ASPECTS OF
THE AUTECOLOGY OF THE PEARL BLUEBUSH, *MAIREANA SEDIFOLIA*

by

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A thesis submitted for the degree of

Doctor of Philosophy

at

The University of Adelaide

(Faculty of Science)

June 1993

TABLE OF CONTENTS

CHAPTER 1: INTRODUCTION

CHAPTER 2: BROAD-SCALE DISTRIBUTION PATTERNS

CHAPTER 3: SPATIAL DISTRIBUTION PATTERNS AND EXISTENCE OF COMPETITION IN BLUEBUSH COMMUNITIES

CHAPTER 4: FACTORS INFLUENCING FLOWERING, FRUITING AND SEED DISPERSAL

CHAPTER 5: GERMINATION CHARACTERISTICS AND THE PROVISION OF SAFE-SITES

CHAPTER 6: PATTERNS OF SEEDLING ESTABLISHMENT, GROWTH AND SURVIVAL

CHAPTER 7: CONCLUDING DISCUSSION

SUMMARY

This study investigates aspects of the ecology of a key chenopod species of the Australian semi-arid rangelands, the pearl bluebush, *Maireana sedifolia* (F. Muell.) Paul G. Wilson. The broad-scale and small-scale distribution patterns, and the recruitment strategies of this species are examined in detail.

A broad-scale phytosociological survey, encompassing 124 sites in semi-arid South Australia and western New South Wales, was carried out to gather information on bluebush distribution, size and abundance. Environmental factors (climate, soils and topography) influencing individual shrubs were determined using generalised linear models and correlation analyses. The most significant variables were rainfall and depth to carbonate (limestone) layers in the soil. Classification analysis was used to delineate the vegetation communities in the region; bluebush was a major component in three of the five main vegetation types. Ordination techniques and multiple discriminant analyses suggested that soil water availability was the major control of vegetation in the study area.

The small-scale spatial distribution patterns of bluebush shrubs were determined from six mapped quadrats (50 x 20 m) located near Whyalla, South Australia, using Batcheler's ratios and tessellation analyses. Bluebush shrubs are predominantly regular in distribution and they commonly exhibit density-dependent growth. Neighbour manipulation trials revealed that these patterns arise primarily as a result of intraspecific competition for soil water over the summer months. However the extent of competition was variable both within and between years.

The recruitment strategies of bluebush were investigated using both laboratory-based experiments and field trials. Specific examinations of flowering/fruiting, seed dispersal by wind and ants, germination and seedling establishment were carried out. Bluebush recruitment was shown to be fundamentally controlled by the co-occurrence of episodic climatic events, with the successful progression from the production of viable seed to germination to establishment of juveniles only possible following several seasons of increased soil moisture. Further investigations demonstrated that other biotic and abiotic factors may have a minor influence of bluebush recruitment, including soil disturbance, the presence of surface litter, mature shrubs and trees, and possibly the grazing and trampling of herbivores.

Proposed strategies for the management of current bluebush populations include the minimization of adult shrub mortality and the maintenance of seedling recruitment levels by manual disturbance of the soil surface, retaining of soil mounds and opportunistic spelling of paddocks. Possible uses of bluebush in revegetation of degraded land were also discussed.

DECLARATION

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

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

Noelene Wotton

ACKNOWLEDGEMENTS

There are many people who must be thanked for their assistance and encouragement during the progress and completion of this thesis.

Firstly, I wish to thank my initial project supervisor, Dr Bob Lange, whose enthusiasm for the arid-zone originally spurned my own interests; thankyou for the ideas and discussions during the early stages of this study. Assoc. Prof. Martin Andrew, who took over supervision following Bob's retirement, must also be thanked for his tireless enthusiasm and bright ideas towards a project that he encountered midstream, and for criticisms of text. I am also grateful to Dr Russ Sinclair for his support during the later half of my doctorate, particularly in the intervening period between Bob's retirement and Martin's supervision.

I particularly wish to thank Dr Ashley Sparrow for his contribution to this thesis. I am especially grateful for his long-term assistance with experimental design and implementation, data analysis and computing, and also for the many thought-provoking ecological discussions. Criticisms of the text, although not always received with a smiling face, were also very much appreciated.

This study would not have been achievable without the interest and help of the Nicolson families of Middleback and Roopena stations over the past five years. Thank you for the ever-welcoming smiles, encouraging chats and cups of tea, and particularly for taking the time to teach a rookie some of the more important aspects of pastoralism. Thanks also for allowing me to conduct numerous experiments at many sites over your stations without complaint. Your presence made all the trips to Middleback much more enjoyable.

I would also like to thank those people who generously donated their time and equipment at various times during this study. I am especially grateful to Hugh Middlemiss from the S.A. Department of Primary Industry, Adelaide, who willingly loaned a brand new micro-meteorological station, and to Leigh Hunt, from the S.A. Department of Primary Industry, Port Augusta, for use of a portable lap-top computer. I would also like to thank Prof. Richard Jarrett, Dr Ari Verbyla and James Pearce, Department of Statistics, The University of Adelaide, for advice on statistical matters, and Dr Rob Murray and Peter Brown, from the Department of Soil Science, The University of Adelaide - Waite Campus, for soil water potential determinations. I am particularly grateful to the many friends and colleagues who accompanied me on field work, especially Ruth Grey-Smith, Ashley Sparrow, Fleur Tiver, Pam Wotton, Karen Beck, James Pearson and Kieren Peterkin. Your time and effort were very much appreciated.

I am also indebted to my friends and colleagues in the Botany Department at The University of Adelaide for their assistance over many years. Specifically, I wish to thank Marcus Brownlow for his help with computing, Fleur Tiver and Angela Renfrey for assistance with the identification of plant voucher specimens, Prof. Andrew Smith for organising the use of a computer over the last few months, Anthony Fox and Lidia Mischis for general technical help, Peter Dorsett and Cathy Hill for administrative back-up and Dr José Facelli for critically reviewing several thesis chapters. Thanks also to these people, and Andrew Rowett, Anne Rathjen and Joe Wiskich, for the numerous discussions, admittedly not always of a scientific nature, which have stimulated and amused me over the years.

Finally, and most particularly, I wish to thank my parents, Pam and Keith Wotton, and Ashley Duckett, for their interest and assistance during this erratic and rather drawn-out period of my life. The endless encouragement and support both emotionally and, at many times financially, which the three of you having so willingly given me over the years has been very much appreciated.

This study was supported by grants covering fieldwork expenses from the Mark Mitchell Research Foundation and the National Estate Grant Program of the Federal Department of the Arts, Sport, Environment and Territories, and by Commonwealth Postgraduate Research and Australian Postgraduate (Priority) Research Award living allowance scholarships from the Federal Department of Employment, Education and Training.

LIST OF ABBREVIATIONS

ANOVA	analysis of variance
C.S.I.R.O.	Commonwealth Scientific and Industrial Research Organisation
DCA	detrended correspondence analysis
GLIM	Generalised Linear Modelling (McCullagh and Nelder, 1983)
LSD	least significant difference
MDA	multiple discriminant analysis
NTP	Numerical Taxonomy Package (Belbin *et al.*, 1984)
PEG	polyethylene glycol
RWC	relative water content
SPSS-X	Statistical Package for the Social Sciences, Version 10 (SPSS Inc., 1986)
TSS	total soluble salts
UPGMA	unweighted pair-group method using arithmetic averages (Sneath and Sokal, 1973)

"The station on which I first stayed was interesting country, and visually not in the least unattractive, especially where belts of black oak (one of the Casuarinas) mingled with open bluebush plain. The bluebush is a favourite plant of mine. I love its round, almost billowing, contours, and the effect of its silver-blue foliage against the bare red."

F.N. Ratcliffe (1947)
Flying Fox and Drifting Sand: the Adventures of a Biologist in Australia
(Angus and Robertson, Sydney)

CHAPTER 1

INTRODUCTION

PROJECT BACKGROUND

AUSTRALIAN RANGELAND ECOSYSTEMS

Australia's rangelands, or pastoral lands, constitute 84% of the continent (Young *et al.*, 1984). Of these areas, approximately 70% (4.5 million km^2) lie in the semi-arid and arid zones (Paul *et al.*, 1986). Here, the rainfall is inadequate for crop production or pasture improvement, but is usually sufficient for extensive sheep and cattle grazing of the native vegetation (Bartholomaeus, 1983). Pastoralism has been carried out in Australia since early European occupation, spreading across the continent with settlement. By world standards, however, the grazing history in the arid rangelands is short, less than 150 years in most regions and only 100 years in some areas (Hill, 1986).

The dominant climatic force within the Australian arid rangelands is rainfall. This is highly variable in quantity, intensity, duration and season. Significant rainfall events do occur over all of arid Australia, although they are highly erratic. Additionally, variations in annual rainfall increase as mean annual rainfall decreases, suggesting that the driest climates also have the least predictability. In contrast, temperature regimes are essentially stable, and are of most influence when soil moisture levels are sufficient for plant growth (Harrington *et al.*, 1984a; Johns *et al.*, 1984).

The vegetation of the Australian arid rangelands is predominantly made up of sclerophyllous species, with a variety of life-forms including ephemerals, perennial herbs, shrubs and trees. These are generally adapted to utilise moisture in the soil at different depths, in different seasons and with varying speed (Harrington *et al.*, 1984a). Forty endemic genera are specific to this area, mainly from the families Chenopodiaceae, Asteraceae and Brassiceae. Common genera include *Acacia*, *Eremophila*, *Atriplex*, *Maireana*, *Triodia* and *Astrebla*. The major plant communities present can be divided into three broad categories - woodlands, shrublands and grasslands - although it is common for several structural layers to be present together. For example, shrubs and grasses often occur as understorey to low tree formations (Stanley, 1983). Detailed descriptions of the vegetation types present in the Australian arid rangelands are given in Williams (1982), Stanley (1983) and Harrington *et al.* (1984a).

MANAGEMENT PRINCIPLES

Management principles for rangelands centre on the maintenance of the natural vegetation in a form which is both productive for animals and protective of the soil resource (Harrington *et al.*, 1984b). Previously, management concentrated on the use of monitoring programs to determine the extent of vegetation change from climax following grazing (Wilson *et al.*, 1984b). Such programs were popularised because they were believed to provide a clearly defined goal (progression toward a climax community) and a measure of health (departure from climax), and allowed each rangeland area to be placed in a discrete condition class (Svejcar and Brown, 1991). Most recent rangeland management theories, however, deny the existence of stable climax status in practice, since the landscapes are subject to frequent disturbance. Instead, current views stress that an understanding of plant population dynamics and community level processes is crucial to management objectives (Westoby, 1980; Harrington *et al.*, 1984a; Archer and Tieszen, 1986; I. Noble, 1986; J. Noble, 1986; Westoby *et al.*, 1989; Call and Roundy, 1991; Provenza, 1991). As Walker (1988) states "Management must concentrate on improving the establishment of desirable species, and on knowing which growth forms will be favoured by particular climatic conditions."

Many aspects of plant dynamics play important roles in the maintenance of viable and productive plant populations. Although the emphasis is most often placed on the grazing tolerance, stress endurance and competitive effectiveness of mature plants, establishment characteristics (seed supply, germination and seedling survival) are also important (Caldwell, 1986). J. Noble (1986) suggests that plant dynamics may be most appropriately studied using demographic studies involving the measurement, description and explanation of parameters influencing plant population size (number of births, deaths, emigrants and immigrants) throughout each stage of the life-cycle of a species. Such information can then be used to describe the processes by which populations are regulated and to discriminate between those processes which are density-dependent and those which are -independent. Regardless of the methods used, all studies of rangeland plant dynamics must take into account three important features of rangeland ecosystems (I. Noble, 1986):

(i) the interactions between biotic elements are often masked by the dominant abiotic elements,
(ii) the plant responses to disturbance factors are highly variable, and
(iii) the ecosystems are dominated by the fortuitous co-occurrence of sequences of events in which each event has a low probability of occurring.

Despite the obvious relevance to management, little is known about the dynamics of many of the major plant species of the Australian arid rangelands. In the past, researchers have often assumed that Australian arid ecosystems function in a similar manner to those studied in North America; as a consequence several North American-derived theories have been applied to Australian ecosystems. Recently, however, there has been considerable debate regarding the validity of such reasoning (Westoby, 1988; Wilson, 1989; Stafford Smith and Morton, 1990). It is now believed that extrapolation is not possible because many important elements of arid Australian ecosystems are fundamentally different from those observed on other continents:

(i) ecological relationships are markedly affected by the extreme events of long, dry periods and flooding events, more so than in any other desert system,
(ii) soils are spatially highly sorted and infertile in comparison to other deserts of comparable aridity, resulting in singular assemblages of plants and animals,
(iii) life history strategies are highly variable and spatially heterogeneous, and
(iv) the dominant plants differ markedly from those of other arid regions - sclerophyllous long-lived perennials are dominant rather than succulents (Stafford Smith and Morton, 1990).

In light of the these criticisms, it is necessary that the information about plant dynamics appropriate to management programs for the Australian rangelands be acquired through studies of relevant Australian species and not through extrapolations of data collected elsewhere.

PROJECT OUTLINE

SELECTION OF STUDY SPECIES

In Australian rangeland environments, the chenopod family of plants is often a key element. Not only do these shrubs play an important role as stabilising elements within ecosystems because they are long-lived, resistant, woody perennials which survive in erratic environments, they are also noted reserve forage sources for sheep during drought. It has been noted, however, that many of these chenopod species require special management considerations (Crisp, 1978; Graetz and Wilson, 1984). Most attention is required because of the reproductive strategies of these plants; in many of the perennial species, establishment by seed is very infrequent and occurs only after favourable rainfall. Such episodic recruitment is thought to be inadequate under continuous grazing, leading Graetz and Wilson (1984) to conclude "many of the populations are relict and at risk." Furthermore, Lange *et al.* (1984) state that preservation of many of the perennial chenopod communities is particularly important because the loss of such shrubs may not be accompanied by the emergence of desirable species such as perennial grasses; instead shrub loss may lead to wind-drift of soils, the invasion of undesirable species and the loss of sustainable carrying capacity.

The subject species chosen for this project, the pearl bluebush *Maireana sedifolia* (F. Muell.) Paul G. Wilson, was selected as it is one of the least-studied chenopod species in Australia. Additionally, as it is a widespread species, the information collected may relate to the ecological processes occurring in the chenopod shrublands more generally. This species is present over much of the southern, semi-arid portion of Australia, occupying large areas of south-west New

South Wales, north-western Victoria, northern South Australia and south-eastern Western Australia (Graetz, 1973; Wilson, 1984) (Figure 1.1). It is believed to cover the largest area of any of the perennial chenopod shrubs (Leigh, 1972), and is a key element in the chenopod shrubland rangeland type which covers approximately 500,000 km^2 of inland Australia.

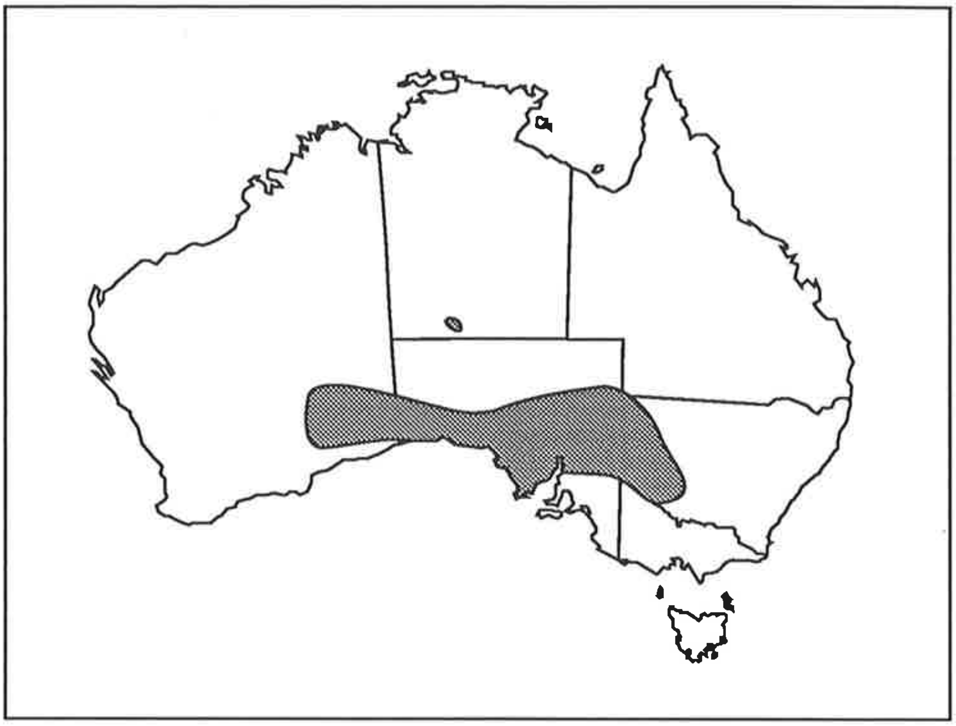

Figure 1.1: Distribution of bluebush, *Maireana sedifolia* (from Wilson, 1984).

AIMS

This study provided baseline autecological data which may be used in the development of management strategies to ensure the continued existence of bluebush populations. In addition, this research aimed to assess the potential of bluebush as a species which may be used in the rehabilitation of degraded areas.

Specific aims of this study were:

(i) To investigate the major environmental factors influencing the broad-scale distribution, size and abundance of bluebush and bluebush-dominated plant communities;

(ii) To determine the small-scale distribution patterns of bluebush shrubs within populations, and the existence and possible effects of intraspecific competition;

(iii) To examine the recruitment characteristics of bluebush including timing of flowering and fruiting, seed dispersal, germination, and seedling establishment and growth in order to identify factors which limit recruitment and methods of enhancing seedling establishment.

The assignment of studies into particular chapters is shown in Figure 1.2.

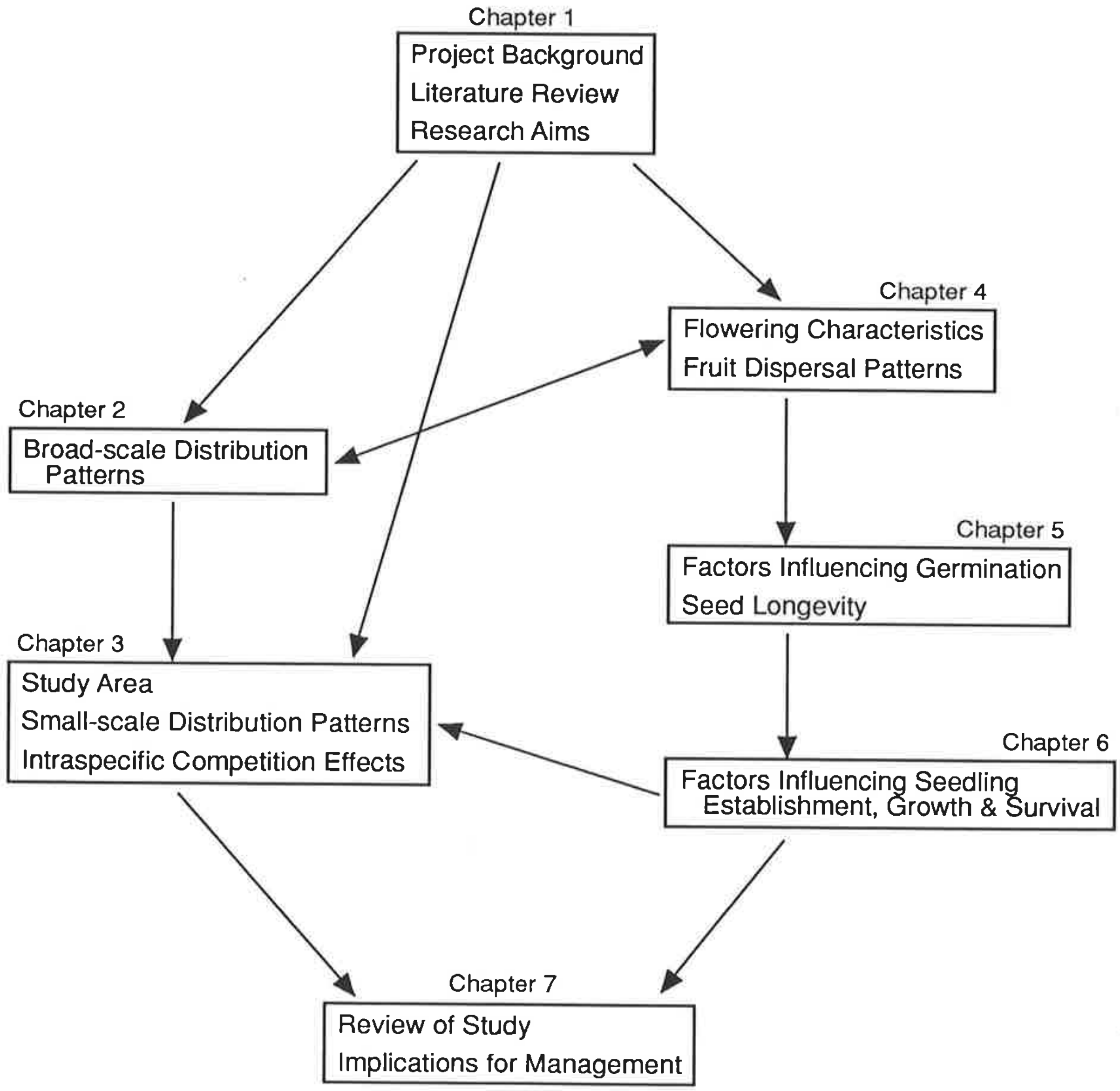

Figure 1.2: Schematic representation of the structure of this thesis.

LITERATURE REVIEW: *MAIREANA SEDIFOLIA*

TAXONOMY

Maireana sedifolia (F. Muell.) P.G. Wilson is a member of the family Chenopodiaceae. Originally known as *Kochia sedifolia*, this species was first described from a specimen collected at Wentworth on the Darling River, N.S.W. It is commonly known as bluebush or pearl bluebush, but may also be referred to as dense bluebush, pearlbush, hoary bluebush or old man bluebush (Cunningham *et al.*, 1981; Wilson, 1984; Jessop and Toelken, 1986).

M. sedifolia has in the past been confused with *Maireana astrotricha*, the low bluebush. Many older herbariums specimens have been found be *M. astrotricha* [illegible]s *M.sedifolia* (e.g. Murray, 1931), although these have since been corrected (Carrodus, 1962). *M. sedifolia* possesses stalkless leaves, flowers consistently in pairs and simple, un-branched hairs while in *M. astrotricha* the leaves are stalked, the flowers borne singly and the hairs branched or forked (Cunningham *et al.*, 1981).

PLANT MORPHOLOGY

Shrub Features

Maireana sedifolia is a perennial shrub which often reaches 1 m in height. Plants are compact and round or columnar in shape with several main woody stems (Plate 1). The leaves and young branchlets are covered by a close, bluish-grey, woolly tomentum which produces the characteristic whitish-blue appearance of this species (Osborn *et al.*, 1935; Leigh and Mulham, 1965; Leigh, 1972; Wilson, 1984). Bluebush leaves are 4-8 mm long and are alternate, fleshy and narrowly clavate (Cunningham *et al.*, 1981; Wilson, 1984). Anatomically, the leaves are succulent with an uncutinised epidermis and a ring of palisade parenchyma usually two cells thick. Large, water-storing, chloroplast-free cells dominate the central leaf tissue, along with oxalate crystals and a central, main vascular strand. The hairs covering the epidermis of the leaves are generally intertwined and contain a living basal cell with a large nucleus, a short stalk cell and a long, dead, spirally-twisted terminal cell. This latter cell possesses thick cellulose walls with no cuticle. The function of these hairs has been assumed to be water absorption, with the dead air-containing cells acting as capillary tubes which draw water into the living basal absorption cell and hence the leaf (Wood, 1923).

Root Studies

M. sedifolia is a relatively deep-rooted species. Excavations have shown that roots are spreading, extending five to six metres from the plant at a depth of 20-30 cm. In addition, secondary roots are prominent, descending to a depth of greater than 2 m from the surface[1]. Roots taper from a diameter of 2 cm at surface level to less than 1 mm at their apices (Osborn *et al.*, 1935). Carrodus (1962) suggested that bluebush roots are capable of penetrating through layers of both nodular and travertine limestone. Because of its deep roots and the ability to penetrate limestone, bluebush is thought to have access to a greater volume of soil than many other shrub species present in the semi-arid zone.

Floral Structures

M. sedifolia is a dioecious species producing pairs of flowers in leaf axils, where only one flower usually matures. Flowers are inconspicuous, with the male hemispherical in shape and the female globular (Plate 2). The fruiting perianth is more obvious, consisting of a short hemispherical to turbinate tube encircled by a horizontal wing around 10 mm in diameter. This wing ranges in colour from green to bright pink, fading to pale brown when dry. The wing is papery and glabrous with faint radial nerves and a single radial slit (Cunningham *et al.,*1981; Figure 1.3).

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[1] The root system of bluebush is similar to that of *Maireana pyramidata* (blackbush), which also has roots to a depth of 2 m (Williams, 1979). In comparison, saltbush (*Atriplex vesicaria*) roots are shallow, concentrated in the upper 25 cm (Wood, 1937; Carrodus, 1962).

Plate 1: Adult bluebush shrub (near Yunta, South Australia). Gradations on the measuring stick shown represent 20 cm in length.

Plate 2: Male bluebush plant in flower (Middleback Station, South Australia, April 1989)

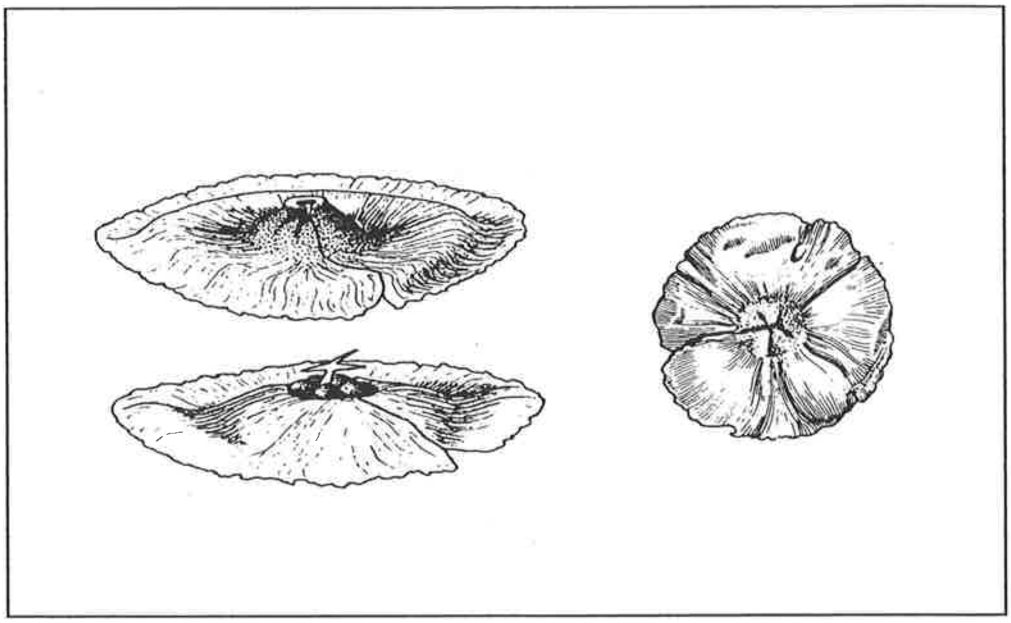

Figure 1.3: Fruiting perianth of Maireana sedifolia (Cunningham *et al.,* 1981; Jessop and Toelken, 1986).

REPRODUCTION AND PLANT GROWTH

Flowering and Fruiting

Reproductive episodes in bluebush are rare with flowering occurring very sparingly and irregularly (Osborn *et al.*, 1935; Ratcliffe, 1936; Wood, 1936; Jessup, 1951; Graetz and Wilson, 1984), leading to the description of this species as 'a very capricious seeder' (Ratcliffe, 1936; Knowles, 1951). It does not seed as heavily nor as frequently as many other Australian chenopods, particularly bladder saltbush (*Atriplex vesicaria*) and blackbush (*Maireana pyramidata*) (Burbidge, 1946; Carrodus, 1962; Leigh and Mulham, 1965). Anecdotal observations of phenology indicate that bluebush can flower at virtually any time of the year, usually following large rainfall events (Hall *et al.*, 1964; Perry, 1972). Flowering has been observed in the 'warmer months' (Burbidge, 1946; Cunningham *et al.*, 1981) and in late winter (Leigh and Mulham, 1965).

Germination and Seedling Establishment

Reports on bluebush germination in the field are very scarce. Hall *et al.* (1964) suggest that germination is possible only in environments where rainfall penetration is high, such as where surface mulch has accumulated or disturbance has occurred. This idea was supported by Butler (1985), who observed germination of bluebush during revegetation trials at Manna Hill, South Australia. He concluded that germination was possible when high levels of soil moisture, low evaporation levels and moderate relative humidities (40-70%) were present. Trumble (1954) also reported high levels of bluebush germination after rain, in areas subjected to heavy grazing. Further evidence suggests that most of this germination occurred beneath existing bluebushes (Burbidge *unpubl.*, in Crisp, 1978). Laboratory studies have shown germination to be rapid and usually complete within 3 days. It occurs over a wide range of temperatures (6.0-36.0°C) and soil saturation levels (20-100%) (Burbidge, 1946).

Successful bluebush establishment occurs infrequently, with the necessary conditions estimated to occur once every 25 years (Wilson *et al.*, 1984a) to 50 years (Graetz and Wilson, 1984). The establishment of bluebush requires a sequence of years of good rainfall and is more likely in areas where the soil has been disturbed leading to increased rainfall infiltration and decreased root competition from other plants. At the T.G.B. Osborn Vegetation Reserve at Koonamore, South Australia, seedlings were recorded only seven times in 35 years, and of these none survived for more than 2 years. It is believed that most bluebush seedlings perish due to insufficient moisture (Hall *et al.*, 1964; Perry, 1972). It is interesting to note that the only successful seedling establishment events which have been documented for bluebush are for re-vegetation trials which have been carried out using mechanical disturbance (Butler, 1985).

Growth Rate

Bluebush is a long-lived plant with an estimated half-life of 150-300 years (Crisp, 1978). In comparison, saltbush has an estimated lifespan of approximately 30 years. Overall growth rates are slow. At the Koonamore Vegetation Reserve, plants that ranged in height from 30-40 cm in 1931 had reached heights of between 55 and 107 cm in 1964 (Hall *et al.*, 1964). It was first suggested that leaf growth in bluebush occurs mainly in the warmer months after periods of effective rainfall, although it was stated that individuals retained the ability to grow at any time of the year following sufficient rain (Leigh and Mulham, 1965). Noble (1977), however, was able to show a long carry-over effect of past rainfall events, by using rainfall response data to calculate that bluebush biomass is best correlated with amount of rainfall received in the previous 24 months.

Drought Tolerance

Bluebush is believed to be an extremely drought-tolerant species. It is capable of utilizing water stored deep in the soil profile via its long tap-roots and has the capability of producing shallow, deciduous feeding roots in times of sufficient water (Leigh and Mulham, 1965). It is said to possess an "efficient water use system" which it can maintain for long periods of time under drought conditions (Williams, 1979). This "even" growth pattern enables bluebush to retain its leaves during drought (Jessup, 1951; Carrodus, 1962; Carrodus and Specht, 1965), an advantage which is only lost when very light rains fall and water infiltration is restricted to surface layers (Wood, 1936). Gates and Muirhead (1967) have reported the ability of *Maireana* species to remain "leafy and viable under high radiation and temperature levels during drought conditions."

Bluebush has also been observed to survive longer periods of drought by defoliation (Hall *et al.*, 1964). Crisp (1978) observed that this defoliation generally does not kill the plant, as the rootstock will readily produce new roots and shoots when the stress is relieved. Chenopod sensitivity to defoliation was recently examined by Crisp (1978) and Graetz and Wilson (1984) who clearly indicated that sensitivity was linked to life expectancy. Bluebush is the least sensitive to defoliation of the listed chenopods and also the longest lived (Table 1.1).

Table 1.1: Sensitivity of several major perennial chenopod species to defoliation (from Graetz and Wilson, 1984).

SPECIES	DEFOLIATION SENSITIVITY	LONGEVITY
A. vesicaria	most sensitive	short lived (10 years)
M. aphylla	↑	↓
M. astrotricha		
M. pyramidata		
M. sedifolia	least sensitive	long lived (150+ years)

Response to Grazing

Early studies examining the effects of grazing on bluebush indicated that bluebush was a robust plant which can withstand high levels of grazing because of its ability to resprout from the base (Ratcliffe, 1936). More recent studies, however, have shown that bluebush populations do decline under heavy grazing, and may be replaced by blackbush or, in more extreme circumstances, by perennial herbs such as *Sclerolaena obliquicuspis* and *Dissocarpus paradoxa* (Crocker and Skewes, 1941; Beadle, 1948; Jessup, 1951; Wilson *et al.*, 1984a). Thus, it has been suggested that bluebush is a decreaser species that can be used as an indicator, where its loss from a pasture indicates poor range condition and a history of heavy grazing (Wilcox and Morrissey, 1980). Crisp (1978) found that grazing affected bluebush survival, and suggested that the natural rate of bluebush decline may be accelerated up to six times under heavy stocking.

In contrast, Trumble (1954) observed an increase in bluebush density with very heavy grazing in a series of experiments carried out at Yudnapinna Station, S.A. Shrubs were shown to possess increased vigour as a result of an inferred increased rate of turnover of the limited nutrient pool and extremely good rains. This cannot be considered as evidence supporting heavy stocking of bluebush, however, as this enhanced growth effect is likely to continue for only a short time, after which the accelerated erosion resulting from heavy grazing would have depleted the system of its labile nutrients and severely reduced the likelihood of self-regeneration (Crisp, 1978). As Barker (1972) pointed out, perennial species are slow to react to environmental modification and any changes which do take place are likely to occur over a long period of time and be irreparable.

Forage Value for Stock

The perennial chenopod shrubs, including bluebush, are important sources of forage for sheep, particularly when herbage layers are depleted or are absent (Graetz and Wilson, 1984). All the major shrub species are readily grazed despite strong palatability preferences. Preference is usually observed in the following order; annual herbage, perennial grasses, saltbush, low bluebush bluebush and blackbush, although seasonal conditions, water quality and the vegetation present may have a minor influence (Ratcliffe, 1936; Eldridge, 1985).

These shrub species are, however, most valuable during drought. Unlike herbage plants, crude protein and digestibility of chenopod shrubs remains constant through-out the year, maintaining higher values than those found for dry herbage. At these times, protein levels are high enough to provide a maintenance diet, although stock must drink extra water to allow for salt excretion (Eldridge, 1985). Comparisons between species show that protein levels in bluebush are higher than that found for bladder saltbush and blackbush (Graetz and Wilson, 1984; Table 1.2).

Table 1.2: Mean values for sodium, potassium, chloride and crude protein and dry matter digestibility for four perennial chenopod species (expressed as % dry weight) (from Graetz and Wilson, 1984).

SPECIES	SODIUM	POTASSIUM	CHLORIDE	PROTEIN	DIGESTIBILITY
A. nummularia	6	3	11	20	71
A. vesicaria	5	4	9	15	53
M. pyramidata	7	2	3	15	58
M. sedifolia	-	-	-	17	-

DISTRIBUTION PATTERNS

Climate

Bluebush is restricted to the southern part of the Australian arid/semi-arid rangeland zone extending from 26-27° to 35-36° S, in areas receiving 125-300 mm of median annual rainfall predominantly during the winter (Hall *et al.*, 1964). Hall *et al.* (1964) also believed temperature to be an important factor influencing the distribution of bluebush, with this species being present in areas where the mean monthly maximum temperature is up to 21-22°C. No other studies have confirmed these speculations.

Soils

There are many references to the distinctive soil types on which bluebush has been observed (Adamson and Osborn, 1922; Murray, 1931; Prescott, 1931; Crocker and Skewes, 1941; Crocker, 1946; Beadle, 1948; Jessup, 1948; Jessup, 1951; Carrodus, 1962; Carrodus and Specht, 1965; Johnson and Baird, 1970; Specht, 1972; Beard, 1975). Generally, it is restricted to red-brown desert soils which are sandy or loamy in texture, and often highly calcareous with travertine (sheet) limestone or calcrete nodules at a depth of 60cm or less (Osborn and Wood, 1923; Prescott, 1931; Osborn *et al.*, 1935; Beadle, 1948; Cunningham *et al.*, 1981). Bluebush usually dominates the vegetation if limestone is present within 60cm of the soil surface, and may form pure stands if limestone is within 30cm (Beadle, 1948). As a result of these observations, bluebush has been described as a 'calcicolous' species and an indicator of alkaline and light-textured soils (Osborn *et al.*, 1935; Beadle, 1948). Carrodus (1962), however, disagrees with these descriptions and reports that the presence of calcareous horizons is not a consistent feature of bluebush soils in the Riverina region, N.S.W. Instead, it was suggested that more appropriate factors which could used to separate perennial *Maireana* from *Atriplex* soils were light surface texture, low surface salinity and deep wetting profile.

Bluebush may be more-or-less replaced by saltbush and low bluebush on the less calcareous desert soils, by blackbush on sandier soils and by *Stipa/Danthonia* grass communities in gilgais (depressions) (Murray, 1931; Crocker and Skewes, 1941; Jessup, 1948; Johnson and Baird, 1970).

Community Studies

Across southern Australia, bluebush community structure varies significantly. Bluebush occurs either in monospecific stands, in association with saltbush, blackbush or low bluebush, or as an understorey to sparse woodland (Leigh, 1972; Figure 1.4).

