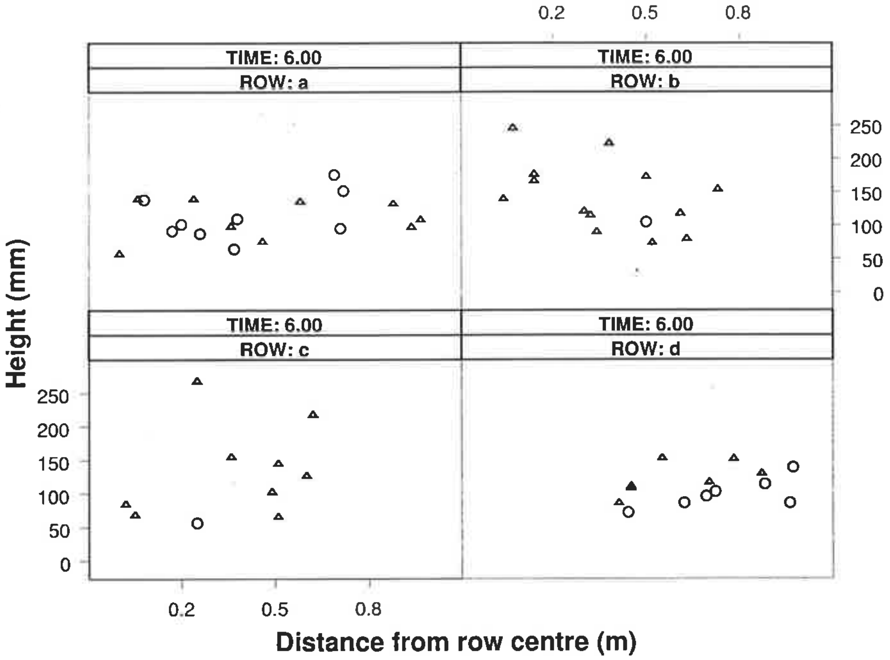
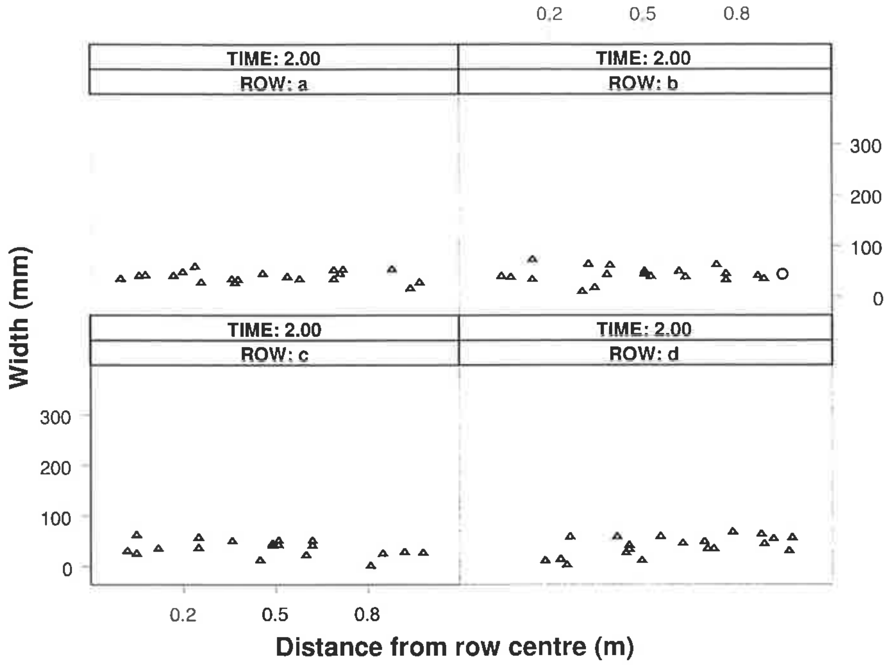


Figure 6.5: The relationship between plant height, plant position and mortality of *E. tomentosa* seedlings grown at differing levels of shading. Row labels as per Figure 6.4. Time 5 = January 2000, Time 6 = February 2000. November 1999 data not shown as there were no new deaths. Triangles = live seedlings, circles = newly dead seedlings.



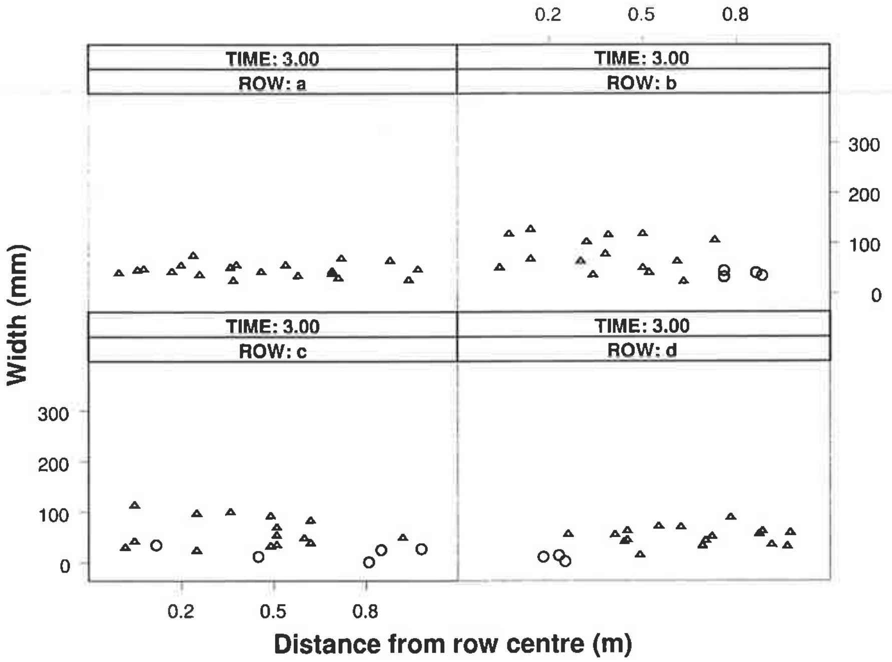


Figure 6.6: The relationship between plant width, plant position and mortality of *E. tomentosa* seedlings grown at differing levels of shading. Row and time labels as per Figures 6.4 and 6.5. Triangles = live seedlings, circles = newly dead seedlings.

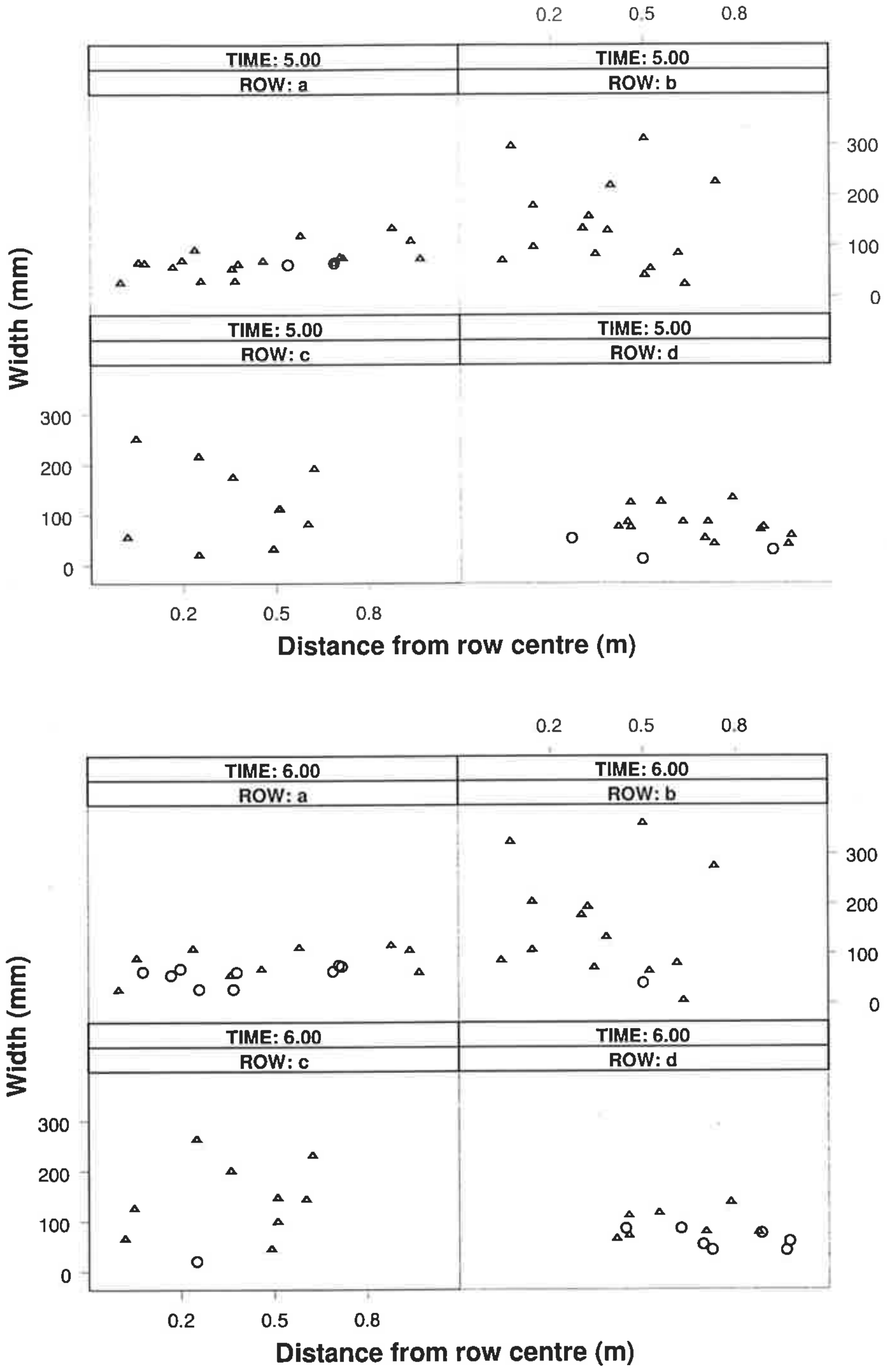


Figure 6.7: The relationship between plant width, plant position and mortality of *E. tomentosa* seedlings grown at differing levels of shading. Row and time labels as per Figures 6.4 and 6.5. Triangles = live seedlings, circles = newly dead seedlings. November 1999 data not shown as there were no new deaths.

of survival. Note that I used the last live size measured for dead plants, which may underestimate size at time of death. On the other hand plant size tended to reduce when plants were stressed (compare January and February 2000 dimensions, Figures 6.5 and 6.7), so I consider that this treatment of the data is unlikely to be a large source of error. Graphs for periods where there were no deaths are not presented.

Regardless of the effects of plant size on survivorship, shading reduced mortality rates in January-February 2000. Comparisons of similarly-sized seedlings show that survival of sunlit plants was lower than survival of shaded plants ($P = 0.0041$, one-tailed test on similar heights; $P = 0.0456$, one-tailed test on similar widths, Fisher Exact Tests). However, the direction of the effect of shading on survivorship changed during the course of the experiment, for survival of sunlit plants was higher than survival of similarly-sized shaded plants in July-October 1999 ($P = 0.0471$, two-tailed test, Fisher Exact Test (May et al., 1993b)).

Mortality rates were not constant, and the effects of the shading treatment on mortality also changed through time (Table 6.2, Figure 6.3b). As these data were skewed and contained many zeroes, I verified that the ANOVA was not unduly influenced by the departures from normality with a two-way factorial permutation test (Time $P = 0.0149$, Treatment $P = 0.2841$, Time∗Treatment $P = 0.0061$, (Manly, 1992)). Mortality was higher in shaded rows than in sunlit rows in July-October 1999, lower in shaded rows in January-February 2000, and did not differ during the other census periods. Mortality rates were highest in January-February 2000, and lowest in June-July, October-November and November-January, with intermediate rates during July-October 1999. Maximum daily soil temperatures in sunlit rows increased by more than 35° C during this period (Plate 6.1), and the difference between sunlit and shaded soil temperatures rose by more than 10° C (Figure 6.8). There were some indications that mortality rates increase with maximum daily soil temperature (Figure 6.3c), although the July-October data indicate that other factors may also affect survival. Note that the soil temperature data presented here were recorded at

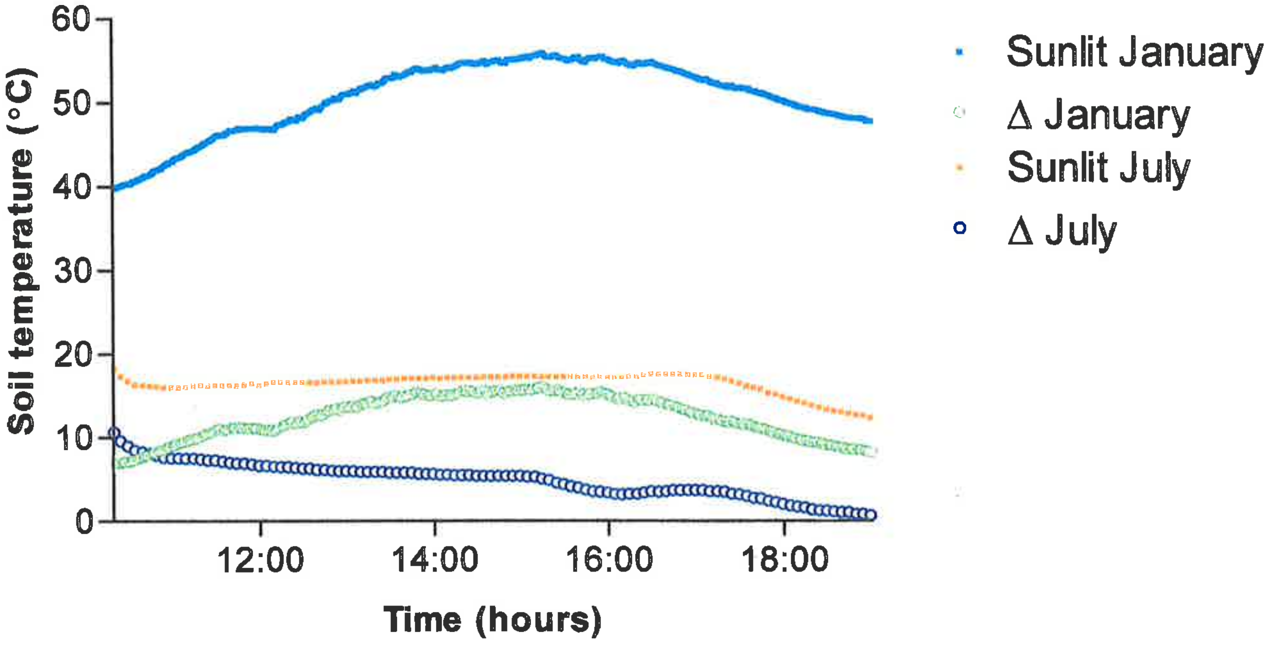


Plate 6.1 Seasonal differences in the effects of shading on daytime soil temperature at a depth of 5.5 cm. Soil temperatures were measured under Big Flat canopies on 26 July 1999 and 18 January 2000 along sunlit and shaded rows. Δ temperatures were calculated by subtracting the temperature at the centre of the all shade row from the temperature at the centre of the no shade row.

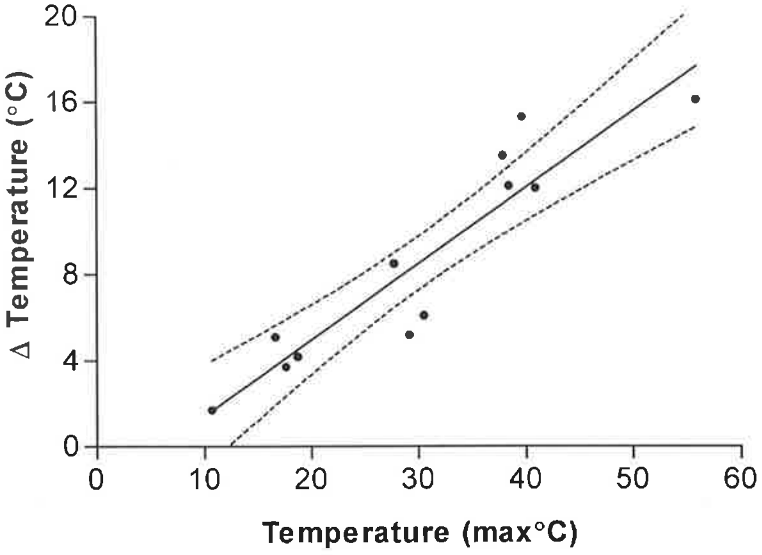


Figure 6.8: The difference in soil temperatures between sunlit and shaded soil as a function of maximum daily sunlit soil temperature. Soil temperatures were measured at a depth of 5.5 cm in the centre of the no shade and all shade rows, or 50 cm south of the canopy centre and in the open. The difference between sunlit and shaded positions was calculated at the time when the maximum daily temperature in the sunlit position was recorded. (Least squares regression $y = 0.3540x - 2.110$, $r^2 = 0.8608$, $P(\text{slope} = 0) < 0.0001$, dashed lines indicate 95% confidence intervals (GraphPad, 1999)).

the census time, and therefore may not be fully representative of the conditions experienced by seedlings during the period since each previous census. The February 2000 temperatures are especially likely to be unrepresentative as the soil was wet when the measurements were made; other measurements made before and after rain show decreases in soil temperatures that cannot be explained by differences in insolation or air temperature (data not presented).