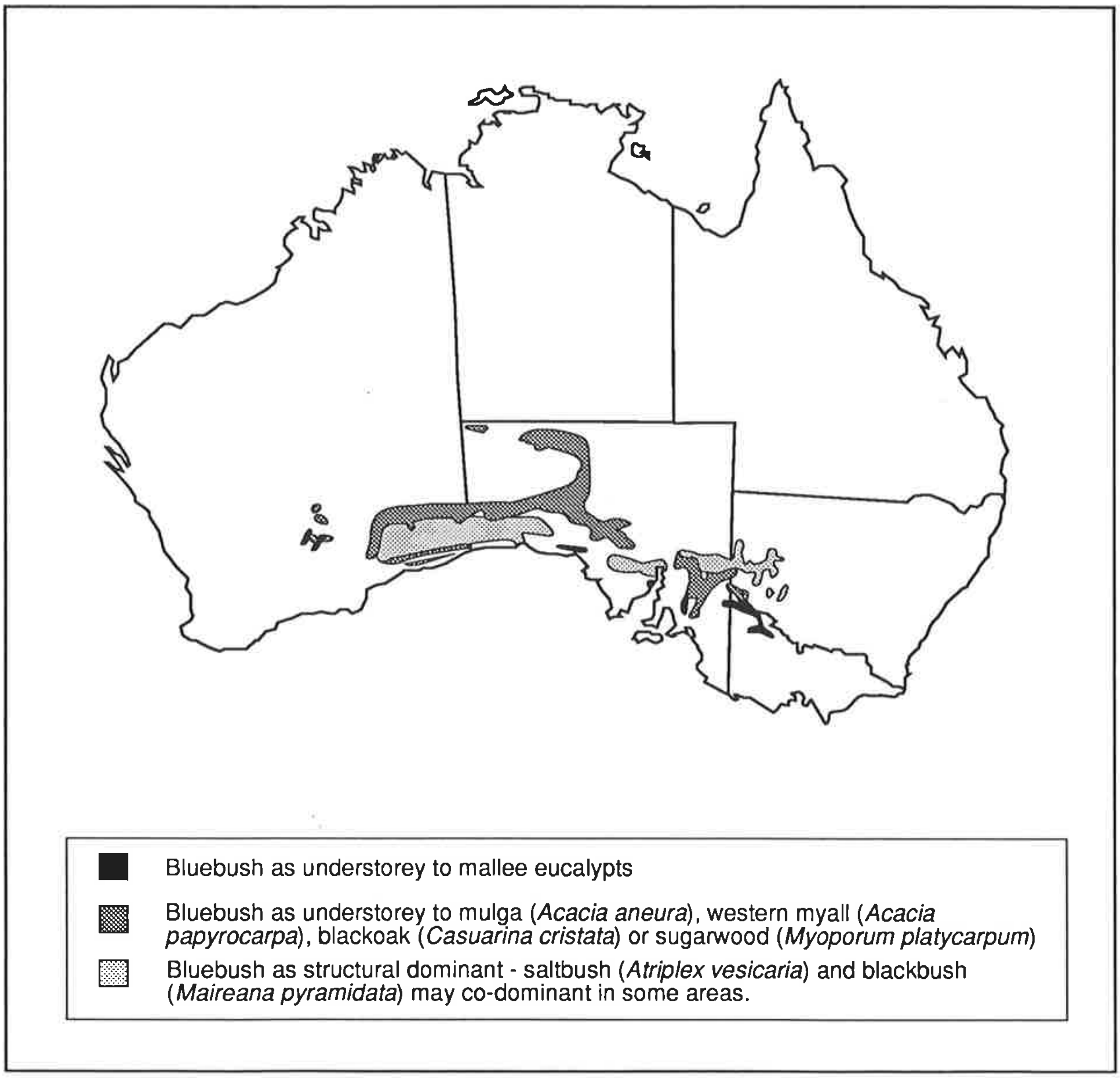

Figure 1.4: Distribution of the major bluebush community types. This composite map is derived from studies by Adamson and Osborn (1922), Osborn and Wood (1923), Collins (1923), Murray (1931), Crocker and Skewes (1941), Crocker (1946), Beadle (1948), Jessup (1948), Jessup (1951), Johnson and Baird (1970) and Specht (1972). This is a more detailed map than Figure 1.1.

In the western portion of its distribution, the higher levels of the Nullarbor Plain carry bluebush as the dominant and almost only perennial shrub species, covering a much greater area than saltbush (Adamson and Osborn, 1922; Johnson and Baird, 1970). To the east of the Nullarbor Plain, bluebush occurs by itself, or as an understorey to mulga (*Acacia aneura*) or western myall (*Acacia papyrocarpa*), or in shrub steppe communities with saltbush/low bluebush or *Maireana triptera/Ptilotus obovatus* (Jessup, 1951). Bluebush is also the abundant, characteristic lower stratum shrub of the extensive western myall/*Myoporum platycarpum* association described on Yudnapinna Station (Crocker and Skewes, 1941). Murray (1931), in her description of the vegetation of the Lake Torrens Plateau, observed bluebush either together with the dominant saltbush, or on the more stable sandhill slopes as part of the mulga scrub association.

Further east, in the mid-north of South Australia, Jessup (1948) reported bluebush in the more northern parts of the study area and as far south as Blanchetown and Swan Reach, where there is a noticeable transition from bluebush to saltbush-dominant communities. In this area, bluebush was the dominant, almost monospecific understorey shrub in the sugarwood (*Myoporum platycarpum*) association and on the more calcareous soils of the black oak (*Casuarina cristata*) communities, and was also encountered more rarely as an understorey species in the *Eucalyptus oleosa/E. brachycalyx* and *E.oleosa/E.gracilis* mallee[1] associations. Osborn and Skewes (1923) described bluebush distribution patterns as "extensively developed" in the Murray Basin, growing with both saltbush and bitter saltbush (*Atriplex stipitata*) under mallee and sugarwood.

In western New South Wales, on the eastern edge of its distribution, observations have been carried out by Collins (1923) and Beadle (1948). In the northern areas of this region, along the Barrier Range, bluebush was reported along the rocky hills and slopes, where it was found in association with blackbush, *Eucalyptus gillii*, *Maireana brevifolia*, *M. villosa*, *Sclerolaena*

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[1] Vegetation formations dominated by multi-stemmed species of *Eucalyptus* (Noble, 1989).

diacantha and *Dissocarpus paradoxa*. It was also described as part of the flora on the surrounding plains, together with saltbush (which was generally co-dominant), blackbush and *Maireana aphylla*. Beadle (1948) also reported bluebush, as well as blackbush, as the understorey in open bull-mallee (*E. oleosa/ E. gracilis/ E.viridis/ E. dumosa*), and abundant in certain areas of the black oak/bullock bush (*Heterodendrum oleifolium*) and mulga associations. Three major types of bluebush association were described including; blackbush/bluebush, bluebush, and bluebush/saltbush in addition to the two blackbush associations; blackbush, and low bluebush/blackbush.

CHAPTER 2

BROAD-SCALE DISTRIBUTION PATTERNS

INTRODUCTION

BACKGROUND

The distribution of all plant species is geographically limited by particular individual environmental constraints on plant establishment and growth. Grime (1977) proposes that the factors which limit plant biomass can be divided into two categories; stress (encompassing shortages and excesses of light, water and nutrients, and temperature extremes) and disturbance (such as herbivory, fire, trampling and pathogens). In semi-arid and arid regions, plant distribution patterns are generally a response to water availability. Many studies have been carried out, particularly in North America, to show this influence on species distribution; competition for soil water occurs both at an intraspecific and interspecific level (Woodell *et al.*, 1969; Fonteyn and Mahall, 1981; Robberecht *et al.*, 1983; Manning and Barbour, 1988).

The species of the Chenopodiaceae occupy a great range of habitats in Australia, which Graetz and Wilson (1984) proposed is due to wide, radiative evolution. It has been suggested that these species are sorted into communities primarily on the basis of edaphic factors and only secondarily by climate, and furthermore, that it is the soil factors that determine plant/water regimes (such as depth of wetting, salinity and texture) that effect species distribution rather than chemical characteristics of soils such as nutrients (Noy-Meir, 1974; Eldridge, 1988).

Only a few studies have been conducted to examine the distribution patterns and environmental requirements of Australian chenopods at an individual species level (Carrodus, 1962; Parr-Smith and Calder, 1979; Williams, 1979). Of these studies, Williams (1979) provides an excellent comparative study relating the ecology of two important perennial species, saltbush (*A. vesicaria*) and blackbush (*M. pyramidata*). While this study is of intrinsic value, it is more broadly useful as it demonstrates how closely-related species dominating structurally-similar vegetation may have very different strategies for reproduction, growth and survival which combine to set distributional limits. As such, it shows how difficult and potentially inaccurate it may be to generalise the information we currently have in this area, and also stresses the need for more species-specific data.

Previous studies suggest that the distribution of bluebush cannot be directly attributed to rainfall or other climatic features. Evidence from community-based studies implies that soil features, particularly texture and the presence of limestone, may define the potential niche of this species (Osborn *et al.*, 1935; Ratcliffe, 1936; Crocker and Skewes, 1941; Crocker, 1946; Beadle, 1948; Hall *et al.*, 1964). Similarly, Carrodus (1962) and Carrodus and Specht (1965), in examinations of the factors influencing the relative distributions of bluebush and saltbush, proposed that bluebush was dominant on deeper soils which wet down to depths, because of its extensive and deep root system.

AIMS

Existing information on bluebush distribution is generally anecdotal and is comprised of community-based field observations. There have been no investigations that have been undertaken using systematic sampling or statistical analysis. In addition, little information has been gathered on the variation in plant size and abundance across the species geographic range, and the possible influence of environmental factors on these plant measures.

As a background to the work on life-cycle characteristics of bluebush, which is described in subsequent chapters, a generalised phytosociological survey was undertaken to gather information on bluebush distribution and broad-scale ecological characteristics with specific aims as follows:

(i) To confirm the previously-published distribution patterns of bluebush;

(ii) To identify the environmental variables which potentially influence the distribution of bluebush;

(iii) To determine the extent of variation in bluebush size and abundance over the geographical range of this species and possible environmental determinants for this variation; and

(iv) To identify the vegetation communities in which bluebush occurs and suggest the environmental factors which limit the distribution of these community types.

SAMPLING METHODS

LOCATION OF SITES

Survey Area

In order to develop sound conclusions regarding the factors influencing bluebush patterns, it was necessary to cover a major portion of the known distribution of this species and surrounding areas. Although the distribution of bluebush extends east-west from Wilcannia, N.S.W., to Kalgoorlie, W. A., field work was restricted to the semi-arid regions of South Australia, Victoria and New South Wales. Sampling was not undertaken in far western South Australia and Western Australia due to constraints of time and funding, and also inaccessibility. Given that the eastern half of the range of bluebush includes a large variation in soils, topography and climate, it was decided that sufficient evidence would be gathered to make a good assessment of vegetation community structure and environmental influences.

Sampling Strategy

Choice of a survey approach is governed to a considerable degree by availability of field time and accessibility within the proposed study area (Greig-Smith, 1983). This latter factor was of particular importance in this study, since station tracks form the only access routes to many areas in this region and are generally unreliable and poorly marked. A regular sampling strategy, restricted to all-weather, easily-traversed access routes, was chosen. This approach minimised travelling time between sites, thereby allowing a large area to be covered. In most cases, sites were located 30 km apart (determined by vehicle odometer). Additional sites were included in some areas to encompass obvious changes in vegetation or environmental features such as soils and topography, while the position of some sites was altered to avoid townships or other disturbances such as vegetation clearance, quarrying, roads and over-grazed areas.

Sampling was concentrated in four main regions, encompassing most of the eastern half of the distribution of bluebush (Figure 2.1):

(i) *North-West* - North of Port Augusta along the Stuart Highway until approximately 80 kilometres south of Coober Pedy, west along the Trans-Australian Railway to Tarcoola, south of Kingoonya and north of Woomera ;

(ii) *Flinders Ranges* - The eastern and western flanks of the Flinders, and across the top of the Ranges from south of Balcanoona to Copley;

(iii) *Eyre Peninsula* - South from Port Augusta to Kimba on north-eastern Eyre Peninsula, from Arno Bay north to Port Augusta along the coast, and in the North Middleback Ranges; and

(iv) *North-east South Australia/Western N.S.W.* - Parallel to the Murray River from Mannum to Mildura, north to Broken Hill and the Barrier Range, and along the Barrier Highway to Peterborough and the eastern flank of the northern Mount Lofty Ranges.

Overall, there was a total of 124 sites, along approximately 3800 km of road transect.

Positioning of Quadrats

A 50 m by 20 m (0.1 ha) sampling quadrat was placed with its long axis perpendicular to the road and its nearest side at least 25 m from the road or other disturbance features (such as fence-lines, vehicle tracks etc.). On a few occasions, when the `natural' vegetation present was restricted to roadside verges, the quadrat was placed parallel to the road and was replaced by a longer but thinner quadrat (e.g.100 m by 10 m).

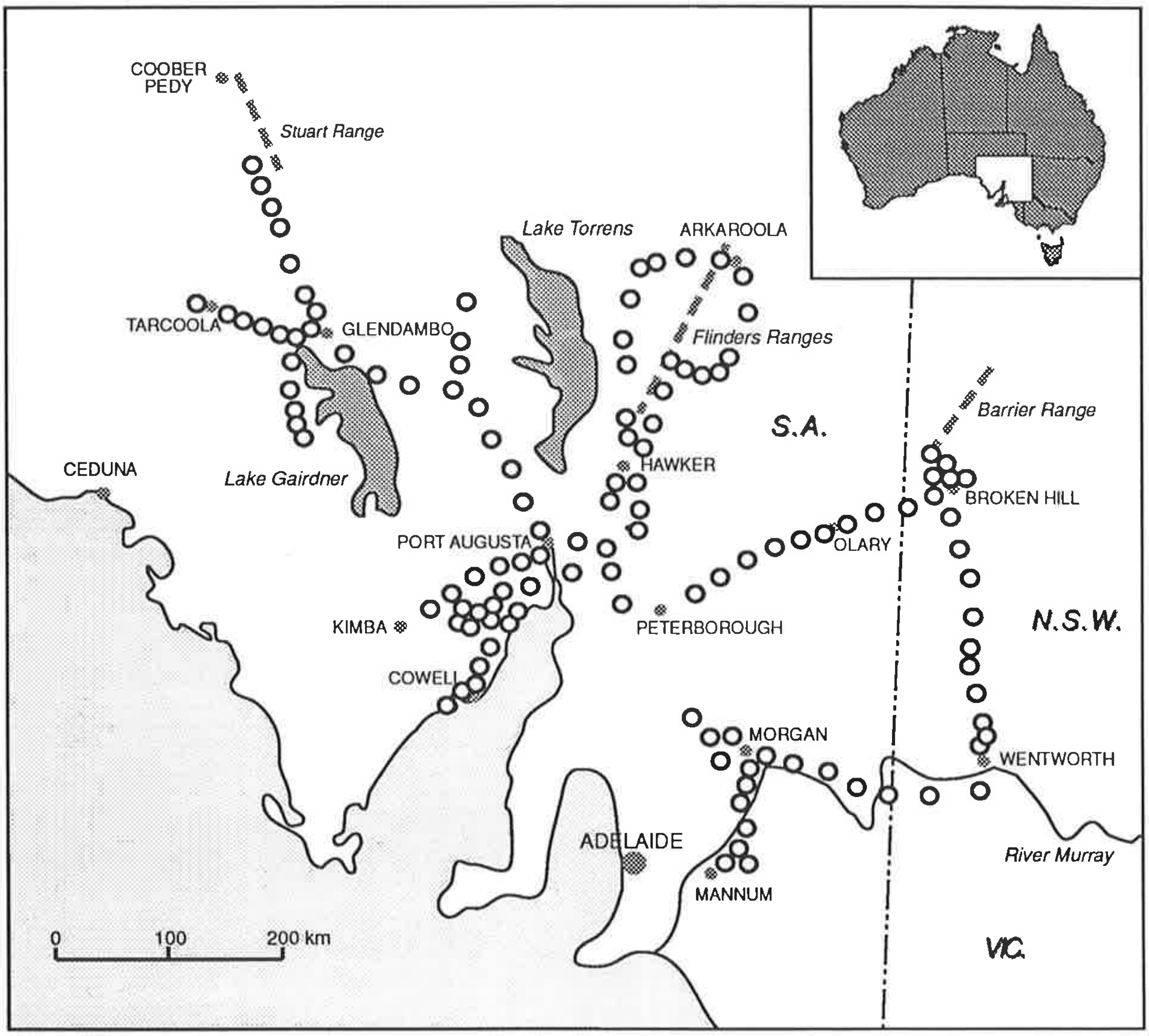

Figure 2.1: Location of the 124 sampling sites (as indicated by open circles) for the broad-scale survey. See text for a summary of the vegetation and environmental information collected at each of these sites.

COLLECTION OF VEGETATION DATA

Field Recordings

General Vegetation Data

At each sampling site, the presence of all perennial species (both native and non-native) was recorded. Some annual species, whose above-ground parts persist in a readily identifiable form after death, such as Wards weed (*Carrichtera annua*) and some grasses, were also recorded. Voucher specimens of species which could not be accurately identified in the field were taken for later examination.

As a quick measure of relative abundance, the projected foliage cover of each species was estimated using a derivation of the Hult-Sernander scale (Table 2.1; from Tiver *et al.*, 1989 after Hult, 1881; see Becking, 1957). This scale, a nearly-logarithmic semi-quantitative cover abundance series, was used in preference to other scales (e.g. Braun-Blanquet, 1932) because of its robustness, ease of use in sparse semi-arid vegetation and comparability with other similar studies in adjoining regions (*e.g.* Hawke, 1986; Sparrow, 1991; Tiver *et al.*, 1989).

Table 2.1: Cover score scale used for visual estimation of projected foliage cover (from Tiver *et al.*, 1989 after Hult, 1881).

COVER SCORE	PROJECTED FOLIAGE COVER %
1	0 - 1
2	1 - 2
3	2 - 5
4	5 - 10
5	10 - 25
6	25 - 50
7	50 - 100

Bluebush Measurements

Further to the species composition information collected, bluebush density and size measurements were made when this species was present. Six 5 m by 10 m sub-quadrats were placed mid-way along the quadrat and the number of bluebush shrubs rooted within each sub-quadrat was recorded (Figure 2.2). Plant size was scored for a maximum of thirty shrubs per site, beginning with those encountered during the density counts. If thirty plants were not present in the six sub-quadrats, plants in the main quadrat (up to thirty) were included in arbitary order of encounter. If the total number of plants within the 50 m by 20 m quadrat was less than thirty, no further plants were measured. The dimensions of these plants were recorded in terms of canopy height, length (longest horizontal axis through canopy) and width (at right angles to the length axis). The presence and height of mounds of soil around the bluebushes was recorded. The number of bluebush seedlings present at each site was noted. Information was gathered on the location of the seedlings relative to trees and open spaces, in addition to their position under live and dead shrubs.

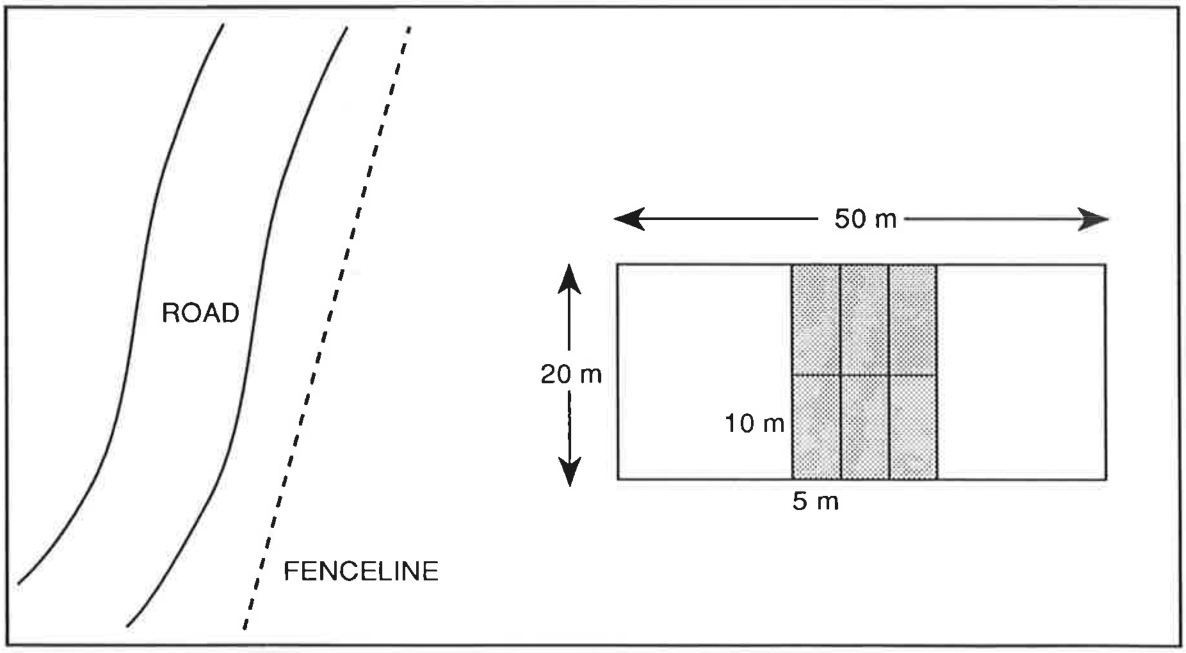

Figure 2.2: Location of the 50 x 20 m quadrat at each of the selected survey sites. The position of the 10 X 5 m sub-quadrats within the main quadrat are also shown.

Laboratory Studies

Voucher specimens were primarily identified using Jessop and Toelken (1986), Cunningham *et al.* (1981), Whibley (1980), Boomsma (1981) and Brooker and Kleinig (1983). A. Renfrey (Botany Department, The University of Adelaide) assisted with the grass identification whilst many other specimens were checked using herbarium specimens of F. Tiver (Botany Department, The University of Adelaide). Jessop and Toelken (1986) was used for standard taxonomic nomenclature.

Some taxonomic groups presented difficulties in identification, both in the field and the laboratory, and were not split into separate taxa. These include *Abutilon octocarpum/ calliphyllum* and *Hakea eyreana/ednieana.* The grasses also proved difficult to identify due to incomplete floral parts. Identification to genus level only was possible for *Aristida, Enneapogon* and *Eragrostis.* All species of *Stipa* were grouped into a single taxon except for *Stipa elegantissima* which was readily identifiable in the field. Two species of samphire, while not identifiable to species level, were clearly different and were assigned to separate taxa. A complete species list is given in Appendix 1.

COLLECTION OF ABIOTIC ENVIRONMENTAL DATA

Field Studies

Field notes were made on soil surface features, particularly the presence of exposed rock, pebbles and/or a lichen crust. Evidence of disturbance such as fence-lines, heavy grazing and vehicular tracks was also noted. Soil hardness was determined using a `falling-weight' penetrometer set at a height of 20 cm and carrying a weight of 2295 g. The number of `drops' required to achieve penetration of the soil surface to a depth of 5, 10 and 20 cm was recorded at five different locations within the quadrat. Topography at each site was recorded as one of seven units, along a scale of approximately increasing topography (Table 2.2). The slope of the quadrat was determined to the nearest $^1/_3$ of a degree using an inclinometer and a standard measuring stick, while aspect (to the nearest degree) was also measured. In the centre of each quadrat a soil core was dug using a 4 inch diameter Jarrett auger. The soil profile was recorded including a measurement of the depth to rock or limestone (up to 70 cm). A soil sample was taken from a depth of 25 cm for later analysis. Where soils were less than 25 cm deep, samples were taken from the maximum depth.

Table 2.2: Topographic units used for the description of land-form pattern at all sites.

UNIT NO.	TOPOGRAPHIC UNIT DESCRIPTION
1	Plain
2	Undulating Plain
3	Interdunal Swale, Creekline
4	Dune
5	Hillside (Slope >1.5° and <20°)
6	Hilltop
7	Steep Hill (Slope>20°), Range Summit

Laboratory Analysis

Soil Analysis

Each of the soil samples were subsequently analysed for the following physical and chemical features:

(i) Colour - moist soil, using Munsell Soil Colour Charts;

(ii) Texture - By the simple method of Northcote (1979). As in Sparrow (1991), textures were ranked on an ordinal scale from 1 to 6 according to the percentage of clay in the soil (as determined by Thompson, 1952; Table 2.3);

(iii) pH - Determined using a 1:5 v/v dry, crushed soil and distilled water suspension mixture which was constantly stirred using a vortex mixer. A Beckman H5 pH meter was used for measurements;

(iv) Total Soluble Salts (TSS) - Measured using the same suspension. A Hanna H18033 conductivity meter calibrated for ambient temperature was used to measure conductivity. Values were then converted to TSS using a standard curve constructed from KCl solutions of known concentration;

(v) *Presence of Carbonates* - Tested by reaction to 0.1N HCl (presence of $CO_3^{=}$ leads to a reaction where gaseous CO_2 is given off visibly). Three results were possible: no reaction, weak reaction and strong reaction; and

(vi) *Soil Wettability* - Sparrow (1991) first described this binary term, defined as the ability of a drop of water to `bead' on the surface of dry and lightly crushed soil.

Table 2.3: Soil texture scale based on clay content (derived from Thompson, 1952 and Northcote, 1979; after Sparrow, 1991).

TEXTURE CLASS	SCORE	MEDIAL % CLAY
Loamy Sand	1	5 - 10
Sandy Loam	2	10 - 15
Loam	3	15 - 20
Silt Loam	4	10 - 20
Sandy Clay Loam	5	25 - 30
Clay Loam	6	35

Climate Data

Rainfall was the only climatic variable considered. Other factors such as temperature and humidity could not be included due to the sparsity of recording stations monitoring these variables in the study area. As several rainfall variables, including seasonality, were considered to be potentially useful, published maps of mean annual rainfall were not used to determine the rainfall regime at each site. Instead, rainfall variables were estimated using collated monthly rainfall records for all towns and pastoral properties within 50 km of study sites for the period 1839-1983 inclusive (Bureau of Meterology, Adelaide, 1984). Rainfall values at each sampling site were estimated using a proportional averaging of values for surrounding rainfall recording stations. Only stations with at least 30 years of continuous recordings were considered in the calculations. Topographic (orographic) influences on rainfall were also incorporated in this procedure and were subjectively considered in estimates. Values were obtained for mean and median annual rainfall, as well as mean winter (April to September) and mean summer (October to March) rainfall. These latter two were included to examine possible seasonal influences. The mean number of rain-days were also calculated for each site on annual, summer and winter bases.

Other Data

The location of each of the sampling sites was determined using 1:250,000 topographic survey maps of the study region (National Mapping Division, Canberra). From these, three variables were estimated; latitude and longitude (Universal Map Grid Northing and Easting) and mean height above sea level (to nearest 10 m).

DATA COLLATION

Following these field and laboratory measurements, data for each of the sampling sites was collated. A complete list of environmental variables considered is given in Table 2.4. The data were stored as three separate matrices; sites by species, sites by environmental variables and sites by bluebush characteristics.

Table 2.4: Environmental variables collected for each of the survey sites. The codes used as abbreviations for these variables in later diagrams is also listed along with the variable type.

VARIABLE	CODE	VARIABLE TYPE
Latitude (U.M.G. Northing)	LAT	Continuous
Longitude (U.M.G. Easting)	LONG	Continuous
Elevation	EL	Continuous
Slope	SL	Continuous
Aspect	A	Circular Continuous
Topography	TOP	Ordinal (7 Classes)
Exposed Rock at Surface	XR	Binary
Litter on Surface	LIT	Binary
Lichen Crust	LICH	Binary
Calcium Carbonate Pebbles	CAPEB	Binary
Other Pebbles	OPEB	Binary
Penetrometer Reading - 5 cm	P5	Continuous
Penetrometer Reading - 10 cm	P10	Continuous
Penetrometer Reading - 20cm	P20	Continuous
Depth to Rock	R	Continuous
Depth to Limestone Nodules	LN	Continuous
Depth to Sheet Limestone	LS	Continuous
pH	PH	Continuous
Total Soluble Salts (TSS)	TSS	Continuous
Colour	COL	Nominal (Many Classes)
Wettability	WET	Binary
Presence of Carbonates	CARB	Ordinal (3 Classes)
Soil Texture	TEX	Ordinal (6 Classes)
Mean Annual Rainfall	AR	Continuous
Mean Summer Rainfall	SR	Continuous
Mean Winter Rainfall	WR	Continuous
Median Annual Rainfall	MED	Continuous
Mean Annual Raindays	ARD	Continuous
Mean Summer Raindays	SRD	Continuous
Mean Winter Raindays	WRD	Continuous

ANALYSIS METHODS

BLUEBUSH DISTRIBUTION PATTERNS

Species Distribution Patterns

The distribution of bluebush was modelled by logistic regression in the form of a generalised linear model (GLIM) using presence/absence data collected for the 124 survey sites. Formal descriptions of this type of model are given by Dobson (1983) and McCullagh and Nelder (1983), and outlined more simply in Crosbie and Hinch (1985) and Nicholls (1991). Applications to vegetation data are discussed by ter Braak and Looman (1986) and Nicholls (1991). In addition to bluebush, three other important chenopod species were also modelled for comparative purposes: saltbush, blackbush and low bluebush. All models were constructed using the computer software package GENSTAT (Statistics Department - Rothamsted Experimental Station, 1987).

Due to the high degree of autocorrelation[1] between the environmental variables listed in Table 2.4, only twelve were included in this, and all subsequent, analyses. These are listed in Table 2.5. Continuous variables were fitted as both linear and quadratic terms to test for possible Gaussian-type bell-shaped response curves as in ter Braak and Looman (1986). The analyses were restrained, however, such that quadratic terms could only be fitted in addition to linear terms. A forward step-wise regression procedure was followed as suggested by Nicholls (1991). This method is recommended when fitting models as an exploratory technique rather than for hypothesis testing. Selection of variables at each step was based on the greatest significant change in deviance tested as a F-statistic. If no difference in residual deviances was detected between the linear and quadratic functions, the

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[1] As tested by Spearman rank correlation. Variables showing a correlation with $p<0.001$ level of significance with at least one other variable were removed. Indirect variables, such as latitude and longitude, were removed in preference to direct variables such as rainfall. The exceptions to this were annual rainfall, summer rainfall and winter rainfall which were retained in the analysis despite high levels of autocorrelation.

simpler linear model was fitted. Finally, the significance of first order interactions was tested for all significant variables fitted.

Table 2.5: Environmental variables used in the statistical analyses following the removal of autocorrelated variables.

VARIABLE	CODE	VARIABLE TYPE
Elevation	EL	Continuous
Slope	SL	Continuous
Topography	TOP	Ordinal (7 Classes)
Depth to Sheet Limestone	SH	Continuous
Depth to Limestone Nodules	NODS	Continuous
Depth to Other Rock	R	Continuous
Soil pH	PH	Continuous
Presence of Carbonates	CARB	Ordinal (3 Classes)
Soil Texture	TEX	Ordinal (6 Classes)
Mean Annual Rainfall	AR	Continuous
Mean Summer Rainfall	SR	Continuous
Mean Winter Rainfall	WR	Continuous

Plant Size and Abundance Patterns

Three estimates of plant size were used: height, projected foliage cover ($\Pi/_4$ x length x width) and hemi-ovoid volume ($\Pi/_6$ x height x length x width). Mean values for each of these factors were obtained for each site using the dimension data collected for the 30 shrubs per quadrat. Three measures of species abundance were also calculated: density (number of shrubs m^{-2}), % cover (density x mean shrub foliage cover) and biomass (density x mean shrub volume). Relationships between species cover and environmental variables were tested by simple rank correlation. Correlations were carried out using the computer software package StatView (Abacus Concepts, 1988).

COMMUNITY ANALYSIS

Classification and Ordination

Classification was carried out using the Bray-Curtis distance metric and UPGMA fusion strategy (see Greig-Smith, 1983 for details) via the software package NTP (Belbin *et al.*, 1984). Data from 124 sampling locations and including 174 perennial species were included to identify the major vegetation types observed.

Ordination was undertaken by detrended correspondence analysis (DCA; Hill, 1979) using the program DECORANA. Relationships between the vegetation gradients represented by the DCA and abiotic factors were tested by rank correlation of individual environmental variables with DCA-axes scores using the NONPAR option in the SPSS-X computer software package (SPSS Inc., 1986). Correlations were presented as vector diagrams for the first two ordination dimensions. Only those variables which showed a $p<0.05$ level of significance with at least one of these principal axes were included on the final diagrams.

Multiple Discriminant Analysis

Discriminant analysis was used to test for significant differences in the abiotic (environmental) characteristics of communities that had been previously delineated by classification. This technique, previously used in vegetation analysis by Batista (1988) and Sparrow (1991), allows discrimination between pre-defined 'noda' (in this instance from classification) on the basis of environmental variables, producing linear discriminant functions which represent principal composite environmental gradients (Ludwig and Reynolds, 1988; Legendre and Fortin, 1989). Multiple discriminant analyses were carried out via Wilk's step-wise procedure using the DISCRIM option in the SPSS-X computer software package (SPSS Inc., 1986).

RESULTS

BLUEBUSH DISTRIBUTION PATTERNS

Distribution Patterns within the Study Area

General Observations

Bluebush was observed in all four regions of the survey area at a total of 58 (47%) of the 124 sampling locations. It was the most commonly encountered chenopod species; saltbush, blackbush and low bluebush were recorded at 54, 37 and 20 sites respectively (Table 2.6). Of these species, bluebush and saltbush were found to be the most widely-spread (Figures 2.3a-b). Low bluebush was restricted to the northern fringes of the surveyed area (Figure 2.3c) while blackbush was found primarily in the central-eastern section of the study region (Figure 2.3d).

Table 2.6: Regional analysis of frequency of occurrence for the four main chenopod species examined.

SPECIES	# SITES	NTH-WEST	EYRE PEN.	FLINDERS R.	EASTERN
M. sedifolia	58	15 (50%)	15 (65%)	11 (38%)	17 (40%)
A. vesicaria	54	14 (47%)	13 (59%)	7 (24%)	20 (47%)
M. pyramidata	37	3 (10%)	5 (23%)	10 (35%)	19 (44%)
M. astrotricha	20	5 (17%)	1 (5%)	10 (35%)	4 (9%)

Climatically, bluebush was restricted to those areas receiving between 125 and 300 mm median annual rainfall. Bluebush locations in the north-western sub-region generally receive less than 150 mm rainfall, while those in the eastern and Eyre Peninsula regions received between 200 and 300 mm of rainfall. All sites where bluebush was recorded can be seasonally-defined as having uniform or winter-dominant rainfall distributions (Figure 2.4).

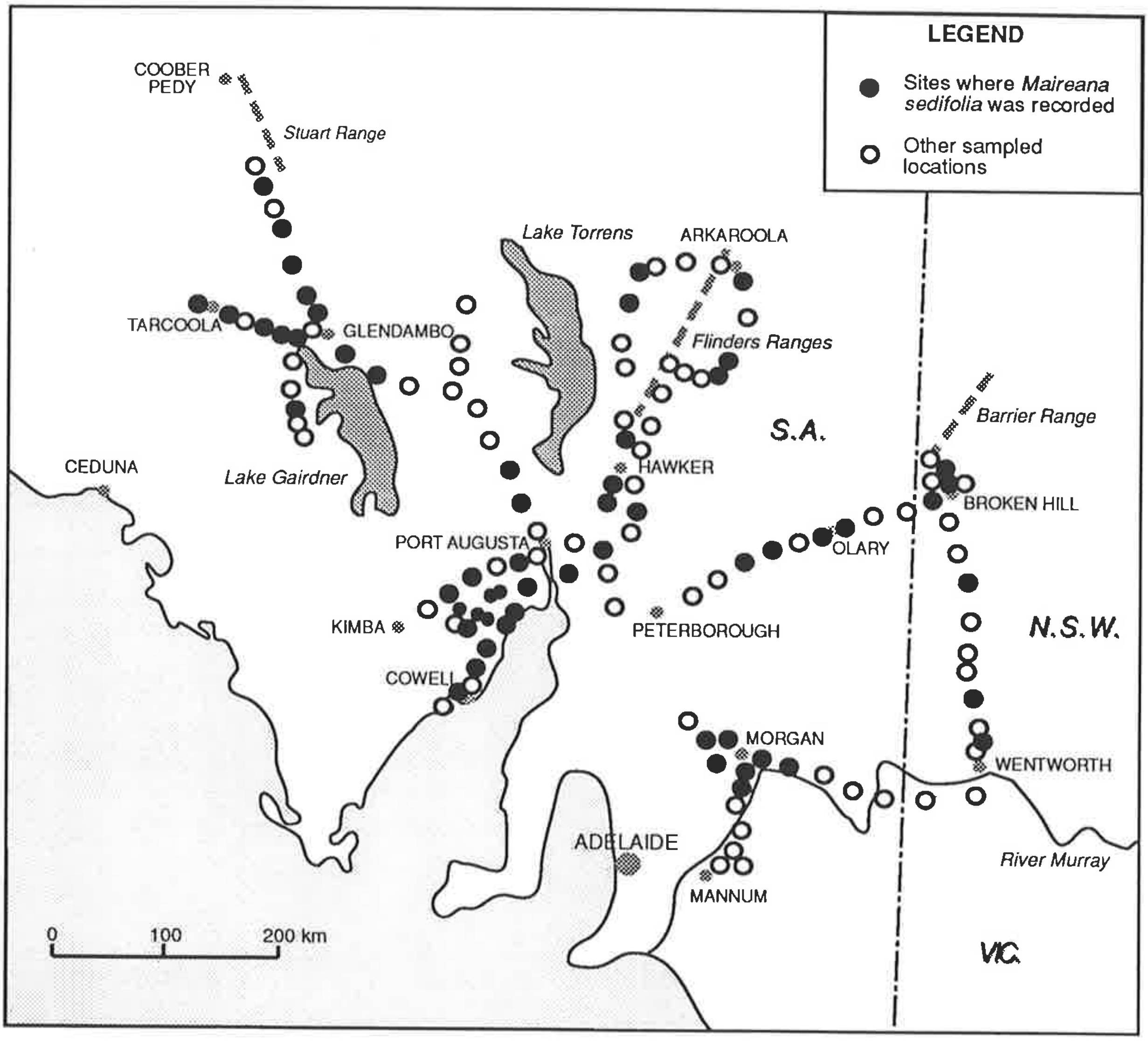


Figure 2.3a: Distribution of bluebush (*Maireana sedifolia*) at the surveyed locations.

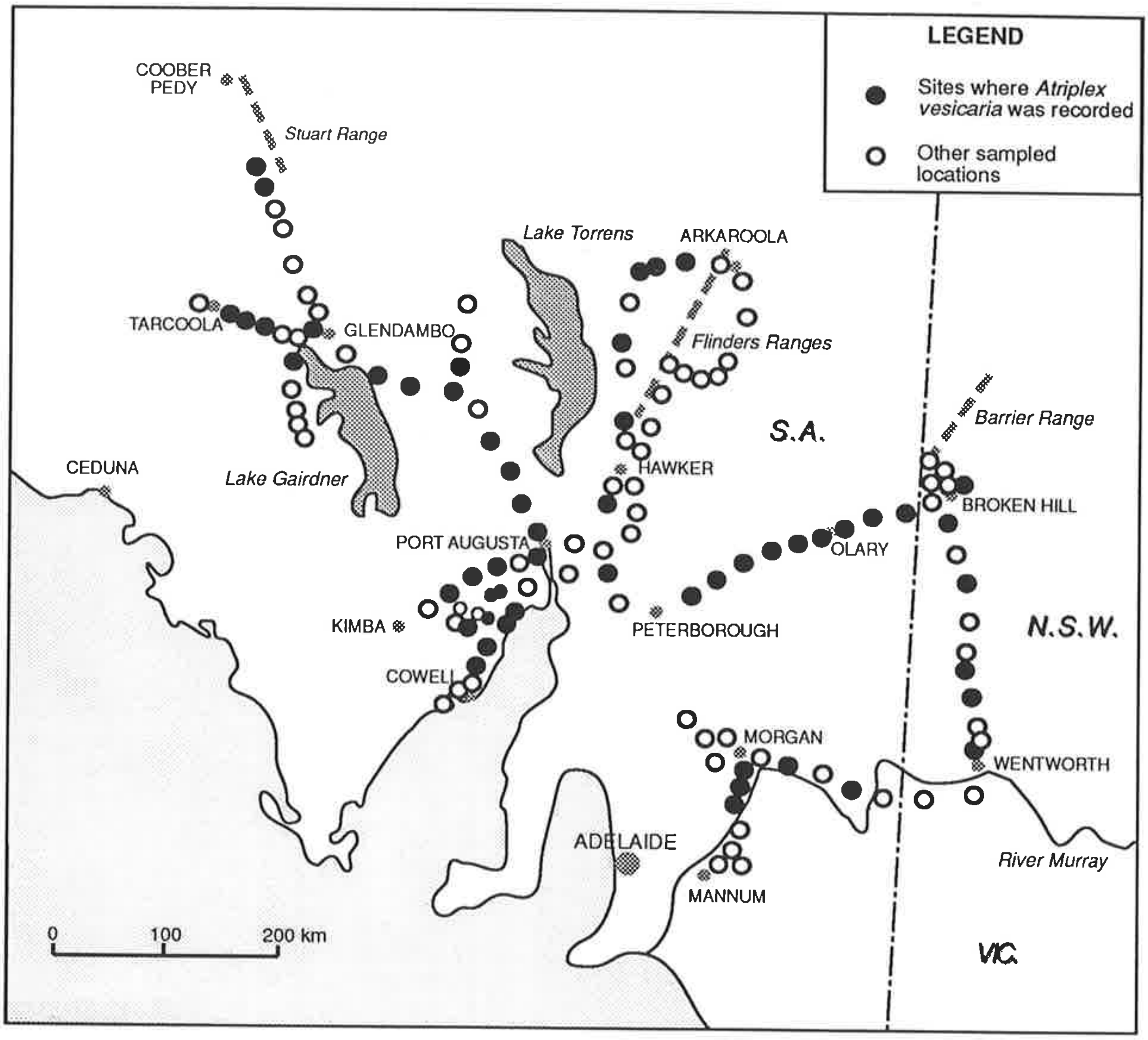


Figure 2.3b: Distribution of saltbush (*Atriplex vesicaria*) at the surveyed locations.

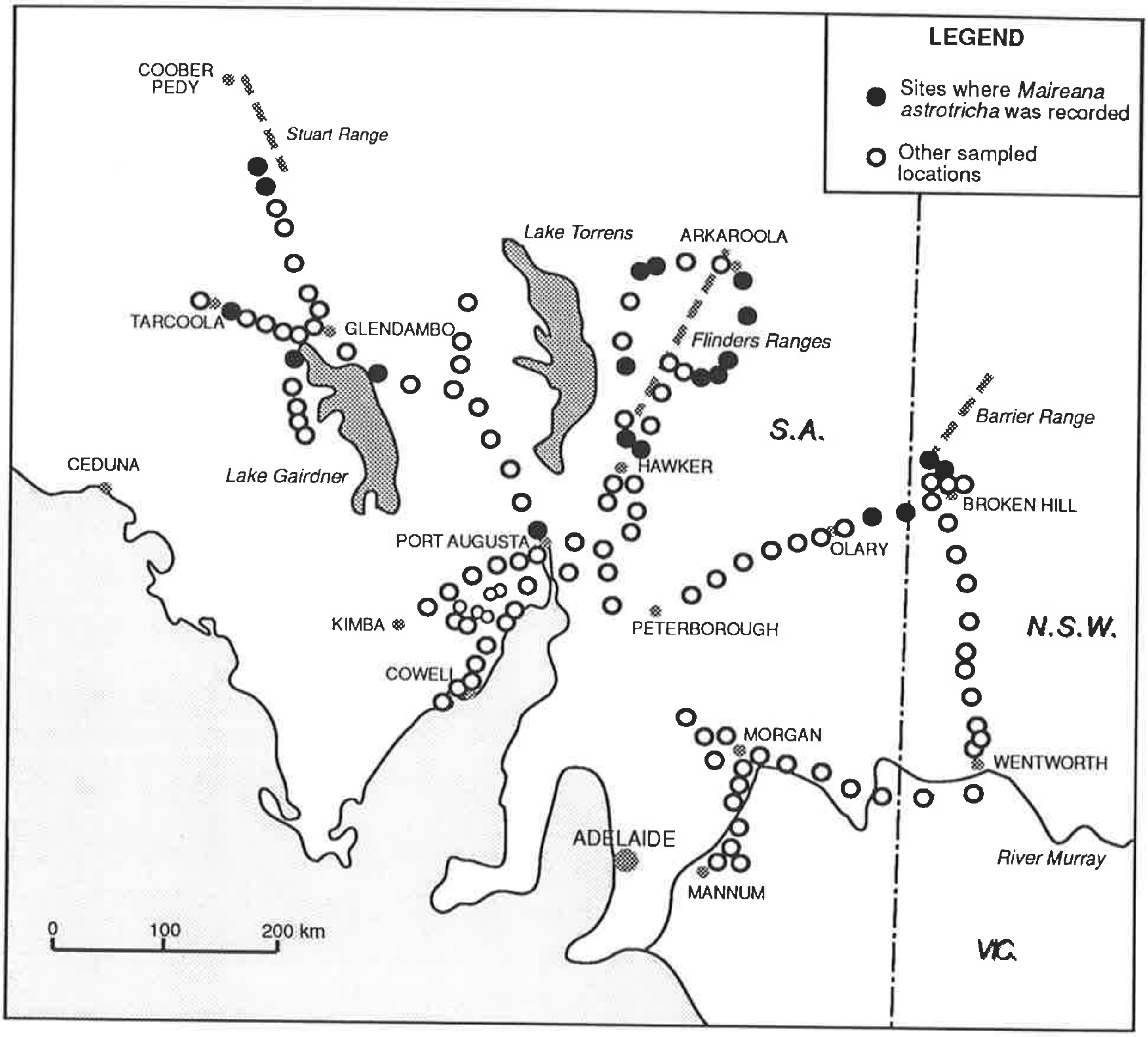


Figure 2.3c: Distribution of low bluebush (*Maireana astrotricha*) at the surveyed locations.

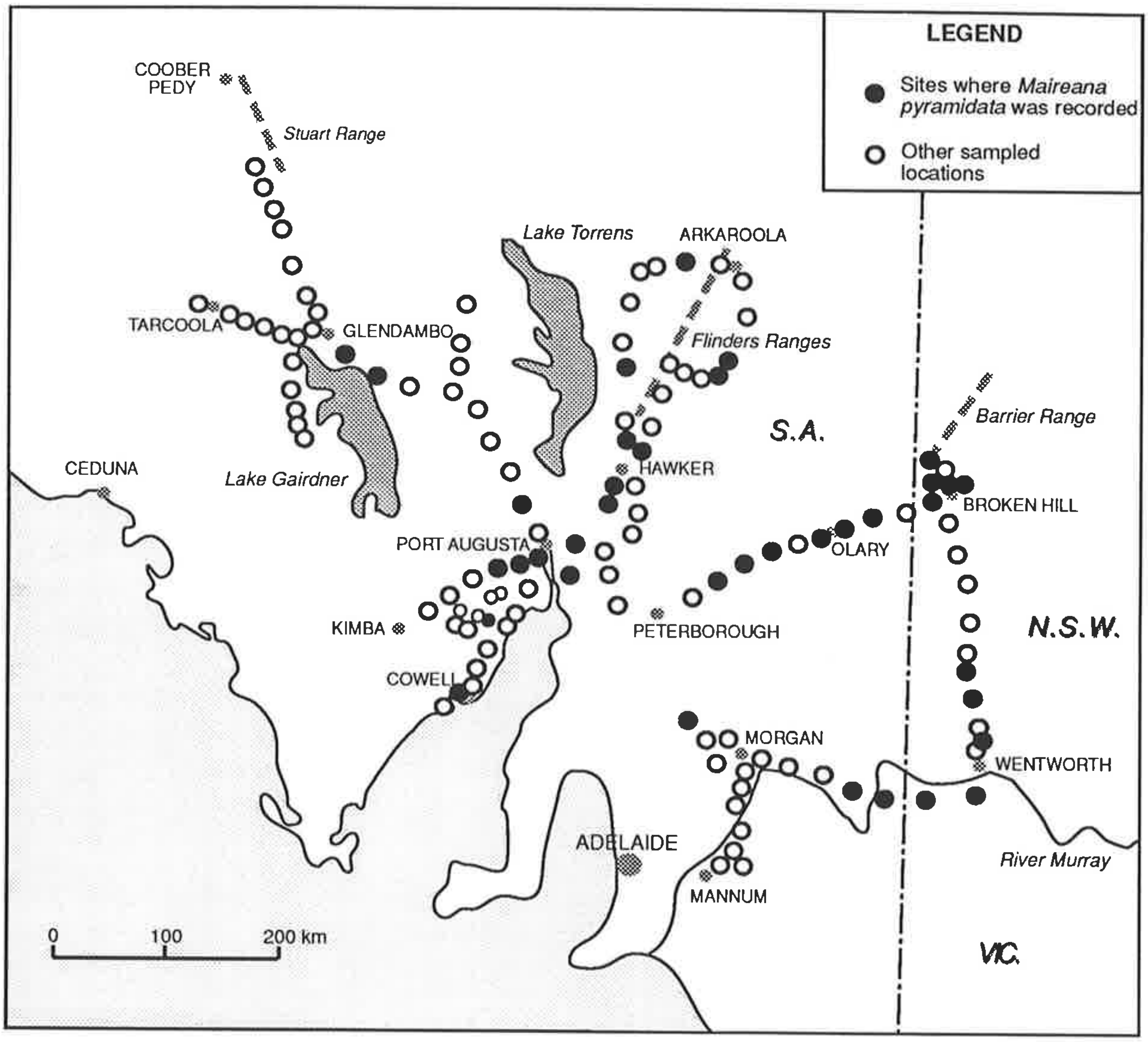


Figure 2.3d: Distribution of blackbush (*Maireana pyramidata*) at the surveyed locations.

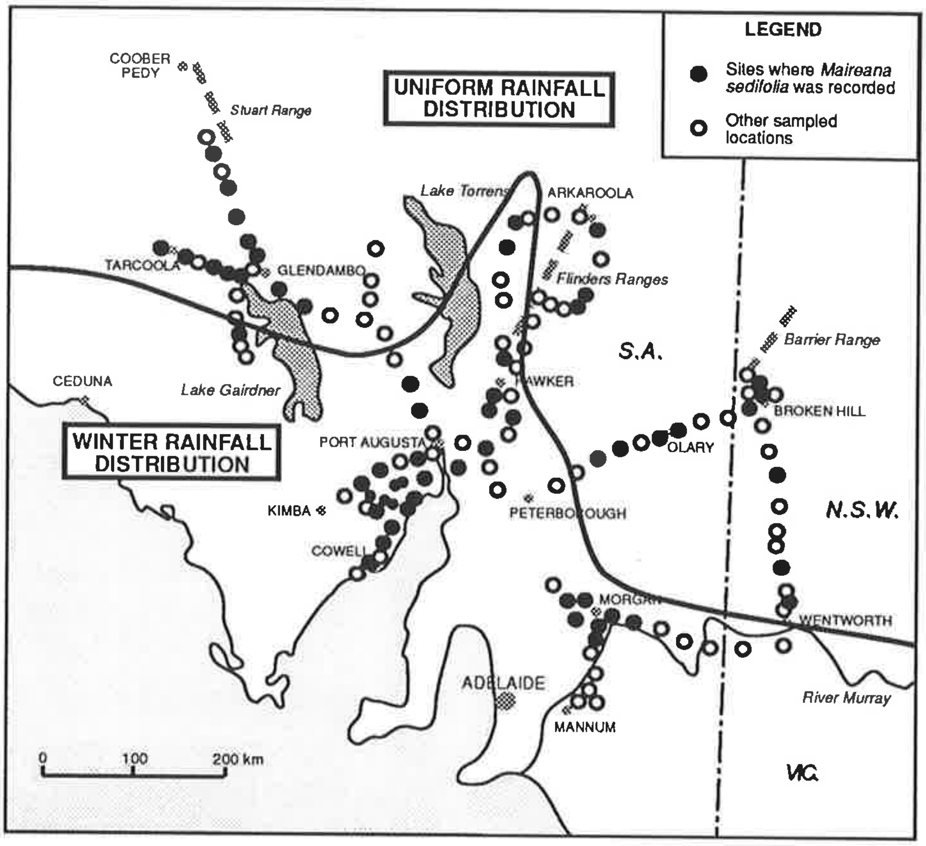


Figure 2.4: Distribution of bluebush in relation to seasonal rainfall patterns. Rainfall data from Atlas of Australian Resources (Division of National Mapping, 1986).

Environmental Correlations

The logistic regression models constructed for bluebush and the three comparison species are shown in Tables 2.7a-d, with a summary table of significant variables given in Table 2.8. The bluebush model indicates that the presence of calcium carbonate (as nodules and sheet limestone or free carbonates) and rainfall are important predictors of the distribution of this species. The negative estimate given for both limestone layer factors suggests that the probability of bluebush occurrence is decreased with increasing depth to limestone. This is illustrated in plots showing the frequency of species along the nodular and sheet limestone gradients (Figures 2.5 a-b). Despite the trend for decreased bluebush frequencies along the sheet limestone gradient, this species is dominant on limestone soils, with a probability of occurrence in excess of 50% when the limestone layer is within 70 cm of the soil surface.

Bluebush is more dominant, relative to the other chenopods, on soils with nodular limestone. Additionally, it is also indicated that bluebush occurs at a much lower frequency than the other chenopods at sites where no limestone layer was detected. Although saltbush is clearly the predominant chenopod in this situation, bluebush is not restricted to calcium carbonate soils. It was present at 12 sites (21% of the 58 observed sightings) where no limestone layer (either nodules or sheet) was present and at 5 sites (8.6%) where neither limestone nor free carbonates were detected in the soil profile.

Mean summer rainfall was included as a quadratic in the model for bluebush. The square term was negative, suggesting a bell-shaped Gaussian-type response curve along the summer rainfall gradient (Figure 2.6). Bluebush, along with saltbush, clearly predominates in areas receiving 90-120 mm of rainfall during October to March, with bluebush present at nearly 50% of sites in this range (Figure 2.6). This plot also reveals trends in distribution for the other three species; *M. astrotricha* is restricted to the lower rainfall regions, while the frequency of blackbush increases with increasing summer rainfall.

The other variable included in the bluebush model was a depth to limestone nodules x mean summer rainfall interaction term; Figures 2.7a-c illustrate this modelled interaction for the three possible carbonate levels. Whilst the interaction is most obvious when free carbonates were not detected in the soil (Figure 2.7a), all plots show that with a decreasing summer rainfall bluebush was more often found on soils where the nodule layer was closer to the surface.

Several other variables not included in the bluebush model were found to be significant for the other species (Table 2.8). These are soil texture and topography (present in the saltbush model), winter rainfall (present in the blackbush and low bluebush models) and elevation (also included in the low bluebush model). In addition, it is interesting to note that at least one rainfall variable was included in all *Maireana* models, while none were included in the saltbush model.

Table 2.7a: Logistic regression model for bluebush (*Maireana sedifolia*). Significance of variables is indicated as follows; *** p<0.001, * 0.01<p<0.05.

NULL MODEL 171.384	D.F. 123
FINAL MODEL 117.384	D.F. 116
DEVIANCE EXPLAINED (R^2) = 0.316***	

MAIN EFFECTS

VARIABLE	ESTIMATE	S. ERROR	RATIO	F VALUE
Constant	-0.800	16.300	-0.05	-
Depth to Nodules	-1.19E-01	5.44E-02	-2.18	17.53 ***
Depth to Sheet Lime	-1.60E-02	4.78E-03	-3.35	14.09 ***
Summer Rainfall	2.44E-01	2.62E-01	0.93	4.59 ***
Summer Rainfall^2	-1.78E-03	1.10E-03	-1.61	6.14 *
Carbonates (0)	0.000	0.000	-	3.25 *
Carbonates (1)	2.071	8.41E-01	2.46	
Carbonates (2)	8.29E-01	5.22E-01	1.59	

INTERACTION TERMS

Nodules x Sum. Rain	8.71E-04	4.63E-04	1.88	4.92 *

Table 2.7b: Logistic regression model for saltbush (*Atriplex vesicaria*). Significance of variables is indicated as follows; *** p<0.001, ** 0.001<p<0.01, * 0.01<p<0.05.

NULL MODEL 169.830	D.F. 123
FINAL MODEL 144.938	D.F. 120
DEVIANCE EXPLAINED (R^2) = 0.172***	

MAIN EFFECTS

VARIABLE	ESTIMATE	S. ERROR	RATIO	F VALUE
Constant	-1.747	0.721	-2.42	-
Depth to Nodules	1.08E-02	4.07E-03	2.65	8.73 **
Soil Texture	2.90E-01	1.24E-01	2.33	5.68 *
Topography	-2.93E-01	1.10E-01	-2.65	6.19 *

Table 2.7c: Logistic regression model for blackbush (*Maireana pyramidata*). Significance of variables is indicated as follows; *** p<0.001, * 0.01<p<0.05.

NULL MODEL	151.154	D.F. 123
FINAL MODEL	132.117	D.F. 119
DEVIANCE EXPLAINED (R^2) = 0.126 ***		

MAIN EFFECTS

VARIABLE	ESTIMATE	S. ERROR	RATIO	F VALUE
Constant	-6.910	1.910	-3.62	
Carbonates (0)	0.000	0.000	-	4.22 *
Carbonates (1)	1.779	7.39E-01	2.41	
Carbonates (2)	1.27E+00	4.97E-01	2.55	
Summer Rainfall	6.25E-02	2.11E-02	2.96	5.26 *
Winter Rainfall	-1.48E-02	7.04E-02	-2.11	3.95 *

Table 2.7d: Logistic regression model for low bluebush (*Maireana astrotricha*). Significance of variables is indicated as follows; *** p<0.001, * 0.01<p<0.05.

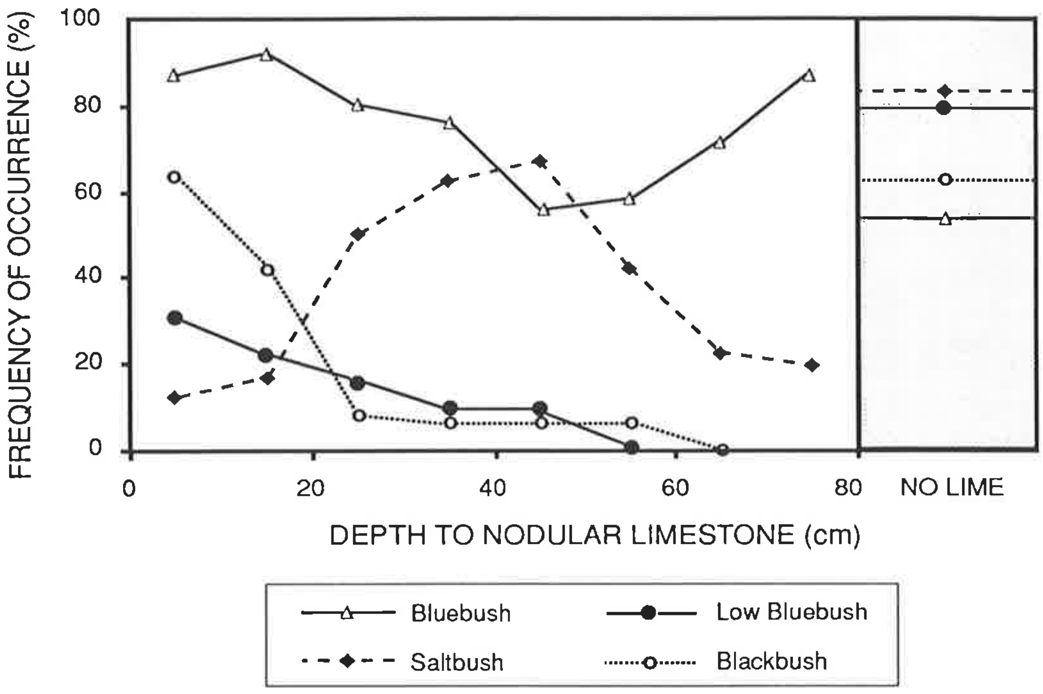
NULL MODEL	109.570	D.F. 123
FINAL MODEL	93.4020	D.F. 121
DEVIANCE EXPLAINED (R^2) = 0.147***		

MAIN EFFECTS

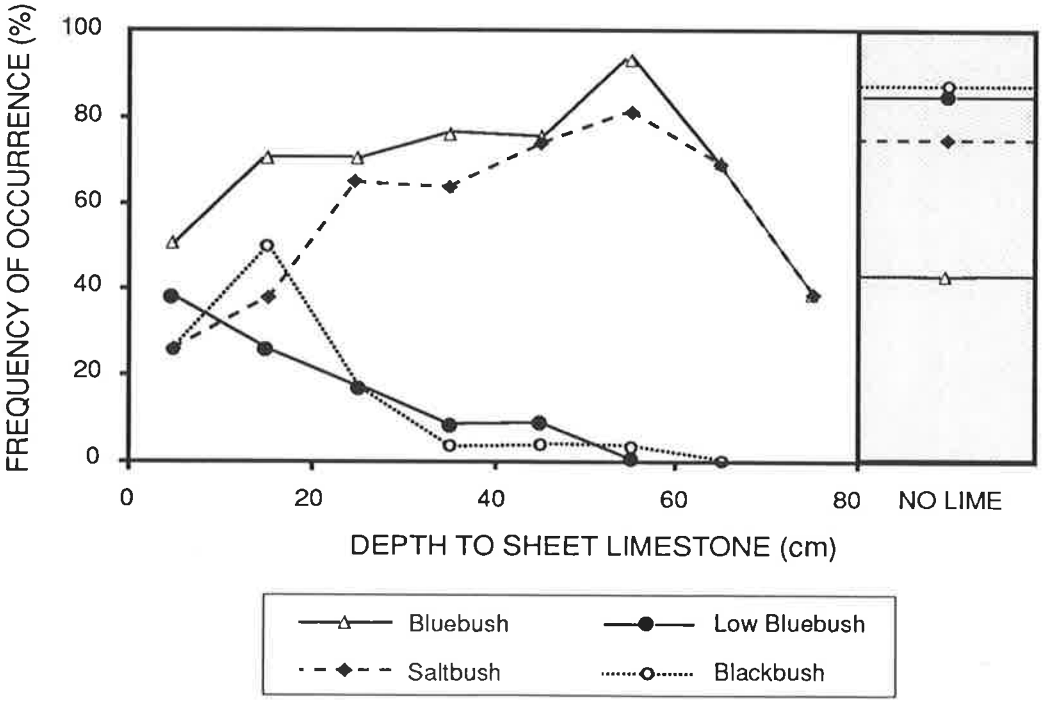
VARIABLE	ESTIMATE	S. ERROR	RATIO	F VALUE
Constant	0.898	0.938	0.96	
Winter Rainfall	-3.18E-02	9.62E-03	-3.31	15.44 ***
Elevation	4.90E-03	2.35E-03	2.09	5.50 *

Table 2.8: Summary of the variables included in the logistic regression models for the four chenopod species. Significance level is indicated as follows; * ,0.01p<0.05; **, 0.001<p<0.01; ***, p<0.001

VARIABLE	*M.sedifolia*	*A.vesicaria*	*M.pyramidata*	*M.astrotricha*
Depth to Nodules	*	**	-	-
Depth to Sheet Lime	***	-	-	-
Carbonates	*	-	*	-
Winter Rainfall	-	-	*	***
Summer Rainfall	*** (+^2*)	-	*	-
Soil Texture	-	*	-	-
Topography	-	*	-	-
Elevation	-	-	-	*
Nodules x Sum. Rain	*	-	-	-



(a) Depth to Limestone Nodules



(b) Depth to Sheet Limestone

Figure 2.5: Frequency of occurrence of the four major chenopod species in relation to limestone depth. Smoothing of these curves was carried out by averaging each three adjacent points.

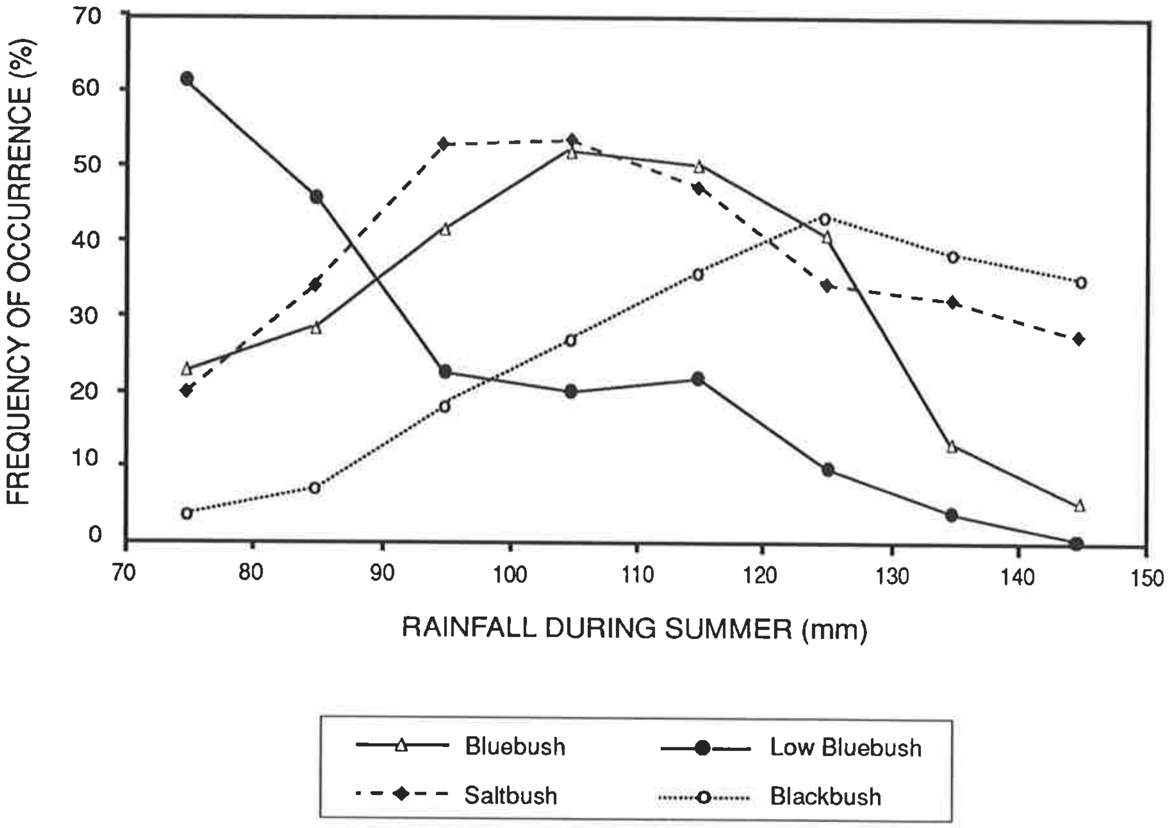


Figure 2.6: Frequency of occurrence of the four major chenopod species in relation to summer rainfall.

Figure 2.7: Predicted trend surface plots of the probability of bluebush occurrence in relation to summer rainfall and depth to limestone nodules for the three levels of soil carbonates. Responses are based on the model in Table 2.7a. Combinations of variables outside the envelope were not encountered during this study.

Legend:

□ $P = 1.00$

░ $0.95 \leq P < 1.00$

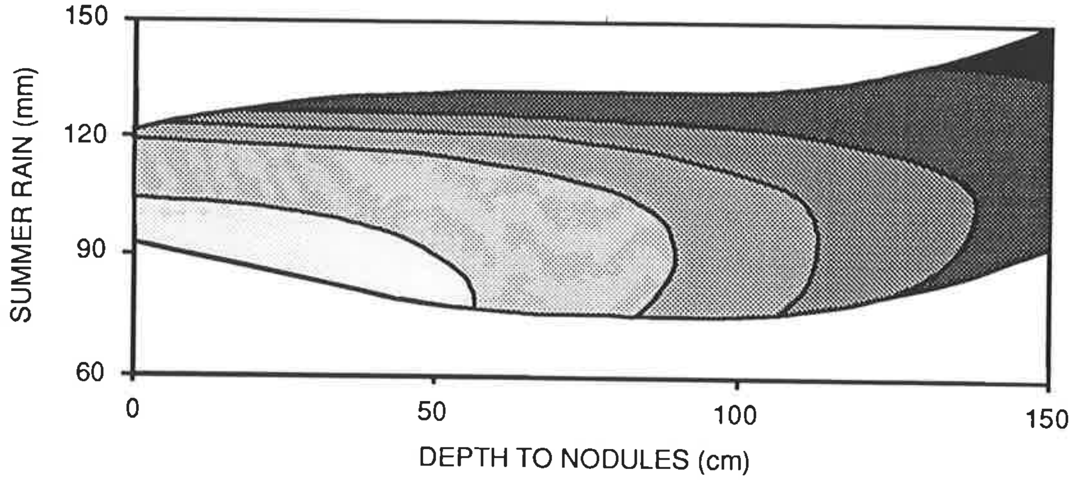
░ $0.90 \leq P < 0.95$

▒ $0.80 \leq P < 0.90$

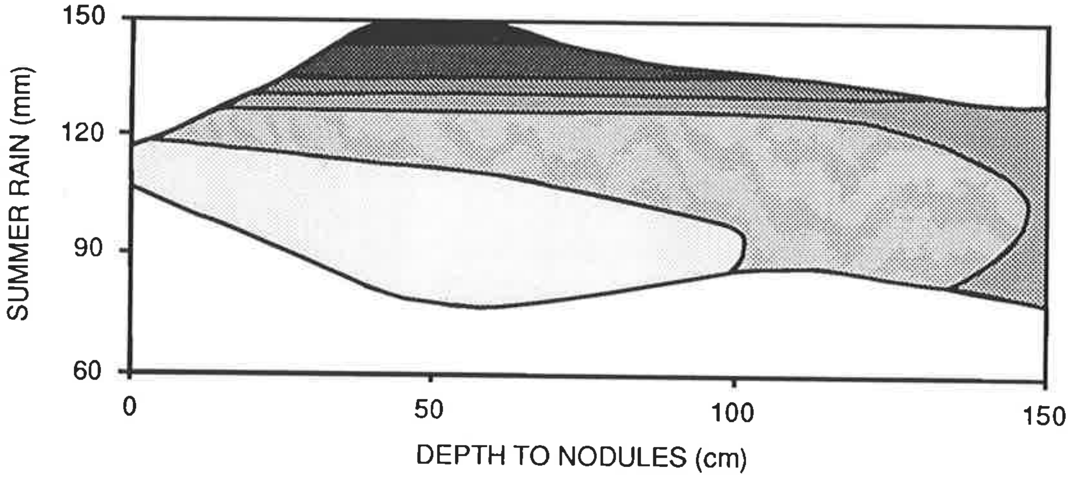
▓ $0.40 \leq P < 0.80$

■ $P < 0.40$

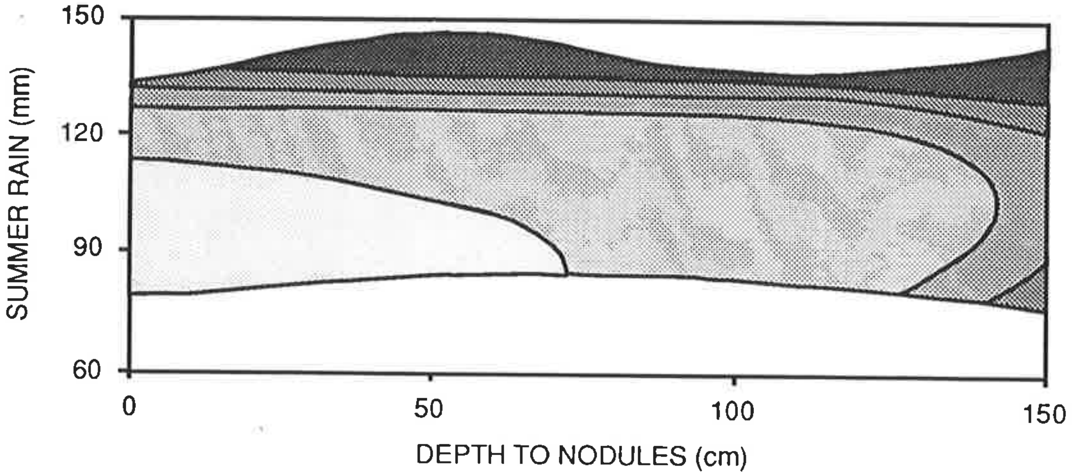
□ Response envelope (combinations not found at any site)



(a) Soil Carbonates Not Present



(b) Soil Carbonates = 1 (Weak Reaction to HCl Acid)



(c) Soil Carbonates = 2 (Strong Reaction to HCl Acid).

Variations in Size and Abundance

On a regional basis, there was little variation in the size and abundance of bluebush shrubs across the study region (Table 2.9a-b). Kruskal-Wallis tests detected significant differences only in shrub density (H=9.189, d.f.=3, p=0.027); density of bluebush shrubs on Eyre Peninsula were higher than in the other three regions. Additionally, some significant relationships between plant size and abundance measures were calculated (Table 2.10); many of these are expected given that estimates were derived from much the same data. It should be noted, however, that increasing shrub size was correlated with overall cover and biomass, despite the negative relationship betwwen shrub size and density.

Table 2.9: Regional and overall averages (means ± S.E.) for bluebush size and density across the survey area.

(a) Bluebush Size

REGION	# SITES	HEIGHT (m)	COVER (m^2)	VOLUME (m^3)
North-Western	15	0.66±0.03	0.47±0.07	0.24±0.04
Eyre Peninsula	15	0.69±0.04	0.41±0.06	0.23±0.04
Flinders Ranges	11	0.76±0.06	0.39±0.04	0.29±0.05
Eastern	17	0.77±0.56	0.58±0.05	0.42±0.13
Overall Mean	58	0.71±0.02	0.47±0.05	0.28±0.04
Lowest Site Estimate	58	0.40	0.078	0.023
Highest Site Estimate	58	1.41	2.174	2.372

(b) Bluebush Abundance

REGION	# SITES	DENSITY (# of shrubs/m^2)	%COVER (m^2 of shrub/m^2) x 100	BIOMASS (m^3 of shrub/ m^2) x 10^{-4}
North-Western	15	0.06±0.01	2.63±0.40	128.03±20.91
Eyre Peninsula	15	0.10±0.02	3.96±0.93	199.07±45.93
Flinders Ranges	11	0.08±0.02	3.19±0.63	173.57±36.31
Eastern	17	0.07±0.03	3.89±1.35	286.65±86.81
Overall Mean	58	0.08±0.01	3.67±0.49	196.75±29.64
Lowest Site Estimate	58	0.001	0.05	1.72
Highest Site Estimate	58	0.464	20.0	1067.4

Table 2.10: Spearman rank correlations between bluebush size and abundance estimates. Significance of correlations:*, 0.01<p<0.05; **, 0.001<p<0.01, ***, p<0.001

POPULATION	INDIVIDUAL PLANT FEATURES		
ESTIMATES	Height	Area	Volume
Density	-0.2052	-0.1040	-0.1312
%Cover	0.1458	0.3477**	0.3143**
Biomass	0.2859*	0.4373***	0.4271***

The size of bluebush shrubs is related to a single factor, depth to limestone (Table 2.11). All three size estimates showed positive correlations with depth to sheet and nodular limestone, implying increasing plant size with increasing depth to limestone. This suggests that although bluebush presence was strongly influenced by the presence of limestone (detected by the GLIM model), smaller plant sizes occur when this limestone is located toward the top of the soil profile.

Although the three abundance measures are derived from the same measurements and are thus logically related, there was some variation in the influence of the various environmental factors on these estimates. Elevation, depth to limestone and winter rainfall were found to be significant for all three abundance estimates. Depth to sheet limestone showed the most significant positive correlation with plant abundance estimates *i.e.* more bluebush can be supported on soils in which the limestone is at a greater depth. The highest correlation of depth to limestone with biomass is a combination of the density and shrub size correlations. Despite the strong correlations between plant size and depth to nodules, there was no significant correlation between density and depth to nodular limestone. Elevation was also significantly correlated to plant abundance, although in this instance a negative correlation coefficient was calculated. This suggests a trend of decreasing plant abundance from areas of low elevation (such as the plains along the River Murray), to areas of higher elevation (Flinders and Stuart Range). Similarly, a topographic influence was shown to be significantly correlated to shrub density and % cover, where abundance was reduced with increasing topography (plains to slopes to hills). In both cases, this may reflect less limestone in the ranges. Abundance was also shown to be positively correlated to winter rainfall, with higher densities and increased overall biomass recorded in areas receiving higher winter rainfall. However, no significant correlation between summer rainfall and plant abundance was seen. This is of particular interest given the importance of summer rainfall in the bluebush distribution model (Table 2.7a).

Significant positive correlations were also observed between the density and % cover estimates and soil texture, implying that higher plant numbers were found on loam-clay soils compared to sand. This may represent a soil water availability effect.