6.3.2 Growth

Seedling size ($\log_e$ plant width and $\log_e$ plant height) differed between positions under canopies and between census times, and the differences between positions changed

Source	SS	DF	F	Prob > F
Time	1.34227	4	5.4768	0.0020
Treatment	0.15766	1	2.5732	0.1192
Time*Treatment	1.45614	4	5.9414	0.0012

Table 6.2: Factorial ANOVA (SAS Institute, 1997) on mortality rates, with census interval (Time) and shading level (Treatment) as factors. Data were arcsin $\sqrt{mortality}$ transformed. $r^2 = 0.6166$.

through time (Plate 6.2, Tables 6.3 and 6.4). Initially there were no differences between treatments, but shaded seedlings were larger than seedlings exposed to full sunlight from November 1999 onwards. Overall $\log_e$ plant width, but not $\log_e$ plant height, decreased between June and July 1999. Both width and height increased between July and October, and between November 1999 and January 2000. Overall width also increased between October and November 1999. There were no changes in overall sizes between January and February 2000.

The relative proportions of *E. tomentosa* shrubs ($\log_e$(height÷width)) also varied through time (Table 6.3) but did not differ with Location or with the interaction between time and Location. Canopy proportion changed between successive censuses up to November 1999, but did not differ between later censuses (Table 6.4).

The significant interactions between time and canopy (Table 6.3) indicate that *E. tomentosa* sizes and proportions differed between canopies at some censuses but not others. This appears to be the result of site-related differences in growth rates between the Reserve and Grazed quadrats.

The relative growth rates of shaded plants were higher than those of sunlit plants, but the difference in relative growth rates between sunlit and shaded rows did not differ during this experiment. Relative growth rates varied between seedling positions and through time, but not with their interaction (Plate 6.3, Table 6.5). Relative

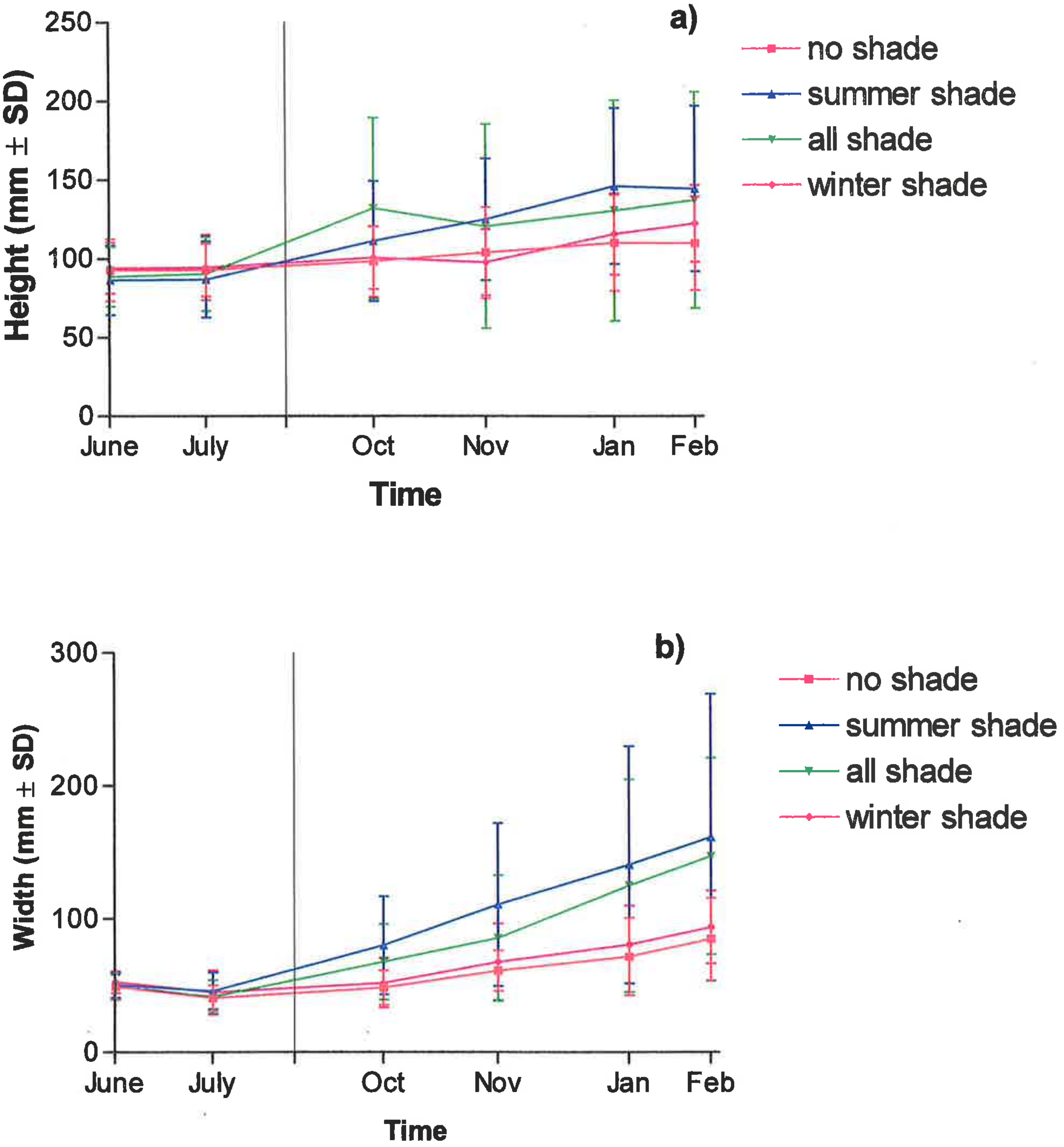
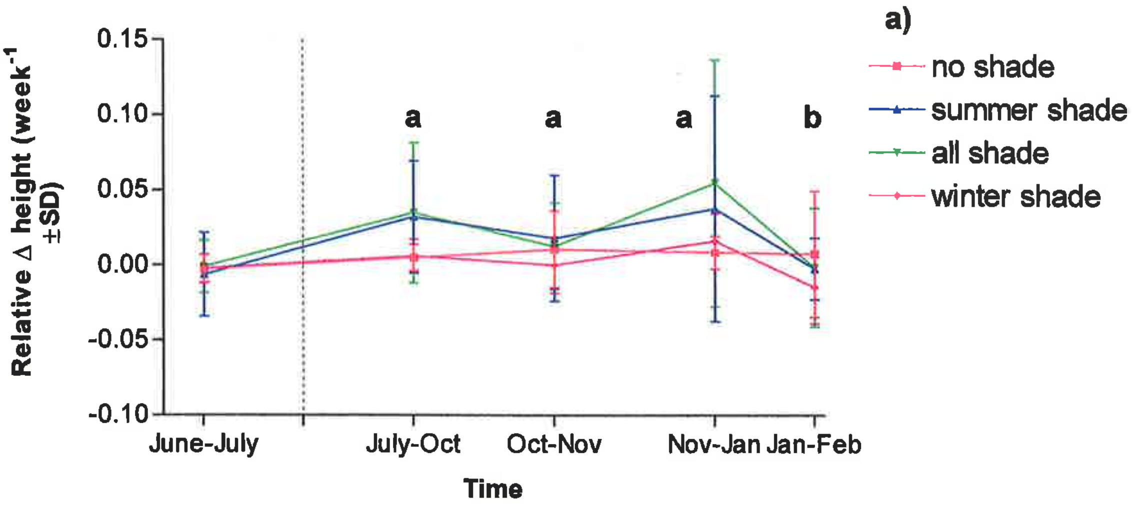


Plate 6.2: Height (a) and width (b) of *E. tomentosa* seedlings planted along four rows with differing levels of shading from direct noon sun (no shade, summer shade, all shade, winter shade). Seedlings were planted on 15-17 June 1999, and their maximum height and width were measured on 17 June, 24 July, 13 October, 24 November 1999, 18 January and 22 February 2000. The vertical dotted line indicates the date when noon shading changed on the summer shade and winter shade rows (*circa* 3 September 1999).



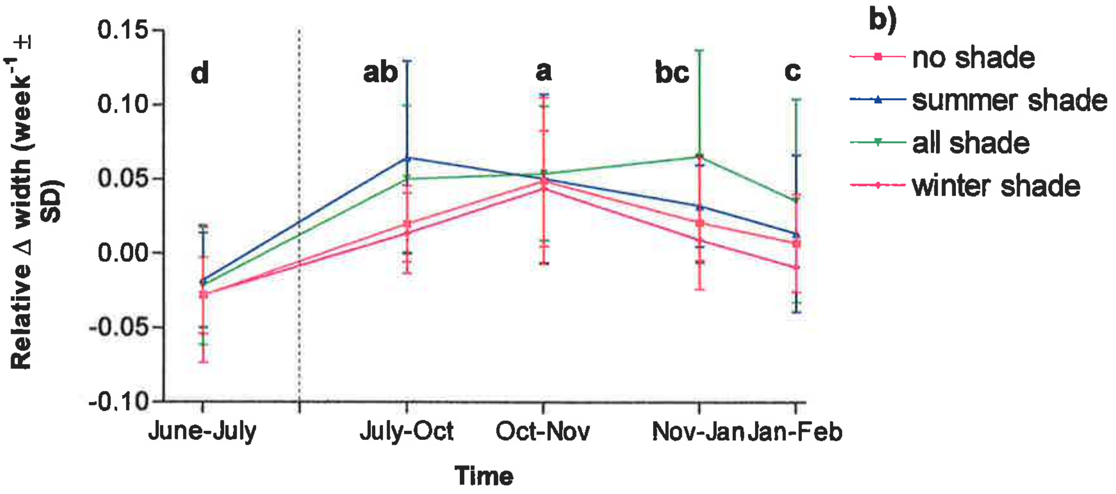


Plate 6.3: Rate of relative change in a) height and b) width of *E. tomentosa* seedlings planted along four rows with differing levels of shading from direct noon sun (no shade, summer shade, all shade, winter shade). The vertical dotted line indicates the date when noon shading changed on the summer shade and winter shade rows (circa 3 September 1999). Pairwise comparisons of $\log_e$ overall growth rates were made between all intervals. June-July relative Δ height was excluded as data were not normal. Different letters indicate significant comparisons at $\alpha' = 0.0085$ (height) and 0.0057 (width).

Source	SS	DF	F	Prob > F
a) $\log_e$ Height	$r^2 = 0.8198$			
Canopy	0.16177	3	0.6374	0.5928
Location[Canopy]	4.03398	27	0.7394	0.8011
Subject[Location, Canopy]	13.175	49	8.6623	<0.0001
Time	3.74183	5	24.1099	<0.0001
Time*Canopy	1.38973	15	2.9848	0.0002
Time*Location	2.72227	35	2.5058	<0.0001
b) $\log_e$ Width	$r^2 = 0.8611$			
Canopy	0.07117	3	0.1600	0.9230
Location[Canopy]	7.6797	27	0.8870	0.6248
Subject[Location, Canopy]	20.5192	49	6.0130	<0.0001
Time	17.9739	5	51.6181	<0.0001
Time*Canopy	6.29528	15	6.0264	<0.0001
Time*Location	6.25458	35	2.5660	<0.0001
c) $\log_e$(Height÷Width)	$r^2 = 0.7355$			
Canopy	0.01571	3	0.0476	0.9862
Location[Canopy]	9.31959	27	1.3287	0.1887
Subject[Location, Canopy]	13.432	49	4.3948	<0.0001
Time	5.69668	5	18.2660	<0.0001
Time*Canopy	3.96431	15	4.2371	<0.0001

Table 6.3: Repeated measures ANOVA (SAS Institute, 1997) on sizes of *E. tomentosa* seedlings grown at differing levels of shading in a field experiment. Seedlings were planted along four rows that were shaded at different times of the year, or never shaded. The ends of shaded rows received more light than the centres, so the level of shading was determined by the row and the distance along the row (factor Location). (Subject[Location, Canopy] used as a random effect.)

Source	Comparison	α'	Prob > F
$\log_e$ Height			
Time*Location	Shaded *vs.* sunlit July	0.0127	0.3237
	Shaded *vs.* sunlit November	0.0127	0.0083*
	Shaded *vs.* sunlit January	0.0127	<0.0001*
	Shaded *vs.* sunlit February	0.0127	0.0002*
Time	June *vs.* July	0.01	0.1134
	July *vs.* October	0.01	<0.0001*
	October *vs.* November	0.01	0.1915
	November *vs.* January	0.01	<0.0001*
	January *vs.* February	0.01	0.7514
$\log_e$ Width			
Time*Location	Shaded *vs.* sunlit July	0.0127	0.2012
	Shaded *vs.* sunlit November	0.0127	0.0019*
	Shaded *vs.* sunlit January	0.0127	<0.0001*
	Shaded *vs.* sunlit February	0.0127	<0.0001*
Time	June *vs.* July	0.01	<0.0001*
	July *vs.* October	0.01	<0.0001*
	October *vs.* November	0.01	<0.0001*
	November *vs.* January	0.01	<0.0001*
	January *vs.* February	0.01	0.6012
$\log_e$(Height÷Width)			
Time	June *vs.* July	0.01	0.0007*
	July *vs.* October	0.01	0.0078*
	October *vs.* November	0.01	<0.0001*
	November *vs.* January	0.01	0.5423
	January *vs.* February	0.01	0.1182

Table 6.4: *Post hoc* contrasts on the effects of shading on *E. tomentosa* plant sizes. Critical alpha levels were calculated as $\alpha' = 1 - (1 - \alpha)^{1/r}$, where r is the number of comparisons. Asterisks denote significant comparisons at α'.

Source	SS	DF	F	Prob > F
a) log$_e$ Relative Δ Height	$r^2 = 0.2828$			
Canopy	0.00443	3	3.1717	0.0291
Location[Canopy]	0.02669	26	2.8238	0.0026
Subject[Location, Canopy]	0.01389	37	0.3841	0.9995
Time	0.01716	3	5.8536	0.0008
b) log$_e$ Relative Δ Width	$r^2 = 0.5079$			
Canopy	0.02191	3	6.6543	0.0004
Row[Canopy]	0.03431	12	2.6157	0.0057
Subject[Row, Canopy]	0.06149	57	0.8987	0.6771
Time	0.1237	4	25.7640	<0.0001
c) log$_e$ Relative Δ Height				
Time*Location[Canopy]	0.05902	72	0.7337	0.9093
d) log$_e$ Relative Δ Width				
Time*Row[Canopy]	0.06953	47	1.3194	0.1045

Table 6.5: Repeated measures ANOVA (SAS Institute, 1997) on change in sizes of *E. tomentosa* seedlings grown at differing levels of shading in a field experiment. Relative Δ size $= \frac{\text{size at t - size at t}_{-1}}{\text{size at t}_{-1} \times \text{ number of weeks}}$. Data for relative Δ height for June-July 1999 are excluded as they departed from normality. Lack of sufficient degrees of freedom in the relative Δ width data necessitated using Row rather than Location to denote plant position. c) and d) show the effect of the time-treatment interaction terms which were subsequently dropped from the models as they were not significant. (Subject[Location/Row, Canopy] used as a random effect).

Source	Comparison	α'	Prob > F
Log$_e$ Relative Δ Height			
Location[Canopy]	Sunlit *vs.* shaded	0.05	0.0002*
	Sunlit inner *vs.* sunlit outer	0.025	0.2994
	Shaded inner *vs.* shaded outer	0.025	0.0028*
Time	July-Oct *vs.* Oct-Nov	0.0085	0.0553
	July-Oct *vs.* Nov-Jan	0.0085	0.6685
	July-Oct *vs.* Jan-Feb	0.0085	<0.0001*
	Oct-Nov *vs.* Nov-Jan	0.0085	0.0431
	Oct-Nov *vs.* Jan-Feb	0.0085	0.0045*
	Nov-Jan *vs.* Jan-Feb	0.0085	<0.0001*
Log$_e$ Relative Δ Width			
Row[Canopy]	Sunlit *vs.* shaded	0.05	0.0266*
Time	June-July *vs.* July-Oct	0.0057	<0.0001*
	June-July *vs.* Oct-Nov	0.0057	<0.0001*
	June-July *vs.* Nov-Jan	0.0057	<0.0001*
	June-July *vs.* Jan-Feb	0.0057	0.0003*
	July-Oct *vs.* Oct-Nov	0.0057	0.0453
	July-Oct *vs.* Nov-Jan	0.0057	0.1231
	July-Oct *vs.* Jan-Feb	0.0057	0.0006*
	Oct-Nov *vs.* Nov-Jan	0.0057	0.0007*
	Oct-Nov *vs.* Jan-Feb	0.0057	<0.0001*
	Nov-Jan *vs.* Jan-Feb	0.0057	0.0362

Table 6.6: *Post hoc* contrasts on *E. tomentosa* relative Δ sizes. Critical alpha levels were calculated as $\alpha' = 1 - (1-\alpha)^{1/r}$, where r is the number of comparisons. Asterisks denote significant comparisons at α'.

Δ height was similar across all rows during July-October, October-November and November-January, but fell during January-February 2000 (Plate 6.3a, Table 6.5). Note that comparisons with the June-July 1999 data were not possible, as they had to be excluded from the main analysis.

Relative Δ width showed a more highly differentiated pattern than that of relative Δ height. Relative Δ width was highest during July-October and October-November 1999 and lowest during June-July 1999 (Plate 6.3b, Table 6.3.2). Growth rates declined during November-January and January-February 2000, but remained above those of June-July 1999.

Relative Δ width was higher in rows that were shaded for most of the experiment's duration than in rows that were predominantly sunlit (Table 6.3.2, Plate 6.3). Height growth rates showed the same pattern, although this comparison did not include data from the June-July period.

Differences in the daily levels of shading also affected relative growth rates. While plant height increased more rapidly in the inner zones of shaded rows than in the outer zones, no such difference was found between zones in sunlit rows (Figure 6.10, Table 6.3.2). So plants that received shading during the middle of the day had higher growth rates than plants that received more of their shading during the morning or the afternoon. There were insufficient degrees of freedom in the main test to allow comparisons between inner and outer zones for relative Δ width.