Table 2.11: Spearman rank correlations between bluebush size and abundance estimates and the measured environmental variables. Correlations with depth to limestone have reduced degrees of freedom as a result of a decreased number of data points. Significance of correlations: *, $0.01<p<0.05$; **, $0.001<p<0.01$, ***, $p<0.001$

(a) Bluebush Size

VARIABLE	D.F.	MEAN HEIGHT	MEAN COVER	MEAN VOLUME
Elevation	57	-0.030	-0.054	-0.026
Slope	57	0.090	0.036	0.051
Topography	57	0.048	-0.003	-0.030
Depth to Nodules	26	0.382 *	0.397 **	0.434 **
Depth to Sheet Limestone	17	0.405 *	0.719 **	0.706 ***
Depth to Other Rock	9	0.290	-0.013	0.076
Annual Rainfall	57	0.091	-0.152	-0.067
Winter Rainfall	57	0.076	-0.161	-0.073
Summer Rainfall	57	0.103	-0.102	-0.020
Soil Texture	57	-0.189	-0.180	-0.185
Soil pH	57	-0.010	-0.026	-0.007
Carbonates	57	0.082	0.053	0.070

(b) Bluebush Abundance

VARIABLE	D.F.	DENSITY	% COVER	BIOMASS
Elevation	57	-0.307 *	-0.361 **	-0.342 *
Slope	57	-0.257	-0.178	0.150
Topography	57	-0.191 *	-0.353 *	-0.130
Depth to Nodules	26	-0.172	0.363	0.454 **
Depth to Sheet Limestone	17	0.563 *	0.645 **	0.700 **
Depth to Other Rock	9	-0.083	-0.126	-0.101
Annual Rainfall	57	0.160	0.172	0.161
Winter Rainfall	57	0.287 **	0.238 *	0.263 *
Summer Rainfall	57	0.163	0.188	0.165
Soil Texture	57	0.375 **	0.313 *	0.178
Soil pH	57	-0.016	-0.008	-0.003
Carbonates	57	-0.183	-0.152	-0.144

COMMUNITY STUDIES

Classification and Ordination

Vegetation Communities

The dendrogram produced from the classification analysis of the 124 sampling sites is shown in Figure 2.8. Primary dendrogram groupings were delineated at the 0.85 dissimilarity level and were assigned as 'vegetation types'. This level was chosen subjectively based on the ability to distinguish these groupings in the field. The most common and characteristic species, detected using the TWTABLE program written by A. Sparrow (Botany Department, University of Adelaide), were used for names of these vegetation types. Twelve vegetation types were identified by this method, ranging in size from a single site (*Eucalyptus odorata*, Type 10; *Acacia aneura/ Cassia phyllodinea,* Type 11; and *Acacia tarculensis/Acacia brachstachya*, Type 12) to 50 sites (*Maireana sedifolia/ M.pyramidata,* Type 3). A majority of the survey sites fell into five vegetation types, the mallee woodland and chenopod shrubland communities, with Types 6-12 encompassing only 19 sites in total.

A secondary level of clustering on the dendrogram was made at the 0.75 dissimilarity level, to produce a two-tiered hierarchical classification (Figure 2.8). In vegetation types 6-12, dominated by species such as *Callitris columellaris, Eucalyptus largiflorens, Acacia victoriae and Acacia ligulata,* chenopod species were found to be uncommon components of the understorey in all types, and were usually replaced by grass or sclerophyllous species. As bluebush was not present in any of these types, they were not examined at a secondary clustering level and will not be described in detail here. From the remaining vegetation types (Types 1 to 5), 11 vegetation sub-types were delineated, ranging in size from 2 sites (Type 4-1 *M. pyramidata/ P.obovatus*) to 31 sites (Type 3-1 *M. sedifolia*). Distribution maps for the vegetation sub-types are shown in Figures 2.9a-e.

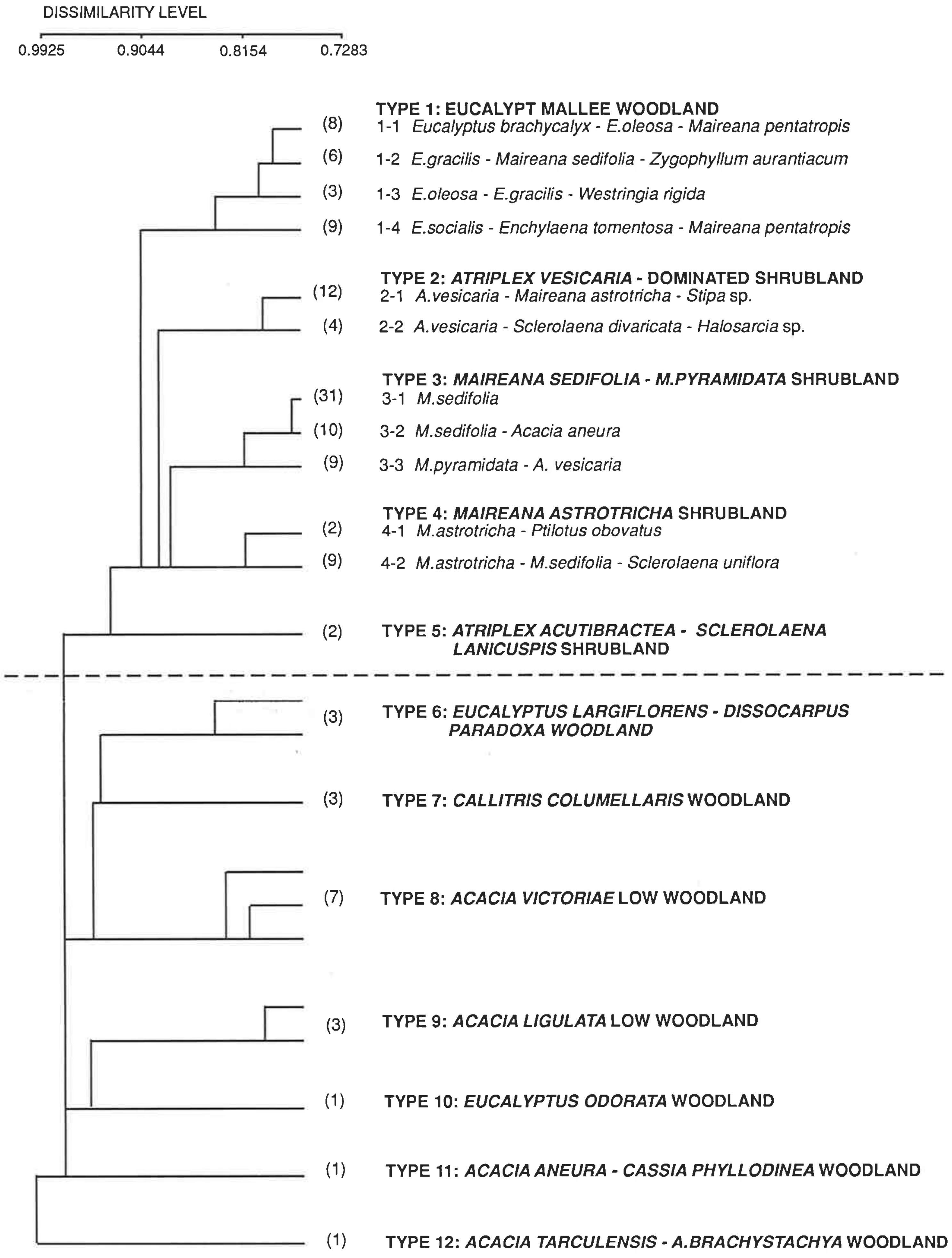
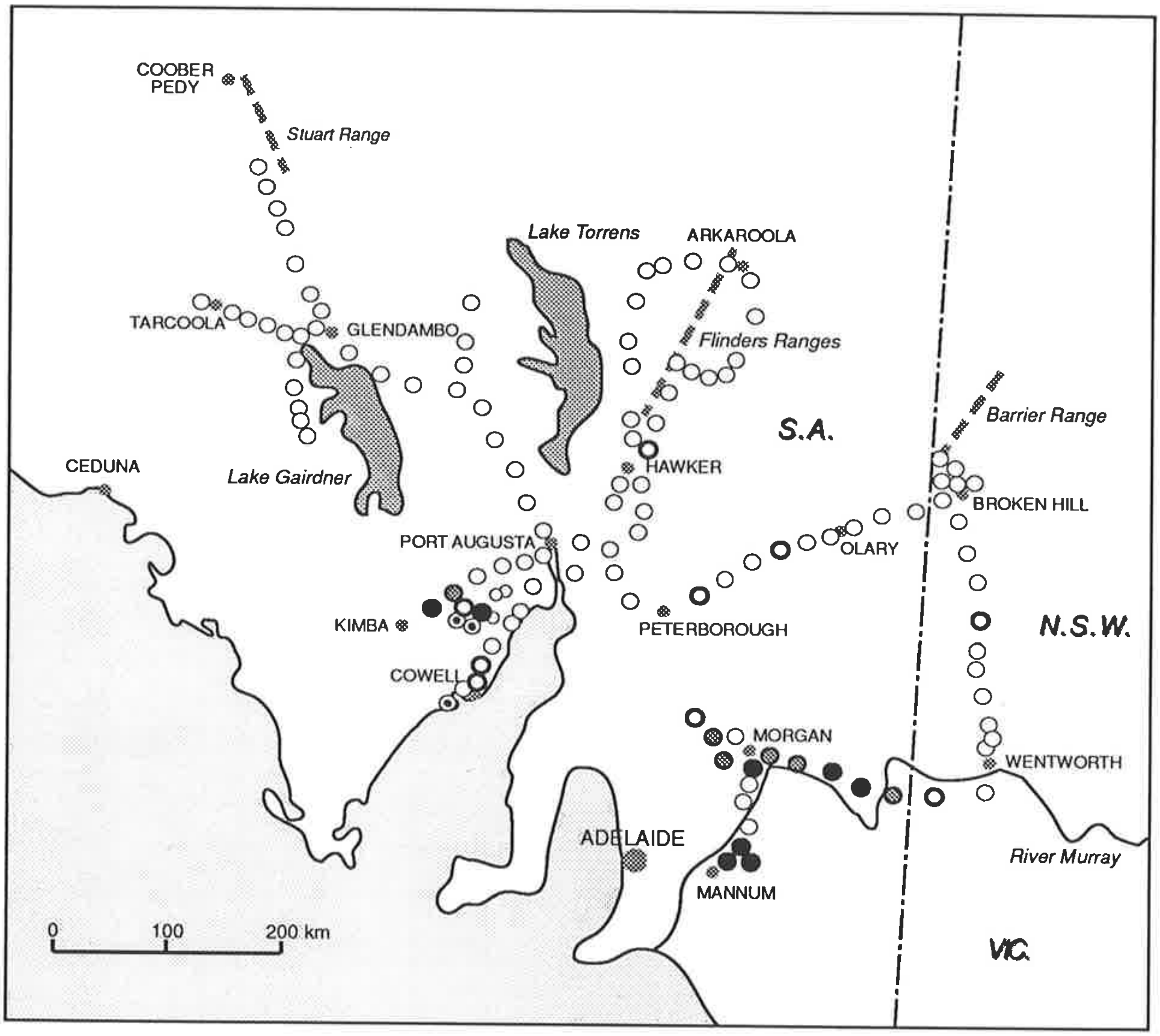


Figure 2.8: Summary dendrogram of the vegetation classification. The dendrogram is truncated at the $d_{BC} = 0.75$ level at which vegetation sub-types were defined. Vegetation types are given in upper case and sub-types in lower case. The number of sites classified into each of the sub-types is shown in parentheses.



●	Type 1-1 *E.brachycalyx - E.oleosa - Maireana pentatropis*
▨	Type 1-2 *E.gracilis - Maireana sedifolia - Zygophyllum aurantiacum*
⊙	Type 1-3 *E.oleosa - E.gracilis - Westringia rigida*
○	Type 1-4 *E.socialis - Enchylaena tomentosa - Maireana pentatropis*

Figure 2.9a: Distribution map for the sub-types of vegetation Type 1 (Eucalypt mallee woodland).

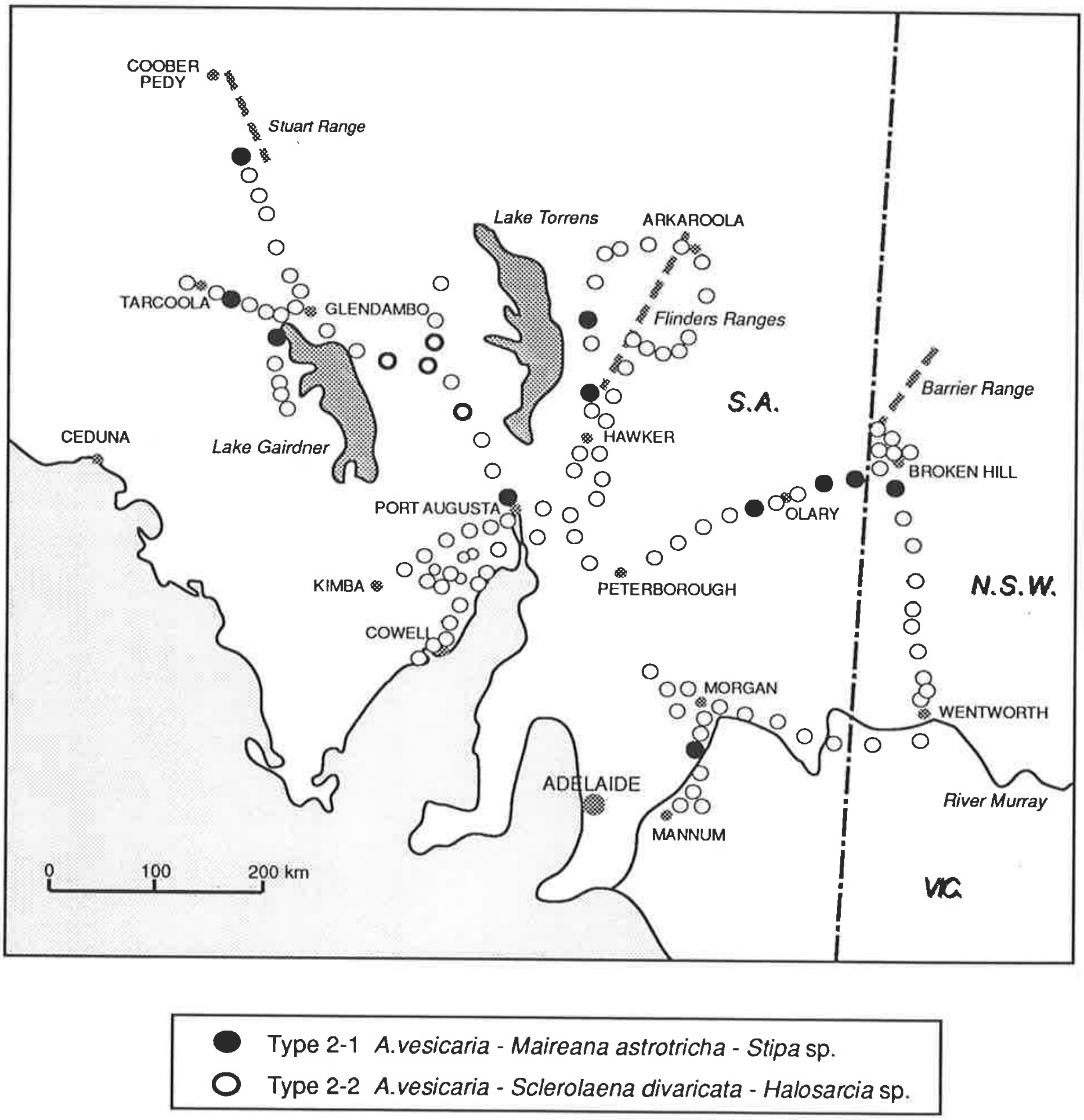


Figure 2.9b: Distribution map for the sub-types of vegetation Type 2 (*Atriplex vesicaria*-dominated shrubland).

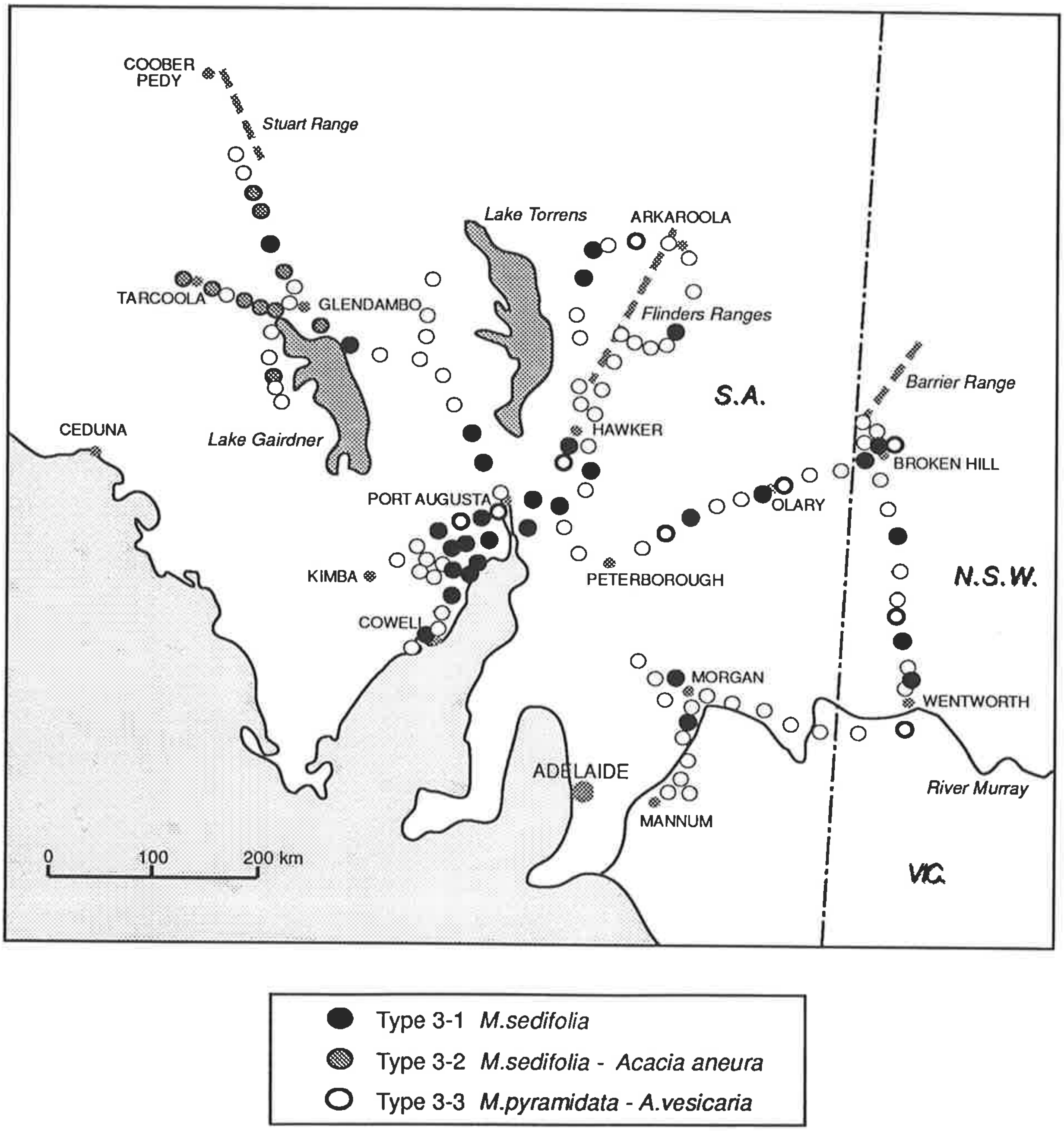
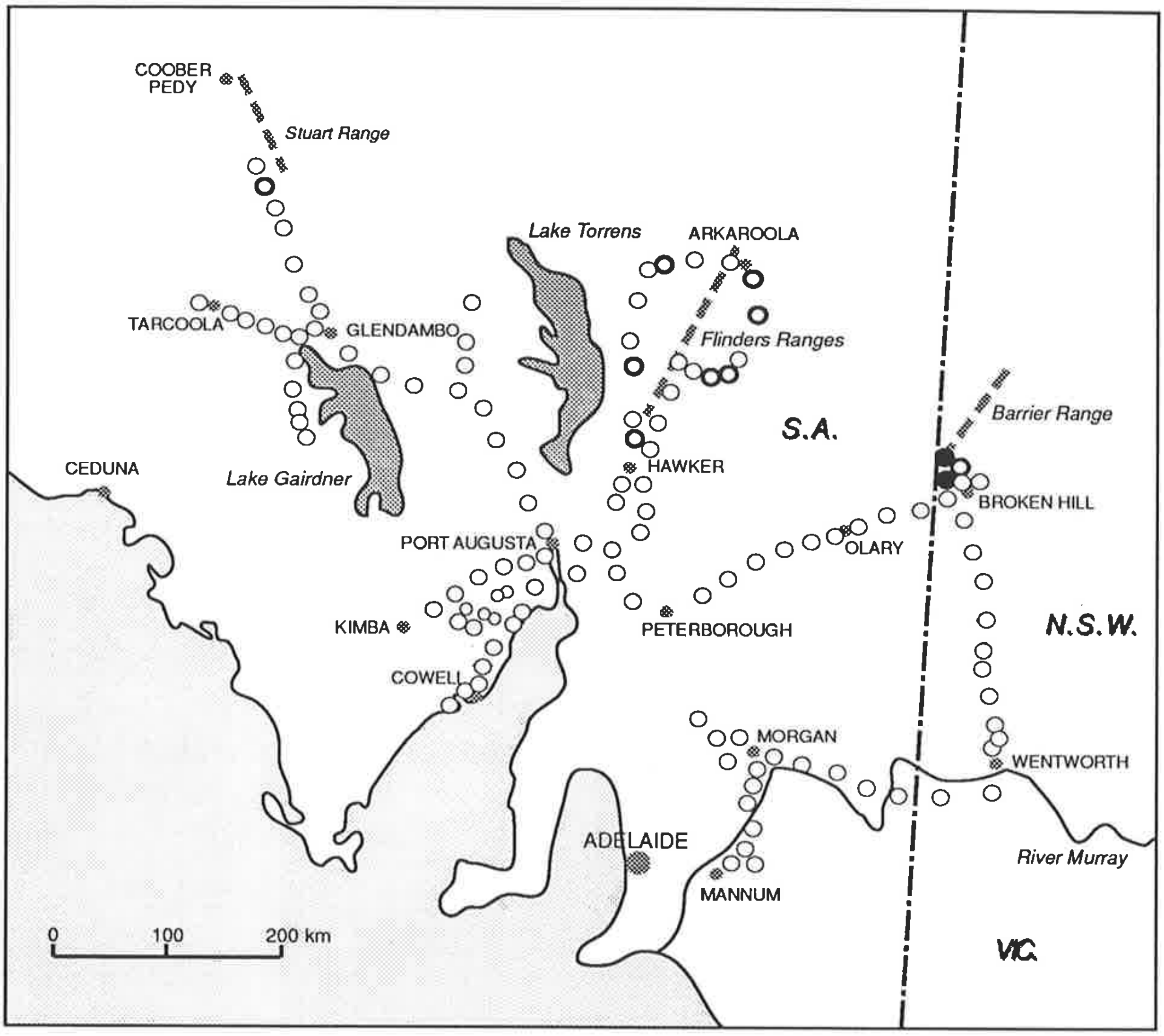


Figure 2.9c: Distribution map for the sub-types of vegetation Type 3 (*Maireana sedifolia/M. pyramidata* shrubland).



● Type 4-1 *M.astrotricha - Ptilotus obovatus*

○ Type 4-2 *M.astrotricha - M.sedifolia - Sclerolaena uniflora*

Figure 2.9d: Distribution map for the sub-types of vegetation Type 4 (*Maireana astrotricha* shrubland).

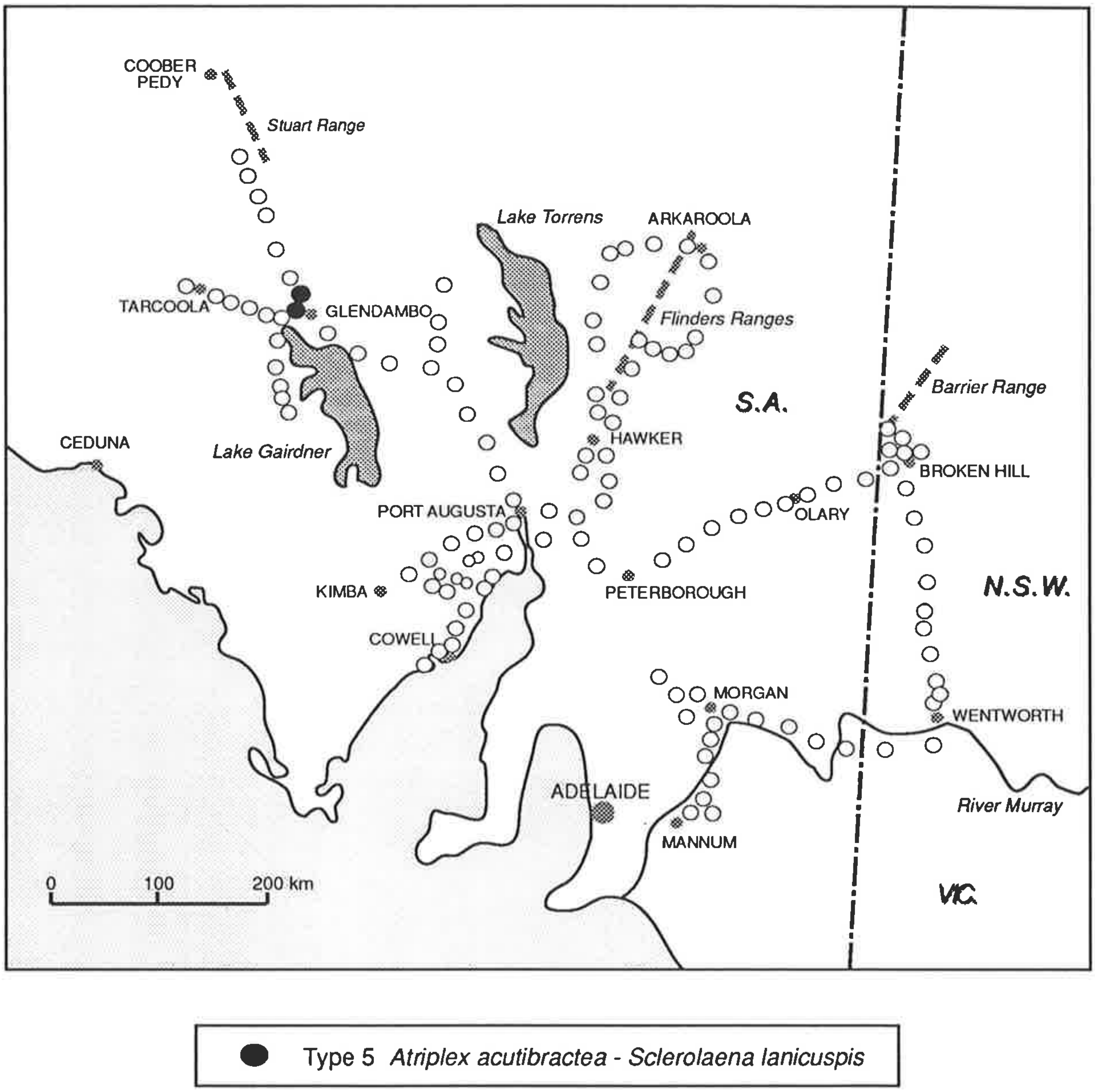


Figure 2.9e: Distribution map for the sub-types of vegetation Type 5 (*Atriplex acutibractea/Sclerolaena lanicuspis* shrubland).

The **Eucalypt Mallee woodland sites (Type 1)** were split into four Sub-types based on the predominant mallee species present. Sub-types 1-1,1-2 and 1-4 showed a strong similarity in understorey composition with a dominance of chenopod species such as *Maireana pentatropis* and *Enchylaena tomentosa*, while Sub-type 1-3 had a more sclerophyllous understorey dominated by members of the genera *Olearia*, *Eremophila* and *Westringia*. The distribution map clearly illustrates the southern distribution of this type.

The ***Atriplex vesicaria*-dominated shrubland (Type 2)** consisted of two sub-types. Type 2-1, occurring at 12 sites, was located over much of the northern part of the study region, with co-dominant species including speargrass (*Stipa* spp.) and low bluebush (*Maireana astrotricha*). Type 2-2, restricted to the top of the large mesa around Pimba, was co-dominated by the chenopods bindyi (*Sclerolaena* spp.) and samphire (*Halosarcia* spp.).

Three sub-types were delineated from **Type 3, *Maireana sedifolia/M.pyramidata* shrubland**. Of these, Type 3-1 (*M.sedifolia*) was most common. The 31 sites classified into this sub-type were encountered over much of the study area with a concentration in the area around Port Augusta. Other chenopod species commonly found in this sub-type include *Sclerolaena obliquicuspis,* blackbush (*M.pyramidata*) and saltbush (*A.vesicaria*). In addition, scattered trees of western myall (*Acacia papyrocarpa*), bullock bush (*Heterodendrum oleifolium*) and blackoak (*Casuarina cristata*) were locally important. Type 3-2 was restricted to 10 sites in the north-west of the study region. Here, mulga (*Acacia aneura*) dominated along with bluebush and *S.obliquicuspis.* Type 3-3 was observed in the eastern section of the region and was dominated by blackbush, saltbush and *S.obliquicuspis.*

The ***Maireana astrotricha* shrubland (Type 4)** was observed over the northern parts of the study area, and was particularly associated with the higher elevation regions such as the Barrier Range (north of Broken Hill), the Flinders Ranges and the Stuart Range (south of Coober Pedy). Type 4-1, recorded at two localities on the Barrier Range, was co-dominated by blackbush, *Ptilotus obovatus* and *Sida calyxhymenia* while the more widespread Type 4-2 was characterised by the presence of bluebush and *Sclerolaena uniflora.*

Finally, vegetation **Type 5 (*Atriplex acutibractea/Sclerolaena lanicuspis shrubland)*** was observed in the Kingoonya-Glendambo region. This type, identified at only two localities, included few other species.

Bluebush was observed as a structurally dominant or co-dominant species, and as an understorey species. It was present in three of the five main vegetation types, particularly dominating Type 3, where it was structurally dominant either on its own or with blackbush. It occurred to a lesser extent as a component of the understorey in the mallee vegetation type (Type 1) and as a structural co-dominant in the M.astrotricha community (Type 4). It was not found in those communities dominated by saltbush species (Types 2 and 5).

Bluebush was also a component in 9 of the 12 vegetation sub-types (Table 2.12). It was dominant or co-dominant in three of these (Types 1-2 E.gracilis, Type 3-1 M.sedifolia and Type 3-2 M.sedifolia/A.aneura) together representing 47 of the 105 sites considered in the reduced analysis (44.8%). Bluebush was particularly dominant in Types 3-1 and 3-2, where average cover scores tallied 3.3 (approximately 7% cover) and 4.3 (15% cover) respectively. It was observed less frequently in Types 1-1, 1-3, 1-4, 3-3, 4-1 and 4-2, where average cover scores ranged from 1 to 2 (up to 2% of cover).

Table 2.12: Estimations of bluebush frequency of occurrence and abundance for each of the vegetation types defined from classification.

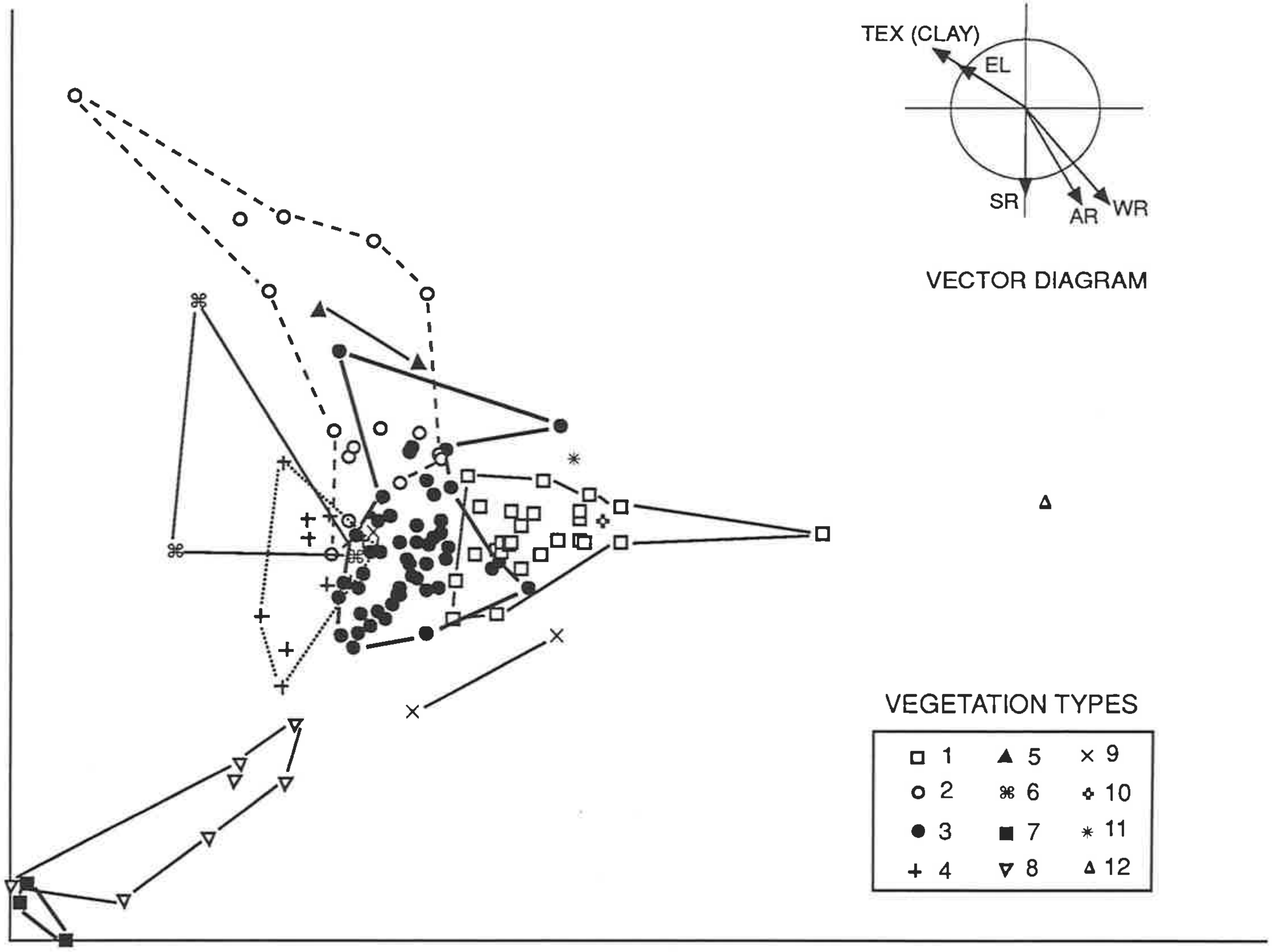
VEGETATION TYPE	# SITES	# SITES WHERE BLUEBUSH PRESENT	% OF SITES IN VEG TYPE	MEAN COVER SCORE
1 - 1	8	2	25.0	2.0
1 - 2	6	5	83.3	1.8
1 - 3	3	1	33.3	1.0
1 - 4	9	3	33.3	1.7
2 - 1	12	0	0.0	-
2 - 2	4	0	0.0	-
3 - 1	31	31	100.0	3.3
3 - 2	10	7	70.0	4.3
3 - 3	9	1	11.1	1.0
4 - 1	2	1	50.0	1.0
4 - 2	9	4	44.0	1.8
5	2	0	0.0	-

Ordination of Communities

Annual rainfall, soil texture and elevation are the most significant linear correlates with the DCA ordination axes, indicating a soil texture/rainfall gradient operating diagonally across the plot (Figure 2.10). The gradational patterns between many of the vegetation types are difficult to observe, however, due to the presence of several independent but equally important gradients which are acting in more than two dimensions on the ordination plot. In an attempt to alleviate some of this 'confusion', Vegetation Types 6 to 12 were removed from the analysis.

The resultant ordination scatterplot and associated vector diagram for the reduced data are shown in Figure 2.11a. One primary gradient was detected by the ordination, running approximately parallel to the first ordination axis. The annotations of vegetation types on to this scatterplot reveal a trend from mallee vegetation (Type 1), through *Maireana*-dominated shrubland (Types 3 and 4) to *Atriplex*-dominated shrubland from left to right along this gradient. There is also slight separation of some groups along a less distinct gradient which is acting diagonally across the plot. Examination of the relative position of vegetation sub-types in relation to the first two ordination axes reveals a degree of overlap between the vegetation types (Figure 2.11b). In particular, strong interdigitation of groups is shown for the mallee sub-types 1-1, 1-2 and 1-3 and the *M.sedifolia/M.pyramidata* sub-types 3-1 and 3-3.

The vector diagram associated with the second DCA ordination reinforces the conclusion that the vegetation gradient is acting primarily in a single direction, as all significant environmental variables lie in approximately the same direction (roughly parallel with the first DCA axis) (Figure 2.10 and 2.11a-b). Annual rainfall and soil texture are again the most significant of the examined environmental variables. Of the other variables considered, depth to sheet limestone, depth to other rock, soil pH and elevation also showed significant correlation with the DCA axes.


TEX (CLAY)
EL
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VECTOR DIAGRAM
VEGETATION TYPES
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✣ 10
✳ 11
△ 12

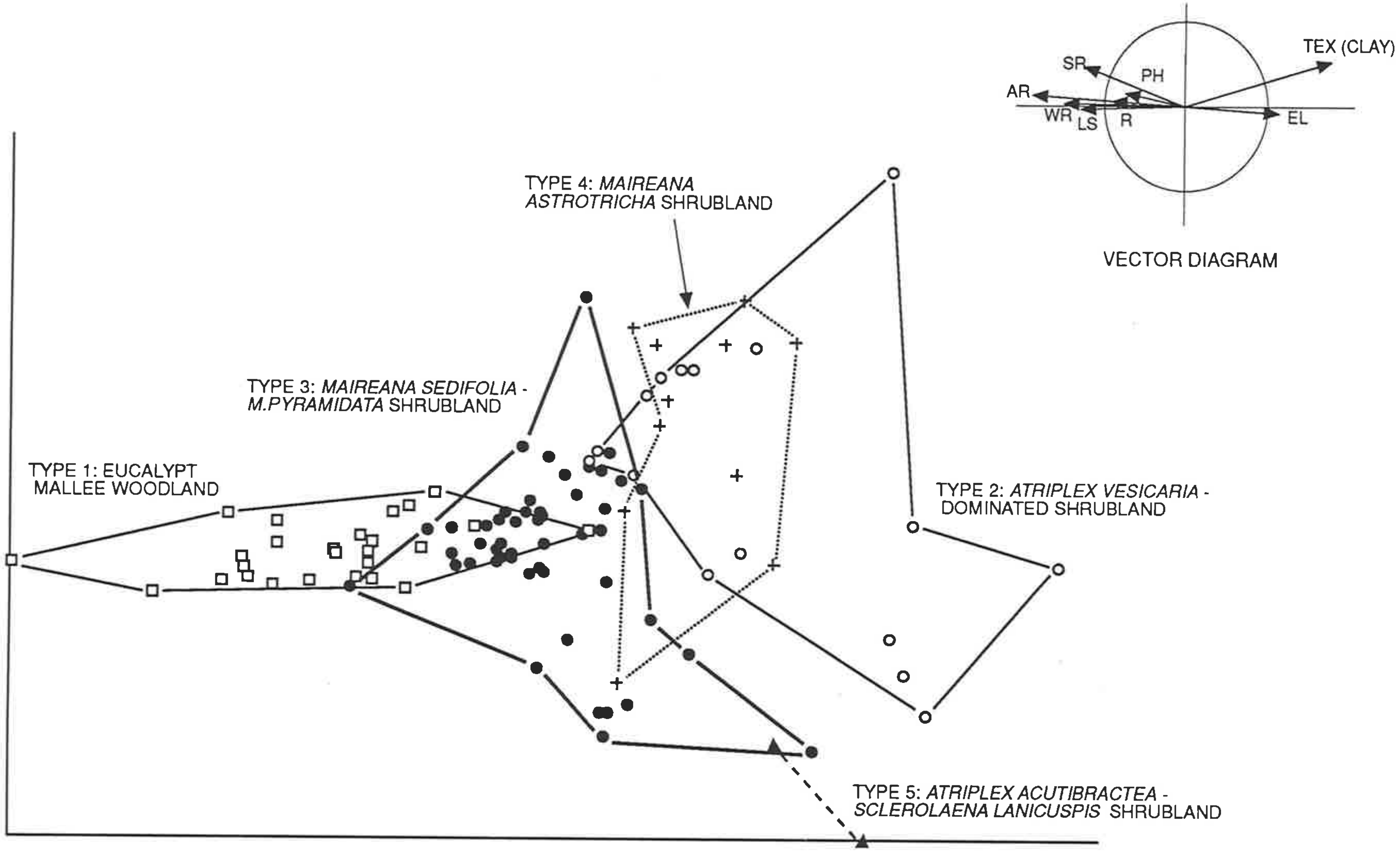


Figure 2.11a: The DCA ordination (axes 1 and 2) for the reduced data set (vegetation types 1-5). The classification from Figure 2.8 is superimposed to show the position of the vegetation types. The vector diagram indicates the rank correlations of environmental variables with the DCA axes as explained in Figure 2.10.