There was no clearcut temporal separation of growth and survival phases. Low rates of lateral growth were measured in the shaded rows during January-February 2000 (Figure 6.9) when mortality rates were high (Figure 6.3). Likewise, growth rates were positive during the other period of high mortality, July-October 1999 (Plate 6.3). However, the long interval between the July and October censuses increases the uncertainty that growth and mortality occurred concurrently.

Sunlit and shaded growth rates tended to converge with increasing rainfall (Figure 6.11). Surprisingly, relative growth rates for height showed a decreasing trend as

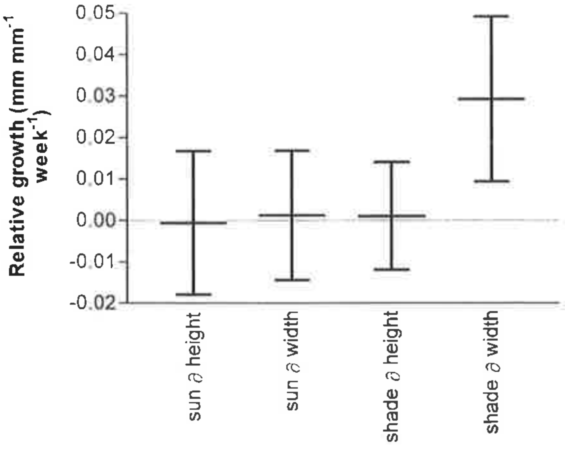


Figure 6.9: Bootstrapped BCa confidence limits of mean Relative Δ sizes of *E. tomentosa* seedlings growing in sunlit and shaded rows during January-February 2000 (MathSoft (1999), 20,000 replicates). Whiskers indicate lower and upper 95 % confidence limits.

rainfall increased, although this is uncertain due to the low levels of replication.

6.4 Discussion

Enchylaena tomentosa growth rates increased and summer mortality rates greatly decreased when the seedlings were provided shading similar to the levels provided by *Alectryon oleifolius* canopies. These results show that growth is affected by both the time of year that shading occurs, and by the daily duration of shading. Furthermore, the much higher summer mortality rates in exposed positions suggest that *E. tomentosa* may not be able to persist in chenopod shrublands in the absence of large shade patches.

The higher summer survival rates of shaded plants may be the result of direct amelioration of habitat, the indirect consequences of shaded plants attaining a greater size before the onset of extreme weather or some combination of the two. While larger plants had higher survival rates, the differences in soil temperatures between shaded and sunlit rows were comparable to the differences that were shown to increase

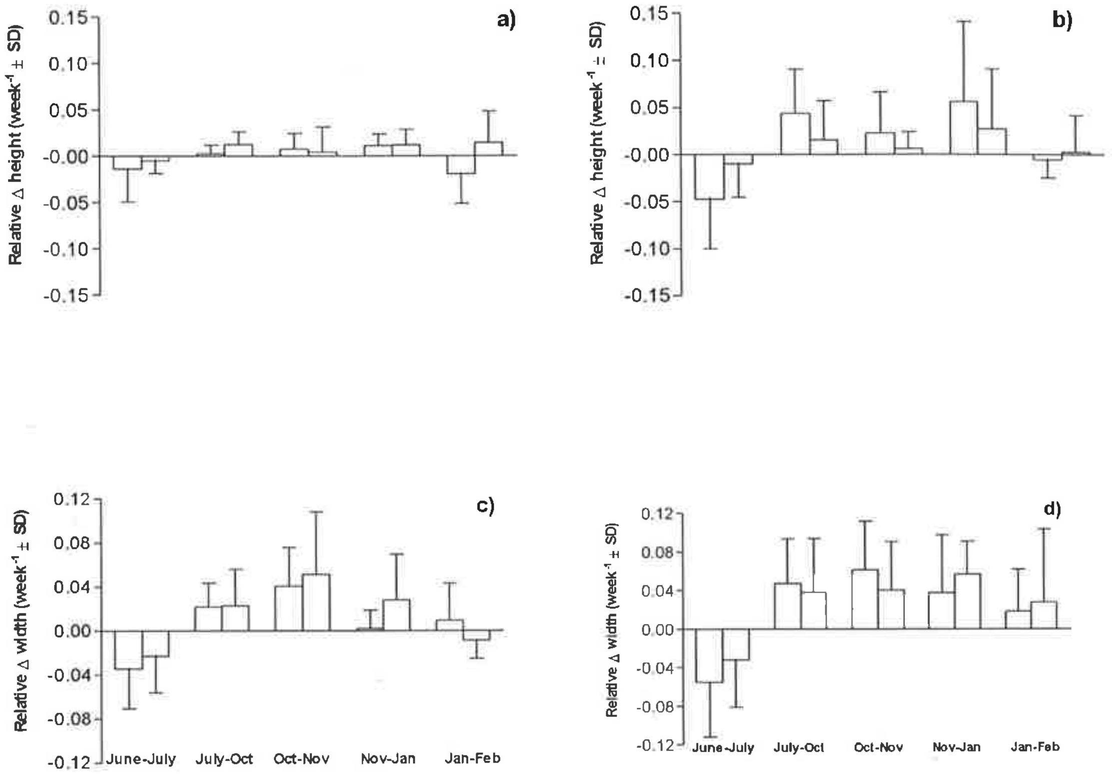


Figure 6.10: Relative Δ *E. tomentosa* height and width. Data are grouped by shading (shaded *vs.* sunlit) and by position within row (inner *vs.* outer) for each census interval. a) sunlit height, b) shaded height, c) sunlit width and d) shaded width; left column of each pair is inner zone and right column is outer zone. Relative Δ height and width is greater in shaded rows than in sunlit rows across all census intervals (data $\log_e$ transformed, non-Gaussian June-July height data excluded). Relative Δ height in shaded rows across all census intervals is greater in the inner zone (P=0.0028, data transformed and censored as above), but zones do not differ in sunlit rows (P=0.2994). Comparisons could not be made between inner and outer zones for relative Δ width due to insufficient *df*.

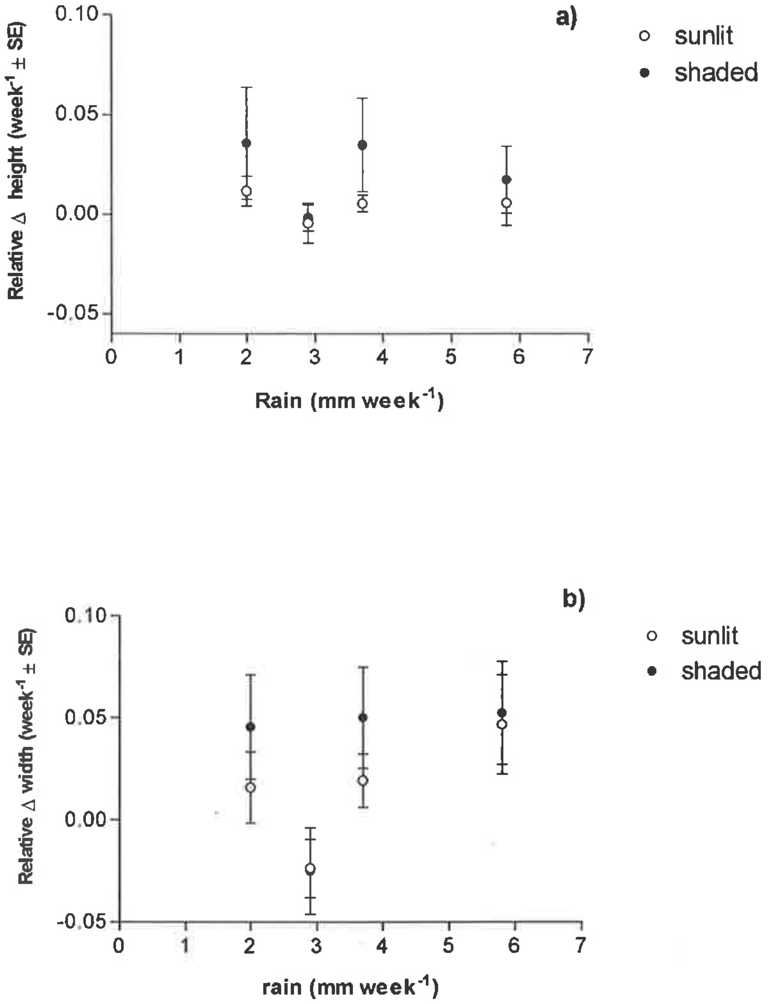


Figure 6.11: Rainfall and relative growth rates of *E. tomentosa* seedlings. Rainfall (recorded at Bindy-i) was averaged over each period between seedling measurements. Data from January-February 2000 were excluded as extreme heat prior to heavy rains may have reduced growth rates. Also note that seedlings were provided supplementary watering during the period corresponding to 2.9 mm week^{-1}. $n = 4$.

mortality in cacti (Turner et al., 1966; Valiente-Banuet and Ezcurra, 1991). This is confirmed by the higher mortality rates among sunlit plants than among similarly-sized shaded plants during the period of greatest stress (January-February 2000). Thus the results of this experiment indicate that both direct and indirect effects of shading determine *E. tomentosa* survival rates.

Plant growth was affected by seasonal patterns in shading; relative growth rates were always higher in shaded rows, so the north-south movement of the canopy shadow determined the location of highest growth. Furthermore, the daily duration of shading also affected growth rates. Plants in the centre of the shaded rows increased their height more rapidly than plants at the row ends, where they were exposed to direct sunlight for a longer period each day. In contrast, there were no differences in growth rates between the centres and edges of sunlit rows, which had no such daily PAR gradient.

These results illustrate the importance of considering the spatial aspects of shading. Many studies have applied shading treatments in a way that is time-homogeneous, so that the level of shading as a percentage of ambient sunlight does not change either daily or seasonally. Such an approach fails to reproduce the nature of the shading cast by plant canopies. My data show that plant growth and survival are affected by both the timing and the duration of shading, which are in turn determined by the size of the shade patch and by the placement of the shading object relative to the target plant. Consequently, the design of shading experiments requires close attention to these parameters if they are to be realistic.

There were fewer indications of seasonal differences in the direction of the overall balance of positive and negative shading effects than I had expected. Generally the effects of shading were clearly positive, possibly as a consequence of the extended periods of low rainfall. This view is supported by the observed convergence of relative growth rates in shaded and unshaded rows as rainfall increased. Low sampling frequency during late winter and spring may have impaired the chances of detecting negative effects, which were found only during June-July 1999. During this period plant sizes decreased in all rows, but the decrease was greater in the shaded rows than in the sunlit rows. Given that the plants received supplementary watering during this period, it would appear that while water was available sunlit plants were able to fix more carbon than shaded plants. This could be related to differences in light intensities or to soil temperatures. Under overcast conditions during winter, shaded *E. tomentosa* seedlings are likely to experience light intensities below point, so sunlit plants would be able to photosynthesise at higher rates while soil moisture levels were adequate. This would provide more resources for root growth, which in turn would further enhance seedling survival and growth. Alternatively, the lower daytime soil temperatures in the shaded rows may have reduced the rate of plant growth (Sohlberg and Bliss, 1987).

Shading increased relative Δ size, and growth rates varied between census periods. However, contrary to existing models (Callaway and Walker, 1997; Brooker and Callaghan, 1998), the difference between the growth rates along shaded and unshaded rows did not differ through time even though environmental conditions became increasingly severe. This could occur if *E. tomentosa* has an approximately linear response to shade-related factors, and if the magnitude of the difference between shaded and unshaded positions does not alter when conditions change. Two other studies (Holzapfel and Mahall, 1999; Tielborger and Kadmon, 2000) also failed to detect consistent links between severity of conditions and the strength and direction of plant interactions. In one case, this appears to have been due to phenological patterns in growth being of greater importance than amelioration of conditions (Holzapfel and Mahall, 1999), while other canopy processes were invoked to explain the discrepancy in the second study (Tielborger and Kadmon, 2000).

There were few indications of negative shading effects, apart from the greater size loss in shaded plants during the first census interval. A small but growing body of evidence suggests that, in general, shading does not become detrimental for many plant species until shade PAR falls below about 100 μmol m^{-2} sec^{-1} (Ryser and Eek, 2000; Coomes and Grubb, 2000). It appears that a combination of morphological (Ryser and Eek, 2000) and physiological (Holmgren, 2000) plasticity allows plants to compensate for the lower light levels. Paradoxically, it appears that a combination of low morphological plasticity and high allocation to roots permits some woody species to tolerate drought under even lower light levels (Coomes and Grubb, 2000).

This experiment shows that mechanisms other than dispersal (Tester et al., 1987) or soil type (Facelli and Brock, 2000) can explain the distribution of *E. tomentosa* in arid chenopod shrublands. Although emergence and growth of *E. tomentosa* were higher in soil from *Acacia papyrocarpa* canopies in a glasshouse experiment (Facelli and Brock, 2000), the rate of emergence in soils from open spaces was around 20% at higher levels of soil moisture. This indicates that *E. tomentosa* is not excluded from exposed habitats by soil characteristics. Rather, the strong association between *E. tomentosa* and tree canopies (Barker, 1972) can be more parsimoniously explained by the fact that shading substantially increases survival rates in this environment.

Most published studies from arid systems in which the effects of shading were separated from differences in soil nutrient levels show positive shade effects on the target species. Seedling mortality was almost invariably reduced (Turner et al., 1966; Valiente-Banuet and Ezcurra, 1991; Walker and Vitousek, 1991; Callaway, 1992; Holzapfel and Mahall, 1999), even at sites with relatively temperate conditions (Kitzberger et al., 2000). Nevertheless, as conditions become more severe, the importance of shading in reducing mortality increased (Greenlee and Callaway, 1996). However, under conditions of extreme resource shortage survival may not be possible even in the presence of positive interactions (Kitzberger et al., 2000) or negative canopy effects may be more important than the positive effects of shading (Tielborger and Kadmon, 2000).

Some studies have shown interactions between shade effects and soil properties on mortality. Weltzin and McPherson (1999) found that shaded *Quercus emoryi* seedlings had lower mortality levels than unshaded seedlings unless they were growing in sites that had been occupied by mature trees, where soil moisture levels were higher. Soil albedo may also indirectly affect mortality. Turner et al. (1966) grew seedlings of the cactus *Carnegia gigantea* in soil from below three different species of trees that act as "nurses" for *Carnegia.* The two darker soils attained higher soil surface temperatures in both full sunlight and shade than did the lighter soils. The mortality rates of shaded seedlings growing in darker soils were higher than shaded seedlings growing in lighter soils, despite the higher nutrient levels of the darker soils. Turner et al. (1966) attributed this to the ~2.5° C higher temperatures of the darker soils.

The few studies that separate the effects of shading and differing levels of soil resources suggest that the effects of shading on growth and productivity are more complex. A glasshouse study on the effects of *Prosopis glandulosa* on the establishment of two other woody plants, *Celtis pallida* and *Acacia smallii,* found an interaction between shading and soil type (Franco-Pizana et al., 1996). Shading reduced the growth of both species, even though *Celtis* is primarily found below *Prosopis* canopies in the field, but the reduction was more pronounced between seedlings growing on the more fertile canopy soils. However, the average maximum PAR levels of the unshaded treatment was only half of that typical of a clear summer day. Consequently the unshaded plants may not have been subject to the levels of soil and leaf heating that would occur under field conditions.

Plant responses to shading may differ between species or functional groups. Weltzin and McPherson (1999) found that whereas herbaceous biomass was higher in shaded plots on grassland and interstitial sites, shading had no effect on herbaceous biomass in canopy plots. This is despite the fact that canopy soils were more fertile than the grassland soils (data on the interstitial soils was not presented). In fact, herbaceous biomass was lower on the canopy soils than at the other sites. In contrast, *Quercus emoyri* seedlings responded to shading most strongly in canopy sites. This response was most pronounced during the period when canopy soils had higher soil moisture contents.

A field experiment at two sites of differing annual rainfall in an *Acacia tortilis* savanna demonstrated that shade-induced changes in productivity are not independent of soil resource levels (Belsky, 1994). Shade increased herbaceous productivity on less fertile soils at the low rainfall site only when fertiliser was added. Shading increased biomass at the high rainfall site outside canopies but not in the grassland, while shading and fertiliser combined produced higher biomass in both zones than shading alone. However, conclusions about the effect of rainfall cannot be made as there are no data on nutrient differences between sites; the study partially confounds rainfall with soil nutrients.

Callaway (1998) discussed whether positive interactions between plants were species-specific, or whether they were the consequence of more general alteration of the physical environment by plants. On the basis of the published literature he concluded that some positive interactions appeared to be due to generalised modification of the physical environment, but that many of the reported cases of facilitation appeared to be the result of species-specific attributes. The evidence to date suggests that the relationship between facilitation and species attributes is more complex than proposed by Callaway (1998). Clearly there is a distinction between survival and growth responses to shading. Shading almost always increases seedling survival in xeric conditions, but growth responses, being apparently determined by a larger set of parameters, tend to be more idiosyncratic. It appears that shading in arid systems is a powerful, widespread mechanism by which woody perennials facilitate seedling survival in a generic fashion, and affect the growth of understorey plants with a complex mix of generic and species-specific interactions that are mediated by abiotic factors such as soil nutrient levels.

The results of this and other experiments suggest that current models require further elaboration. There is a good case for differentiating between survival and growth responses; these should be viewed in the context of the two-phase resource dynamic hypothesis (Goldberg and Novoplansky, 1997). Ecologists also need to explicitly consider ontogenetic and size-related differences: smaller or younger plants will have less access to soil resources during interpulse intervals.