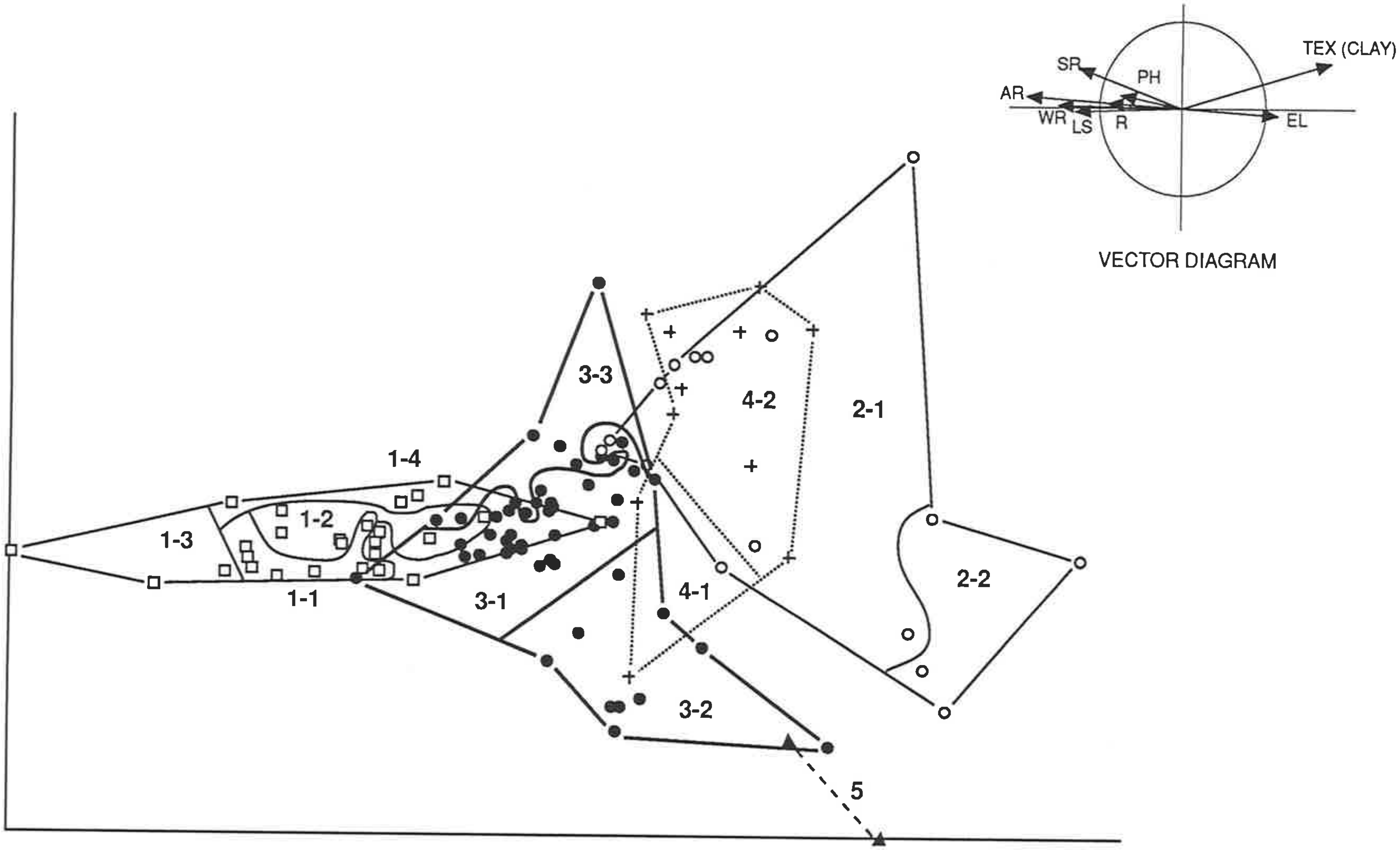


Figure 2.11b: The DCA ordination (axes 1 and 2) for the reduced data set (vegetation types 1-5). The classification from Figure 2.8 is superimposed to show the position of the vegetation sub-types. The vector diagram indicates the rank correlations of environmental variables with the DCA axes as explained in Figure 2.10.

Multiple Discriminant Analysis

The MDA shows rainfall was the most significant environmental factor in discriminating between the vegetation communities previously defined by classification, although winter rainfall was selected in the vegetation type analyses and annual rainfall in the sub-type analyses (Table 2.13a-b). Soil texture, topography, pH, depth to limestone (as nodules and sheet) and the presence of soil carbonates were also important descriptors.

The scatterplot of the first two linear discriminating functions for vegetation types and sub-types shows some separation of pre-defined groups. For vegetation types, function 1 (60.85% of the variation between groups) separates the mallee (Type 1) and *Maireana sedifolia/M. pyramidata* (Type 3) groups from the remainder along a gradient which primarily represents rainfall, soil texture and elevation, while function 2 (25.87% of variation) separates the *Atriplex*-dominated communities (Types 2 and 5) and Types 1 and 3 from *Maireana astrotricha* (Type 4) sites along a calcium carbonate gradient (Figure 2.12a). Bluebush communities appear to occupy a position midway along the first gradient and at the high carbonate/shallow limestone layer end of the second gradient. Group separation appears less distinct on the scatterplot for vegetation sub-types (Figure 2.12b). Function 1 (41.42% of variation) again represents a rainfall gradient, separating Types 5 (*Atriplex acutibractea/ Sclerolaena lanicuspis*) and 3-2 (*M.sedifolia/A.aneura*) at the 'dry' end of the gradient from Type 3-3 (*M.pyramidata/A.vesicaria*) and the mallee communities (Type 1) at the wetter end. There is some separation of groups by Function 2 (20.18% of variation), although this was not correlated to any of the measured environmental variables.

Using all discriminant functions, 63.81% of the sites were correctly assigned to the pre-defined vegetation types. Prediction was highest for the mallee type (Type 1) and lowest for the *Maireana sedifolia/M. pyramidata* (Type 3) and *Atriplex acutibractea/ Sclerolaena lanicuspis* (Type 5) groups (Table 2.14a). Group membership predictions were lower for vegetation sub-types (54.29% correctly classified; Table 2.14b). Sub-types 1-3, 2-2, 3-2, 4-1 and 5 were predicted in all cases while sub-types 1-4, 3-1 and 4-2 showed the lowest predictability.

Table 2.13: Variables accepted in the multiple discriminant analyses for vegetation types and subtypes. Significance of variables is tested using Wilks' Lambda. A summary of the main discriminant functions and their contribution to group separation is also given.

(a) Vegetation Types

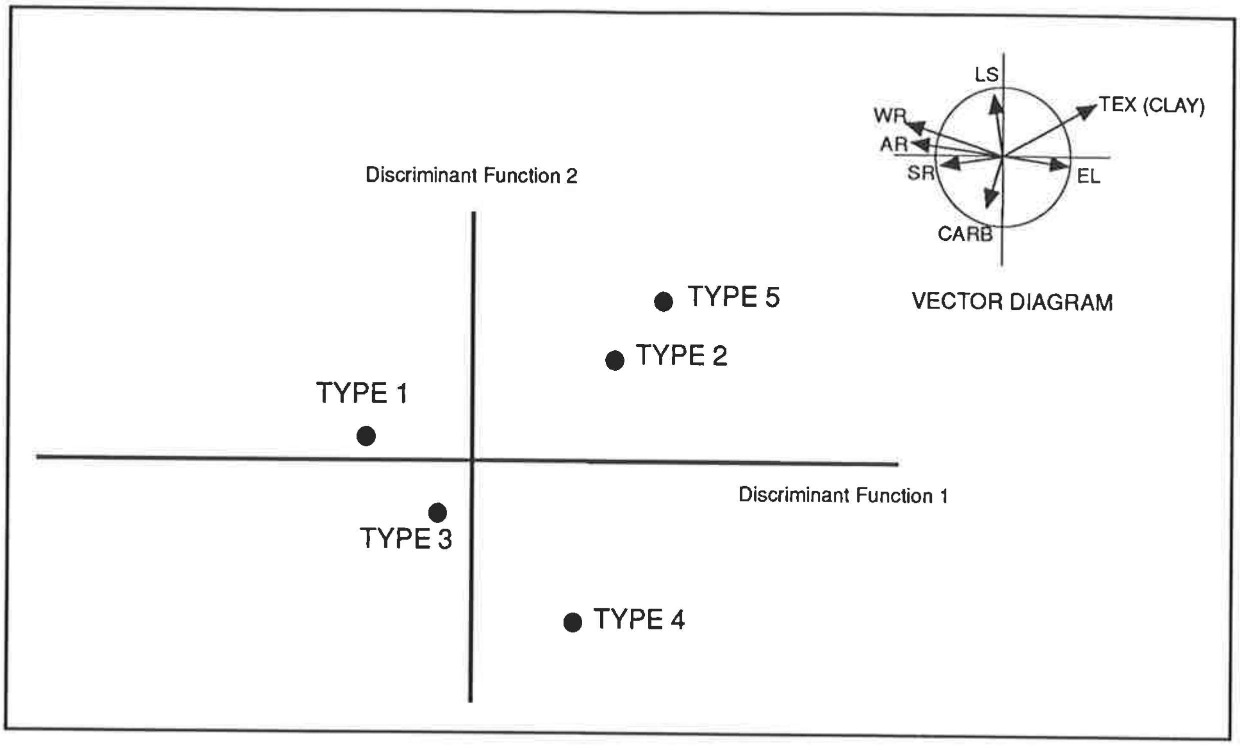
STEP	VARIABLE	WILKS' LAMBDA	PROB.
1	Winter Rainfall	0.7020	***
2	Soil Texture	0.5212	***
3	Topography	0.4623	***
4	pH	0.4213	***
5	Summer Rainfall	0.3860	***
6	Depth to Sheet Limestone	0.3519	***
7	Depth to Nodules	0.3200	***
8	Presences of Carbonates	0.2999	***
9	Elevation	0.2865	***

FUNCTION	VARIANCE EXPLAINED (%)	CUMULATIVE VAR.
1	60.85	60.8500
2	25.87	86.7200
3-4	13.28	100.000

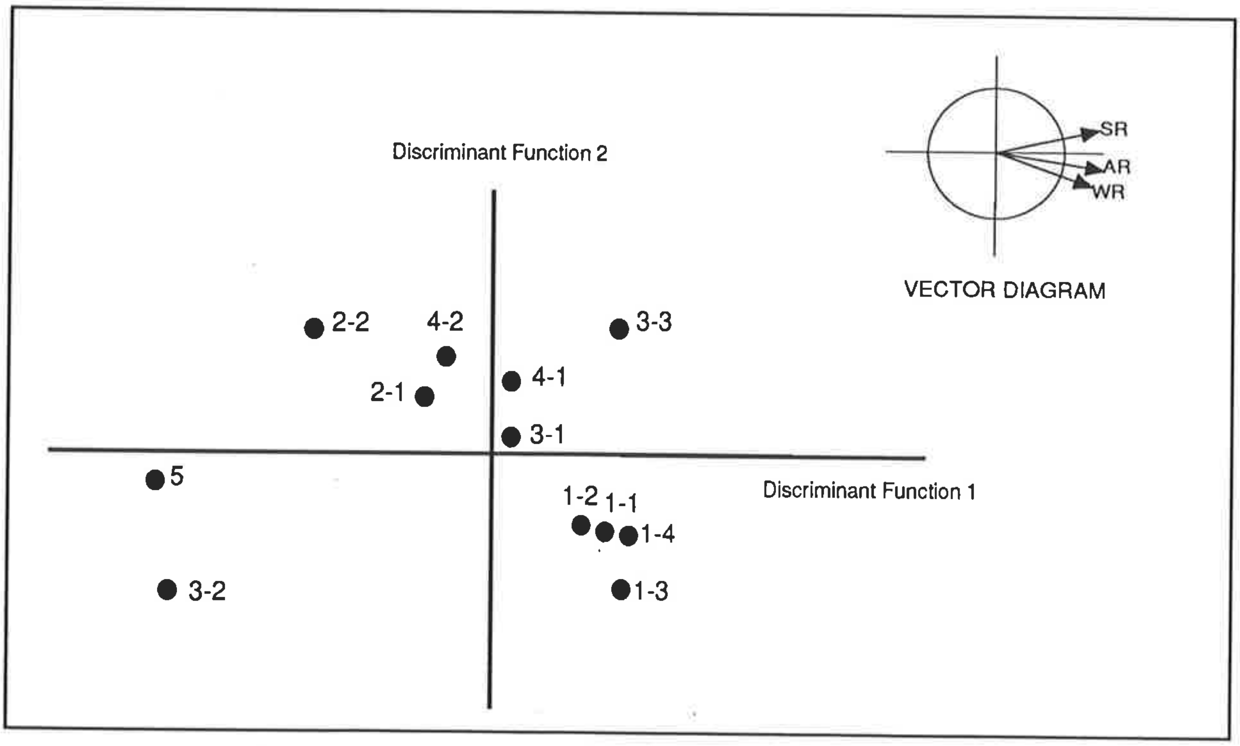
(b) Vegetation Sub-types

STEP	VARIABLE	WILKS' LAMBDA	PROB.
1	Annual Rainfall	0.5181	***
2	Soil Texture	0.3444	***
3	Summer Rainfall	0.2407	***
4	Elevation	0.1609	***
5	Depth to Nodules	0.1214	***
6	Depth to Sheet Limestone	0.0931	***
7	Topography	0.0734	***
8	pH	0.0599	***
9	Depth to Other Rock	0.0514	***
10	Presence of Soil Carbonates	0.0453	***

FUNCTION	VARIANCE EXPLAINED (%)	CUMULATIVE VAR.
1	41.42	41.42
2	20.18	61.61
3-11	38.39	100.00



(a) Vegetation Types



(b) Vegetation sub-types

Figure 2.12: Multiple discriminant analysis plots of the catenation of the centroids of the vegetation types and sub-types. Correlations of environmental variables with each of the discriminant functions is shown as for the environmental correlations with DCA ordination axes (Figure 2.10).

Table 2.14: Classification of Vegetation Types and Sub-types from the discriminant analysis.

(a) Vegetation Types 1 to 5

ACTUAL MEMBERSHIP	PREDICTED GROUP MEMBERSHIP				
	Type 1	Type 2	Type 3	Type 4	Type 5
Type 1	80.8	7.7	11.5	0.0	0.0
Type 2	6.3	75.0	6.3	12.5	0.0
Type 3	16.0	14.0	52.0	12.0	6.0
Type 4	0.0	36.4	0.0	63.6	0.0
Type 5	0.0	50.0	0.0	0.0	50.0

(b) Vegetation Sub-types 1-1 to 5

ACTUAL MEMBERSHIP	PREDICTED GROUP MEMBERSHIP (SUB-TYPE)											
	1-1	1-2	1-3	1-4	2-1	2-2	3-1	3-2	3-3	4-1	4-2	5
Type 1-1	25	12.5	25	25	12.5	0	0	0	0	0	0	0
Type 1-2	0	66.7	0	16.7	0	0	0	0	16.7	0	0	0
Type1-3	0	0	100	0	0	0	0	0	0	0	0	0
Type1-4	22.2	22	11.1	44.4	0	0	0	0	0	0	0	0
Type 2-1	8.3	0	0	0	50	0	8.3	25	0	0	8.3	0
Type 2-2	0	0	0	0	0	100	0	0	0	0	0	0
Type 3-1	6.5	22.6	3.2	3.2	3.2	6.5	35.5	3.2	6.5	0	6.5	3.2
Type 3-2	0	0	0	0	0	0	0	100	0	0	0	0
Type 3-3	11.1	0	0	0	11.1	11.1	0	0	66.67	0	0	0
Type 4-1	0	0	0	0	0	0	0	0	0	100	0	0
Type 4-2	11.1	0	0	0	11.1	0	0	11.1	0	22.2	44.4	0
Type 5	0	0	0	0	0	50	0	0	0	0	0	50

DISCUSSION

DISTRIBUTION OF BLUEBUSH

Distribution Patterns within the Study Area

Bluebush was the most commonly encountered shrub species within the study region, occurring in all four sub-regions; this is not surprising given that the study area was selected to encompass much of the known distribution of bluebush. This actual pattern of distribution, however, corresponds well with the previously recorded distributions of this species; comparison with the composite map (derived from community-based surveys and anecdotal observations; Figure 1.4) indicates little difference in the observed distributions of bluebush. Climatically, bluebush is restricted to the rainfall range suggested earlier, with the driest sites occurring in the north-western populations. While Hall *et al.* (1964) stated that this species is restricted to the winter rainfall belt, more recent descriptions of the seasonal rainfall regions of Australia would position the northern half of its distribution in the uniform rainfall belt. Sites in the north-west and east in particular fall into this climatic region.

Environmental Influences Controlling Distribution

Eldridge (1988) suggested that soil water availability primarily controls the distribution of Australian chenopod shrubs. Results presented here support this statement; all environmental factors included in the species response models for bluebush and the three comparison chenopods may influence the availability of water in the soil.

Rainfall

Rainfall variables, an obvious factor influencing moisture availability, can be used as a good predictor of *Maireana* species distribution within the study area. Bluebush distribution patterns, in particular, were closely related to the amount of rain falling in the summer months (October to March). Similar correlations between species distribution patterns and rainfall have been observed for the Australian species *Maireana erioclada* and *Callitris verrucosa* in addition to several species from the genus *Eucalyptus* (Sparrow, 1991). North American examples showing relationships between rainfall and plant distribution patterns include *Larrea tridentata* (Beatley, 1974) and sub-species of *Artemisia tridentata* (Bonham *et al.*, 1991).

The observed bell-shaped (Gaussian) response to summer rainfall is derived from the concept of physiological optima, as proposed by Ellenberg (1954). This concept suggests that the distribution pattern of a species over its geographic range arises from both the physiological requirements and tolerances of the species and the competitive availability of resources. A species 'importance value' is generally greatest at the centre of its environmental range, becoming less important towards tolerance extremes (Westman, 1980; Gauch, 1982; Greig-Smith, 1983). Evidence indicates, however, that most distribution curves along major environmental gradients are distorted by other minor environmental factors causing skewness, bimodality or flattening of the basic bell shape (Austin, 1976; Westman, 1980). For bluebush, the response to summer rainfall was approximately bell-shaped, with the highest frequency of occurrence when falls averaged 90-120 mm over the summer period (Figure 2.6). Saltbush showed a similar response to summer rain although this factor was not included in the species response model. In contrast, monotonic responses were observed for low bluebush (*M. astrotricha*) and blackbush; the former species clearly dominated in low summer rainfall areas while the frequency of blackbush increased at the wetter end of the gradient. Such results suggest that the optimum amount of summer rainfall for these two species lies beyond the limits of the examined rainfall gradient. Both species might be expected to exhibit Gaussian responses to summer rainfall if their distributions were examined over a wider section of the gradient. Similarly, all four species would be expected to show approximately bell-shaped responses to winter and annual rainfall because of the high degree of autocorrelation between the rainfall variables.

Depth to Limestone/Presence of Carbonates

A strong relationship was detected between bluebush presence/absence and the occurrence of calcium carbonate in the soil. This preference has been reported previously (Osborn and Wood, 1923; Prescott, 1931; Osborn *et al.*, 1935; Beadle, 1948; Cunningham *et al.*, 1981) and has led to bluebush being described as 'calcicolous' (Osborn *et al.*, 1935). Jeffrey (1987) disputes the use of this term, however, believing that it suggests a resource requirement rather than a tolerance for adverse factors. As he points out, the presence of carbonates indicates an extreme habitat where there is often a reduction in nutrient availability and changes in soil moisture.

Carbonates in the soil influence water availability primarily when they are present as a barrier (or layer) in the soil. Cunningham and Burk (1973) illustrated this control during a study examining the water status of *Larrea* shrubs in southern New Mexico. Here, "caliche" (or limestone) was shown to influence the amount of water available to plants following rainfall, with variations due to the depth to limestone, the amount of rainfall and the rooting depth of individual plant species. They concluded that the shallow-rooted *Larrea* plants were favoured on limestone soils receiving only small rainfalls (as the water did not penetrate to any great depth), while deeper-rooted species were advantaged during heavier rainfalls. In the latter case, water penetrated down the soil profile through the carbonate layer to become available only to those plants with deep roots.

On limestone soils, deep-rooted bluebush shrubs may be similarly advantaged over more shallow-rooted species (such as saltbush), particularly as many of the rain events occurring during summer can be considered as "heavy" (Jackson, 1958; Noble, 1979; Reid, 1984). As a consequence, it is not surprising that the highest frequency of bluebush occurrence was on the shallowest soils where the ability to penetrate through the limestone layer would have the greatest influence on water availability, and hence plant growth and survival. This competitive advantage is also suggested by the inclusion of the summer rainfall x depth to nodules interaction into the bluebush model, which reveals that with decreasing summer rainfall this species is more commonly found on progressively shallower soils overlying nodular limestone. At these drier sites, shallow-rooted species may be restricted by the limited amount of soil available over the limestone; this hypothesis is supported, at least in part, by the negative relationship between saltbush occurrence and nodules at shallow depth (as shown in Figure

2.5a). Although this appears a plausible explanation, it is unclear as to why an interaction between summer rainfall and depth to sheet limestone was not included in the bluebush model. Similar conclusions relating the importance of wetting depth on the distribution of bluebush and saltbush were reached by Carrodus and Specht (1965). They suggested that bluebush is restricted to soils which are deep-wetting (60 cm or more) while saltbush occurs on soils with a heavy clay subsoil or hardpan which impedes water penetration beyond 30 cm.

The presence of soil carbonates may influence species distribution patterns via the control of nutrient availability. Calcareous soils often exhibit lower absolute quantities of major nutrients, sub-optimal availability of all nutrients and a reduced cation exchange capacity. Positive aspects of high carbonate levels include plentiful calcium cations, useful for membrane function and cell development, and the availability of nitrogen as nitrate (Jeffrey, 1987). Such variations in the supply of nutrients have been shown to influence the growth of many plant species (Grime, 1965; Lloyd and Pigott, 1967) and may be particularly important when considering the occurrence of bluebush and blackbush which both show a positive relationship between species presence and high soil carbonate levels. Specific mineral nutrition trials are needed to test these ideas.

Other Factors

Three other environmental factors could be used as predictors of chenopod distribution patterns within the study region; soil texture, topography (both included in the saltbush model) and elevation (included in the low bluebush model).

Walter and Stadelmann (1974) and Noy-Meir (1974) have discussed the implications of soil texture changes on the availability of water stored in the soil profile. Both studies concluded that the increases in particle and pore sizes associated with sandy soils produces lower runoff and deeper penetration of rainfall, a decrease in the loss of water by surface evaporation and a lower potential for extraction by roots. Accordingly, a preference for heavy-textured soils (those with a higher clay content) may indicate a tolerance to low levels of moisture in the soil.

Additionally, however, it is suggested that the preference of saltbush for heavy soils may also indicate a tolerance to high levels of total soluble salts (TSS) in the soil. There is a high level of autocorrelation between these variables (r_S=0.3575, d.f. 123, $P<0.001$). This tolerance of high salt levels in the soil is not surprising and has been reported previously (Beadle, 1960; Charley, 1965; Williams, 1979). As a halophyte, saltbush has a lower growth rate and is less competitive under less saline conditions (Williams, 1979).

Topography was also included as a useful predictor of saltbush distribution, with the negative estimate indicating a preference for plains and slight slopes over hills. Again, this may indicate a water availability effect. Walter and Stadelmann (1974) illustrated how hills and ridge-tops with shallow soils and high levels of exposed rocks acted in a similar manner to deep sands. In contrast to these environments, plains and slight slopes are usually more xeric.

The inclusion of elevation into the low bluebush (*M. astrotricha*) model may be somewhat spurious as only a small area of this species' distribution was sampled. While low bluebush is known to occur in the more northern regions of South Australia and adjacent states, in this study such sites were located predominantly in areas of high elevation (such as the Barrier Range, Flinders Ranges and Stuart Range). Only a limited number of sampling sites were positioned on the gentle slopes and plains where this species has been recorded previously (see Jessup, 1951 and Wilson, 1975). Therefore, it is suggested that rainfall may be a more ecologically meaningful overall predictor of low bluebush distribution than elevation.

Individual Species Niches

The chenopod species response models indicate that although the availability of water in the soil appears to be the major factor influencing distribution patterns, the realised niches of each species remains difficult to describe. This is particularly so because of the high degree of species co-occurrence at individual sites[1] and the similar morphologies of some of the species. Such co-existence may be possible because of the slow growth rates of shrubs and the lack of structural superiority of any particular species; it is possible that two species may co-occur as long as germination and seedling establishment has occurred in areas left vacant following plant death or disturbance.

Despite this high degree of species co-occurrence, it is possible to characterize broadly the environments in which the four examined chenopod species tend to dominate; differences between species appear to occur as a result of variation in the innate physiological water requirement of each species, the tolerance to adverse factors, including nutrient and salinity levels, and also some morphological attributes. The morphological and physiological characteristics of bluebush lead it to be dominant on the lighter texture soils where a majority of the water is maintained deep in the soil profile. Here, the deep and extensive tap-root system is able to reach this water, giving bluebush an opportunity to avoid competition with shallow-rooted species by providing a stable reserve of water which can be used slowly and regularly during dry periods to maintain perennial structures and a reasonable rate of photosynthesis (Williams, 1979). Bluebush appears to be unable to tolerate more arid conditions, however, being replaced by low bluebush (*M. astrotricha*) in areas with less rainfall; this suggests that the latter species may be more physiologically-adapted to drought tolerance than bluebush. Little is known of this species, however, and this can only be speculated at this time. Bluebush was not found in some of the areas occupied by saltbush, possibly as a result of a combination of salinity and water availability effects. As saltbush is shallow-rooted and exhibits faster growth, this species dominates in areas where water is maintained high in the soil profile, such as in clay soils. It may also tolerate more saline conditions (Williams, 1979). Blackbush can possibly be considered a 'less arid' species than bluebush; this species tends

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[1] Examination of the raw data shows the co-occurrence of two chenopod species at 43 sites, 3 species at 13 sites and 4 species at at single site. The following combinations were also noted: *M.sedifolia* & *A.vesicaria* - 26 sites, *M.sedifolia* & *M.pyramidata* - 20 sites, *M.sedifolia* & *M.astrotricha* - 8 sites, *A.vesicaria* & *M.pyramidata* - 16 sites, *A.vesicaria* & *M.astrotricha* - 10 sites and *M.pyramidata* & *M.astrotricha* - 8 sites.

to dominate in areas where there is a greater availability of soil water, such as washes and run-on areas, and was not observed at all in areas of low rainfall.

The bluebush response model demonstrated a better fit than the comparison models (r^2=0.316 compared to 0.126-0.172 for the other models), although possibly a result of the comparatively high numbers of bluebush occurrences in the data set. It appears likely that the distribution of bluebush may be more geographically isolated than the other chenopods examined and that this species may respond to wide environmental extremes (Sparrow, 1991).

Variations in Size and Abundance

The variations in size and abundance of bluebush over the surveyed range can be also be correlated to patterns of environmental factors which may be related either directly or indirectly to soil moisture levels.

Although there was a higher frequency of occurrence on limestone soils, the size of the individual bluebush shrubs was reduced when the limestone layer was close to the surface. As discussed earlier, the presence of a limestone layer can alter both soil water relations and nutrient availability, and generally indicates an extreme habitat (Jeffrey, 1987). The results presented here lend support to the idea proposed by Jeffrey that the presence of a species on carbonate soils represents a tolerance of adverse factors rather than a resource requirement. It is most likely that bluebushes growing on shallow soils overlying limestone are located in more stressful environments and hence are reduced in size.

Bluebush abundance was correlated to several of the measured environmental factors. The most obvious of these factors to show relation to the availability of moisture in the soil profile is rainfall; plant numbers and overall % cover and biomass estimates were shown to increase with increasing rainfall in the winter months. Observations did show a trend of increasing plant size and abundance along the north-west to south-east diagonal rainfall gradient. Such a response is not surprising in a water-driven environment, and has previously been demonstrated for *Larrea* species by Woodell *et al.* (1969), Barbour and Diaz (1973) and Barbour *et al.* (1977). These studies, however, have shown significant correlation between plant abundance and annual rainfall. For example, Woodell *et al.* (1969) demonstrated the relationship between plant density and annual rainfall for *Larrea divaricata*, revealing a "fairly good"[1] correlation between these factors. With removal of one data point from the analysis (which was considered to be unusual as the plants were subject to continuous high wind and were obviously different in habit), the correlation of density with rainfall was stated to be "very close".[2] In my study, a significant positive correlation between winter rainfall and density estimates was shown. This finding is particularly interesting given that the species response model indicated that the amount of summer rainfall is the best predictor for bluebush presence/absence. These results may suggest that the amount of rain received during the hot summer months, when drought effects would be most prominent, limits the distribution (*i.e.* the regeneration niche) of this species, while the rain received during winter may govern the biomass that can be supported.

Depth to sheet limestone was positively correlated to all of the abundance measures indicating that bluebush was more abundant on soils in which the sheet limestone layer was located at greater depths. Presumably, this relationship may indicate similar circumstances to those discussed for plant size. A comparable relationship between bluebush abundance and depth to nodular limestone was not generally detected; this may relate to differences in water availability in sheet and nodular limestone.

Topography and elevation showed negative correlations with bluebush abundance, suggesting that bluebushes were less dense and of less overall % cover and biomass when located in areas of high elevation/sloping topography (locations previously said to have higher

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[1] A correlation analysis of the data presented in Table 2 of (Woodell *et al.*, 1969) gave the following: $r_s=0.658$, n=11, p=0.03

[2] $r_s=0.793$, n=10, p=0.01.

water availability[1]). Although this may be surprising at first glance, such a result may be explained on examination of bluebush distribution patterns and the location of areas of high elevation/ sloping topography within the survey region. Observations clearly show that these topographical zones are restricted to the northern portion of the survey region, at the northern distribution limits of bluebush. As there is likely to be a decreased probability of limestone in the ranges due to geological patterning, and as less annual rainfall is recorded in this area, a decrease in bluebush abundance would not be unexpected.

Finally, soil texture appeared to have an influence on the abundance of bluebush, with higher plant numbers and percentage cover estimates in areas with heavier soil. Although this may appear a surprising result given that sand and loam soils have increased water availability compared to clay (Walter and Stadelmann, 1974), it may also indicate that other factors such as the rainfall regime and soil depth are influential. Examination of the data does suggest that this correlation may be misleading; further analysis revealed significant autocorrelation between soil texture and winter rainfall for those sites where bluebush was present.[2] This positive association demonstrates that heavier-textured soils were generally located in areas with greater winter rainfall. As a consequence, the abundance of heavy soil texture does not necessarily imply a decrease in the amount of soil moisture available. Alternatively, the decrease in bluebush abundance on sandy soils may reflect a competitive effect. In this more favourable environment, bluebush may be partially replaced by faster-growing, more competitive species which can obtain sufficient water for survival.

Analysis of the data also revealed correlation between bluebush size and abundance measures. A strong correlation was detected between individual shrubs and the total % cover and biomass estimated, suggesting that shrubs get larger with increasing overall coverage. Previous discussions indicate that these increases occur as a result of increased soil water availability. Although not statistically significant, there was also a trend for decreasing plant

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[1] As discussed in the section *Environmental Influences Controlling Distribution*
[2] Rank correlation analysis gave the following: $r_s=0.268$, d.f.=57, $0.01<P<0.05$.

numbers (*i.e.* densities) with increasing plant size. A possible interpretation of this result suggests that decreases in density occurred following intraspecific competition among individual bluebushes. It is hypothesised that larger plants require larger areas for resource acquisition, leading to a reduction in the density of plants (White and Harper, 1970). As the distribution, size and abundance of bluebush were all shown to be linked to soil water availability, competition for this resource is most likely. Such effects are examined in detail in Chapter 3.

COMMUNITY STUDIES

Vegetation Communities - Comparison with the Literature

Bluebush was observed as an important component in many of the vegetation types and subtypes detected in the survey region, both as a structural dominant or co-dominant and as an understorey species. It was found to commonly co-occur with mulga (*Acacia aneura*), western myall (*Acacia papyrocarpa*), mallee (particularly *Eucalyptus gracilis*) and blackbush (*M. pyramidata*) as well as forming almost mono-specific stands. The communities defined in this study compare favourably to those reported in the literature despite appearing rather discordant at first glance. The differences arise mainly from the decision to use the most common and characteristic species as group identifiers, rather than the more conservative approach of using structural dominants (*i.e.* tree species). These latter species were not generally included as community descriptors in this study as they were patchy in distribution and only of local importance.

The bluebush communities described in this study are very similar to those previously reported. The mallee associations (Type 1) correspond well to the mallee communities of Crocker (1946), Jessup (1948), Beadle (1948) and Hawke (1986), although in these previous studies vegetation associations were generally characterised by three or four species of eucalypt rather than a single species. Hawke (1986), in his study of the biogeographic boundary separating the arid and temperate zone on north-eastern Eyre Peninsula, S.A., also delineated mallee associations on the basis of undestorey species. Two mallee associations were identified; one with a chenopod understorey and the other with a mixed chenopod/ sclerophyllous understorey. These roughly correspond respectively with the mallee vegetation subtypes (Types 1-4 and 1-1 to 1-3) described in this survey.

The *Maireana*-dominated chenopod shrubland associations (Types 3 and 4) have been variously described in the past. Type 3-1 (*M.sedifolia* shrubland) appears to encompass several of the vegetation communities reported including the *A.papyrocarpa-C.cristata* edaphic complex of Crocker (1946), the *M. platycarpum* and *C.cristata* communities of Jessup (1948), the *A. papyrocarpa* community of Jessup (1951), the *M.platycarpum/A.papyrocarpa* association of Crocker and Skewes (1941), the *M.platycarpum* community of Osborn and Wood (1923) and the *A.papyrocarpa/M.sedifolia* association of Hawke (1986). This vegetation subtype may also encompass the *A.vesicaria/M.sedifolia* communities of Collins (1923), Osborn and Wood (1923) and Beadle (1948) and the *M.sedifolia/M.pyramidata* communities of Collins (1923) and Osborn and Wood (1923). Vegetation Type 3-2 (*Acacia aneura* with *M.sedifolia* understorey) appears to correspond with the mulga communities described by Murray (1931), Beadle (1948) and Jessup (1951). Bluebush was also a relatively common component of vegetation Type 4-2 (*M.astrotricha* shrubland). This association appears most similar to the *M.astrotricha/M.sedifolia* community described by Jessup (1951) in the north-west of South Australia.

Comparisons between these published communities and those identified during this study raise several points for comment. Firstly, it should be noted that many of the previously-defined associations were clustered together in this study. This is most likely to occur as a consequence of sampling over a much wider area than the comparison surveys. Secondly, with additional examination of the raw data, it can be concluded that not all species associations were recorded with similar frequencies to those reported in the literature. Only a few sites were shown to be *M.platycarpum/M.sedifolia* or *C.cristata/M.sedifolia* dominated despite large portions of the survey area being previously classified as such. As my personal observations would suggest that these species associations do occur more frequently than indicated by this study, the lack of recordings in this instance may be linked more strongly to site placement than rarity of association. In contrast, bluebush and saltbush occurred together only infrequently, despite the many references to mixed *A.vesicaria/M.sedifolia* communities (e.g. Osborn and Wood, 1923; Beadle, 1948; Jessup, 1951). Bluebush was not present in the saltbush-dominated communities (Type 2), while saltbush was recorded as only a minor part of Type 3-1, occurring with a cover score in excess of 2 (*i.e.* greater than 2% projected foliage cover) for only 2 of the 31 sites. Additionally, no equivalent to the *M.sedifolia/ Maireana triptera/Ptilotus obovatus* community recorded by Jessup (1951) was noted in this study. A comment should also be made regarding the inclusion of the mulga vegetation association by Beadle (1948). Although only identified in the north-west portion of the current survey, Beadle's observations indicate a more easterly distribution of this association; bluebush was said to be abundant in the understorey of the mulga association in north-western New South Wales. Although it may have been present in unsampled, isolated locations within the eastern section of the study region, it is more likely that this association would have been encountered if the survey was extended further to the east.

Ordination of Communities

The main floristic gradient detected during ordination is observed approximately parallel to the first axis on the partial ordination plot. This demonstrates the transition from mallee with sclerophyllous understorey, through mallee with chenopod understorey to chenopod-dominated shrublands with scattered tree species. Some separation of subtypes was observed along the second ordination axis although this was less distinct and did not appear to indicate a single parallel gradient.

The most striking feature of the ordination plots, however, is the strong overlap of vegetation communities; very few of the vegetation types and sub-types appear as clearly delineated clusters. Particularly high degrees of overlap were observed between the *Maireana* *sedifolia/M.pyramidata* (Type 3) communities and the mallee communities with chenopod understorey (Types 1-1,1-2 and 1-4), and between the *Maireana astrotricha* (Type 4) and *Atriplex vesicaria* (Type 2) vegetation types. Much of this overlap results from high levels of floristic continuity between groups, particularly among the chenopod species. Species co-occurrence among this group was demonstrated to be common during examination of individual chenopod species distributions; this arises as a result of similarity in habitat requirements.