Resource pulses and plant interactions

Goldberg and Novoplansky (1997) proposed a two-phase resource dynamic hypothesis that differentiates between growth and survival phases in environments where resource availability was strongly pulsed. They argued that most stress-related mortality occurs during periods of resource shortages. During such times growth rates are very low, and competitive interactions minimal. Conversely, growth rates and competitive interactions are both high during resource pulses, whereas stress-related mortality is minimal. These concepts can be logically extended to more generalised models of plant interactions that incorporate both positive and negative interactions. Such models would have positive interactions dominating in inter-pulse periods, and negative interactions more important during periods of resource pulses. However, my data do not support the contention that growth and stress-induced mortality are temporally separated in systems where resources are strongly pulsed. Nor have other studies (Weltzin and McPherson, 1999; Holzapfel and Mahall, 1999; Tielborger and Kadmon, 2000; Kitzberger et al., 2000) been entirely consistent with the two-phase resource dynamic hypothesis or with facilitation models. There is good evidence that mortality mainly occurs during periods of low resource availability, and that facilitation has a greater effect at such times. But there are limits to the effectiveness of facilitation in extreme conditions. There is a threshold beyond which habitat amelioration may be insufficient to permit any seedling survival (Kitzberger et al., 2000). Furthermore, my results show that although shade facilitated growth for most of the experiment, it did not have a more pronounced effect when conditions were more severe.

6.4.1 Summary

The results of this experiment demonstrate that shading similar to that provided by trees facilitates both growth and survivorship in the seedlings of a common understorey shrub, *E. tomentosa*. This provides evidence that the presence of trees in chenopod shrublands may affect community composition and could possibly increase plant productivity. The results also demonstrate that the relationship between facilitation and environmental severity is more complex than previously thought, and that facilitation affects growth and survivorship differently. Thus local environmental modification due to shading by trees may affect plant community compositions, but the effects of shading are complex and differ between aspects of plant performance.

Chapter 7

Modelling facilitation: linking localised modification with plant interactions.

7.1 Introduction

Most published models of facilitation are simple graphical representations of observed patterns along environmental gradients (Bertness and Callaway, 1994; Callaway and Walker, 1997; Callaway, 1997). They depict a schema in which facilitation is more commonly observed, and where its effects become stronger, as conditions become increasingly adverse to plant growth and survival. As such, these models lack any mechanistic basis; rather, they are based on concepts adopted from competition theory. In particular, they assume that competition becomes more intense with increased productivity. This is a controversial idea, and has been the subject of years of debate between Grime (1973, 1977) and Tilman (1988). Furthermore, a recent meta-analysis of field experiments on herbaceous plants found that competition intensity often declined as productivity increased (Goldberg et al., 1999), providing little support to either side of the debate.

Rather than rely on such a questionable premise, I argue for a more sophisticated approach, one that explicitly links modification of the local environment by plants with plant responses to their environment. Such an approach offers the promise of a more quantitative explanation of plant interactions along environmental gradients. Two models use such mechanistic methods to explain particular phenomena related to facilitation (Holmgren et al., 1997; Tielborger and Kadmon, 2000). Both provide explanations in terms of plant responses to moisture and light, one to explain the apparent paradox between the nurse plant phenomenon and the physiological trade-off between shade and drought tolerance (Holmgren et al., 1997), the other to explain why shrubs had negative effects on reproductive success of desert annuals in very dry years and positive effects in wetter years (Tielborger and Kadmon, 2000). Models such as these offer greater predictive power and more satisfactory explanations of observed patterns.

Several studies (Holzapfel and Mahall, 1999; Tielborger and Kadmon, 2000) (see also Chapter 6.3.2) show that, contrary to current theory (Bertness and Callaway, 1994), facilitation does not always become stronger or more 'important' when environmental conditions become more severe. In order to investigate why the intensity of facilitation increased under more severe conditions in some studies but not in others, I used graphical and algebraic methods to explicitly examine the relationship between modification by plants and the response by neighbouring plants to such modifications.

7.2 Model methods

Plant survivorship, growth and fecundity are known to be determined by the levels of a number of environmental factors. Some, such as light, water and mineral nutrients, are variously essential for survival and growth and are generically labelled as resources. Others, such as salinity, may result in loss of biomass, increased mortality or reduced fecundity. I shall refer to such factors as being impediments. The distinction between resources and impediments is sometimes ambiguous, for plant performance may decline as resource levels increase beyond certain points, *e.g.* mineral nutrients (Marschner, 1986), or may increase as impediment levels increase up to certain points, *e.g.* halophytes at differing Na^+ concentrations (Marschner, 1986). I shall for the present put these exceptions to one side; they generally represent levels of environmental factors that are only encountered in extreme conditions or unusual metabolic adaptations to such conditions.

Absolute measures of plant performance at given resource levels often vary with plant size. For example, at any particular light intensity a large plant may show a larger increase in biomass than a smaller plant of the same species. Consequently it is more informative to consider standardised measures, such as the increase in biomass per unit biomass. Moreover, because the performance increment will also change with time, standardised measures of rates of change provide better bases for comparisons.

I constructed two-dimensional graphical models where resources or impediments were represented on the x axes, and relative rates of plant performance were represented on the y axes. Thus plant responses to changes in the level of a single resource or impediment were represented. The models assume that changes in the level of one resource or impediment will not affect plant responses to other resources or impediments.

I considered three biologically plausible scenarios; one in which the relationship between plant performance and environmental factors is linear (Figure 7.1), another in which the relationship monotonically approaches an asymptotic maximum (Figure 7.2), and a third in which the relationship has both upper and lower bounds (Figure 7.3). Within each scenario I considered two possible outcomes of plant modification, one where the difference between modified and unmodified levels (hereafter $\triangle_{modify}$) was constant, and the other where $\triangle_{modify}$ was linearly dependent on the unmodified level l_u. Although little is known about the relationship between the level of environmental factors and the magnitude of plant modification, linear relationships

Symbol	Definition
l	level of environmental factor
l_u	level of environmental factor in absence of plant modification
l_m	level of environmental factor produced by plant modification acting at l_u
$g(l)$	function that determines l_m for any given l_u, determines size of $\triangle_{modify}$
$\triangle_{modify}$	change in l due to plant modification; given by $l_m - l_u$
$f(l)$	function that determines plant response for any given l
$\triangle_{response}$	change in plant response due to modification; given by $f(l_m) - f(l_u)$

Table 7.1: Definitions of notation used in models.

are known to occur *e.g.* the relationship between unshaded soil temperature and the magnitude of the change in soil temperature due to shading (Chapter 6.3.1).

Plant response attributable to modification by neighbouring plants is the difference between performance rates at modified and unmodified levels; where plant responses to modified levels are greater than plant responses to unmodified levels it can be said that the modifying plant has facilitated the responding plant. The size of this difference is a measure of the intensity of facilitation. I tested whether or not facilitation became stronger as conditions become less favourable for plant growth and survival by comparing the difference between modified and unmodified levels along the environmental gradient represented by the x axis. Assigning measures of 'importance' of facilitation is a more complex issue that may depend on the context, so it will not be considered any further here.

7.3 Analysis and results

For the sake of analytical tractability I have assumed simple, well-known response functions. The linear function (Figure 7.1) is of the form

$$f(l) = f_0 + a(l - l_0),$$

the monotonic increasing asymptotic function (Figure 7.2) is of the form

$$f(l) = f_0 + b(1 - e^{-c(l-l_0)}),$$

and the sigmoidal function (Figure 7.3) is of the logistic form

$$f(l) = \frac{K}{1 + \left[\frac{K-f_0}{f_0}\right] e^{-b(l-l_0)}}$$

where a, b and c are constants, l_0 is the minimum level of the environmental factor, f_0 is $f(l_0)$, and K is the upper asymptotic limit. I further define l_u as being the unmodified level, and l_m as being the level under the influence of plant modification. The function $g(l)$ models the effect that the modifying plant has on its surroundings, and determines l_m for any l_u. The difference between modified and unmodified levels is given by $\triangle_{modify}$, where

$$\begin{aligned} \triangle_{modify} &= l_m - l_u \\ &= g(l_u) - l_u \end{aligned}$$

I consider two cases, one where $\triangle_{modify}$ is constant:

$$\begin{aligned} g(l_u) &= l_u + k \\ &= l_m \end{aligned}$$

and the other where $\triangle_{modify}$ changes with l_u:

$$\begin{aligned} g(l_u) &= kl_u + B \\ &= l_m \end{aligned}$$

where k and B are constants. In the second case, $\triangle_{modify}$ increases if $k > 1$ and decreases if $k < 1$. In all three scenarios the magnitude of $\triangle_{response}$ is determined by $f(l)$ and the magnitude of $\triangle_{modify}$ (Figures 7.1, 7.2 and 7.3). So

$$\begin{aligned}\triangle_{response} &= f(l_m) - f(l_u) \\ &= f(g(l_u)) - f(l_u)\end{aligned}$$

For the first case, where $\triangle_{modify}$ is constant, this means that

$$\triangle_{response} = f(l_u + k) - f(l_u) \tag{7.1}$$

while in the second case, where $\triangle_{modify}$ is a linear function of l

$$\triangle_{response} = f(kl_u + B) - f(l_u) \tag{7.2}$$

7.3.1 Linear functions

Case 1: constant $\triangle_{modify}$

For linear response functions, the intensity of facilitation remains constant whenever $\triangle_{modify}$ is constant (Figure 7.1). In other words, the intensity of facilitation does not change as environmental conditions change whenever the modification size is constant. This can be shown formally; from Equation 7.1:

$$\begin{aligned}\triangle_{response} &= f(l_u + k) - f(l_u) \\ &= a(l_m - l_u) \\ &= a\triangle_{modify} \\ &= ak\end{aligned}$$

therefore $\triangle_{response}$ is constant and independent of l_u.

Case 2: variable $\triangle_{modify}$

If the magnitude of $\triangle_{modify}$ varies with l, the intensity of facilitation can differ along environmental gradients (Figure 7.1). When $\triangle_{modify}$ increases as l increases, the

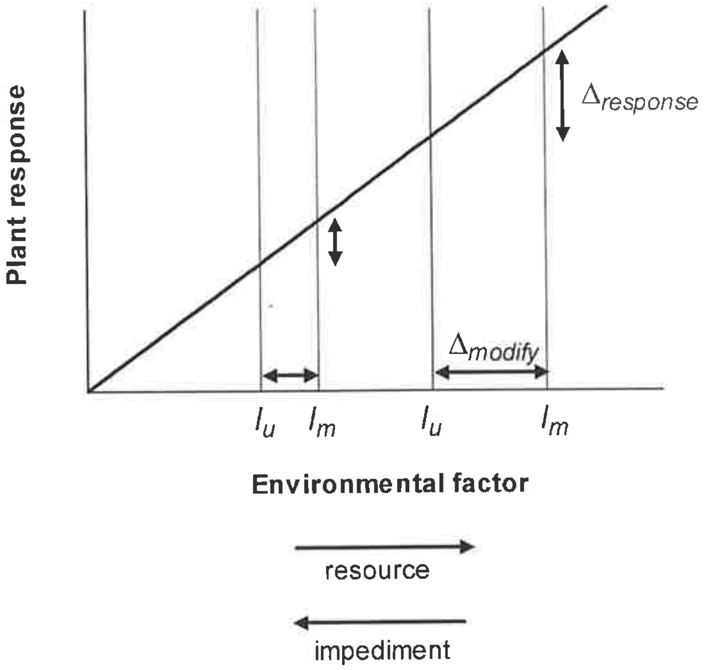


Figure 7.1: Predicted plant response to changes in the level of an environmental factor due to modification by another plant, assuming a linear response. Plant responses may increase (resource) or decrease (impediment) with increases in levels of the factor. The difference between factor levels in unmodified (l_u) and modified (l_m) states is the quantity $\triangle_{modify}$. The difference in the levels of plant responses ($\triangle_{response}$) at l_u and l_m represents the intensity of facilitation.

intensity of facilitation increases as conditions become more favourable. Conversely, if $\triangle_{modify}$ decreases as l increases, the intensity of facilitation decreases as conditions become more favourable. This can be shown from Equation 7.2:

$$\begin{aligned}\triangle_{response} &= f(kl_u + B) - f(l_u) \\ &= a\left[l_u(k-1) + B\right]\end{aligned}$$

therefore $\triangle_{response}$ is dependent on l_u, increasing as l_u increases if $k > 1$ and decreasing as l_u increases if $k < 1$.

7.3.2 Monotonic increasing asymptotic functions

Here the general form of $\triangle_{response}$ is given by:

$$\begin{aligned}\triangle_{response} &= f(l_m) - f(l_u) \\ &= b(1 - e^{-c(l_m - l_0)}) - b(1 - e^{-c(l_u - l_0)})\end{aligned}$$

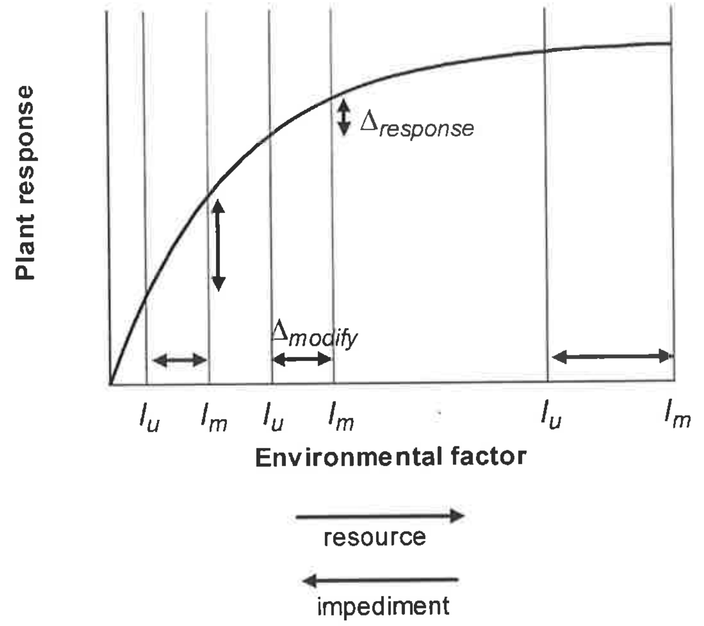


Figure 7.2: Predicted plant response to changes in the level of an environmental factor due to modification by another plant, assuming a monotonic increasing asymptotic response.

$$= be^{cl_0}(e^{-cl_u} - e^{-cl_m}) \tag{7.3}$$

Case 1: constant $\triangle_{modify}$

For asymptotic increasing functions facilitation will be greater under unfavourable conditions than under favourable conditions if the size of $\triangle_{modify}$ remains constant (Figure 7.2). From Equations 7.1 and 7.3

$$\begin{aligned}\triangle_{response} &= be^{cl_0}(e^{-cl_u} - e^{-c(l_u+k)}) \\ &= be^{-c(l_u-l_0)}(1 - e^{-ck})\end{aligned}$$

Thus $\triangle_{response}$ becomes smaller as $l_u - l_0$ increases, *i.e.* $\triangle_{response}$ decreases as l_u increases.

Case 2: variable $\triangle_{modify}$

The intensity of facilitation may or may not change along environmental gradients when the level of modification changes linearly with l_u, and when the response function

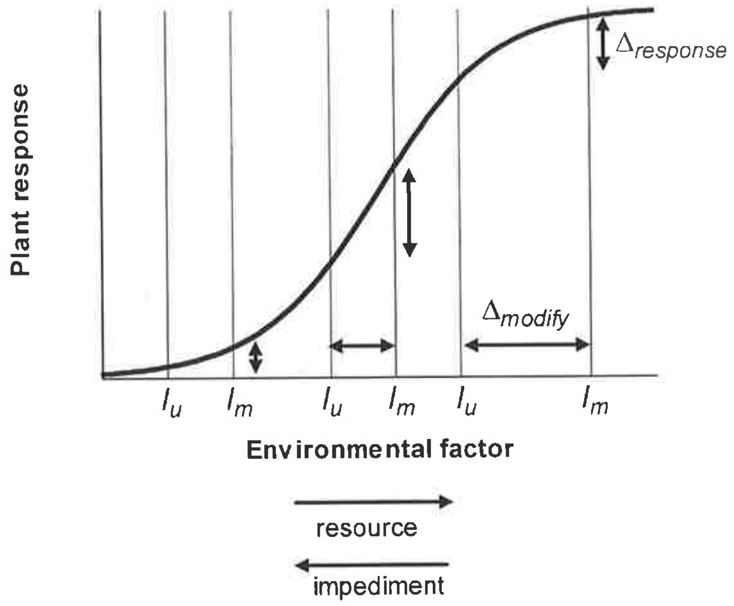


Figure 7.3: Predicted plant response to changes in the level of an environmental factor due to modification by another plant, assuming a logistic response.

is asymptotic increasing. From Equations 7.2 and 7.3:

$$\triangle_{response} = be^{cl_o}(e^{-cl_u} - e^{-c(kl_u+B)})$$

Thus $\triangle_{response}$ depends on $e^{-cl_u} - e^{-c(kl_u+B)}$, as be^{cl_o} will be constant for any given environmental gradient (Figure 7.2). Writing

$$h(l) = e^{-cl_u} - e^{-c(kl_u+B)}$$

we can see that $\triangle_{response}$ increases with l_u when $\frac{dh}{dl} > 0$, is constant when $\frac{dh}{dl} = 0$, and decreases with l_u when $\frac{dh}{dl} < 0$. Thus the direction of the changes in the intensity of facilitation along environmental gradients will be determined by the parameters c, k and B.

7.3.3 Sigmoidal functions

The general form of $\triangle_{response}$ for logistic functions is given by:

$$\begin{aligned} \triangle_{response} &= f(l_m) - f(l_u) \\ &= \frac{K}{1+\left[\frac{K-f_o}{f_o}\right]e^{-b(g(l_u)-l_o)}} - \frac{K}{1+\left[\frac{K-f_o}{f_o}\right]e^{-b(l_u-l_o)}} \end{aligned} \qquad (7.4)$$

It can be seen that the algebraic analysis of the behaviour of $\triangle_{response}$ as l_u changes will be complex, and is outside the scope of this thesis. Instead, I will provide a graphical analysis.