Additionally, the overlap between the mallee and bluebush communities reveals an independent change in understorey and overstorey species along the environmental gradient. Clearly, the transition from sclerophyll to chenopod species in the understorey did not correspond to the overstorey change from eucalypt mallee species to *Acacia*, *Casuarina* and *Myoporum* species, although they appeared to be responding to the same environmental gradient. A similar phenomenon has been noted previously by Wood (1929, 1937), Noy-Meir (1971, 1974) and Sparrow (1991). In the latter study, this effect was observed during the examination of the distribution patterns of mallee communities further to the south of the current study area. Sparrow was able to show a shift in the overstorey species (from *E. diversifolia* to *E.incrassata-E.foecunda* and then *E.socialis)* which did not correspond to shifts in the understorey species (from calciphilic subshrubs to *Melaleuca uncinata* then *Triodia irritans* and finally chenopod shrubs).

Environmental Correlations

Soil water availability is strongly implicated in the distribution patterns of vegetation communities within the survey region. In both the full and partial ordination analyses, and in the multiple discriminant analyses (MDA), the primary vegetation gradients were correlated with rainfall and soil texture. These factors interact to alter water availability down the soil profile (Noy-Meir, 1971; Walter and Stadelmann, 1974) as explained for the individual species response models. Similar conclusions regarding the primary controls of the distribution of plant communities in south-eastern Australia have been reached by several authors including Noy-Meir (1971, 1974), Hawke (1986), and Sparrow (1991).

In this study, the left to right trend for decreasing rainfall/heavier-textured soils across the partial ordination plot would imply a decreasing water availability. Annotation of vegetation types onto this plot suggests that, as would be expected, the mallee communities occur at the mesic end of the gradient while the saltbush-dominated communities are positioned toward the xeric end. The communities in which bluebush frequently occurs occupy a midway position along this gradient. Additionally, the rainfall/soil texture gradient can be seen to be modified by other minor environmental factors. While these do not represent gradients which exist across all vegetation groups, their inclusion does provide further environmental distinction between some of the vegetation communities.

The environmental factors important in the delineation of vegetation sub-types are more difficult to specify. The large degree of overlap on the ordination and MDA plots and a lower rate of prediction for vegetation subtypes (compared to types) by the MDA analysis implies floristic continuity and habitat overlap between many of the communities. However, some of the vegetation subtypes could be visually separated on the ordination and MDA plots; not surprisingly, these correspond to communities where group classification was predicted most successfully. Mallee eucalypt subtypes were sorted along axis 1 to a certain extent by rainfall and soil type; Type 1-3 (*E.oleosa/E.gracilis* woodland with sclerophyllous understorey) was restricted to coarser-textured soils in higher rainfall areas, while Types 1-1, 1-2 and 1-4 (mallee woodland with chenopod understorey) were present in areas with a slightly lower rainfall and on variable soil types where a limestone layer may be present. Factors leading to the separation of the mallee community with a bluebush understorey (Type 1-2) and those with a mixed chenopod understorey cannot be determined accurately from either the ordination or MDA analyses. Similarly, identification of environmental variables distinguishing sub-types of Types 2, 3 and 4 are also ambiguous. These groups were generally separated along ordination axis 2, to which none of the measured environmental variables were significantly correlated. Subtypes of the *Maireana sedifolia/M.pyramidata* community (Type 3) are distinguishable to a limited extent along the water availability gradient; sites classified as Type 3-2 (*A.aneura/M.sedifolia*) are located further towards the xeric end of the gradient than the sites classified into Types 3-1 (*M.sedifolia*) and 3-3 (*M.pyramidata/A.vesicaria*). Individual species response results suggest that the features characterising these latter two types may relate to depth to limestone, soil depth, pH and elevation, although more specific community analysis studies would be required to confirm these ideas.

Overall, the lack of correlation between the measured environmental variables and the vegetation subtypes, particularly the bluebush communities, suggest that observed differences must arise primarily as a result of influences from alternative, untested variates. Possible factors proffered as influences on vegetation community distributions in southern Australia but which were not examined in this study include the co-occurrence of episodic climatic events, historical factors and disturbance due to fire or grazing (Noy-Meir, 1971; Tiver *et al.*, 1989; Sparrow, 1991; Ireland, 1992).

CONCLUSIONS

- Bluebush distributions noted in this study agree closely with those previously described.

- Bluebush distribution was related to soil water availability and the tolerance of high soil carbonate levels. Highest frequencies of occurrence were noted on soils where a detectable limestone layer occurred close to the surface and summer rainfall averaged 90-120 mm. Differences in the distributions of major chenopod species appeared to arise from physiological and morphological adaptations related to water requirement and acquisition, and the tolerance of adverse nutritional conditions.

- Bluebush size and abundance was dependent on soil water availability and the presence of a limestone layer in the soil. Fewer and smaller plants were observed when the limestone layer was shallow implying a tolerance of limestone rather than a resource requirement.

- Plant communities delineated within the survey area correspond well to those previously described, although results suggested a high degree of floristic continuity and habitat overlap between groups. Bluebush was a major component of many of the vegetation communities described, occurring with myall, mulga, mallee, blackbush and in almost monospecific stands.

- Rainfall and soil texture appeared to be the primary influences on the distribution of plant communities within the survey area through the control of soil water availability. A major gradient related to changes in rainfall/soil texture was detected, although this was modified by other factors including the presence of a limestone layer, soil depth and pH, and elevation. Environmental distinction between the various bluebush communities was often difficult to quantify accurately.

CHAPTER 3

SPATIAL DISTRIBUTION PATTERNS AND THE EXISTENCE OF COMPETITION WITHIN BLUEBUSH COMMUNITIES

INTRODUCTION

BACKGROUND

The simple physiognomic structure of many semi-arid and arid ecosystems has encouraged the study of plant spatial distributions. These studies have particularly aimed at examining the effects of plant-plant interactions both at an interspecific and intraspecific level, and their influence on distribution patterns and plant behaviour. As a result of these studies, the existence of within-population competition for limited resources in arid and semi-arid plant communities has been debated for many years (see review by Fowler, 1986).

Pielou (1962) suggests that competition in plant populations is manifested in two ways: (i) through a positive correlation between inter-plant distances and plant size, and (ii) by each established plant possessing a territory in which no other plant can become established. This prediction infers that competition leads to density-dependent growth and survival, converting clumped distributions to random distributions, and random to regular. Consequently, competitive effects have been inferred through the detection of regularity in pattern (Shreve, 1942; Woodell *et al.*, 1969) or through the correlation of plant size with distance to neighbouring plants (Pielou, 1960). Very few studies, however, have conclusively shown regular distribution patterns for individual species, even though such patterns would seem to be the logical consequence of the laws of self-thinning (Silvertown, 1987). Consistent regular patterns have only been found in populations of the Iranian shrub *Zygophyllum eurypterum* (Moore and Bhadresa, 1978) and the Chilean shrub *Baccharis concava* (Serey, 1980 in Fowler, 1986). Regular patterns have been detected in other studies (Beals, 1968; Woodell *et al.*, 1969; Waisel, 1971; Barbour and Diaz, 1973; Fonteyn and Mahall, 1981; Phillips and

MacMahon, 1981), although in these instances regularity was not stable and was generally detected only infrequently. Positive correlations between plant size and separation distance have been observed for many North American shrub species including *Ambrosia dumosa* (Phillips and MacMahon, 1981), *Encelia farinosa* (Ehleringer, 1984) and *Larrea tridentata* (Yeaton and Cody, 1976).

Studies in the semi-arid zone of Australia carried out by Anderson and his colleagues revealed changing patterns in the distribution of saltbush (*Atriplex vesicaria*) plants with age. Results showed that juveniles tended to be clumped in distribution while older bushes tended towards random spacing. These patterns were generally attributed to micro-topographical variations in the soil, which presumably influence recruitment success, rather than competition effects (Anderson, 1967; Anderson, 1970; Anderson, 1971; Anderson *et al.*, 1969). Similar North American studies have been made of the spacing patterns of the creosote-bush (*Larrea tridentata*), a plant widespread across the deserts of south-western United States. Conclusions about the distribution of this species varied (Barbour, 1969; Woodell *et al.*, 1969; Barbour, 1973; Fonteyn and Mahall, 1981; Phillips and MacMahon, 1981). Fonteyn and Mahall (1981) reported regular dispersion in low rainfall areas and clumping in high rainfall areas, which suggests that "regular spacing in areas of low rainfall is caused and maintained by root competition for available water".

More recently, studies have concentrated on the direct demonstration of competition via neighbour manipulation experiments (reviewed by Aarssen and Epp, 1990). Studies have clearly shown competition for soil water (Robberecht *et al.*, 1983; Ehleringer, 1984; Smith and Goodman, 1986; Manning and Barbour, 1988; Sala *et al.*, 1989), and soil nutrients (Caldwell *et al.*, 1985; Fisher, 1988). Sufficient substantiating evidence, at either the intraspecific or interspecific level, has been provided in each case to lead Fowler (1986), in her review of competition in arid and semi-arid environments, to conclude "competition among plants is both common and strong enough to be easily detected".

AIMS

Most of the analyses demonstrating the presence of competition have been undertaken in North American xeric plant communities, whether by pattern analysis, examination of the relationship between plant size and performance or direct field demonstration. Although the existence of such effects in Australian arid and semi-arid regions has been presumed for many years (Anderson *et al.*, 1969; Crisp, 1978; Barker, 1979; Williams, 1979), studies to date have not used either regularity in species distributions or neighbour manipulation experiments to verify these claims. Such verification is highly desirable in face of recent criticism of extrapolation of North American rangeland theories to Australian ecological circumstances (Westoby *et al.*, 1989; Wilson, 1989; Stafford Smith and Morton, 1990).

Little work has been carried out examining the influence of competition on the perennial shrubs in the Australian rangelands using modern statistical approaches. Evidence presented in the broad-scale survey (Chapter 2) suggests that bluebush size may relate to the density of plants, and that decreasing densities occur with decreasing rainfall. This implies that density-dependent growth and intraspecific competition for soil moisture occur between individual bluebushes. This chapter reports on work carried out to investigate the presence of competition within bluebush populations using the three main methods mentioned above.

METHODS

THE STUDY AREA

Introduction

Field work for this study, with the exception of the broad-scale survey, was carried out on Middleback and Roopena Stations (32° 57′S, 137° 24′E), approximately 20 km north-west of Whyalla, on the north-east of Eyre Peninsula, South Australia. Additional sites were located on the adjacent stations of Myola and Cooyerdoo (Figure 3.1). A brief description of the area, as background for experimental work reported in this and following chapters, is given below.

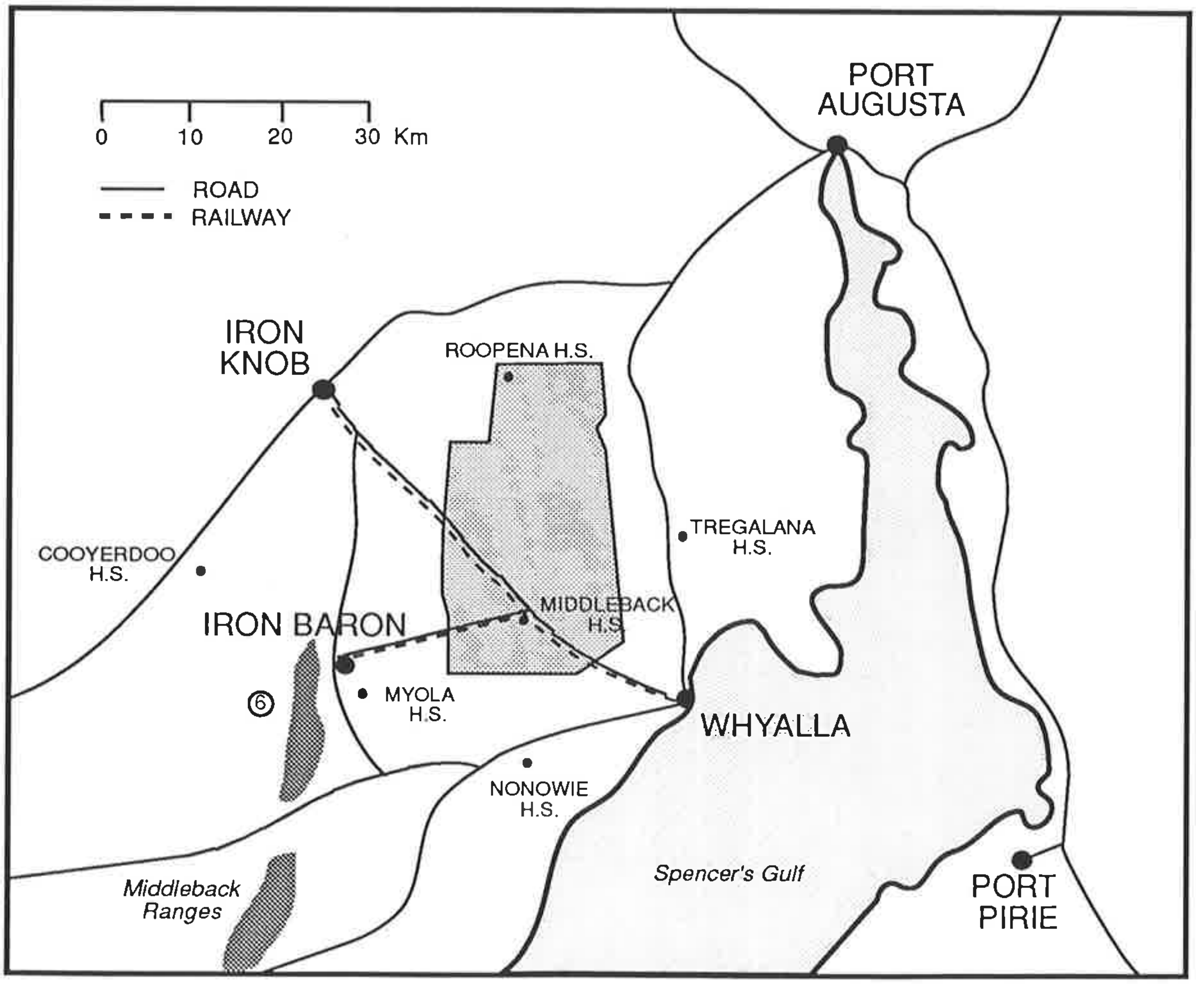

Figure 3.1: Map showing the general location of the study area on north-eastern Eyre Peninsula. The location of the permanent quadrat set up on Cooyerdoo Station is shown by the number 6, west of the North Middleback Ranges; see text for details.

Geology and Soils

Much of the structural geology of the region has been obscured by fluviatile (river) and aeolian (wind) deposits of late Tertiary and Quaternary origin. These have given rise to the low undulating topography predominant in the area, described as a distinct system of interfluvial slopes and plains, washes and basins (Laut *et al.*, 1977; Johns, 1985). The main topographic feature of the region is the Middleback Ranges, located 45 km to the west of Whyalla on the western edge of Myola Station. These ranges are composed of a mixture of iron and limestone formations and metasediments which have been metamorphosed by tectonic events to produce the outcroppings of folded jaspilite approximately 250 m above the surrounding plains (Parkin, 1969; Furber and Cook, 1976).

Brown calcareous earths (DD2) predominate over much of the study area in the form of flat plains with isolated tracts of dunes. Surface soils, commonly dark reddish-brown in colour, range from sand to clay-loam in texture. There is a gradual texture increase down the soil profile with marked horizons of calcium carbonate, usually as nodular limestone (Northcote, 1960-68; Wright, 1985). Two minor soil types have been described in the region;

(i) Gc1.12 - where calcium carbonate is readily observable in the surface horizons and is at maximum concentration before a depth of 30 cm, and

(ii) Gc1.22 - where an acid test is needed to detect $CaCO_3$ at the surface and the maximum concentration is at depths of at least 40-50 cm (Northcote, 1960-68).

Wright (1985) also described the minor soil type Dr 1.43, crusty duplex soils which are characteristic of the basins and washes. The soils of the Middleback Ranges are described as shallow, dense, loamy soils (Um 5.41) with a uniform medium texture.

Climate

The climate of north-eastern Eyre Peninsula is characterised by long, hot summers and short, cold winters, with low and erratic rainfall. Temperatures in Whyalla, on the Spencer Gulf coast, range from a mean daily maximum of 28.9°C in January (summer) to a mean daily minimum of 7.3°C in July (winter) (Commonwealth Bureau of Meteorology data; Figure 3.2). At Middleback

Station, the summer maximum is usually 4-5°C hotter and the winter minimum is 2-3°C colder due to its inland position (Reid, 1984).

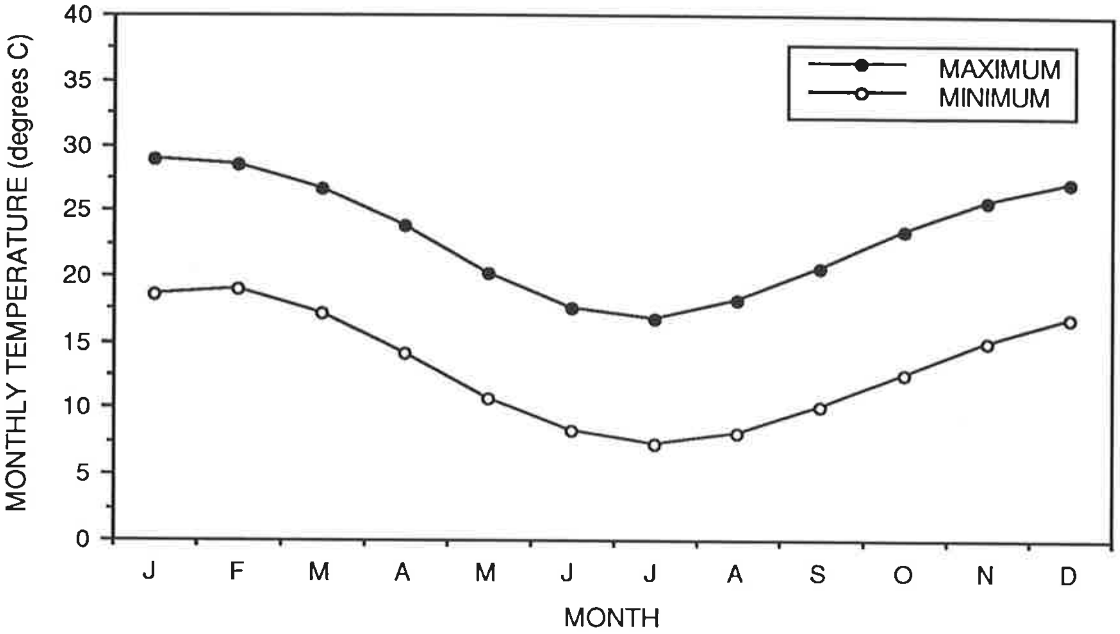

Figure 3.2: Mean daily maximum and minimum temperatures for Whyalla, 20 km south-east of Middleback Station (Commonwealth Bureau of Meterology, 1992).

Contrasting with the predictable, cyclic rainfall of the southern temperate regions of South Australia, rainfall in the study area is erratic and unpredictable. The total annual rainfall varies greatly from year to year with records at Roopena homestead showing totals of between 79 mm (1927) and 537 mm (1974). Within a given year, there is little variation in the average monthly rainfall suggesting a lack of seasonal influences on rainfall (Figure 3.3). This is not entirely the case, however, as the mean number of wet days per month is higher in winter, indicating frequent light rainfall events in winter and rare but heavy falls in the summer months. The mean annual rainfall for Whyalla is 270 mm with the more arid inland stations of Middleback and Roopena receiving 210 mm. Iron Knob, also inland, receives a slightly higher average of 221 mm which may be due to orographic influences from the Middleback Ranges. In the

Whyalla area, mean annual rainfall is approximately one-tenth of the average annual pan A evaporation (Jackson, 1958).

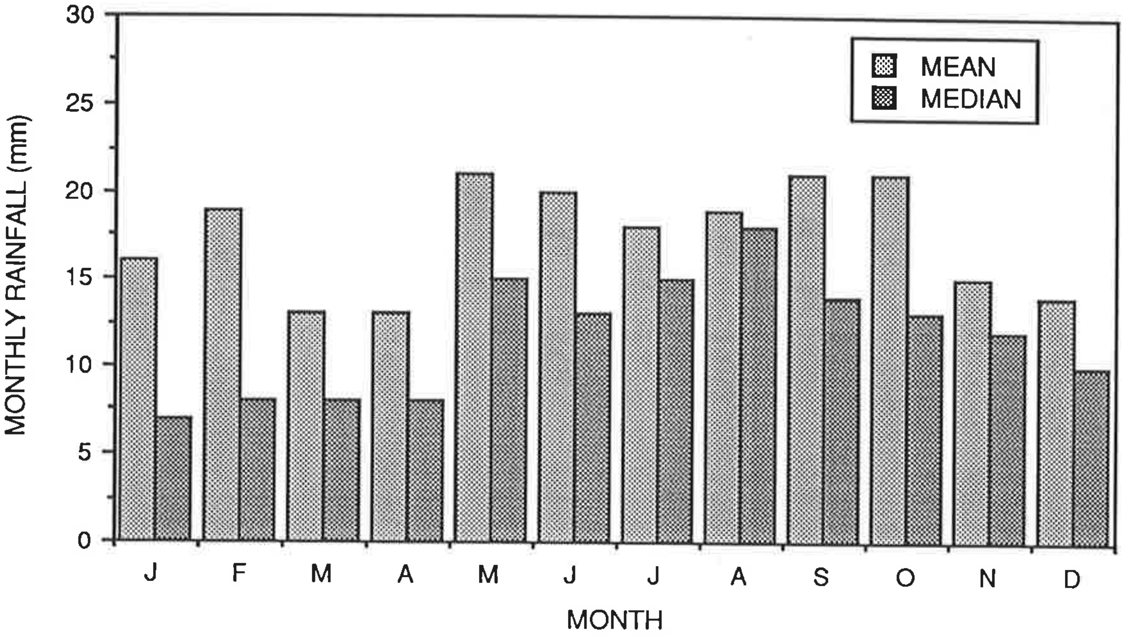

Figure 3.3: Mean and median monthly rainfall for Roopena Homestead (1891-1984) (Commonwealth Bureau of Meterology Data, 1984).

Vegetation

General Vegetation Patterns

The vegetation of Eyre Peninsula has been investigated by Prescott (1929), Wood (1937) and Crocker (1946). Of these, Crocker (1946) represents possibly the most detailed and accurate interpretation (see Sparrow, 1991). He classified north-eastern Eyre Peninsula into two edaphic complexes as follows:

(i) *Acacia papyrocarpa - Casuarina cristata* EDAPHIC COMPLEX containing 4 associations;

a.*Acacia papyrocarpa - Myoporum platycarpum*

b.*Casuarina cristata - Maireana sedifolia*

c.*Atriplex vesicaria - Maireana sedifolia*

d. *Maireana sedifolia*, and

(ii) *Eucalyptus oleosa - E.gracilis - E. dumosa* (also thought to include *E.socialis*[1])

EDAPHIC COMPLEX containing 6 associations, of which three occur on north-east Eyre Peninsula;

a. *E.oleosa - E.incrassata*

b. *E.oleosa - E.brachycalyx*

c. *E.oleosa - E.gracilis*

Middleback and Roopena Stations

The vegetation of the area encompassing Middleback and Roopena Stations can be broadly considered as chenopod shrubland and can be classified into the first of Crocker's edaphic complexes given above. Sites from this area also form part of the *Maireana sedifolia/M.pyramidata* shrubland vegetation type (Type 3) described in Chapter 2.

Reid (1984) suggested three vegetation associations were present in the general area:

(i) *Chenopod low open-shrubland* - In this community type, saltbush is often dominant in low lying basins and washes, with bluebush and saltbush on the interfluvial slopes and plains. In areas subjected to heavier grazing pressure, washes and basins are dominated by blackbush and slopes and plains by bluebush. Other important shrub species include *Rhagodia ulicina* and *Lycium australe*;

(ii) *Western myall low open-woodland* - This vegetation association, occurring over much of the study area, is characterised by the sparse but dominant western myall over chenopod steppe. Tree density is higher in lower lying areas, where other tree and tall shrub species, such as bullock bush (*Heterodendrum oleifolium*) and sugarwood (*Myoporum platycarpum*) may also attain local dominance. Other important species include *Pittosporum phylliraeoides* and *Eremophila scoparia.* The understorey is composed of similar species to

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[1] See Hawke (1986)

chenopod open shrubland, except under tree canopies where the berry-fruited chenopods *Enchylaena tomentosa* and *Rhagodia spinescens* dominate; and

(iii) *Black oak low woodland* - Due to its clonal nature,black oak (*Casuarina cristata*) often forms extensive groves. Generally, the understorey is a mix of bluebush, saltbush or blackbush and berry-fruited chenopods.

Middleback Ranges

The vegetation changes significantly in the western portion of the study area with the presence of a biogeographic boundary between the northern arid zone and the southern temperate zone (Prescott, 1929; Crocker, 1946; Hawke, 1986). Here, the vegetation changes from the characteristic chenopod shrubland found in the east section of the study region, to mallee eucalypt woodland. This woodland, described by Crocker (1946) as the *E.oleosa - E.gracilis - E. dumosa* edaphic complex, has been shown to include vegetation associations with chenopod, sclerophyll and mixed understories. The Middleback Ranges straddle the biogeographic boundary and possess a somewhat unique flora including species of the genera *Dodonaea, Beyeria* and *Alyxia* in addition to chenopod and mallee species (Wotton, 1987).

Land Use

Sheep pastoralism for wool production has been carried out in this region for over 120 years. The first grazing lease was taken up in 1868, but it was not until the early 1900's that continuous pastoralism took place due to the advent of more permanent water supplies. Middleback and Roopena Stations have been managed using the principles of the Waite/Nicolson model since 1919 (Lange *et al.*, 1984). Such practises involve the use of small paddocks (200 ha or less) each with a permanent watering point and less than 350 sheep, giving an average stocking rate of approximately 6 hectares per sheep. Destocking of paddocks is not carried out even during drought because of these conservative stocking rates. The only other major land use in the region is iron-ore mining, conducted in the Middleback Ranges. This area represents South Australia's largest exploited mineral deposit, with 175 million tonnes of iron ore having been removed between 1900 and 1984 (Johns, 1985).

ESTABLISHMENT OF PERMANENT QUADRATS

To study aspects of spatial distribution patterns, in addition to the life-cycle and ecology of bluebush, such as flowering, germination and seedling establishment, a series of permanent study quadrats were set up in the Middleback area in 1988. The locations of these quadrats were chosen to represent a wide range of topographic and vegetation features present within the general area (Table 3.1). Five of the sites were located on Middleback Station in areas of chenopod shrub steppe (Figure 3.4) while the sixth was positioned in mallee vegetation on Cooyerdoo Station, west of the Middleback Ranges (Figure 3.1). All sites were positioned in paddocks grazed by sheep, except for the Field Centre site, which was situated in an animal-proof exclosure near to the Middleback Field Centre. Descriptions of sites are given in Appendix 2.

Table 3.1: Descriptions of sites selected for spatial pattern analysis of bluebush. Percent canopy cover is estimated from length and width measurements of individual plants.

SITE	TOPOGRAPHY	DOMINANT VEGETATION	% COVER *M.sedifolia*
Field Centre	Slope	*M.sedifolia/R.ulicina*	12.78
Two-Mile	Wash	*M.pyramidata/M.sedifolia*	6.62
Purpunda	Plain	*M.sedifolia*	10.67
North-east Overland	Slope	*M.sedifolia/A.vesicaria*	8.64
South-west Overland	Plain	*M.sedifolia/A.papyrocarpa*	12.61
Cooyerdoo	Plain	*E. socialis/ M. sedifolia*	7.09

Each of the quadrats was positioned 50 to 100 m from a vehicular track and was marked for later identification by the placement of large iron posts at each of the four corners. Quadrats were 50 x 20 m in size, with the long axis placed in an approximate north-south direction. At each site abiotic environmental information was collected as for the broad-scale survey. Topography, elevation and slope was assessed and a soil profile was described. A soil sample, collected from the centre of the quadrat at a depth of 25 cm, was analysed in the laboratory for soil features. All perennial plants rooted within these quadrats were identified and the location of the centre of each plant's base was mapped to the nearest 5 cm. The dimensions of these plants were recorded in terms of canopy height, length (longest horizontal axis through the canopy) and width (at right angles to the length axis).

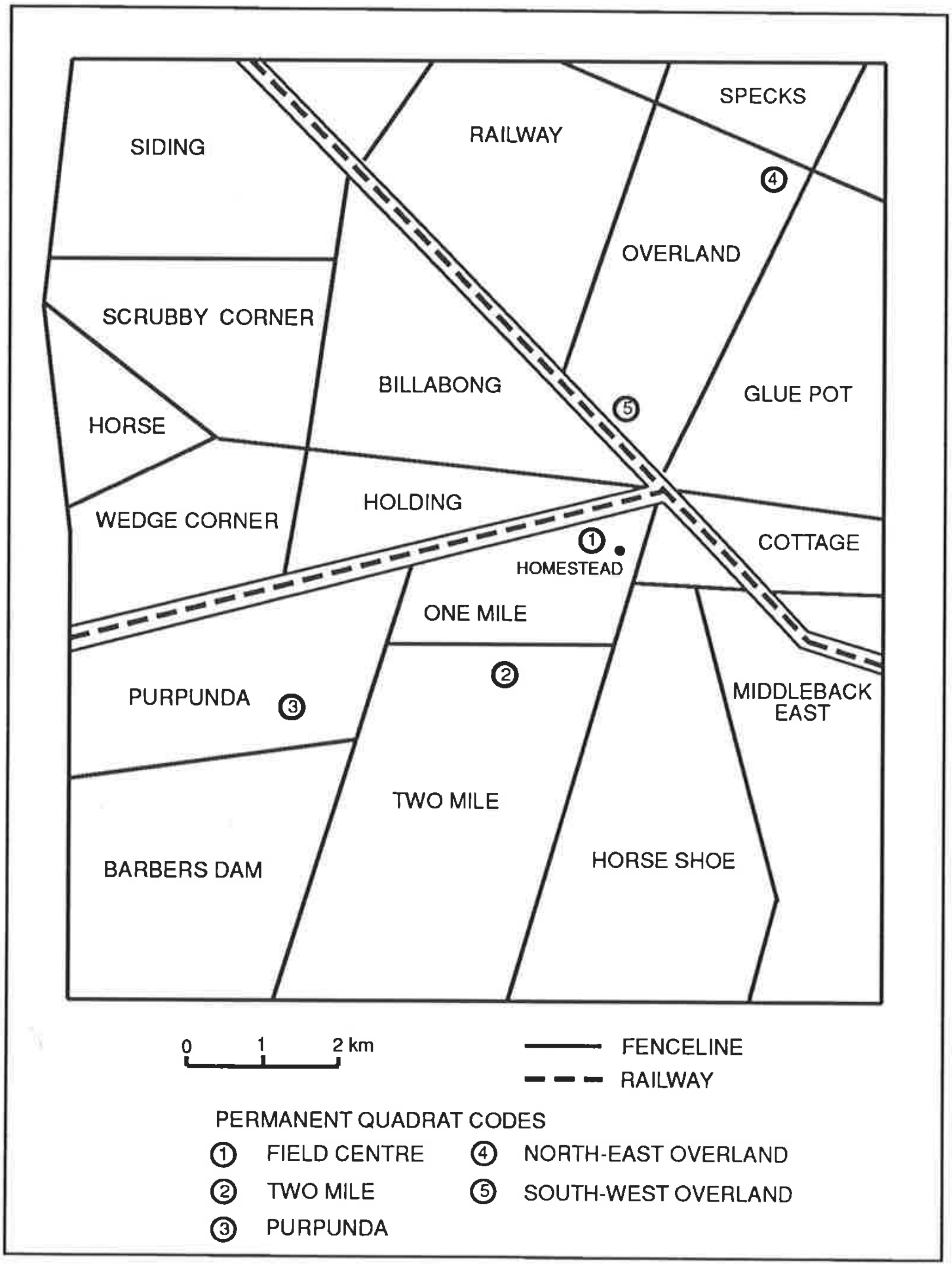

Figure 3.4: Map showing the location of the paddocks near Middleback Homestead and the position of the five permanent quadrats set up early in 1988.

EXPERIMENTAL AND ANALYSIS METHODS

Spatial Distribution Patterns

Methods Available

In the past, spatial pattern analysis tests measured the departure from randomness using plant frequency data from a large number of small (contiguous) quadrats. Here, the actual distribution of numbers of individuals in sampled quadrats was compared to that expected for the Poisson distribution, which would be found if the plants were randomly distributed. Significance in these instances was tested by Chi-square analysis or the variance:mean ratio (Fonteyn and Mahall, 1981; Greig-Smith, 1983). However, this method has been severely criticized because of the effect that the initial quadrat size can have on the detection of pattern (Kershaw and Looney, 1985). Consequently, pattern analysis was undertaken using a nest of contiguous grid of quadrats, where the grid is laid out with increasing quadrat sizes being built up by 'blocking' adjacent quadrats in pairs, fours, eights etc. An analysis of variance can then be carried out with the variance partitioned between different block sizes. If the mean square (variance) is then plotted in relation to increasing block size, the different scales of pattern appear as peaks at a block size corresponding to the mean area of the clump (Kershaw and Looney, 1985).

Alternatively, methods for detecting pattern have been developed which involve distance values rather than quadrat counts. In such tests, the basic sampling unit is a point, which is considered in relation to neighbouring events. Many tests have been designed to test for departure from randomness by this method; a review is given in (Greig-Smith, 1983). Most methods use a formula to obtain a significance value for any departures towards regularity or clumping using either nearest-neighbour, inter-event or point to nearest event data. One method which have been used to detect spatial pattern using nearest neighbour and point to nearest neighbour data is Batchelers Ratio (Batcheler, 1971; see Chapin *et al.*, 1989 as an example).

Field Data Collection and Analysis

Spatial distribution patterns were examined using bluebush data collected from the permanent quadrats. Positional data was in the form of X-Y co-ordinates. Batcheler's ratio (Batcheler, 1971) was used to indicate the spatial distribution patterns of bluebush in each of the permanent quadrats. These were calculated using a FORTRAN program written by J. Pearce, Statistics Department, University of Adelaide. From the quadrat maps, distances were computed from a random point to the nearest shrub and from that shrub to its nearest neighbour to obtain the ratio of point-plant:plant-plant distance (Rp/Rn). When averaged over the population, the distribution of shrubs can be either clumped (ratio > 0.88), random (ratio = 0.88) or regular (ratio < 0.88). Significance was determined by comparison with simulated data sets as no formal test could be applied in this instance (Prof. R. Jarrett, Statistics Department, University of Adelaide, pers. comm.).

Plant Separation:Performance Relationship

Methods Available

Positive correlations between the size of individual plants and the distance to nearest neighbours have also been used to indicate competition using many methods (Pielou, 1960; Fonteyn and Mahall, 1981). Traditionally, the distance to nearest neighbour was related to estimates of plant size using correlation analysis (Pielou, 1960; Phillips and MacMahon, 1981; Smith and Goodman, 1986). More recently, Dirichlet (Thiessen) polygons have been commonly used as the measure of shrub separation. These polygons, first employed to describe plant spacing patterns by Mead (1966), delineate an area around each plant which contains all points closer to that plant than to any other, and hence give a measure of the area potentially available to each plant for resource acquisition. Mathematically they are defined by the equal division of space between the centres of each pair of shrubs within a given area (Figure 3.5). This method of estimating neighbour influences may be preferred over the simpler physical distance measures as it is considered to produce a more accurate measure of the overall neighbouring influences. The problem of determining those shrubs which might be considered as neighbours is also greatly reduced by this method, as neighbouring shrubs are simply defined as those which contribute to the sides of the polygons (Mead, 1966; Matlack and Harper, 1986; Kenkel, 1990).

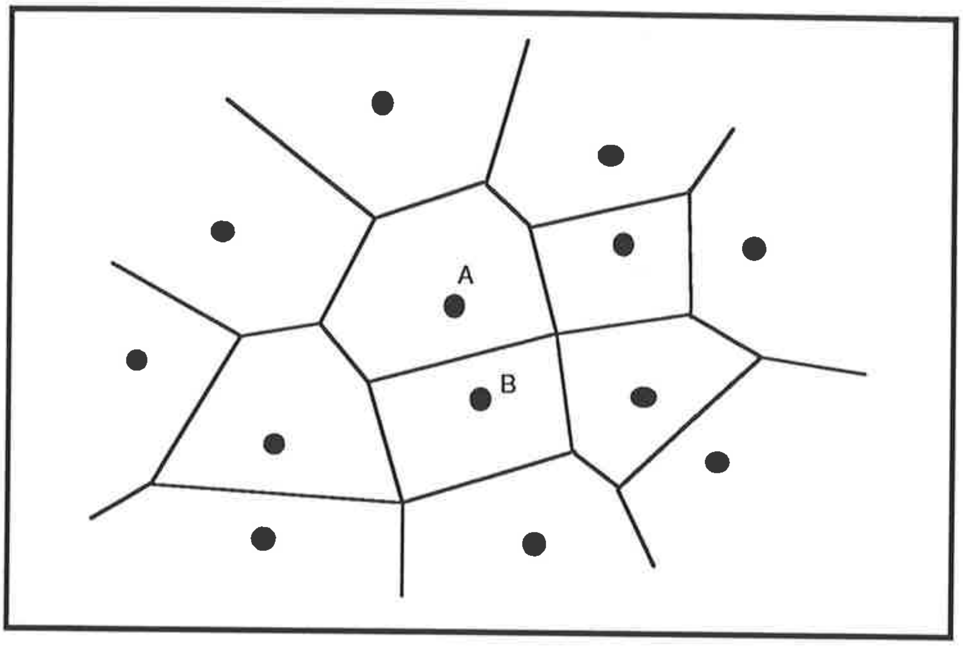

Figure 3.5: Dirichlet polygons used to delineate the area potentially available to each plant. Polygons are constructed by the equal division of space between the centres of each pair of shrubs (such as those labelled A and B in the above).

The spatial arrangement of plants can be described in terms of five features of the polygons (Liddle *et al.*, 1982). These include:

(i) Number of neighbours - number of plants contributing to the sides of the polygon,

(ii) Area - surface area of the polygon,

(iii) Perimeter - the sum of the lengths of the sides of the polygon,

(iv) Displacement (Abcentricity) - measure of the distance of the subject plant from the centre of gravity of its polygon relative to other dimensions; and

(v) Eccentricity (Eccircularity) - measure of the difference of the polygon from a circle, where a circular polygon has a value of 0 and an ellipse has a value of 1.