An important feature of sigmoidal functions is the point of inflection, where the slope of $f(l)$ changes from increasing to decreasing and the second derivative $(\frac{d^2f}{dl^2})$ changes from positive to negative (Figure 7.3). This point of inflection can be found by setting $\frac{d^2f}{dl^2}$ to zero.

$$\frac{d^2f}{dl^2} = f(l)b^2(1-\frac{f(l)}{K})(1-\frac{2f(l)}{K})$$

Thus the point of inflection occurs when $\frac{f(l)}{K} = 1$ or $\frac{f(l)}{K} = \frac{1}{2}$, *i.e.* when $f(l) = K$ or $f(l) = \frac{K}{2}$. Note that only the latter solution is meaningful in the context of this model.

Case 1: constant $\triangle_{modify}$

If the size of $\triangle_{modify}$ remains constant for all l_u, the strength of facilitation increases as $f(l)$ approaches the point of inflection $(\frac{K}{2})$, and then decreases when $f(l) > \frac{K}{2}$. In other words, the intensity of facilitation will be greater at intermediate levels of the environmental factor than at low or high levels.

Case 2: variable $\triangle_{modify}$

Where $\triangle_{modify}$ changes linearly with l_u, a multitude of outcomes are possible (Figure 7.3). When the level of modification decreases as l_u increases, the intensity of facilitation cannot increase continuously, but may increase over some intervals. When the level of modification increases as l_u increases, the intensity of facilitation cannot decrease continuously, but may decrease over some intervals. The outcomes will be determined, at least in part, by whether or not the magnitude of the rate at which $\triangle_{modify}$ changes is greater than the rate at which $f(l_u)$ changes.

7.4 Discussion

These models provide testable predictions that are not in accord with current models of facilitation, and they establish some of the conditions under which facilitation will increase with environmental severity. They reveal that changes in the level of a single environmental variable can result in a variety of responses, and that the intensity of facilitation may show complex changes along environmental gradients. Furthermore, the patterns of change are determined by both the patterns of plant responses to environmental factors, and by the patterns of environmental modification by plants. In general, the intensity of facilitation will not change along an environmental gradient if plants respond to change linearly and if the effect of plant modification does not change in magnitude. Contrary to earlier models (Bertness and Callaway, 1994; Callaway and Walker, 1997; Callaway, 1997), the intensity of facilitation will increase as resource levels increase under some circumstances, especially when the effect of plant modification increases with resource levels. Clearly, we can no longer countenance a simplistic qualitative relationship between environmental 'severity' and the intensity of facilitation.

My approach is in contrast to that of earlier models (Callaway and Walker, 1997; Brooker and Callaghan, 1998) based on anticipated patterns of competition along environmental gradients. I chose instead to construct this model around parameters that are less abstract and more directly quantifiable. The core concept of the model is that plants modify their environments, and that those modifications can affect the performance of neighbouring plants. Consequently the processes of modification and response are explicitly and quantitatively modelled. Thus the measures of facilitation are derived directly from modelled plant performance, not from anticipated patterns of competition.

I also differ in my choice of measure of plant response. I sought robust measures that are transferable between systems and situations. Recognising that the modular nature of plants can create size-related biases in measures of growth and fecundity, I elected to use *per capita* measures of rates of change.

These models assume that changes in the level of a single factor do not affect plant responses to other factors. However, the absence of interactions between factors is not always a reasonable assumption. For example, increased plant growth in response to elevated nutrient levels may result in competition for light. Nevertheless, in conditions where some resources are scarce while others are in plentiful supply, increasing the availability of a scarce resource may not result in pronounced interactions between plant responses and other resources.

In the case where there are substantial interactions consequent upon changes in the level of a single resource, the net outcomes are likely to be non-linear regardless of the nature of the response functions for individual resources. It is unlikely, though not impossible, that an increased plant response due to an increase in the level of a single resource will be exactly counterbalanced by a decreased plant response emanating from interacting effects on the availability of other resources.

Non-linear plant responses may be effectively linear along environmental gradients that encompass a narrow range of levels. Whereas light and soil moisture gradients commonly cover large ranges, permitting most or all of the possible range of plant responses, other gradients may be much shorter. For instance, few ecosystems would provide the range of soil nutrients required to encompass the full gamut of plant responses. In such cases the ranges encountered under field conditions may correspond to a portion of the plant response curve that barely deviates from linearity. Given the vagaries of field experimentation, such minor deviations from linearity may not be detectable by current methods.

Surprisingly little quantitative information is available on the responses to resource levels by non-agricultural plant species. This bias means that most data concern responses by annual grasses, legumes or brassicas. Although the general nature of responses to light, nutrients and water is known, it will not be possible to make quantitative predictions on the effects of plant modification until more data become available. Even less is known about how the effects of plant modification on resource availability change with ambient resource levels. I have shown that the effect of shading on soil temperature increases linearly with ambient soil temperature (Figure 6.8), but I am not aware of other comparable data.

Plant growth is usually represented as a non-negative response to resource levels. While this may be a reasonable approximation of growth responses in benign habitats, it does not accurately model growth under the adverse conditions where facilitation is purportedly stronger and more common. Negative growth may occur when resource levels are insufficient to maintain an individual plant's extant biomass. This is not infrequently observed in perennial plants growing in the absence of vertebrate herbivores in arid systems (Chapter 6.3.2, J. Facelli *pers. comm.*).

Although these models show that facilitation may not necessarily be stronger under adverse conditions, it is unclear as to how frequently facilitation will fail to be so. This will depend on how frequently the different response functions are encountered, the levels found along environmental gradients and on the way in which plant modification changes with those levels. In arid systems, water and often soil nutrients are scarce. Where plant responses to these resources are sigmoidal (Marschner, 1986), the intensity of facilitation may change little when resources are very scarce, yet suddenly become much stronger if conditions begin to improve. On current knowledge, this would appear to be not unlikely. Cases where facilitation is not more intense under adverse conditions may be relatively common.

7.4.1 Conclusions

The prime importance of these models is that they explicitly link modification by plants with interactions between plants. They are also extendable, and can be used to model competition or the effects of impediments along gradients. As such, they provide a new conceptual framework for considering interactions between sessile modular organisms. The models also explicitly clarify the relationship between facilitation and competition, representing them as outcomes of the same processes under different conditions rather than being separate processes in their own right.

The models provide a rational framework for considering the processes of plant modification within the context of the surrounding environment. This is akin to the approach of considering plant responses as a function of resource levels ($f(l)$ in the model); here the effects of plant modification are considered as a function of environmental levels ($g(l)$ in the model). Furthermore they clearly show the differences in plant responses that are attributable to plant modification.

The models are currently limited by their depiction of responses to changes in a single resource. Nevertheless they have provided valuable information; they establish the bounds of what plant interactions are possible along environmental gradients, and they define a set of prerequisite conditions that result in interactions being of equal strength along gradients. Furthermore, the model parameters are quantifiable, and the predictions are testable. Extending the models to incorporate interactions between environmental factors is a challenge that I intend to pursue on completion of this thesis.

Chapter 8

Conclusions

8.1 Tree canopies and their effects

The objectives of this study were to investigate the heterogeneity associated with trees, to identify processes by which canopies may create heterogeneity, and to test the effects of canopy processes on the performance of some of the plant species that occur in canopy micro-environments. During the course of this work I developed novel experimental techniques, using shadecloth structures to model the effects of tree canopies on light and rainfall redirection. I also developed a new conceptual framework for modelling plant interactions along environmental gradients.

8.1.1 Trees and spatial heterogeneity

Considerable heterogeneity in both soil resources and plant species composition and cover were associated with the presence of *Alectryon oleifolius*. Nutrient levels in soils under *A. oleifolius* canopies were higher than the levels in soils from adjacent open areas, confirming that fertile islands are associated with this species. Similarly, the plant species composition under canopies differed from that in open areas. Some species, such as *Enchylaena tomentosa* and *Rhagodia spinescens*, were more abundant in areas near larger trees where soil nutrient levels were higher, while others such as *Eriochiton sclerolaenoides* and grasses were more abundant in the surrounding areas where trees had less influence.

8.1.2 Evidence of biological modification

Several lines of evidence were consistent with a biological origin for the fertile islands associated with *A. oleifolius*. Correlations between some soil resources differed with distance from the tree trunk, suggesting that the processes of decomposition, mineralisation and leaching change with distance from the trunk. These processes are sensitive to changes in temperature and moisture levels (Aerts, 1997; Caldwell et al., 1998), so tree canopies may affect nutrient accumulation by modifying the local microclimate.

Perhaps the strongest evidence that fertile islands are of biological origin comes from the changes that occur to soils, litter density and plant communities under *A. oleifolius* as the trees grow and age. The processes of change appear to be cumulative, and they have a distinct size-related threshold. While there were few differences between open areas and those under the canopies of small trees, differences became increasingly pronounced once tree height exceeded about 3.5 m. Shrub cover increased, the species composition of the understorey changed, leaf litter density increased and soil organic carbon levels were higher. Furthermore, the level of modification associated with trees in clusters tended to be higher than the level associated with isolated trees of similar size. This suggests that at least some of the processes of change are associated with shading, as the canopies of adjoining trees provide a much larger shade patch than single trees of similar size.

Further evidence that shading, rather than soil resources, influences plant distributions, was provided by variation in the abundance of some plant species (*E. tomentosa, M. appressa,* and *R. spinescens*) between trees of differing canopy shapes. This may be a consequence of the differences in the levels of shading provided by each canopy shape when the sun is low in the sky, as trees of similar size should provide comparable levels of shading when the sun is high regardless of canopy shape. In particular, these differences may assume greater importance in autumn during periods of prolonged drought, when plants will be experiencing severe water stress.

8.1.3 Facilitation, shrubs and fertile islands

It is not yet clear how fertile islands are created, but it appears that shrubs are an integral part of the processes of nutrient accumulation under *A. oleifolius*. The survey data show that shrub densities below *A. oleifolius* do not increase until the trees are about 3.5 m high, suggesting that *A. oleifolius* trees modify the microclimate sufficiently to increase the probability of successful shrub recruitment when they attain this size. The survey data also indicate that nutrient accumulation does not proceed until this occurs. Several plausible non-exclusive mechanisms of nutrient accumulation exist; shrubs may assist nutrient accumulation because they increase leaf litter retention rates, they may produce higher-quality leaf litter that decomposes more readily and increases rates of nutrient cycling, and they may increase the amount of leaf litter through increased site productivity.

8.1.4 Effects of modification by canopies

Experimental methodology

In testing the effects of plant canopies on other plant species, it was important to avoid the confounding effects of differences in soil resources between under-canopy and open areas. I circumvented this problem by developing a set of artificial canopies that modelled shading and rainfall redirection by tree canopies. These artificial canopies were designed to provide generic effects, rather than to specifically mimic a particular plant species. Attention was paid to the geometry of shading. I not only selected shadecloth of an appropriate density, but also constructed the canopies to provide shade patches that were within the range of sizes that were to be found at my field site. Furthermore, the rates at which the shade patches moved across the ground ensured that total daily PAR levels under artificial canopies were biologically realistic.

Rainfall redirection was also successfully emulated by one type of artificial canopy. Although I was unable to make quantitative comparisons between the artificial canopies and trees, I was successfully demonstrated that the V-shaped canopies directed a substantial proportion of rainfall towards their centres.

Shade

Shading by artificial canopies affected the performance of several plant species, increasing seedling emergence rates in *C. annua* and *D. caespitosa* during spring and again in summer following heavy rain. Furthermore, emergence rates were higher in large shade patches than in small shade patches. Growth rates and survivorship of *E. tomentosa* were also affected by shading. During summer shaded *E. tomentosa* had much lower mortality rates than exposed plants, but during spring plants experiencing a transition from shaded to exposed or *vice versa* had higher mortality rates than plants that remained shaded or sunlit. Shading also increased *E. tomentosa* growth rates during spring and summer, but not during winter. These results indicate that the provision of shade by trees is an important process of environmental modification that has consequences for recruitment, survivorship and productivity in chenopod shrublands.

Rainfall redirection

Surprisingly, there was little evidence that rainfall redirection had any effect on *C. annua* or *D. caespitosa* emergence. However, damage to some experimental treatments reduced the power of my experiments to detect rainfall redirection effects. Nevertheless, my results show that shading has a greater effect on seedling emergence in these species than any effects of rainfall redirection that may exist.

Unfortunately, two experiments testing the effects of rainfall redirection on growth of *C. annua* and *D. caespitosa* failed (data not presented), so I am unable to comment on the importance of this process to productivity.

8.1.5 Does local-scale heterogeneity matter?

One important issue that remains unresolved is whether or not the localised modifications associated with trees have larger scale consequences for biodiversity, productivity and nutrient cycling. It is conceivable that there may be other counteracting processes that negate the changes associated with trees, or that the magnitude of the changes are insufficiently large to have anything more than a negligible impact, given that they affect only a small proportion of the landscape. My results indicate that the local effects of trees have the potential to enhance both biodiversity and productivity, and they appear to act as focal points for nutrient cycling. However, the sorts of large-scale long term manipulative experiments that would be needed to settle this question would be logistically infeasible, and there is still insufficient quantitative data available to attempt to use models to find answers.

8.2 Facilitation

My work also addressed theoretical issues regarding facilitation. In particular, I explicitly tested changes in the intensity of facilitation along environmental gradients. Some aspects of the work also provide evidence regarding species-specificity in positive interactions between plants.

8.2.1 Environmental gradients and facilitation

Contrary to current theory, results from the growth experiment show that facilitation does not necessarily become stronger as conditions become more adverse. The effect of shading on *E. tomentosa* growth was no stronger during the height of summer than it was under less extreme conditions. However, the effects of shading on mortality changed in magnitude over the same period, showing that the effects of facilitation can vary between different aspects of plant performance. Furthermore, low levels of growth still occurred during periods when mortality was highest. This suggests that mortality is due to something other than a shortage of the resources required to sustain growth, or that some mortality agents may have little effect on growth.

Facilitation intensity may show complex patterns of change along environmental gradients. I modelled plant performance and local modification by plants as hypothetical functions of a single environmental factor. The results showed that the patterns of the change in the intensity of facilitation are determined by both the characteristics of the plant response function and the characteristics of the modification function. Change in the intensity of facilitation along gradients is not necessarily linear, nor is it necessarily monotonic.

8.2.2 Is facilitation species specific?

It has been suggested that positive interactions between plants tend to be the species-specific consequences of atypical plant traits (Callaway, 1998). However, the results of the three field experiments suggest that at least some processes may have more generic positive effects. In each experiment shading increased plant performance, with the sole exception of *E. tomentosa* survival rates in winter-spring. This is despite the use of three species from different families, with contrasting life forms and habitat preferences. Clearly, facilitation by shading is not species-specific. Rather, positive interactions are more likely to be hierarchical, with different species accruing benefits or penalties at different levels along environmental gradients.

8.3 Coda

This study has quantified aspects of the heterogeneity associated with *A. oleifolius*, and provided evidence that soil resource heterogeneity may result from cumulative processes associated with the presence of these trees. I employed novel experimental methods to demonstrate the effects of shading by canopies on the emergence, survivorship and growth of *C. annua, D. caespitosa* and *E. tomentosa.* I found that shading increased emergence in both *C. annua* and *D. caespitosa*, while rainfall redirection had a much smaller effect on emergence of these two species. Shade facilitated *E. tomentosa* growth throughout winter, spring and summer, but differed between seasons in its effects on *E. tomentosa* survivorship.

I found that facilitation does not necessarily become more intense as conditions become more severe, and that the effects of facilitation can simultaneously differ between survivorship and growth. More importantly, I used simple graphical methods to construct more sophisticated models linking modification by plants with plant interactions. These models predict the strength and direction of plant interactions along environmental gradients, providing testable explanations for my experimental results.

Bibliography

Aerts, R. (1997). Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. *Oikos*, 79:439–49.

Aguiar, M., Soriano, A., and Sala, O. (1992). Competition and facilitation in the recruitment of seedlings in Patagonian steppe. *Functional Ecology*, 6:66–70.

Allison, L. (1965). Organic carbon. In Evans, D., Ensminger, L., Clark, F., and White, J., editors, *Methods of soil analysis. Part 2. Chemical and microbiological properties*, Agronomy, pages 1367–1378. American Society of Agronomy, Madison, Wisconsin.

Amundson, R., Ali, A., and Belsky, A. (1995). Stomatal responsiveness to changing light intensity increases rain-use efficiency of below-crown vegetation in tropical savannas. *Journal of Arid Environments*, 29:139–153.

Andrew, M. H. (1978). *The initial impact of depasturing sheep on arid chenopod shrublands.* Ph.D., The University of Adelaide, South Australia.

Andrew, M. H. and Lange, R. T. (1986). Development of a new piosphere in arid chenopod shrubland grazed by sheep. 2. changes to the vegetation. *Australian Journal of Ecology*, 11:411–424.

Andrewartha, H. and Birch, L. (1954). *The Distribution and Abundance of Animals.* The University of Chicago Press, Chicago.

Aphalo, P. and Ballaré, C. (1995). On the importance of information-acquiring systems in plant-plant interactions. *Functional Ecology*, 9:5–14.

Archer, S., Scifres, C., and Bassham, C. (1988). Autogenic succession in a subtropical savanna: conversion of grassland to thorn woodland. *Ecological Monographs*, 58:111–127.

Aston, A. (1979). Rainfall interception by eight small trees. *Journal of Hydrology*, 42:383–396.

Ball, M., Hodges, V., and Laughlin, G. (1991). Cold-induced photoinhibition limits regeneration of snow gum at tree-line. *Functional Ecology*, 5:663–668.

Ball, M. C. (1994). The role of photoinhibition during tree seedling establishment at low temperatures. In Baker, N. and Bowyer, J., editors, *Photoinhibition of Photosynthesis: From Molecular Mechanisms to the Field.*, pages 365–376. Bios Scientific, Oxford.

Barker, S. (1972). *Effects of sheep stocking on the population structure of arid shrublands in South Australia.* Ph.D., University of Adelaide, Adelaide.

Barnes, P. W. and Archer, S. (1996). Influence of an overstorey tree (*Prosopis glandulosa)* on associated shrubs in a savanna parkland: Implications for patch dynamics. *Oecologia*, 105:493–500.

Barritt, A. R. and Facelli, J. M. (*in press*). Effects of *Casuarina pauper* litter and grove soil in emergence and growth of understorey species in arid lands of South Australia. *Journal of Arid Environments.*

Barth, R. (1980). Influence of pinyon pine trees on soil chemical and physical properties. *Soil Science Society of America Journal*, 44:112–114.

Bartholomew, B. (1970). Bare zone between California shrub and grassland communities: The role of animals. *Science*, 170:1210–1212.

Belsky, A., Amundson, R., Duxbury, J., Riha, S., Ali, A., and Mwonga, S. (1989). The effects of trees on their physical, chemical, and biological environments in a semi-arid savanna in Kenya. *Journal of Applied Ecology*, 26:1005–1024.

Belsky, A., Mwonga, S., Amundson, R., Duxbury, J., and Ali, A. (1993). Comparative effects of isolated trees on their undercanopy environments in high- and low-rainfall savannas. *Journal of Applied Ecology*, 30:143–155.

Belsky, A. J. (1994). Influences of trees on savanna productivity: tests of shade, nutrients, and tree-grass competition. *Ecology*, 75:922–932.

Belsky, A. J. and Canham, C. D. (1994). Forest gaps and isolated savanna trees. *BioScience*, 44:77–84.

Bernhard-Reversat, F. (1982). Biogeochemical cycle of nitrogen in a semi-arid savanna. *Oikos*, 38:321–332.

Bertness, M. D. and Callaway, R. (1994). Positive interactions in communities. *Trends in Ecology and Evolution*, 9:191–193.

Bertness, M. D. and Leonard, G. H. (1997). The role of positive interactions in communities: lessons from intertidal habitats. *Ecology*, 78:1976–1989.

Blair, D. (2000). The geometry of incoming solar radiation. http:// www. uniwinnipeg.ca/ ~ blair/ physclim/ lab2.htm.

Bradstreet, R. (1965). *The Kjeldahl method for organic nitrogen.* Academic Press, New York.

Breshears, D. D., Nyhan, J. W., Heil, C. E., and Wilcox, B. P. (1998). Effects of woody plants on microclimate in a semiarid woodland: soil temperature and evaporation in canopy and intercanopy patches. *International Journal of Plant Sciences*, 159:1010–1017.

Breshears, D. D., Rich, P. M., Barnes, F. J., and Campbell, K. (1997). Overstorey-imposed heterogeneity in solar radiation and soil moisture in a semiarid woodland. *Ecological Applications*, 7:1201–1215.

Brock, D. J. (1993). *The localised influence of the Western Myall (Acacia papyrocarpa Benth.) on plant community structure in the arid zone at Middleback Station, Whyalla.* Bachelor of Science with Honours, University of Adelaide.

Brokaw, N. V. (1985). Disturbance regimes in temperate forests. In Pickett, S. and White, P., editors, *The ecology of natural disturbance and patch dynamics.*, pages 53–69. Academic Press, Orlando, Florida.

Brooker, R. W. and Callaghan, T. V. (1998). The balance between positive and negative plant interactions and its relationship to environmental gradients: a model. *Oikos*, 81:196–207.

Burgess, S. S., Adams, M. A., Turner, N. C., and Ong, C. K. (1998). The redistribution of soil water by tree root systems. *Oecologia*, 115:306–311.

Caldwell, M. and Richards, J. (1989). Hydraulic lift: water efflux from upper roots improves effectiveness of water uptake by deep roots. *Oecologia*, 79:1–5.

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

Callaway, R. (1992). Effect of shrubs on recruitment of *Quercus douglasii* and *Quercus lobata* in California. *Ecology*, 73:2118–2128.

Callaway, R. M. (1995). Positive interactions among plants. *The Botanical Review*, 61:306–349.

Callaway, R. M. (1997). Positive interactions in plant communities and the individualistic-continuum concept. *Oecologia*, 112:143–149.

Callaway, R. M. (1998). Are positive interactions species-specific? *Oikos*, 82:202–207.

Callaway, R. M. and Nadkarni, N. M. (1991). Seasonal patterns of nutrient deposition in a *Quercus douglasii* woodland in central California. *Plant and Soil*, 137:209–222.

Callaway, R. M., Nadkarni, N. M., and Mahall, B. E. (1991). Facilitation and interference of *Quercus douglasii* on understory productivity in central California. *Ecology*, 72:1484–1499.

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

Carrodus, B., Specht, R., and Jackman, M. E. (1965). The vegetation of Koonamore Station, South Australia. *Transactions of the Royal Society of South Australia*, 89:41–59.

Cescatti, A. (1997). Modelling the radiative transfer in discontinuous canopies of asymmetric crowns. 1. Model structure and algorithms. *Ecological Modelling*, 101:263–274.

Chambers, J. C. and MacMahon, J. A. (1994). A day in the life of a seed: movements and fates of seeds and their implications for natural and managed systems. *Annual Review of Ecology and Systematics*, 25:263–292.

Chapin, F. and Kedrowski, R. (1983). Seasonal changes in nitrogen and phosphorus fractions and autumn retranslocation in evergreen and deciduous taiga trees. *Ecology*, 64:376–391.

Charley, J. L. and West, N. E. (1975). Plant-induced soil chemical patterns in some shrub-dominated semi-desert ecosystems of Utah. *Journal of Ecology*, 63:945–963.

Chazdon, R. L. (1988). Sunflecks and their importance to forest understorey plants. *Advances in Ecological Research*, 18:1–63.

Cheal, D. C. (1999). *Fire and soil interactions in a mallee heartland: the generation of heterogeneity in an homogeneous landscape.* Ph.D., University of Melbourne.

Clements, F. E. (1916). *Plant succession: an analysis of the development of vegetation.* Carnegie Institute of Washington, Washington.

Connell, J. H. (1978). Diversity in tropical rain forest and coral reefs. *Science*, 199:1302–1310.

Coomes, D. A. and Grubb, P. J. (2000). Impacts of root competition in forests and woodlands: A theoretical framework and review of experiments. *Ecological Monographs*, 70:171–207.

Cowling, S. (1978). Coupling of nutrient to water flows in rangeland ecosystems. In Howes, K., editor, *Water in rangelands.*, volume 3 of *Studies of the Australian arid zone.*, pages 110–121. CSIRO, Melbourne.

Crisp, M. and Lange, R. (1976). Age structure, distribution and survival under grazing of the arid-zone shrub *Acacia burkittii*. *Oikos*, 27:86–92.

Crisp, M. D. (1978). Demography and survival under grazing of three Australian semi-desert shrubs. *Oikos*, 30:520–528.

Curtis, W. and Kincaid, D. (1984). Leaf conductance responses of *Viola* spp. from sun and shade habitats. *Canadian Journal of Botany*, 62:1268–1272.

Davis, M. A., Ritchie, B., Graf, N., and Gregg, K. (1995). An experimental study of the effects of shade, conspecific crowding, pocket gophers and surrounding vegetation on survivorship, growth and reproduction in *Penstemon grandiflorus* . *American Midland Naturalist*, 134:237–243.

Dawson, T. E. (1993). Hydraulic lift and water use by plants: implications for water balance, performance and plant-plant interactions. *Oecologia*, 95:565–574.

Dawson, T. E. (1996). Determining water use by trees and forests from isotopic, energy balance and transpiration analyses: the roles of tree size and hydraulic lift. *Tree Physiology*, 16:263–272.

De Soyza, A. G., Whitford, W. G., Martinez-Meza, E., and Van Zee, J. W. (1997). Variation in creosotebush (*Larrea tridentata*) canopy morphology in relation to habitat, soil fertility and associated annual plant communities. *American Midland Naturalist*, 137:13–26.

Dean, W., Milton, S., and Jeltsch, F. (1999). Large trees, fertile islands, and birds in arid savanna. *Journal of Arid Environments*, 41:61–78.

Dean, W. and Milton, S. J. (1991). Disturbances in semi-arid shrubland and arid grassland in the Karoo, South Africa: Mammal diggings as germination sites. *African Journal of Ecology*, 29:11–16.

Deregibus, V. A., Sanchez, R. A., Casal, J. J., and Trlica, M. J. (1985). Tillering responses to enrichment of red light beneath the canopy in humid natural grasslands. *Journal of Applied Ecology*, 22:199–206.

Drake, B., Raschke, K., and Salisbury, F. (1970). Temperatures and transpiration resistances of *Xanthium* leaves as affected by air temperature, humidity and wind speed. *Plant Physiology*, 46:324–330.

Dufrene, M. and Legendre, P. (1997). Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs*, 67:345–366.

Dunham, K. M. (1991). Comparative effects of *Acacia albida* and *Kigelia africana* trees on soil characteristics in Zambezi riverine woodlands. *Journal of Tropical Ecology*, 7:215–220.

Ellenberg, H. (1988). *Vegetation Ecology of Central Europe*. Cambridge University Press, Cambridge.

Everett, R. L., Sharrow, S. H., and Meeuwig, R. O. (1983). Pinyon-juniper woodland understory distribution patterns and species associations. *Bulletin of the Torrey Botanical Club*, 110:454–463.

Facelli, J. M. (1994). Multiple indirect effects of plant litter affect the establishment of woody seedlings in old fields. *Ecology*, 75:1727–1735.

Facelli, J. M. and Brock, D. J. (2000). Patch dynamics in arid lands: Localized effects of *Acacia papyrocarpa* on soils and vegetation of open woodlands of South Australia. *Ecography*, 23:479–491.

Facelli, J. M. and Carson, W. P. (1991). Heterogeneity of plant litter accumulation in successional communities. *Bulletin of the Torrey Botanical Club*, 118:62–66.

Facelli, J. M. and Kerrigan, R. (1996). Effects of ash and four types of litter in the establishment of *Eucalyptus obliqua* . *Ecoscience*, 3:319–324.

Facelli, J. M. and Ladd, B. (1996). Germination requirements and responses to leaf litter of four species of eucalypts. *Oecologia*, 107:441–445.

Facelli, J. M. and Pickett, S. (1991a). Indirect effects of litter on woody seedlings subject to herb competition. *Oikos*, 62:129–138.

Facelli, J. M. and Pickett, S. T. (1991b). Plant litter: its dynamics and effects on plant community structure. *The Botanical Review*, 57:1–32.

Fenner, M. (1978). A comparison of the abilities of colonizers and close-turf species to establish from seed in artificial swards. *Journal of Ecology*, 66:953–963.

Fenner, M. (1985). *Seed Ecology*. Chapman and Hall, London.

Flores-Martinez, A., Ezcurra, E., and Sanchez-Colon, S. (1994). Effect of *Neobuxbaumia tetetzo* on growth and fecundity of its nurse plant *Mimosa luisana*. *Journal of Ecology*, 82:325–330.

Franco, A. and Nobel, P. (1989). Effect of nurse plants on the microhabitat and growth of cacti. *Journal of Ecology*, 77:870–886.

Franco-Pizana, J. G., Fulbright, T. E., Gardiner, D. T., and Tipton, A. R. (1996). Shrub emergence and seedling growth in microenvironments created by *Prosopis glandulosa* . *Journal of Vegetation Science*, 7:257–264.

Frost, W. E. and McDougald, N. K. (1989). Tree canopy effects on herbaceous production of annual rangeland during drought. *Journal of Range Management*, 42:281–283.

Fuentes, E. R., Otaiza, R. D., Alliende, M. C., Hoffmann, A., and Poiani, A. (1984). Shrub clumps of the Chilean matorral vegetation: Structure and possible maintenance mechanisms. *Oecologia*, 62:405–411.

Fulbright, T. E., Kuti, J. O., and Tipton, A. R. (1995). Effects of nurse-plant canopy temperatures on shrub seed germination and seedling growth. *Acta Oecologia*, 16:621–632.

Garcia-Moya, E. and McKell, C. M. (1970). Contribution of shrubs to the nitrogen economy of a desert-wash plant community. *Ecology*, 51:81–88.

Garner, W. and Steinberger, Y. (1989). A proposed mechanism for the formation of 'fertile islands' in the desert ecosystem. *Journal of Arid Environments*, 16:257–262.

Georgiadis, N. J. (1989). Microhabitat variation in an African savanna: Effects of woody cover and herbivores in Kenya. *Journal of Tropical Ecology*, 5:93–108.

Gerdol, R., Brancaleoni, L., Menghini, M., and Marchesini, R. (2000). Response of dwarf shrubs to neighbour removal and nutrient addition and their influence on community structure in a subalpine heath. *Journal of Ecology*, 88:256–266.

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

Goldberg, D. E., Rajaniemi, T., Gurevitch, J., and Stewart-Oaten, A. (1999). Empirical approaches to quantifying interaction intensity: competition and facilitation along productivity gradients. *Ecology*, 80:1118–1131.

GraphPad (1999). GraphPad Prism version 3.02 for Windows.

Greenlee, J. T. and Callaway, R. M. (1996). Abiotic stress and the relative importance of interference and facilitation in montane bunchgrass communities in Western Montana. *American Naturalist*, 148:386–396.

Grime, J. (1973). Competitive exclusion in herbaceous vegetation. *Nature*, 242:344–347.

Grime, J. (1977). Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist*, 111:1169–1194.

Grime, J. P. (1979). *Plant strategies and vegetation processes.* John Wiley and Son, New York.

Grouzis, M. and Akpo, L.-E. (1997). Influence of tree cover on herbaceous above- and below-ground phytomass in the Sahelian zone of Senegal. *Journal of Arid Environments*, 35:285–296.

Gutterman, Y. (1986). Influences of environmental factors on germination and plant establishment in the Negev Desert highlands of Israel. In *Rangelands: A resource inder siege. Proceedings of the Second International Rangelands Congress*, pages 441–449. Australian Academy of Science, Canberra.

Gutterman, Y. and Herr, N. (1981). Influences of porcupine (*Hystrix indica*) activity on the slopes of the northern Negev Mountains - germination and vegetation renewal in different geomorphological types and slope directions. *Oecologia*, 51:332–334.

Guttierrez, J. R., Meserve, P. L., Contreras, L. C., Vasquez, H., and Jaksic, F. M. (1993). Spatial distribution of soil nutrients and ephemeral plants underneath and outside the canopy of *Porlieria chilensis* shrubs (Zygophyllaceae) in arid coastal Chile. *Oecologia*, 95:347–352.

Hacker, S. D. and Gaines, S. D. (1997). Some implications of direct positive interactions for community species diversity. *Ecology*, 78:1990–2003.

Halligan, J. P. (1974). Relationship between animal activity and bare areas associated with California sagebrush in annual grassland. *Journal of Range Management*, 27:358–362.

Hastwell, G. T. and Facelli, J. M. (2000). Effects of leaf litter on woody seedlings in xeric successional communities. *Plant Ecology*, 148:225–231.

Haworth, K. and McPherson, G. R. (1995). Effects of *Quercus emoryi* trees on precipitation distribution and microclimate in a semi-arid savanna. *Journal of Arid Environments*, 31:153–170.

Hofstede, R., Chilito, E., and Sandovals, E. (1995). Vegetative structure, microclimate, and leaf growth of a paramo tussock grass species, in undisturbed, burned and grazed conditions. *Vegetatio*, 119:53–65.

Holling, C. (1992). Cross-scale morphology, geometry, and dynamics of ecosystems. *Ecological Monographs*, 62:447–502.

Holly, C., Laughlin, G., and Ball, M. (1994). Cold-induced photoinhibition and design of shelters for establishment of eucalypts in pasture. *Australian Journal of Botany*, 42:139–147.

Holmgren, M. (2000). Combined effects of shade and drought on tulip poplar seedlings: Trade-off in tolerance or facilitation? *Oikos*, 90:67–78.

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

Holzapfel, C. and Mahall, B. E. (1999). Bidirectional facilitation and interference between shrubs and annuals in the Mojave desert. *Ecology*, 80:1747–1761.

Howard, J. (1966). Spectral energy relations of isobilateral leaves. *Australian Journal of Biological Science*, 19:757–766.

Huston, M. (1979). A general hypothesis of species diversity. *American Naturalist*, 113:81–101.

Isichei, A. O. and Muoghalu, J. I. (1992). The effects of tree canopy cover on soil fertility in a Nigerian savanna. *Journal of Tropical Ecology*, 8:329–338.

Jackson, J. and Ash, A. J. (1998). Tree-grass relationships in open eucalypt woodlands of northeastern Australia: Influence of trees on pasture productivity, forage quality and species distribution. *Agroforestry Systems*, 40:159–176.

Jessop, J. P. and Toelken, H. R. (1986). *Flora of South Australia, Vol.I-IV*. South Australian Government Printing Division, Adelaide.

Joffre, R. and Rambal, S. (1988). Soil water improvement by trees in the rangelands of southern Spain. *Acta Oecologia /Oecologia Plantarum*, 9:405–422.

Joffre, R. and Rambal, S. (1993). How tree cover influences the water balance of mediterranean rangelands. *Ecology*, 74:570–582.

Johnson, A. W. (1978). *Vegetation suppression in the Whyalla region, with particular reference to the phenomena around Casuarina cristata.* Honours, University of Adelaide.

Jorgensen, S. E. (1986). *Fundamentals of Ecological Modelling.* Elsevier, Amsterdam.

Karssen, C. and Hilhorst, H. (1992). Effect of chemical environment on seed germination. In Fenner, M., editor, *Seeds: the ecology of regeneration in plant communities.*, pages 327–348. C.A.B. International, Wallingford UK.