A number of studies have investigated the relationship between individual plant performance with some of these polygon (available area) features. Experiments have been carried out relating polygon area to dry biomass (Liddle *et al.*, 1982; Matlack and Harper, 1986; Firbank and Watkinson, 1987), and the probability of mortality (Watkinson *et al.*, 1983; Kenkel *et al.*, 1989; Owens and Norton, 1989).

Field Data Collection and Analysis Methods

Plant size:separation distance relationships were examined using bluebush data collected from the permanent quadrats. Positional data was in the form of X-Y co-ordinates and plant size estimates were calculated from height, length and width measurements (as in the broad-scale survey). Dirichlet polygons were constructed for every bluebush in the mapped quadrats using the FORTRAN program TESSELLATE (A.Sparrow, Botany Department, University of Adelaide). Estimates of three of the polygon features described earlier (number of sides, area and perimeter) were also calculated using this program. Polygons which were located on the edge of the quadrats and found to be incomplete were excluded from further analysis. Plant size was estimated from the dimension data in terms of height, cover (as an ellipse) and volume (as a hemi-ovoid). The relationship between plant size estimates and polygon features was determined by Spearman rank correlation analysis using the computer software package SPSS-X (SPSS Inc., 1986).

Direct Demonstration of Competition

Methods Available

It was once difficult to directly demonstrate and quantify the extent of intraspecific or interspecific competition effects, when plant distribution patterns had been determined. Over the last twenty years, however, neighbourhood manipulation experiments in natural environments have been used extensively to give dramatic, quantifiable evidence for competition (Manning and Barbour, 1988). Such field experiments involve the alteration, in density or morphology, of one or several species, with the response measured in either a single target plant or all the remaining vegetation components. Aarssen and Epp (1990) reviewed the three main types of manipulation experiments that have been used:

(i) Introductions - this involves the transplanting of whole plants or seeds into existing vegetation, with the response measured in both the introduced and existing vegetation (*e.g.* Friedman, 1971; Keddy, 1981; Werner, 1977);

(ii) Trenching - this method, used primarily to examine root competition, involves the digging of a trench around a small plot to sever the roots of surrounding plants (*e.g.* Robertson, 1947; Goldberg, 1985; Monk and Gabrielson, 1985); and

(iii) Vegetation Removals - this is the most common neighbour manipulation approach involving the removal of some part or parts of the vegetation and measuring the response in either the remaining components of the vegetation or, more generally, single target plants (*e.g.* Clements *et al.,* 1929; Gurevitch, 1986; Manning and Barbour, 1988).

Field Data Collection and Analysis Methods

Competition effects were directly investigated by following the status of target bluebushes after the removal of neighbouring shrubs. Trials were conducted over two periods, June 1989-April 1990 and September 1990-June 1991. In Trial 1, only the effects of neighbour removal were investigated. In the second trial, the effects of irrigation and nutrients (to determine the existence of competition for nutrients) were also examined.

Trial 1 was set up in Pony Paddock, approximately 500 m south of the Field Centre permanent quadrat within an apparently homogeneous area of bluebush, saltbush and scattered western myall trees. Nine mature bluebush plants were randomly selected and each shrub was made the centre of a circular plot with a radius of 2.5 m. Plant dimensions were recorded for the central bluebush and for all other shrubs within the plot as for spatial pattern analysis. These target bluebushes were subjected to one of three treatments in late June 1989:

(i) Control - no plants removed;

(ii) All surrounding bluebushes within the radius of 2.5 m removed; and

(iii) All surrounding plants within the radius of 2.5 m removed.

Allocation of treatments was by stratified randomization giving 3 replicates per treatment. The plants removed from the plots were cut off at surface level with minimum disturbance of the soil surface and were carried from the immediate study area. All subsequent regrowth of the 'removed' plants was also removed in this way.

The pre-dawn xylem pressure potential was measured for each central shrub on the day following the manipulation, and at approximately four week intervals from November 1989 to April 1990, using the Scholander pressure chamber technique (Scholander *et al.*, 1965). The small size of the leaves of bluebush (4-8 mm in length) made it necessary for terminal shoots to be used in the pressure chamber rather than individual leaves; non-woody shoots containing 10 to 15 leaves were selected. Generally, only three shoots from each plant were sampled to minimize the destruction of the central shrub. Harvested shoots from each shrub were stored in plastic bags; testing was carried out after each individual shrub had been sampled, reducing storage times to less than 15 minutes for all shoots. Soil samples were also collected from the experimental plot at depths of 10 cm and 25 cm from the surface for determination of gravimetric soil water content. Rainfall records were recorded at Middleback Homestead.

Trial 2 was conducted over the following summer period, in an area of bluebush-saltbush-*Rhagodia ulicina* -*Acacia papyrocarpa* vegetation just south of Middleback homestead. Thirty-six mature bluebushes were chosen in an approximate 6 x 6 grid, with a distance of 8 to 10 m between plants. A radius of 2.5 m was marked around each target plant while a low levee bank was built at a radius of 0.75 m. Plants were subjected to one of six treatments as follows:

(i) Control - no plants removed;

(ii) All surrounding bluebushes within the radius of 2.5 m removed;

(iii) All surrounding plants within the radius of 2.5 m removed;

(iv) Nutrient addition;

(v) Irrigation; and

(vi) Nutrient addition and irrigation .

Restricted stratified randomization gave 6 replicates per treatment. Removal of plants from the appropriate plots was carried out as per Trial 1. Nutrient and irrigation treatments were first applied in September 1990. Fertilizer (Complete Garden Food, Defender Brand[1]) was applied at a rate of 10g N m^{-2}, dissolved in 5 L of water, while irrigation simulated 25.4 mm of rainfall per plot (45 L). Plots in which nutrients had not been added were also irrigated with 5 L of water. Tags were also applied to each target plant to measure growth over the following months. Ten tags of fine, plastic-coated wire were carefully tied around ten individual shoots on each plant.

Predawn xylem pressure potentials were measured for four of the six replicates of each treatment on the morning of manipulation, and at four week intervals from September 1990 to June 1991 using the technique described for Trial 1. Not all plants were measured at each time interval to reduce the destruction of plants through removal of shoots; plants measured were chosen randomly. Each month, the number of leaves and shoot length were recorded for each of the tagged shoots, while small shoots were collected from the sampled plants for later determination of relative water content and % water content. Gravimetric soil water content and rainfall data was also collected as for Trial 1.

To determine shoot water contents, shoots were placed in sealed plastic containers immmediately after harvesting and were then stored in an insulated container before being weighed for determination of fresh weight (weighing was carried out within 30 minutes of harvesting). Shoots were then placed in distilled water for 24 hours, after which time they were blotted dry and reweighed for determination of turgid weight. Dry weights were measured after subsequently oven-drying shoots for 24 hours at 100°C. Relative water content was calculated as (fresh weight - dry weight)/(turgid weight - dry weight) and % water content as (fresh weight - dry weight)/(fresh weight) x 100.

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[1] Chemical composition reported as: Nitrogen as Ammonia- 7.26%, Nitrogen as Organic - 0.75%, Total Phosphorus - 4.65%, Potassium as Potassium Chloride- 9.00%, Sulphur as Sulphates - 9.07%, Total Calcium - 5.5%, Magnesium as Magnesium Carbonate - 0.5%.

Time series analysis using repeated measures analysis of variance was used to examine differences in water potentials between treatments in Trial 1. Treatments with significantly different water potentials on any one recording date were identified using ANOVA with pairwise comparisons of Least Significant Differences (LSD). For Trial 2, time series analysis was again used to examine patterns in both water potential and shoot relative water content of the target shrubs. In this instance, however, a series of planned comparisons as contrasts were undertaken to detect differences between groups of treatments. Such comparisons have recently been shown to be more powerful than unplanned comparisons, as they test more specific hypotheses (Day and Quinn, 1989). All analyses were carried out using the GLM procedure in the computer software package SAS (SAS Institute, 1985).

RESULTS

SPATIAL PATTERN ANALYSIS

The spatial arrangement of bluebushes in the permanent quadrats was variable (Table 3.1). All populations exhibited some degree of regularity (all ratios were less than 0.88), with significant regularity detected at four of the six sites (Field Centre, Purpunda, North-east Overland and South-west Overland). At sites where the bluebush distribution was random (Two-Mile and Cooyerdoo), fewer bluebushes and lower % cover estimates were reported.

Table 3.1: Batcheler's ratios calculated using co-ordinates from each of the permanent quadrats. Significance is indicated as follows: * , P<0.05. Estimates of % cover are calculated from length and width measurements of individual plants.

SITE	# OF BLUEBUSH IN QUADRAT	% COVER BLUEBUSH	BATCHELER'S RATIO	PATTERN
Field Centre	199	12.78	0.7047 *	Regular
Two-Mile	114	6.62	0.7318	Random
Purpunda	180	10.67	0.6553 *	Regular
NE Overland	233	8.64	0.6796 *	Regular
SW Overland	231	12.61	0.6876 *	Regular
Cooyerdoo	135	7.09	0.8100	Random

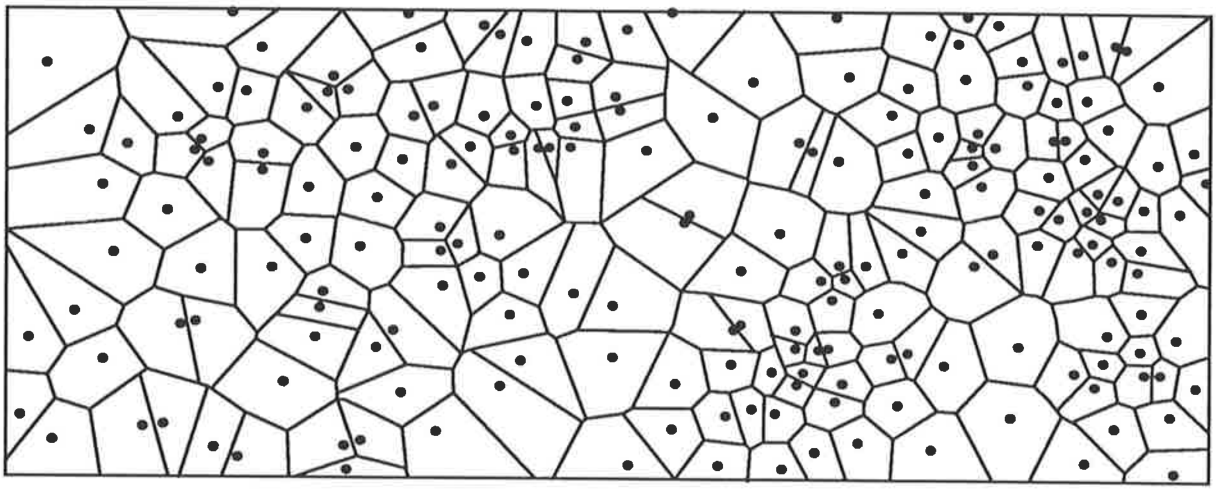
PLANT SEPARATION:PERFORMANCE RELATIONSHIPS

The Dirichlet polygons constructed for individual bluebushes at each site are shown in Figure 3.6. Mean estimates of plant size and polygon values are given in Figures 3.7 and 3.8; rank correlations between variables are shown in Table 3.2.

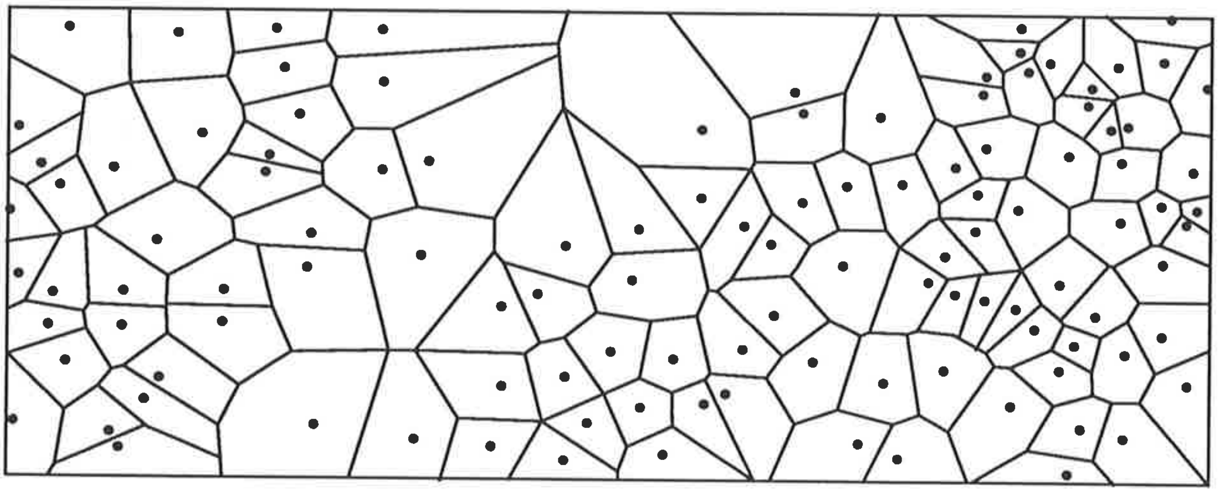
Little difference in the mean height of bluebush could be detected between the six sites with all averaging heights of 59.38 - 66.65 cm (Figure 3.7). Estimates of cover and volume, however, suggest that bluebush in the North-east Overland site are comparatively 'smaller' than for the other sites. Here, mean projected foliage cover per bluebush was 0.371 m^2 compared to between 0.525 and 0.642 m^2 at the other sites. Polygon area and perimeter length were, not surprisingly, largest at sites where overall bluebush density was low (Two-Mile and Cooyerdoo; Figure 3.8). In comparison, there was little detectable difference in the mean number of sides to the polygon (taken to represent the number of neighbours of influence) at each of the sites.

Significant positive correlations were detected between the plant size estimates and some of the polygon features shown, although trends did vary between sites (Table 3.2). Significant relationships were detected between plant size (cover and volume) and available area (polygon area) and perimeter at every site, although this relationship was less significant at the Two-Mile site. Further analyses, however, revealed similar strong correlations at the Two-Mile site when both bluebush and blackbush (representing 6.62 and 8.04 % cover respectively) were examined simultaneously (Table 3.3). Overall, the results suggest that larger shrubs occupy larger polygons and hence are spaced further away from neighbours than smaller shrubs. Polygon size appeared to have less influence on plant height; a strong correlation between these variables was detected only at the Field Centre and North-east Overland sites. The correlation between plant size and the number of sides of each polygon (taken to indicate the number of neighbouring plants) differed noticeably between the sites.

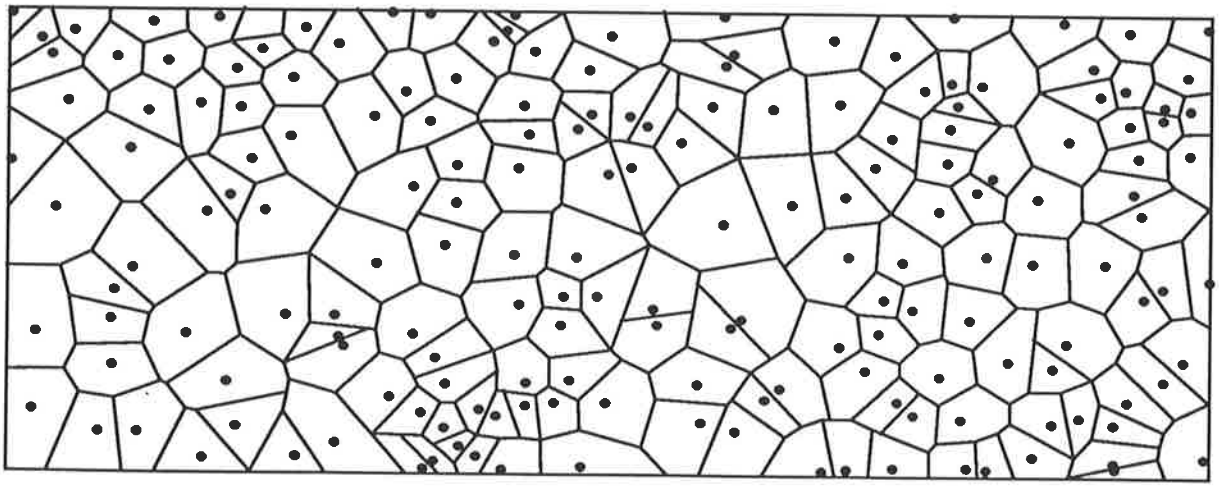
Figure 3.6: Dirichlet polygons constructed for each bluebush within the permanent quadrats. Each polygon delineates an area around the central shrub which contains all points closer to that shrub than to any other.



(a) Field Centre Site

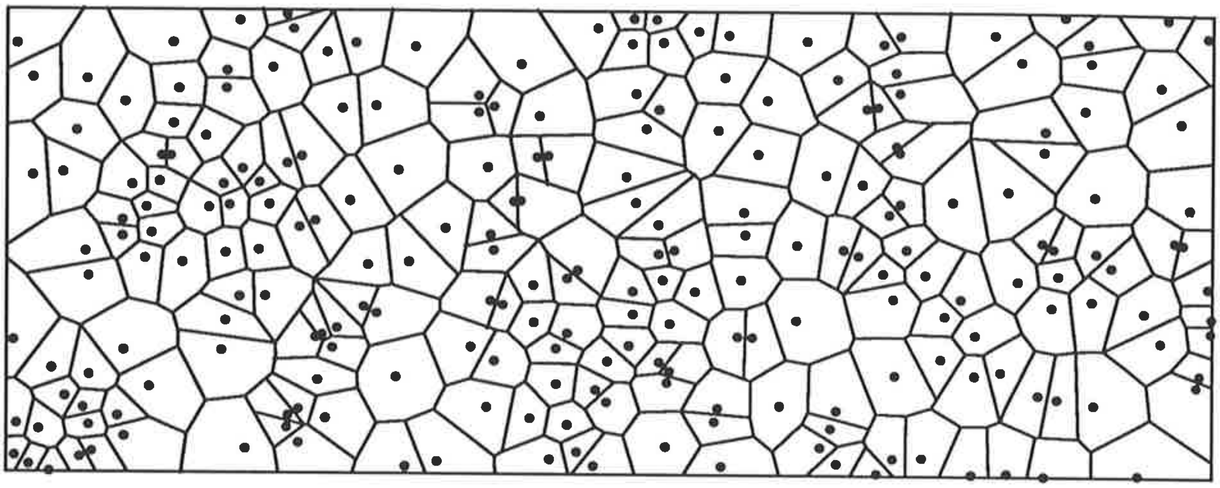


(b) Two-Mile Site

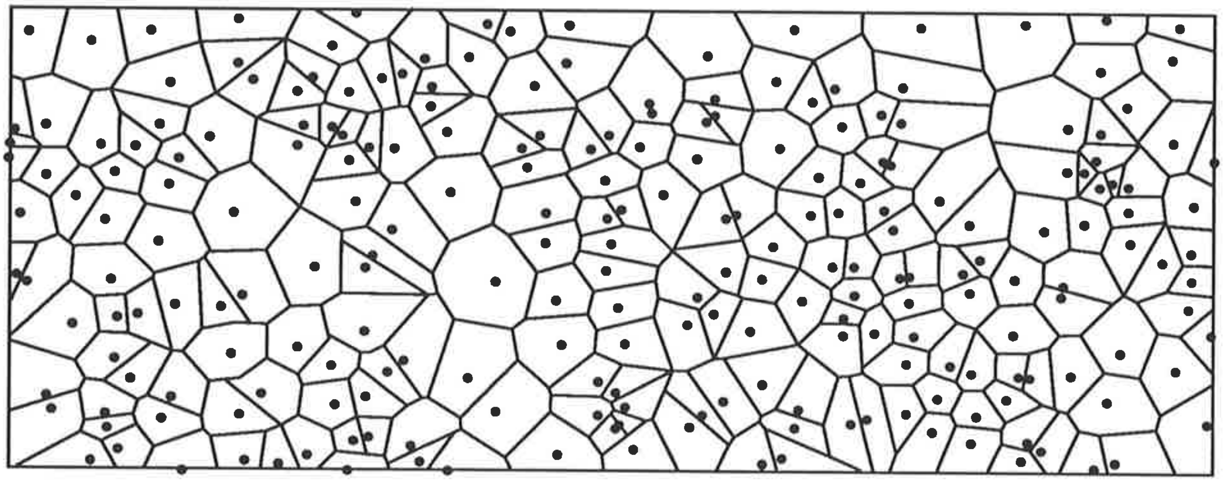


(c) Purpunda Site

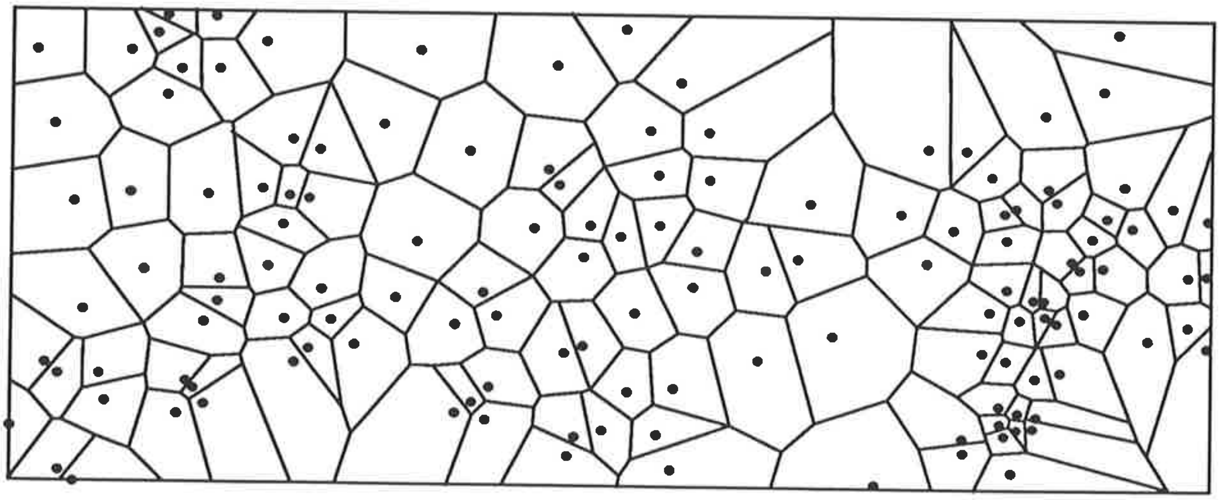
Figure 3.6 (cont.): Dirichlet polygons constructed for each bluebush within the permanent quadrats. Each polygon delineates an area around the central shrub which contains all points closer to that shrub than to any other.



(d) North-east Overland Site

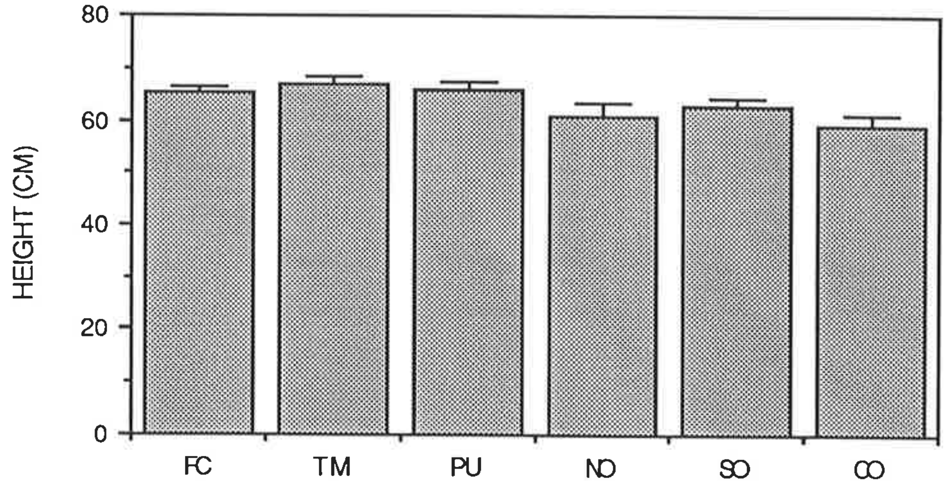


(e) Southwest Overland Site

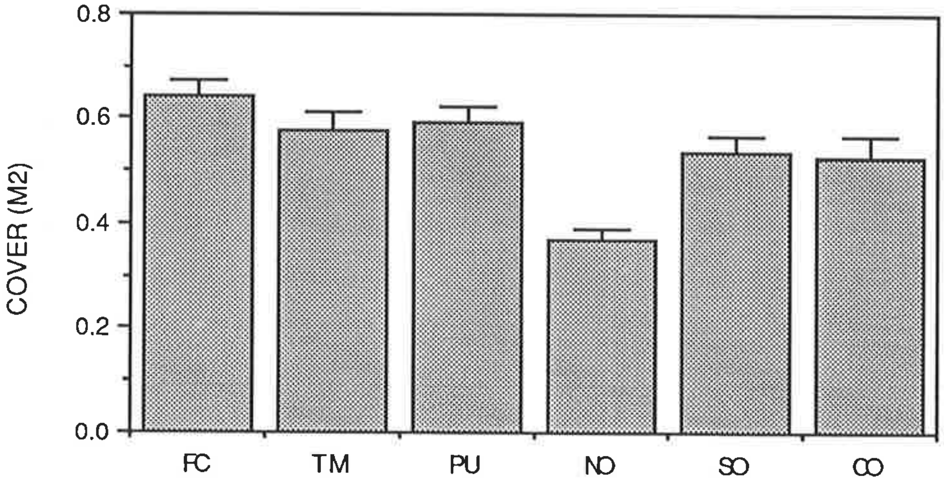


(f) Cooyerdoo Site

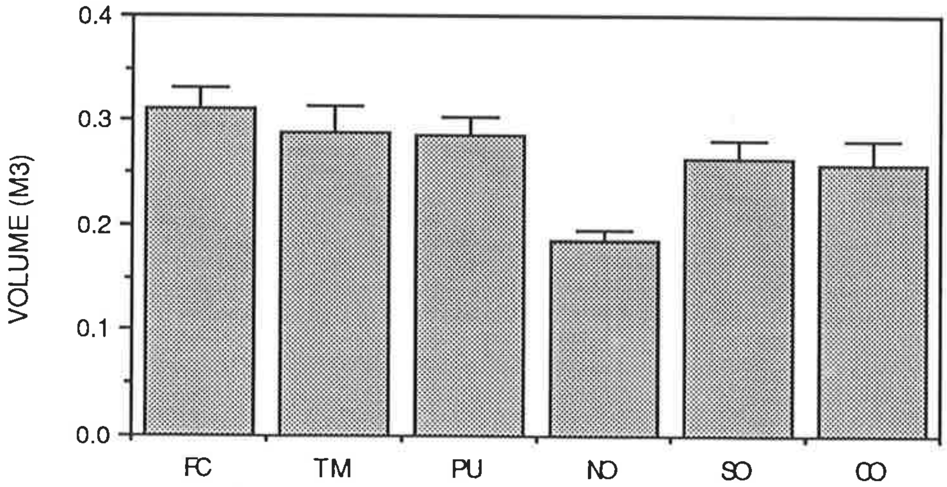
Figure 3.7: Estimates of mean bluebush size (± S.E.) at each of the study sites. Site abbreviations are as follows: FC, Field Centre; TM, Two-Mile; PU, Purpunda; NO, North-east Overland; SO, South-west Overland; CO, Cooyerdoo.



(a) Plant Height

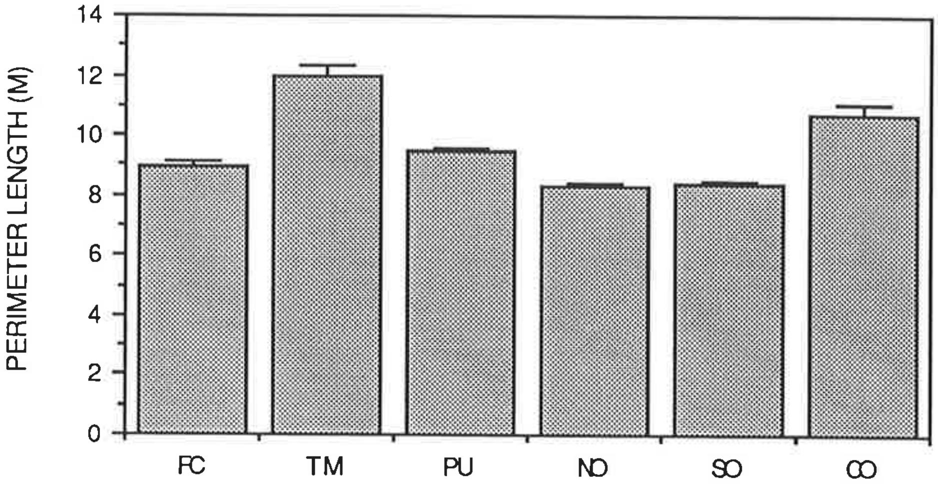


(b) Plant Cover

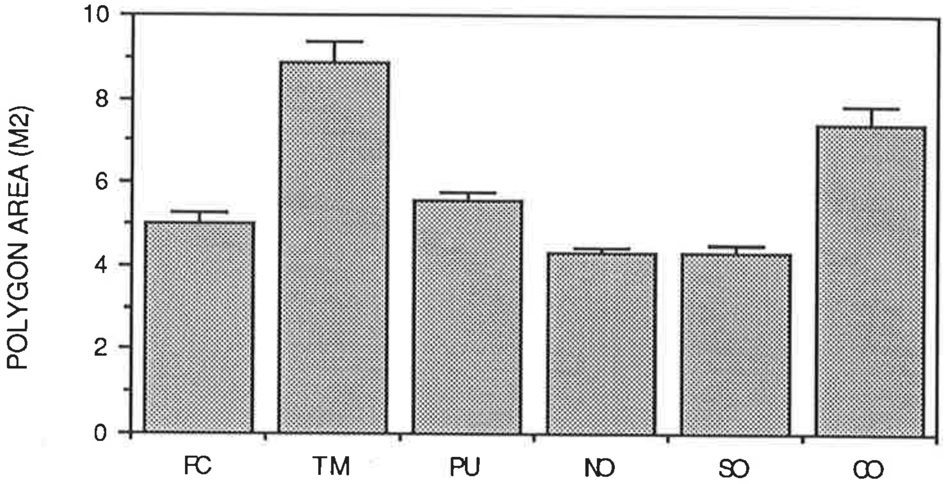


(c) Plant Volume

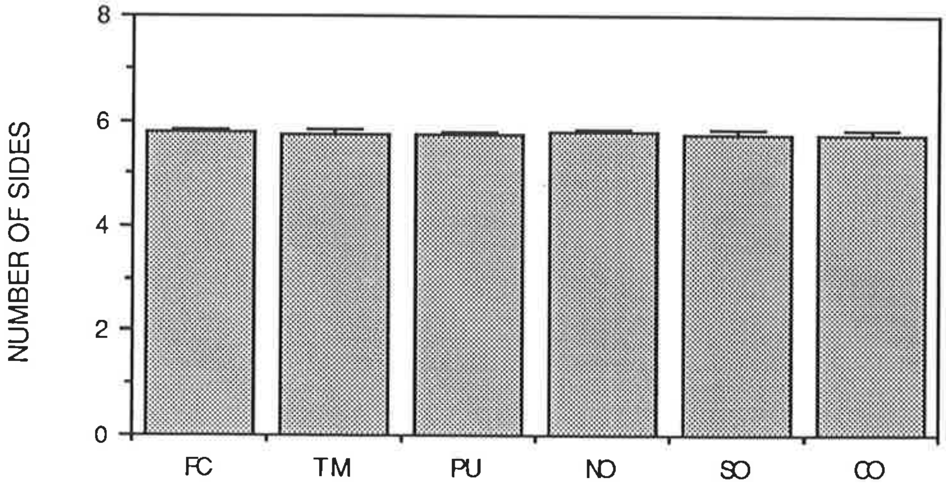
Figure 3.8: Estimates of Dirichlet polygon features (mean ± S.E.) for each of the study sites. Site abbreviations are as follows: FC, Field Centre; TM, Two-Mile; PU, Purpunda; NO, North-east Overland; SO, South-west Overland; CO, Cooyerdoo.



(a) Length of polygon perimeter



(b) Polygon Area



(c) Number of Polygon Sides

Table 3.2: Spearman rank correlations between plant size estimates and Dirichlet polygon features. Significance of correlations as follows; *, 0.01<p<0.05; **, 0.001<p<0.01; ***, p<0.001. Polygon features are abbreviated as *peri*, length of polygon perimeter; *area*, polygon area; *sides*, number of sides contributing to the polygon; *a:p*, polygon area to perimeter ratio, *a:s*,polygon area to sides ratio.

(a) Shrub height

SITE	D.F.	PERI	AREA	SIDES	A:P	A:S
Field Centre	198	0.307***	0.317***	0.041	0.320***	0.308***
Two-Mile	113	0.110	0.137	0.017	0.139	0.155*
Purpunda	179	0.111	0.127	0.099	0.144*	0.108*
North-east Overland	232	0.372***	0.404***	0.175**	0.416***	0.360***
South-west Overland	230	0.105	0.143*	0.177**	0.165**	0.051
Cooyerdoo	134	0.252**	0.284	0.168*	0.292***	0.232***

(b) Shrub cover

SITE	D.F.	PERI	AREA	SIDES	A:P	A:S
Field Centre	198	0.431***	0.428***	0.079	0.410***	0.428***
Two-Mile	113	0.158*	0.167*	0.044	0.131	0.171*
Purpunda	179	0.291***	0.317***	0.213**	0.312***	0.294***
North-east Overland	232	0.344***	0.366***	0.156**	0.365***	0.328***
South-west Overland	230	0.185**	0.235***	0.214**	0.257***	0.140*
Cooyerdoo	134	0.302***	0.343***	0.171**	0.359***	0.296***

(c) Shrub volume

SITE	D.F.	PERI	AREA	SIDES	A:P	A:S
Field Centre	198	0.427***	0.427***	0.075	0.412***	0.423***
Two-Mile	113	0.147	0.163*	0.041	0.140	0.165*
Purpunda	179	0.283***	0.310***	0.223**	0.310***	0.281***
North-east Overland	232	0.371***	0.398***	0.171**	0.402***	0.356***
South-west Overland	230	0.172**	0.220***	0.219***	0.242***	0.119*
Cooyerdoo	134	0.309***	0.350***	0.189*	0.364***	0.296***

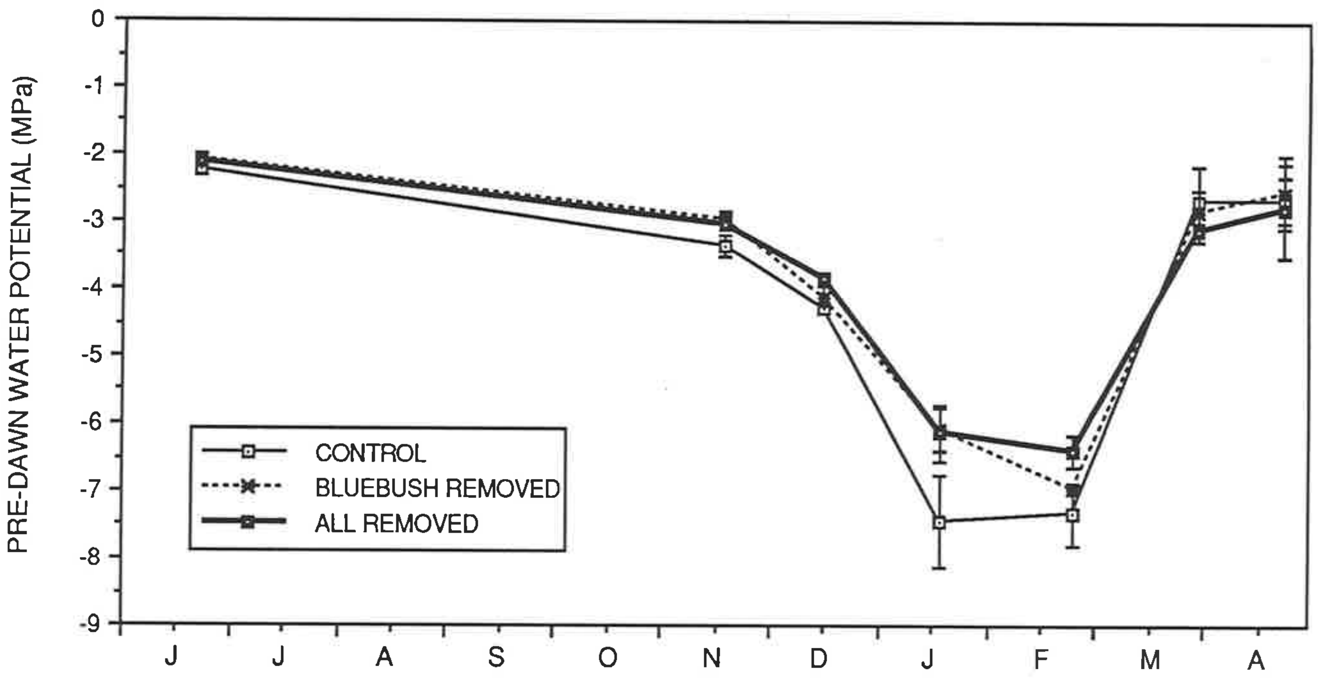
Table 3.3: Spearman rank correlations between bluebush size estimates and three polygon features for the Two-Mile site. Two sets of polygons were constructed; the first including bluebush and the second including both bluebush and blackbush. Significance of correlations and abbreviations are as for Table 3.2.