Kellman, M. (1979). Soil enrichment by neotropical savanna trees. *Journal of Ecology*, 67:565–577.

Kellman, M. and Kading, M. (1992). Facilitation of tree seedling establishment in a sand dune succession. *Journal of Vegetation Science*, 3:679–688.

Kelly, R. H. and Burke, I. C. (1997). Heterogeneity of soil organic matter following death of individual plants in shortgrass steppe. *Ecology*, 78:1256–1261.

Kitzberger, T., Steinaker, D. F., and Veblen, T. T. (2000). Effects of climatic variability on facilitation of tree establishment in northern Patagonia. *Ecology*, 81:1914–1924.

Klemmedson, J. and Tiedemann, A. (1986). Long-term effects of mesquite removal on soil characteristics: 2. Nutrient availability. *Soil Science Society of America Journal*, 50:476–480.

Knops, J. M., Nash, T. H. I., and Schlesinger, W. H. (1996). The influence of epiphytic lichens on the nutrient cycling of an oak woodland. *Ecological Monographs*, 66:159–179.

Ko, L. J. and Reich, P. B. (1993). Oak tree effects on soil and herbaceous vegetation in savannas and pastures in Wisconsin. *American Midland Naturalist*, 130:31–42.

Kursar, T. and Coley, P. (1993). Photosynthetic induction times in shade-tolerant species with long and short-lived leaves. *Oecologia*, 93:165–170.

Lambert, D. (1992). Zero-inflated poisson regression, with an application to defects in manufacturing. *Technometrics*, 34:1–14.

Lange, R. T. and Purdie, R. (1976). Western myall (*Acacia sowdenii*), its survival prospects and management needs. *Australian Rangeland Journal*, 1:64–69.

Lee, D. (1987). The spectral distribution of radiation in two neotropical rainforests. *Biotropica*, 19:161–166.

Li, X. and Wilson, S. D. (1998). Facilitation among woody plants establishing in an old field. *Ecology*, 79:2694–2705.

Loustau, D., Berbigier, P., and Granier, A. (1992). Interception loss, throughfall and stemflow in a maritime pine stand. 2. An application of Gash's analytical model of interception. *Journal of Hydrology*, 138:469–485.

Ludwig, J. A. and Tongway, D. J. (1995). Spatial organisation of landscapes and its function in semi-arid woodlands, Australia. *Landscape Ecology*, 10:51–63.

Manly, B. F. (1992). RT version 1.02 for MS-DOS.

Maranon, T. and Bartolome, J. (1993). Reciprocal transplants of herbaceous communities between *Quercus agrifolia* woodland and adjacent grassland. *Journal of Ecology*, 81:673–682.

Marschner, H. (1986). *Mineral nutrition of higher plants.* Academic Press, London.

Martens, S. N., Breshears, D. D., and Meyer, C. W. (2000). Spatial distributions of understorey light along the grassland/forest continuum: Effects of cover, height, and spatial pattern of tree canopies. *Ecological Modelling*, 126:79–93.

Martens, S. N., Breshears, D. D., Meyer, C. W., and Barnes, F. J. (1997). Scales of above-ground and below-ground competition in a semi-arid woodland detected from spatial pattern. *Journal of Vegetation Science*, 8:655–664.

Martinez-Meza, E. and Whitford, W. G. (1996). Stemflow, throughfall and channelization of stemflow by roots in three Chihuahuan Desert shrubs. *Journal of Arid Environments*, 32:271–287.

MathSoft (1999). S-Plus 2000 Professional Edition for Windows.

MathSoft (2000). RobLib library for S-Plus, beta release.

Mauchamp, A. and Janeau, J. (1993). Water funnelling by the crown of *Flourensia cernua*, a Chihuahuan Desert shrub. *Journal of Arid Environments*, 25:299–306.

May, R., Hunter, M., and Gabriel, R. (1993a). NPFact 1.0 for MS-DOS.

May, R., Hunter, M., Masson, M., and Wells, J. (1993b). NPStat 3.8 for MS-DOS.

McCune, B. and Mefford, M. (1999). PC-ORD for Windows, version 4.14.

McDonnell, M. J. and Stiles, E. W. (1983). The structural complexity of old-field vegetation and the recruitment of bird dispersed species. *Oecologia*, 56:109–116.

Miller, T. (1987). Effects of emergence time on survival and growth in an early old-field plant community. *Oecologia*, 72:272–278.

Molofsky, J., Lanza, J., and Crone, E. E. (2000). Plant litter feedback and population dynamics in an annual plant, *Cardamine pensylvanica*. *Oecologia*, 124:522–528.

Mooney, H., Gulmon, S., Rundel, P., and Ehleringer, J. (1980). Further observations on the water relations of *Prosopis tamarugo* of the Northern Atacama Desert. *Oecologia*, 44:177–180.

Morrison, R. (1981). *A field guide to the tracks and traces of Australian animals.* Rigby Field Guide. Rigby, Adelaide, Australia.

Mueller-Dombois, D. and Ellenberg, H. (1974). *Aims and methods of vegetation ecology.* John Wiley, New York.

Muller, C. H. (1953). The association of desert annuals with shrubs. *American Journal of Botany*, 40:53–60.

Muller, C. H. (1969). Allelopathy as a factor in ecological process. *Vegetatio*, 18:348–357.

Murdoch, A. J. and Ellis, R. H. (1992). Longevity, viability and dormancy. In Fenner, M., editor, *Seeds: the ecology of regeneration in plant communities.*, pages 193–229. C.A.B. International, Wallingford, UK.

Myster, R. W. (1994). Contrasting litter effects on old field tree germination and emergence. *Vegetatio*, 114:169–174.

Navar, J. and Bryan, R. (1990). Interception loss and rainfall redistribution by three semi-arid growing shrubs in northeastern Mexico. *Journal of Hydrology*, 115:51–63.

Nilsen, E. and Schlesinger, W. (1981). Phenology, productivity and nutrient accumulation in the post-fire chapparral shrub, *Lotus scoparius*. *Oecologia*, 50:217–224.

Nobel, P. S. (1989). Temperature, water availability, and nutrient levels at various soil depths - consequences for shallow-rooted desert succulents, including nurse plants. *American Journal of Botany*, 76:1486–1492.

Noble, I. R. (1975). *Computer simulations of sheep grazing in the arid zone.* Ph.D, University of Adelaide.

Noy-Meir, I. (1981). Spatial effects in modelling of arid ecosystems. In Goodall, D., Perry, R., and Howes, K., editors, *Arid-land ecosystems: Structure, functioning and management.*, volume 2, pages 411–432. Cambridge University Press., Cambridge, United Kingdom.

Nulsen, R., Bligh, K., Baxter, I., Solin, E., and Imrie, D. (1986). The fate of rainfall in a mallee and heath vegetated catchment in southern Western Australia. *Australian Journal of Ecology*, 11:361–371.

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

Parker, V. and Muller, C. (1982). Vegetational and environmental changes beneath isolated live oak trees (*Quercus agrifolia*) in a California annual grassland. *The American Midland Naturalist*, 107:69–81.

Pearman, G. (1966). The reflection of visible radiation from leaves of some Western Australian species. *Australian Journal of Biological Science*, 19:97–103.

Peterson, C. J. and Facelli, J. M. (1992). Contrasting germination and seedling growth of *Betula alleghaniensis* and *Rhus typhina* subjected to various amounts and types of plant litter. *American Journal of Botany*, 79:1209–1216.

Pickett, S. and White, P. (1985). Patch dynamics: a synthesis. In Pickett, S. and White, P., editors, *The ecology of natural disturbance and patch dynamics*, pages 371–484. Academic Press, Orlando, Florida.

Pons, T. L. (1992). Seed responses to light. In Fenner, M., editor, *Seeds: the ecology of regeneration in plant communities.*, pages 259–284. C.A.B. International, Wallingford, UK.

Poorter, H. and Nagel, O. (2000). The role of biomass allocation in the growth response of plants to different levels of light, CO2, nutrients and water: A quantitative review. *Australian Journal of Physiology*, 27:595–607.

Pound, L. M. (1998). *The effect of the shrub Maireana pyramidata on annual plant communities.* Honours, University of Adelaide.

Pressland, A. (1973). Rainfall partitioning by an arid woodland (*Acacia aneura* F. Muell.) in south-western Queensland. *Australian Journal of Botany*, 21:235–245.

Probert, R. (1992). The role of temperature in germination ecophysiology. In Fenner, M., editor, *Seeds: the ecology of regeneration in plant communities.*, pages 285–325. C.A.B International, Wallingford.

Pugnaire, F., Haase, P., Puigdefabregas, J., Cueto, M., Clark, S., and Incoll, L. (1996a).

Facilitation and succession under the canopy of a leguminous shrub, *Retama sphaerocarpa*, in a semi-arid environment in south-east Spain. *Oikos*, 76:455–464.

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

Ratliff, R. D., Duncan, D. A., and Westfall, S. E. (1991). California oak-woodland overstorey species affect herbage understorey: management implications. *Journal of Range Management*, 44:306–310.

Richards, J. and Caldwell, M. (1987). Hydraulic lift: Substantial nocturnal water transport between soil layers by *Artemisia tridentata* roots. *Oecologia*, 73:486–489.

Romney, E., Wallace, A., Kaaz, H., and Hale, V. (1980). The role of shrubs on redistribution of mineral nutrients in soil in the Mojave Desert. *Great Basin Naturalist Memoirs*, 4:124–133.

Roos, P. and Allsopp, N. (1997). Soil nutrient ecology associated with *Acacia sieberana* at different tree densities in a South African savanna. *African Journal of Range and Forage Science*, 14:39–44.

Rousset, O. and Lepart, J. (1999). Shrub facilitation of *Quercus humilis* regeneration in succession on calcareous grasslands. *Journal of Vegetation Science*, 10:493–502.

Rousset, O. and Lepart, J. (2000). Positive and negative interactions at different life stages of a colonizing species (*Quercus humilis*). *Journal of Ecology*, 88:401–412.

Ruel, J. J. and Ayres, M. P. (1999). Jensen's inequality predicts effects of environmental variation. *Trends in Ecology and Evolution*, 14:361–366.

Runkle, J. R. (1985). Disturbance regimes in temperate forests. In Pickett, S. and White, P., editors, *The ecology of natural disturbance and patch dynamics.*, pages 17–33. Academic Press, Orlando, Florida.

Ryel, R., Beyschlag, W., and Caldwell, M. (1993). Foliage orientation and carbon gain in two tussock grasses as assessed with a new whole-plant gas-exchange model. *Functional Ecology*, 7:115–124.

Ryel, R., Beyschlag, W., and Caldwell, M. (1994). Light field heterogeneity among tussock grasses: theoretical considerations of light harvesting and seedling establishment in tussocks and uniform tiller distributions. *Oecologia*, 98:241–246.

Ryser, P. and Eek, L. (2000). Consequences of phenotypic plasticity vs. interspecific differences in leaf and root traits for acquisition of aboveground and belowground resources. *American Journal of Botany*, 87:402–411.

SAS Institute (1997). JMP 3.1.4 for Windows.

Schauffler, M., Jacobson, G. L. J., Pugh, A. L. I., and Norton, S. A. (1996). Influence of vegetational structure on capture of salt and nutrient aerosols in a maine peatland. *Ecological Applications*, 6:263–268.

Schlesinger, W. H. and Pilmanis, A. M. (1998). Plant-soil interactions in deserts. *Biogeochemistry*, 42:169–187.

Schlesinger, W. H., Raikes, J. A., Hartley, A. E., and Cross, A. F. (1996). On the spatial pattern of soil nutrients in desert ecosystems. *Ecology*, 77:364–374.

Scholes, R. and Archer, S. (1997). Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics*, 28:517–544.

Schupp, E. W. (1995). Seed-seedling conflicts, habitat choice, and patterns of plant recruitment. *American Journal of Botany*, 82:399–409.

Schupp, E. W. and Fuentes, M. (1995). Spatial patterns of seed dispersal and the unification of plant population ecology. *Ecoscience*, 2:267–275.

Silvertown, J. W. (1980). Leaf-canopy induced seed dormancy in a grassland flora. *New Phytologist*, 85:109–118.

Sinclair, R. and Thomas, D. (1970). Optical properties of leaves of some species in arid South Australia. *Australian Journal of Botany*, 18:261–273.

Skalski, J. R. (1987). Selecting a random sample of points in circular field plots. *Ecology*, 68:749.

Skillman, J., Strain, B., and Osmond, C. (1996). Contrasting patterns of photosynthetic acclimation and photoinhibition in two evergreen herbs from a winter deciduous forest. *Oecologia*, 107:446–455.

Smith, H., Samson, G., and Fork, D. (1993). Photosynthetic acclimation to shade: Probing the role of phytochromes using photomorphogenic mutants of tomato. *Plant, Cell and Environment*, 16:929–937.

Smith, S., Patten, D., and Monson, R. (1987). Effects of artificially imposed shade on a Sonoran Desert ecosystem: Microclimate and vegetation. *Journal of Arid Environments*, 13:65–82.

Smith, T. and Huston, M. (1989). A theory of the spatial and temporal dynamics of plant communities. *Vegetatio*, 83:49–69.

Sohlberg, E. and Bliss, L. (1987). Responses of *Ranunculus sabinei* and *Papaver radicatum* to removal of the moss layer in a high-arctic meadow. *Canadian Journal of Botany*, 65:1224–1228.

Specht, R. L. (1972). *The vegetation of South Australia (2nd Edition)*. Government Printer, Adelaide.

Stafford Smith, M. (1984). *Behavioural Ecology of Sheep in the Australian Arid Zone.* PhD, Australian National University.

Telfer, W. R. (1998). *The effects of shrubs on the recruitment of Eucalyptus incrassata in an abandoned pasture.* Honours, University of Adelaide.

Tester, M., Paton, D., Reid, N., and Lange, R. (1987). Seed dispersal by birds and densities of shrubs under trees in arid South Australia. *Transactions of the Royal Society of South Australia*, 111:1–5.

Thurow, T., Blackburn, W., Warren, S., and Taylor, C. J. (1987). Rainfall interception by midgrass, shortgrass, and live oak mottes. *Journal of Range Management*, 40:455–460.

Tiedemann, A. and Klemmedson, J. (1986). Long-term effects of mesquite removal on soil characteristics: I. nutrients and bulk density. *Soil Science Society of America Journal*, 50:472–475.

Tiedemann, A. R. and Klemmedson, J. O. (1973). Nutrient availability in desert grassland soils under mesquite (*Prosopis juliflora*) trees and adjacent open areas. *Soil Science Society of America Proceedings*, 37:107–111.

Tielborger, K. and Kadmon, R. (2000). Temporal environmental variation tips the balance between facilitation and interference in desert plants. *Ecology*, 81:1544–1553.

Tilman, D. (1988). *Plant strategies and the dynamics and structure of plant communities.* Princeton University Press, Princeton, New Jersey, USA.

Tilman, D. and Wedin, D. (1991). Oscillation and chaos in the dynamics of a perennial grass. *Nature*, 353:653–655.

Tongway, D. and Ludwig, J. (1990). Vegetation and soil patterning in semi-arid mulga lands of Eastern Australia. *Australian Journal of Ecology*, 15:23–34.

Triggs, B. (1996). *Tracks, scats and other traces: a field guide to Australian mammals.* Oxford University Press, Melbourne, Australia.

Tromble, J. M. (1983). Interception of rainfall by tarbush. *Journal of Range Management*, 36:525–526.

Turner, J. (1960). An examination of some energy and microclimate relationships in a mulga community. In *Arid zone technical conference*, volume 1, pages 7.1–7.15, Warburton, Victoria. C.S.I.R.O.

Turner, M. G. (1989). Landscape ecology: the effect of pattern on process. *Annual Review of Ecology and Systematics*, 20:171–97.

Turner, R. M., Alcorn, S. M., Olin, G., and Booth, J. A. (1966). The influence of shade, soil, and water on saguaro seedling establishment. *Botanical Gazette*, 127:95–102.

Underwood, A. (1997). *Experiments in ecology: their logical design and interpretation using analysis of variance.* Cambridge University Press, Cambridge, United Kingdom.

Valiente-Banuet, A. and Ezcurra, E. (1991). Shade as a cause of the association between the cactus *Neobuxbaumia tetetzo* and the nurse plant *Mimosa luisana* in the Tehuacan Valley, Mexico. *Journal of Ecology*, 79:961–971.

van Breeman, N. and Finzi, A. C. (1998). Plant-soil interactions: ecological aspects and evolutionary implications. *Biogeochemistry*, 42:1–19.

Venables, W. N. and Ripley, B. D. (1999a). MASS library for S-Plus. http:// www.stats.ox.ac.uk/ pub/ MASS3/ sites.html.

Venables, W. N. and Ripley, B. D. (1999b). *Modern Applied Statistics with S-PLUS.* Statistics and computing. Springer-Verlag, New York, 3rd edition.

Vetaas, O. R. (1992). Micro-site effects of trees and shrubs in dry savannas. *Journal of Vegetation Science*, 3:337–344.

Vinton, M. A. and Burke, I. C. (1995). Interactions between individual plant species and soil nutrient status in shortgrass steppe. *Ecology*, 76:1116–1133.

Vleeshouwers, L., Bouwmeester, H., and Karssen, C. (1995). Redefining seed dormancy: an attempt to integrate physiology and ecology. *Journal of Ecology*, 83:1031–1037.

Walker, L. R. and Vitousek, P. M. (1991). An invader alters germination and growth of a native dominant tree in Hawaii (USA). *Ecology*, 72:1449–1455.

Watanabe, F. and Olsen, S. (1965). Test of an ascorbic acid method for determining P in water and $NaHCO_3$ extracts from soil. *Proceedings of the Soil Science Society of America*, 29:677–678.

Watt, A. S. (1947). Pattern and process in the plant community. *Journal of Ecology*, 35:1–22.

Welsh, A., Cunningham, R., Donnelly, C., and Lindenmayer, D. (1996). Modelling the abundance of rare species: statistical methods for counts with extra zeros. *Ecological Modelling*, 88:297–308.

Weltzin, J. F. and Coughenour, M. B. (1990). Savanna tree influence on understory vegetation and soil nutrients in northwestern Kenya. *Journal of Vegetation Science*, 1:325–334.

Weltzin, J. F. and McPherson, G. R. (1999). Facilitation of conspecific seedling recruitment and shifts in temperate savanna ecotones. *Ecological Monographs*, 69:513–534.

Whitford, P. C. and Whitford, P. B. (1978). Effects of trees on ground cover in old-field succession. *American Midland Naturalist*, 99:435–443.

Whitford, W. G., Anderson, J., and Rice, P. M. (1997). Stemflow contribution to the 'fertile island' effect in creosotebush, *Larrea tridentata*. *Journal of Arid Environments*, 35:451–457.

Wilson, J. B. and Agnew, A. D. (1992). Positive-feedback swtiches in plant communities. *Advances in Ecological Research*, 23:263–336.

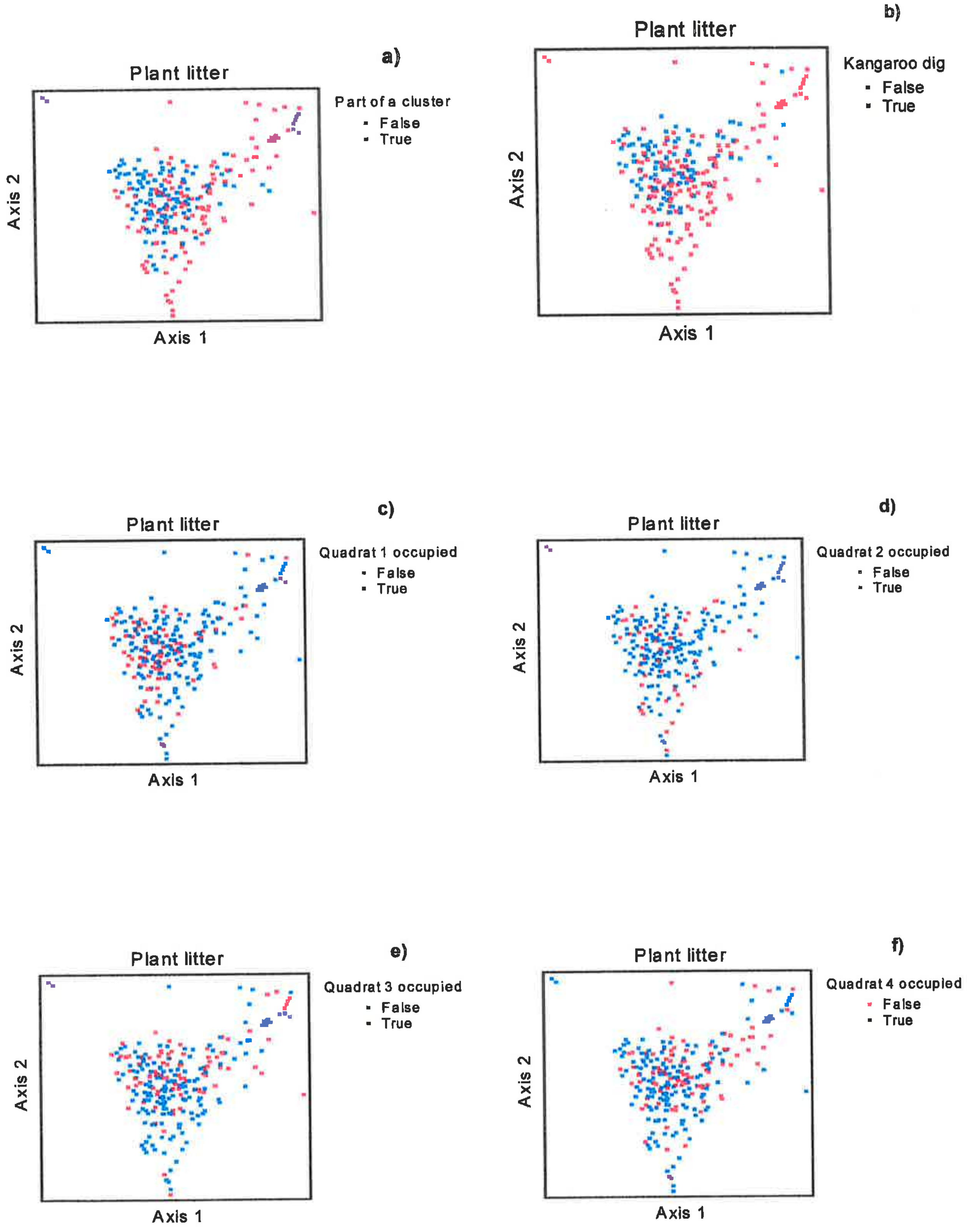
Wilson, W. G. and Nisbet, R. M. (1997). Cooperation and competition along smooth environmental gradients. *Ecology*, 78:2004–2017.

Yau, K. K. (2000). ZipmixMenu library for S-Plus. http:// www.fbstaff.cityu.edu.hk/ mskyau/ materials/ zipmix.txt.

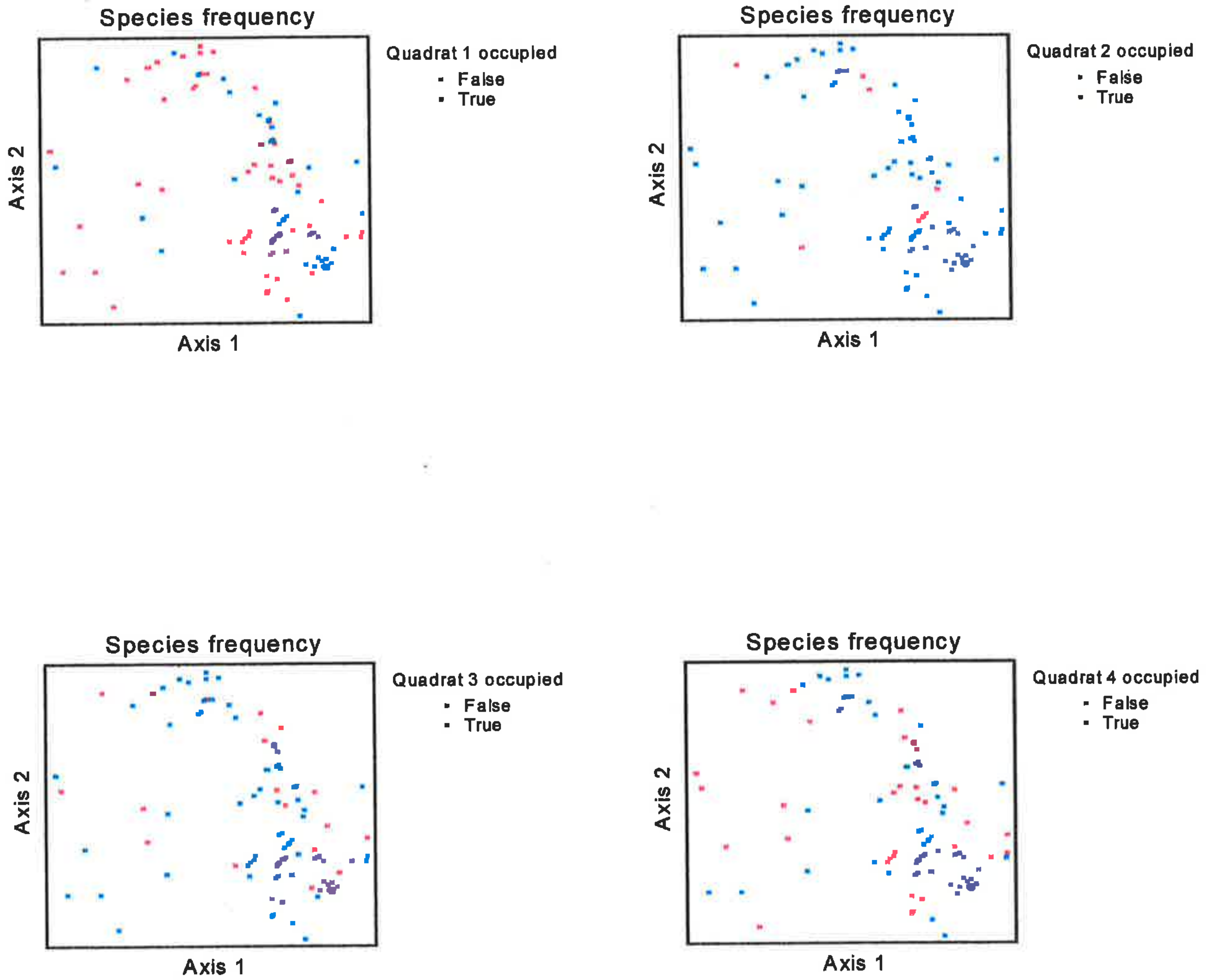
Zar, J. H. (1999). *Biostatistical analysis.* Prentice-Hall, 4th edition.

Zinke, P. J. (1962). The pattern of influence of individual forest trees on soil properties. *Ecology*, 43:130–133.

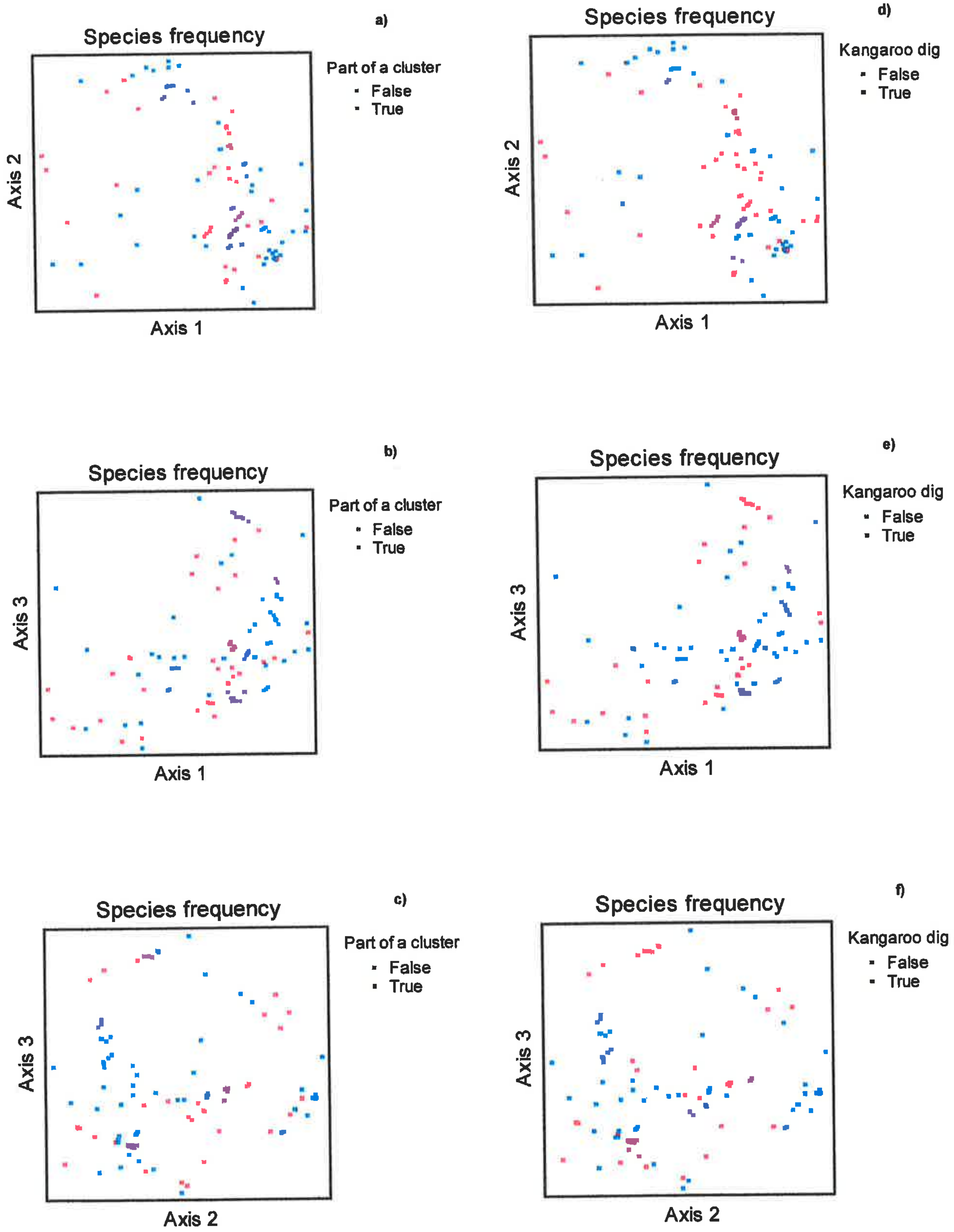
fin



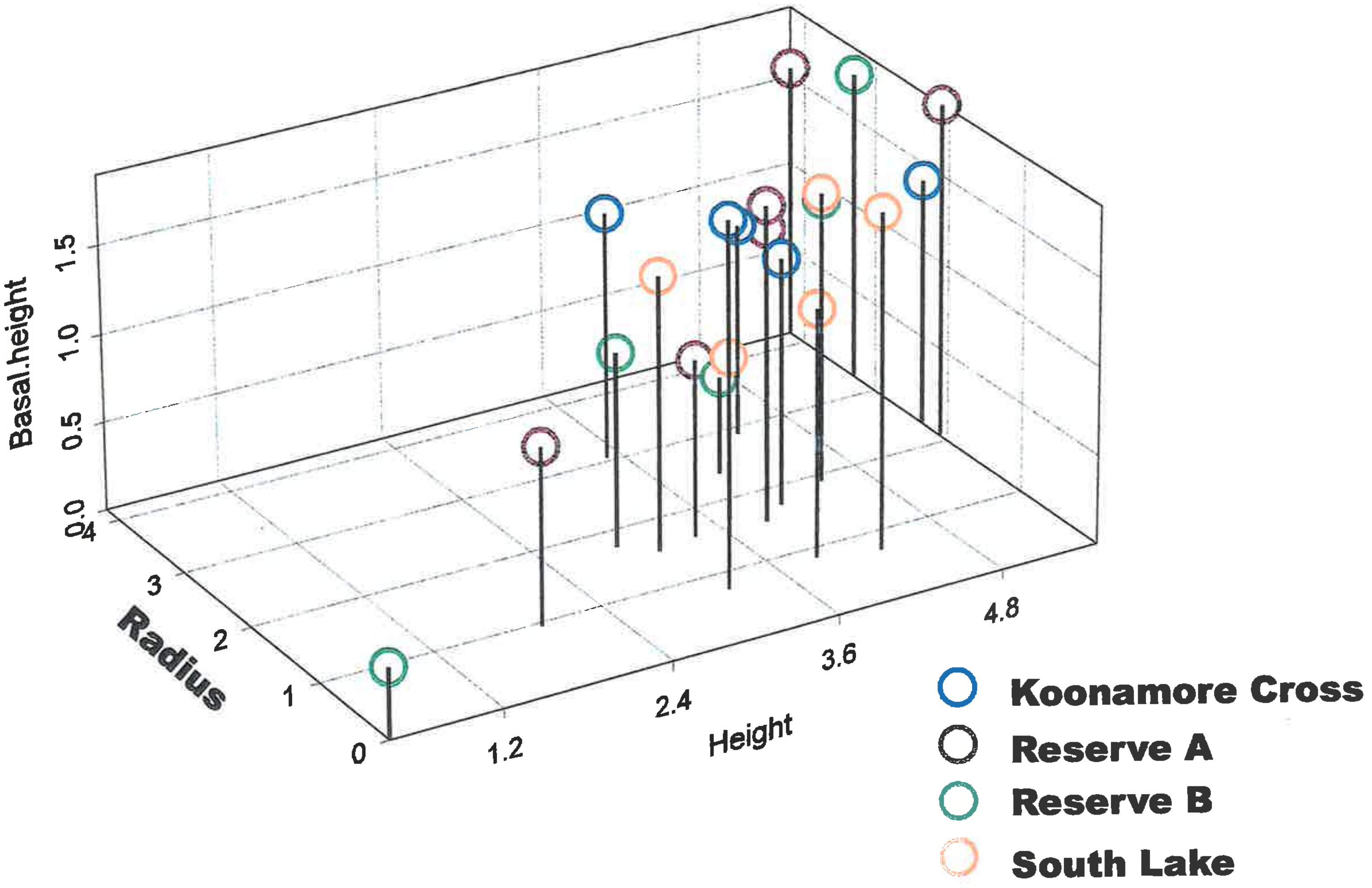
Appendix - Ordinations of plant litter samples classed by a) whether or not *Alectryon* canopies were contiguous with other tree canopies, b) absence/presence of kangaroo scrapes under the canopies, d-f) absence/presence of other trees ≥ 1.5 m high within 15 m of the trunk of the sampled tree.



Appendix - Ordination of plant species frequencies with samples classed by presence or absence of trees ≥ 1.5 m high within 15 m of the trunk of the tree being sampled. Quadrant 1 = 0 - 90° bearing, quadrant 2 = 91 -180°, quadrant 3 = 180-270°, quadrant 4 = 271-360°.



Appendix - Ordination of survey plant species frequencies around *Alectryon oleifolius* against environmental measures on three axes. a-c) samples grouped according to whether or not *Alectryon* canopies were contiguous with other tree canopies. d-f) samples grouped according to whether or not kangaroo scrapes were present under the canopies.



Appendix - Canopy dimensions of the *Alectryon oleifolius* trees sampled in the survey.