SIZE ESTIMATE	SPECIES	PERIMETER	AREA	# SIDES
COVER	*M.sedifolia*	0.1580*	0.167*	0.044
	M.sedifolia-M.pyramidata	0.2681***	0.2731***	0.1033*
VOLUME	*M.sedifolia*	0.147	0.163*	0.041
	M.sedifolia-M.pyramidata	0.2397***	0.2375***	0.0824

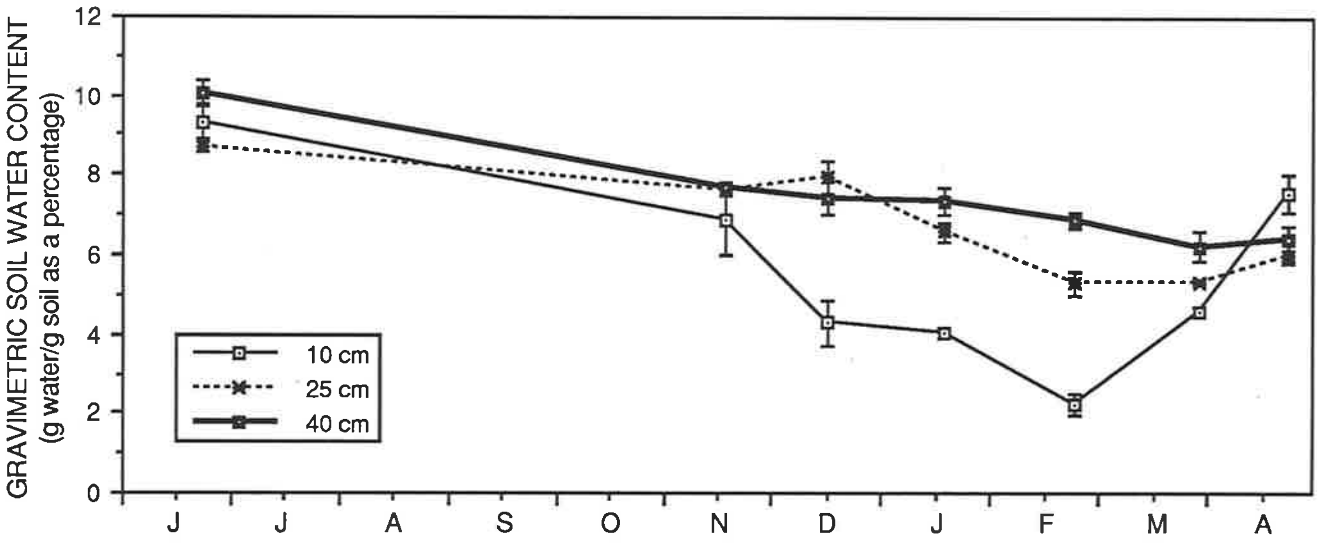
DIRECT DEMONSTRATION

Trial 1 Results

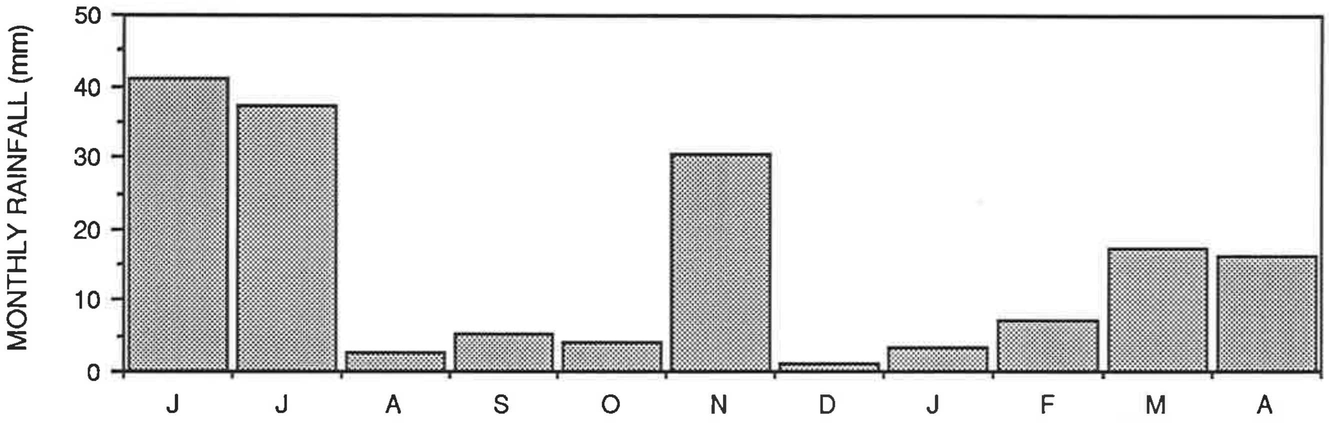
A seasonal trend in pre-dawn xylem pressure potentials is evident for all 3 treatments, following seasonal trends in monthly rainfall, maximum temperature and soil water content (Figure 3.9). As might be expected, there was a decrease in water potential measurements (*i.e.* plants were more water-stressed) over the late summer period (December through February) when the pressures fell to between -6 and -7 MPa. This was followed by a rapid recovery to between -2.5 and -3 MPa as a response to rain and cooler temperatures in late March. More interestingly, significant differences in the pattern of water potential were detected between the variously-treated shrubs (Table 3.4). Monthly ANOVA results and pairwise comparison tests show that these differences occurred predominantly between the control and two removal treatments; removal of surrounding shrubs significantly increased water potentials of the target shrubs on four occasions (Table 3.5). While no difference was detected in June (this was expected as removal was carried out only on the previous day), the control bluebush had more negative water potentials from November 1989 through to February 1990. This suggests that the shrubs within the removal plots were less water-stressed than the control shrubs over most of the summer. This difference was not observed in the March and April recordings when all plants were less stressed as a result of rainfall and cooler temperatures. Significant differences between the two removal treatments were detected only in December, when the water potentials for the bluebush-only removal treatment were higher (less negative) than for the treatment where all neighbouring species were removed.



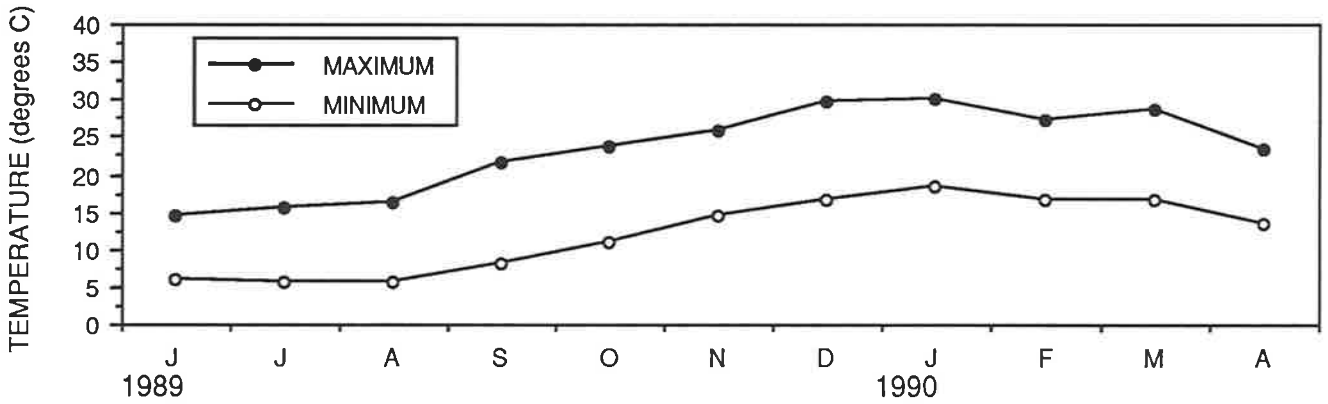
(a) Pre-dawn Water Potentials



(b) Soil Water Contents at Depths of 10, 25 and 40 cm



(c) Monthly Rainfall at Middleback Homestead



(d) Mean Monthly Maximum and Minimum Temperatures at Whyalla

Figure 3.9: Seasonal trends in water potential, soil water content, rainfall and temperature during neighbour removal Trial 1 (June 1989-April 1990). Error bars shown represent standard errors.

Table 3.4: Time series analysis used to examine differences in bluebush water potential over the Trial 1 experimental period. F was calculated by Wilk's criterion.

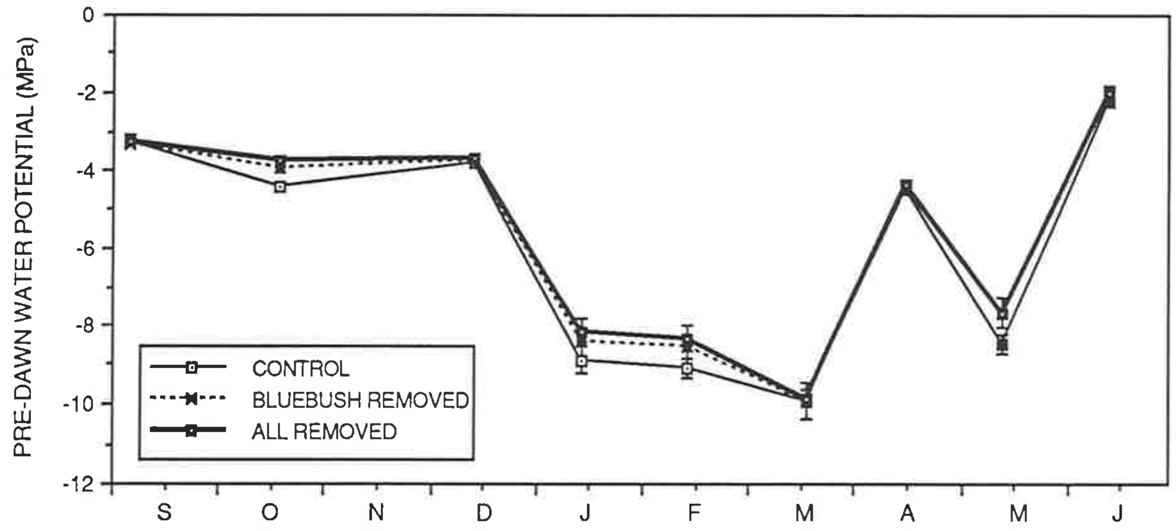
VARIABLE	D.F.	F-VALUE	SIGNIFICANCE
BETWEEN SUBJECT EFFECTS			
Treatment	2	7.24	0.0251 *
WITHIN SUBJECT EFFECTS			
Time	6	1678.953	0.0187 **
Treatment x Time	12	2.672	0.3045

Table 3.5: Monthly mean water potentials (MPa) for each treatment during Trial 1. Similar superscript letters indicate values which are not significantly different at $p<0.05$ (as indicated by ANOVA and pairwise tests of L.S.D).

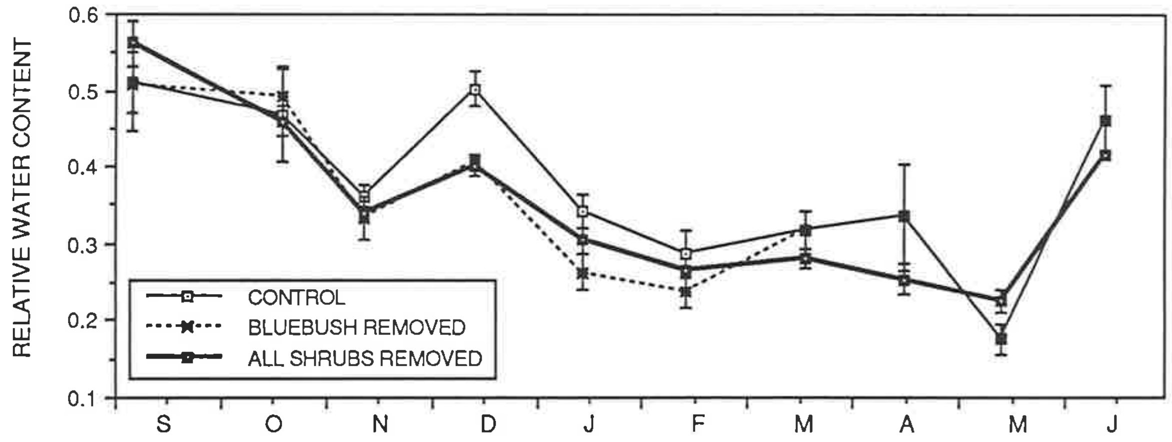
TREATMENT	JUN 22	NOV 17	DEC 14	JAN 16	FEB 22	MAR 29	APR 23
Control (No Removal)	-2.23^{a}	-3.36^{a}	-4.30^{a}	-7.44^{a}	-7.33^{a}	-2.69^{a}	-2.66^{a}
Bluebush Removed	-2.08^{a}	-2.95^{b}	-4.10^{b}	-6.14^{b}	-6.95^{ab}	-2.84^{a}	-2.55^{a}
All Shrubs Removed	-2.12^{a}	-3.02^{b}	-3.86^{c}	-6.07^{b}	-6.41^{b}	-3.13^{a}	-2.81^{a}
F-VALUE	2.58	10.47 *	26.00**	5.33*	7.00*	1.33	0.62

Trial 2 Results

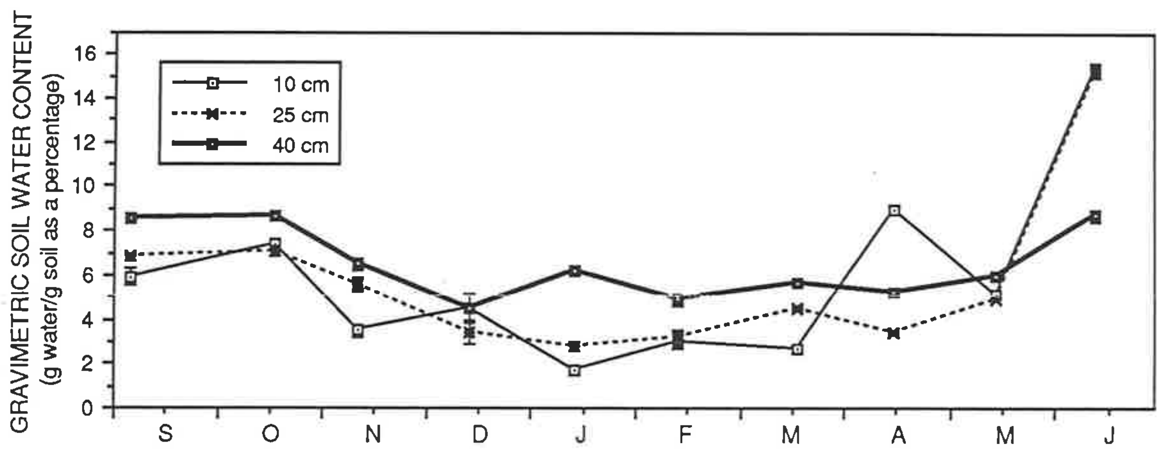
During the second trial, similar seasonal variations in the pre-dawn water potentials of bluebushes were detected (Table 3.6); the results for the control and removal treatments are illustrated in Figure 3.10. During the hotter, drier months, the water potentials were lower than those observed the previous year, with recorded pressures of -9 to -10 MPa. As a response to rainfall and cooler temperatures in April, the pre-dawn water potentials increased to -4 MPa, but subsequently decreased to -7 and -8 MPa in May following scant follow-up rains. The plants showed a rapid increase in water potential following large rainfall events in early and mid June. The relative water content of individual shoots from the control and neighbour-removal plants decreased progressively over the summer, although slight increases were observed following rainfall (December and June) (Table 3.7; Figure 3.10). Unfortunately, many problems were encountered with the plastic tags attached to individual shoots for growth measurements. As a result, growth of target plants could not be estimated during Trial 2.



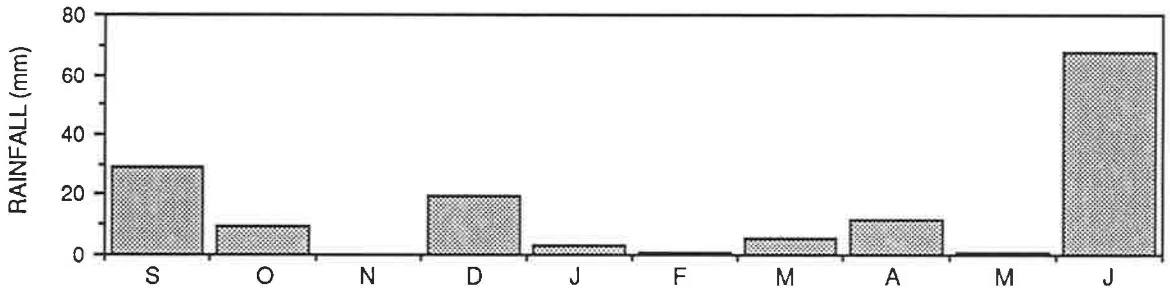
(a) Pre-dawn Water Potentials



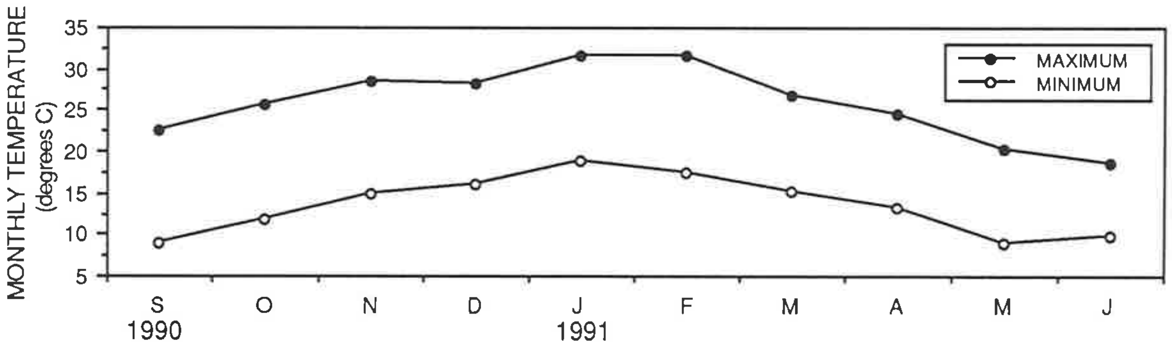
(b) Relative Water Contents of Shoots



(c) Soil Water Contents at depths of 10, 25 and 40 cm



(d) Monthly Rainfall at Middleback Homestead



(e) Mean Monthly Maximum and Minimum Temperatures at Whyalla

Figure 3.10: Seasonal trends in pre-dawn water potential, shoot relative water content, soil water content, rainfall and temperature during neighbour removal Trial 2 (September 1990-June 1991). Error bars shown represent standard errors.

Table 3.6: Pre-dawn water potentials (mean ± S.E.) for all six treatments. Treatments abbreviated as: C, Control; BR, Bluebush removed; AR, All shrubs removed; I, Irrigation; N, Nutrient addition; I+N, Irrigation and Nutrients.

	SEP	OCT	DEC	JAN	FEB	MAR	APR	MAY	JUN
C	-3.25 (±0.13)	-4.41 (±0.06)	-3.83 (±0.70)	-8.89 (±0.32)	-9.09 (±0.23)	-9.91 (±0.44)	-4.46 (±0.13)	-8.49 (±0.24)	-2.24 (±0.10)
BR	-3.33 (±0.09)	-3.94 (±0.14)	-3.75 (±0.17)	-8.42 (±0.34)	-8.52 (±0.30)	-9.91 (±0.44)	-4.46 (±0.13)	-8.49 (±0.24)	-2.24 (±0.01)
AR	-3.25 (±0.14)	-3.75 (±0.09)	-3.67 (±0.06)	-8.19 (±0.36)	-8.34 (±0.35)	-9.85 (±0.22)	-4.37 (±0.05)	-7.67 (±0.38)	-1.97 (±0.15)
I	-3.21 (±0.11)	-3.94 (±0.11)	-3.40 (±0.07)	-8.32 (±0.48)	-8.39 (±0.43)	-9.22 (±0.28)	-4.14 (±0.06)	-8.81 (±0.40)	-2.16 (±0.04)
N	-3.29 (±0.11)	-4.19 (±0.06)	-3.87 (±0.02)	-8.56 (±0.57)	-8.68 (±0.56)	-10.02 (±0.18)	-4.44 (±0.04)	-8.64 (±0.35)	-2.17 (±0.11)
I+N	-3.31 (±0.11)	-3.75 (±0.16)	-3.52 (±0.12)	-8.40 (±0.47)	-8.51 (±0.46)	-9.45 (±0.21)	-4.21 (±0.07)	-8.91 (±0.22)	-2.09 (±0.12)

Table 3.7: Relative water content of shoots (mean ± S.E.) for all six treatments. Treatments abbreviated as for Table 3.5.

	SEP	OCT	NOV	DEC	JAN	FEB	MAR	APR	MAY	JUN
C	0.510 (±0.042)	0.468 (±0.060)	0.361 (±0.015)	0.503 (±0.022)	0.342 (±0.022)	0.286 (±0.031)	0.318 (±0.024)	0.335 (±0.068)	0.176 (±0.020)	0.510 (±0.045)
BR	0.508 (±0.060)	0.492 (±0.043)	0.333 (±0.028)	0.407 (±0.003)	0.264 (±0.023)	0.239 (±0.021)	0.318 (±0.024)	0.335 (±0.068)	0.176 (±0.020)	0.462 (±0.045)
AR	0.562 (±0.032)	0.460 (±0.021)	0.340 (±0.009)	0.402 (±0.015)	0.304 (±0.018)	0.266 (±0.003)	0.281 (±0.011)	0.254 (±0.020)	0.225 (±0.015)	0.417 (±0.004)
I	0.499 (±0.010)	0.520 (±0.040)	0.311 (±0.021)	0.381 (±0.010)	0.304 (±0.037)	0.272 (±0.019)	0.224 (±0.032)	0.290 (±0.025)	0.243 (±0.053)	0.465 (±0.020)
N	0.543 (±0.013)	0.510 (±0.050)	0.333 (±0.010)	0.484 (±0.028)	0.317 (±0.018)	0.275 (±0.007)	0.295 (±0.026)	0.265 (±0.054)	0.212 (±0.024)	0.488 (±0.044)
I+N	0.494 (±0.030)	0.500 (±0.069)	0.324 (±0.021)	0.430 (±0.013)	0.2941 (±0.011)	0.269 (±0.009)	0.287 (±0.061)	0.300 (±0.023)	0.215 (±0.035)	0.419 (±0.024)

There were few detectable differences in water potential and shoot water content between treatments during the Trial 2 (Tables 3.8 and 3.9). The removal of neighbouring shrubs significantly influenced the water status of the target bluebushes on only one occasion (October, the middle of spring). At this time, the water potential of the control shrubs was lower than the removal treatments indicating that the control shrubs were more water-stressed. Comparisons between removal treatments suggest that much of this variation was due to removal of neighbouring bluebushes and not other species. The water potential of the irrigation-nutrient treatmented shrubs was also less than the control shrubs; this variation is largely due to the addition of irrigation rather than nutrients. Differences in the relative water content of shoots (RWC) from the target plants were significant only in December when the RWC of the treatment shrubs was observed to be lower than the control shrubs. This is a surprising result , given that the water potentials of target bushes in both the removal and irrigated treatments was higher (less negative) than the control shrubs at this time.

During the summer period through to autumn, the water potentials of the removal treatment shrubs were not significantly different to those measured for the control, suggesting that all were equally water-stressed over the hot, dry summer period. In contrast, differences between the control and irrigation-nutrient treatments were detected in December and April (early and late summer), suggesting that irrigation promoted the maintainance of higher water potentials (less negative) in the target shrubs in both the irrigation+nutrients and irrigation-only treatments at these times. As in the October observations, the variations in water status of target shrubs was not always reflected by similar fluctuations in the relative water content of the shoots. In December, there were significant differences in shoot water content between the control shrubs and both the removal and irrigation-nutrient treatments at this time, whereas in April, no differences between any of the treatments were found.

Table 3.8: Planned contrast comparisons used to examine differences in water potential between groups of treatments on each recording. Values given are the F-ratios calculated for each comparison with significance indicated as: *, $0.01<p<0.05$; **, $0.001<p<0.01$; ***, $p<0.001$. Abbreviations for treatments are: Con, Control; Rem, Removal; I-N, Irrigation and/or Nutrient Addition. Note: no measurements of water potential were taken in November.

COMPARISON	D.F.	SEP	OCT	DEC	JAN	FEB	MAR	APR	MAY	JUN
Con v Rem.	1	0.07	17.11***	1.01	1.22	1.71	0.00	1.56	0.85	3.83
Con v I-N	1	0.02	12.27***	4.40*	0.86	1.25	1.21	5.94*	0.49	0.79
Among Rem.	1	0.21	1.39	0.41	0.14	0.10	0.17	0.08	2.46	0.18
Among I-N	2	0.20	3.82*	6.55**	0.08	0.08	2.03	5.15**	0.14	0.24

Table 3.9: Planned contrast comparisons used to examine differences in shoot relative water content between groups of treatments on each recording date. Values given are the F-ratios calculated for each comparison. Significance and abbreviations as above.

COMPARISON	D.F.	SEP	OCT	NOV	DEC	JAN	FEB	MAR	APR	MAY	JUN
Con v Rem	1	0.45	0.51	1.24	9.76**	4.12	0.26	1.56	1.34	0.68	1.18
Con v I-N	1	0.01	0.00	3.43	5.74*	1.87	0.23	1.91	0.95	1.88	0.01
Among Rem	1	1.89	2.06	0.08	0.02	1.63	3.97	0.38	0.39	1.13	0.05
Among I-N	2	0.88	0.83	0.39	3.98*	0.23	0.02	1.53	0.25	0.27	1.47

DISCUSSION

SPATIAL PATTERN ANALYSIS

Comparisons with Previous Studies

The distribution of bluebush within the study region is predominantly regular inferring the presence of competition between individual bluebushes for one or more resources (Woodell *et al.*, 1969; Fowler, 1986). This finding is particularly noteworthy given that this is the first demonstration of regular spatial distribution patterns among Australian semi-arid plant species and also because of the surprisingly few examples of regularly-spaced plant distributions reported anywhere (Fowler, 1986).

Within populations of Australian chenopod species, previous studies have revealed shrub spatial patterns which are distinctly non-regular. Examinations have demonstrated that many species, including saltbush and blackbush are often clumped as seedlings, tending towards randomness with age (Anderson, 1967; Anderson, 1970; Anderson *et al.*, 1969). Anderson and his colleagues attributed this change in pattern to intraspecific competition and, more particularly, environmental heterogeneity claiming that regularity could not be achieved in the Australian rangelands because of patchy variation in microtopography, soil moisture and associated nutrients (Anderson *et al.*, 1969). It would appear in hindsight, however, that much of the lack of detected regularity may be due to the use of inappropriate spatial analysis methods. In each of these studies pattern was determined using quadrat-based data, with sample units of at least 1 m^2. More recent studies have suggested that these methods are more powerful in showing the scale at which a clumped pattern may occur, rather than determining the type of pattern present (Kershaw and Looney, 1985). As such, it is likely that Anderson's methods may have failed to detect relevant spatial patterns, particularly considering that interactions which produce a regular distribution of individuals of desert shrubs are more likely to operate over a small distance *i.e.* less than 1m for small shrubs such as saltbush (Phillips and MacMahon, 1981).

Variations in Pattern

As with other studies which have detected regularity in plant populations (Beals, 1968; Woodell *et al.*, 1969; Waisel, 1971; Fonteyn and Mahall, 1981; Phillips and MacMahon, 1981), this pattern was not observed as a consistent feature of bluebush populations on north-eastern Eyre Peninsula. Similar results have also been demonstrated in populations of the North American creosote bush (*Larrea tridentata*) by Barbour (1973) using the results from several studies conducted in the Mojave, Sonoran and Chihuahuan Deserts. *Larrea* was found to be regularly dispersed at 10 locations, random at 22 locations and clumped at 18 locations. Woodell *et al.* (1969) attributed the differences in the spatial patterns of *Larrea* to competition for soil water. They concluded that shrubs tended to be clumped in high rainfall areas and regularly spaced at low rainfalls suggesting that plants became more regular in distribution as a result of decreases in resource availability. This hypothesis was later opposed by Anderson (1971) who suggested that rainfall had little influence on distribution of plants given that different patterns were reported in areas with similar rainfalls.

At first glance, it would be easy to infer that a change in bluebush patterning from regularity to randomness directly reflects an increase in resource availability (in particular the availability of moisture from the soil) as suggested by Woodell *et al.* (1969). Examination of the environmental data reveals that the soil water availability at the two sites with random bluebush distributions (Cooyerdoo and Two-Mile) may be higher than for the other sites; Two-Mile site is located in a wash (run-on area) where the soil texture is sandier especially in the upper profile, while the Cooyerdoo site is on sandy soil in an area which may also receive slightly higher annual rainfall. Interestingly, however, as shown in Table 3.1 bluebush density and % cover were comparatively low at the Cooyerdoo and Two-Mile sites (6.62 and 7.09% cover respectively compared to between 8.64 and 12.78% cover at the other sites). As this is a response that would not be expected following an increase in resource availability (Smith and Goodman, 1986), other factors may have a significant influence on distribution.

The observed differences in bluebush spatial patterns may be explained in part by the existence of interspecific competition within the Cooyerdoo and Two-Mile quadrats. Here, the presence of other plant species appears to limit the abundance of bluebush, thus reducing the importance of competition between neighbouring bluebushes and diminishing the likelihood of a regular spatial pattern. Bluebush abundance at the Cooyerdoo site may be influenced by the presence of more temperate sclerophyllous shrub and tree species such as *Eucalyptus socialis*, *Eremophila scoparia* and *Geijera linearifolia*; estimates of % foliage cover calculated from the quadrat data for this site reveals these species represent approximately 45.30, 4.89 and 5.62 % cover respectively. These species, able to persist at this site because of higher water availability, would have a competitive advantage over slower-growing species such as bluebush. At the Two-Mile site, the random spatial pattern of bluebush is more difficult to explain. First observations would suggest that competition from the more abundant blackbush (8.04% estimated cover compared with 6.62% for bluebush) may limit the distribution of bluebush shrubs. This does not appear to be case, however, given the results of the pattern analysis examining bluebush and blackbush distributions simultaneously. They have similar gross morphologies and thus may be in direct competition, but regularity in pattern was not detected (Batcheler's Ratio=0.8794, p>0.05, random distribution). Few other species were present within the quadrat to influence spatial patterns (cover of all other species was estimated at less 4%). As a result of the rejection of interspecific competition effects, the lack of regularity in this quadrat appears to be due to natural variations in the abiotic environment. Although such variations would be present to a certain extent in all sampled quadrats, they may have been enhanced at the Two-Mile site; the environmental data collected for this site shows this site has been subjected to noticeable water erosion in some areas and has been heavily grazed over recent years due to a watering trough in the near vicinity. This hypothesis would support the ideas of Anderson (1969) who believed that variations in microtopography, nutrients levels and the re-distribution and infiltration of rainfall obstructed the formation of regular spatial patterns in populations of many Australian chenopod species. They would also reinforce the ideas of Matlack and Harper (1986), who state "it is difficult to distinguish changes in density and pattern due to competition from changes due to micro-habitat dispersion and independent germination and mortality".

PLANT SEPARATION:PERFORMANCE RELATIONSHIPS

Detection of Density-dependent Growth

Density-dependent bluebush biomass was observed at every site with significant correlations between shrub size and many of the examined polygon characteristics. Larger bluebushes were seen to occupy 'larger' polygons implying that competition had produced patterns of biomass and survival which were strongly related to the position of neighbouring plants. These results, therefore, provide evidence for competitive effects indicated by spatial pattern studies. Traditional nearest-neighbour analyses have previously revealed density dependent growth in many North American arid and semi-arid species including *Ambrosia dumosa* (Phillips and MacMahon, 1981), *Yucca schidigera* and *Opuntia* spp. (Yeaton and Cody, 1976), *Atriplex polycarpa* (Phillips and MacMahon, 1981) and *Larrea tridentata* (Yeaton *et al.*, 1977; Phillips and MacMahon, 1981; Schlesinger and Jones, 1984). Similar results using tessellation methods have been reported for the perennial grass *Festuca rubra* (Liddle *et al.*, 1982), the perennial herb *Silene dioca* (Matlack and Harper, 1986) and the jack pine, *Pinus banksiana* (Kenkel *et al.*, 1989).

Results from this study revealed a general trend for increasing bluebush cover and volume with the increased availability of water and nutrients. Bluebush height, in contrast, did not appear to be related to the resource availability since there were inconsistent relationships with all polygon features. This may suggest that bluebush possesses less plastic control over upward growth than over vertical spread. Of the tessellation features examined, bluebush size was most strongly related to polygon area. As previous studies have shown this feature to measure the resources available to a plant most closely (Matlack and Harper, 1986), the significance of this relationship is not unexpected. Comparably, polygon perimeter was also correlated with plant size. Previously, this feature has been used as an indicator of polygon shape, where polygons with larger perimeters have more 'border' with potential competitors and hence are more vulnerable to interference (Matlack and Harper, 1986). In this study, increasing perimeter length did not appear to indicate such interference effects as a greater length was correlated with increased plant size. Instead perimeter length was strongly related to polygon area (Spearman rank correlation coefficient (r_S) = 0.972 , d.f. 1072, p<0.001). In contrast, the number of neighbours (polygon sides) was related to plant size only weakly at four of the six sites, and not at all at the other two. Previous studies examining this association (Mack and Harper, 1977; Matlack and Harper, 1986) have also shown tenuous and variable relationships with no bias in sign. Such variation was believed to suggest that growth plasticity allowed plants to exploit the area available to them regardless of the number of neighbours. In the current study, all correlations between plant size and number of polygon sides were positive implying that individual shrubs performed better with more neighbours. Further analysis, however, suggests that this relationship simply reflects an increase in the number of polygon sides with increasing polygon area (Spearman rank correlation coefficient (r_S) = 0.452 , d.f. 1072, p<0.001).

Evidence of density-dependent growth may also be gained by comparing bluebush size estimates and plant densities at each of the study sites. Although little difference in mean plant size was detected between five of the sites, North-east Overland can be seen to possess noticeably smaller shrubs and the highest plant density. This observation supports the hypothesis that individual plants will be smaller when in denser stands as a result of a decline in the average resource availability (Harper, 1977; Silvertown, 1987; Gurevitch *et al.*, 1990).

Variation in Relationships

Although the general trends were consistent, relationships between plant size and polygon features did vary to a limited extent between sites. Strong correlations (mostly P<0.001) were reported for the four sites in which regular spatial patterns were detected. At the Two-Mile site, however, the relationships were much less distinct with most correlations only weakly significant. These results may reflect the low density and random spatial pattern of bluebush reported previously, and reinforce earlier speculation about the lack of competition at both the intraspecific and interspecific levels at this location. Further analyses did not support this theory, however, as strong density-dependent growth was revealed when bluebush size was correlated to available area estimates derived from polygons constructed using both bluebush and blackbush plants (Table 3.3). Fowler (1986) believes such a situation is possible, claiming "the absence of such a [regular] distribution is not evidence for the absence of competition" because of the effects of spatial heterogeneity in the environment and restricted seed dispersal. Environmental heterogeneity has already been implicated as a factor influencing the distribution of bluebushes within the Two-Mile quadrat.

The strong correlation between bluebush size and separation distance detected at the Cooyerdoo site also warrants comment. Although bluebush density was low and spatial pattern analysis revealed a random distribution, correlation analysis indicated significant relationships between bluebush size and most of the polygon features considered. Although it may be speculated that these relationships arise as a result of interspecific competitive effects, it would be necessary to undertake more specific studies to confirm this hypothesis.

DIRECT DEMONSTRATION OF COMPETITION

Presence of Competition

The neighbour removal trials demonstrated that competition for soil moisture occurred between neighbouring shrubs for at least some of the time during both experiments. This was demonstrated through an improved water status of target bushes following the removal of neighbouring shrubs during Trials 1 and 2, and also by showing higher water potentials in irrigated shrubs in Trial 2. Competition for soil water is not a new discovery; many similar findings have been recorded for both crop plants and North American rangeland species (*e.g. Ambrosia* and *Larrea* (Fonteyn and Mahall, 1978; Fonteyn and Mahall, 1981), *Hilaria rigida*

(Robberecht *et al.*, 1983) and *Haplopappus cooperi* (Manning and Barbour, 1988)). The results show, however, that competitive effects are readily demonstrated in bluebush populations, reinforcing previous suggestions that competition is a relatively frequent phenomenon within semi-arid communities. The ability to demonstrate directly the presence of competition in populations of long-lived perennial species such as bluebush is particularly important as the discovery of regular spatial patterning gives little information about the frequency of competition (Fowler, 1986).

Intraspecific Versus Interspecific Competition

Competition for soil water occurred primarily at an intraspecific level (*i.e.* between neighbouring bluebushes); on only one occasion during both trials was a significant difference detected between the bluebush-removed and all shrubs-removed treatments. The lack of detected interspecific competition may be indicative of successful niche separation processes (Fowler, 1986). These usually allow the segregation of resources in space and/or time thereby reducing the intensity of competition and promoting species co-existence. Semi-arid species have evolved a wide range of adaptations that assist in the separation of water use. These include the ability to become physiologically active at different times, spatial separation along microtopographical and other environmental gradients and the evolution of different patterns of root distribution. This latter factor has been demonstrated as an important factor determining the distribution of several perennial species (including *Larrea*, *Franseria* and *Opuntia*) in plant communities of the Arizona Upland (Yeaton *et al.*, 1977) and the subshrub species *Haplopappus* and *Chrysothamnus* (Manning and Barbour, 1988). Studies by Wieland and Bazzaz (1975), Davis and Mooney (1986) and Sala *et al.* (1989) also show that species co-existence may be possible because of differences in rooting depth and water use.

Similarly, root separation appears to be the most likely factor restricting interspecific competition between bluebush and other perennial shrub species. Bluebush is noted as a deep-rooted species (Osborn *et al.*, 1935; Carrodus, 1962) possessing tap-roots which extend to a greater depth than many other shallow-rooted species such as saltbush (*A. vesicaria*). Such root morphology enables bluebush to penetrate comparatively deeper into the soil for water acquisition thereby reducing the competition for soil water with shallow-rooted species. As no other known deep-rooted species *e.g.* blackbush occurred at the experimental site (saltbush and *Rhagodia ulicina* were the other common species), it is not surprising that the removal of neighbouring species other than bluebush had little effect on the water status of the target bluebushes. It must be noted, however, that the results of this trial should not be taken to imply that interspecific competition from other shrubs is not necessarily an important factor influencing the distribution of bluebush. At other locations in the general area, such effects would be expected to be more pronounced. For example, the removal of blackbush (*Maireana pyramidata*), also a deep-rooted species, is likely to show interspecific competitive effects with bluebush as these two species are morphologically similar and possess comparable root distributions.

Variability in Competitive Effects

Competition was also seen to be variable over time. It was demonstrated over most of the summer during trial 1 (where differences between the control and removal treatments ranged from ≈ 0.03 to 1.3 MPa) but only during spring in trial 2 (where differences between the control and removal treatments was ≈ 0.6 MPa). Although such temporal variation is not unexpected in areas of erratic climate (Fowler, 1986), it may appear surprising that it was detected for a longer period of time during the first trial, given that this was conducted over a milder and wetter summer period (see Table 3.10). Under these conditions, it would be expected that more water would be available in the soil profile and that competition would be reduced; a similar comparison examining the water relations of *Artemisia tridentata* over wet and dry years illustrates the maintenance of higher water potentials during wet years (Campbell and Harris, 1977).

Table 3.10: Summary of climatic conditions during the two neighbour removal trials. Rainfall records are from Middleback Homestead with temperature data from Whyalla (Bureau of Meterology).

TRIAL NUMBER	RAINFALL (mm) YEAR TO SEPT.	RAINFALL (mm) OCT - APRIL	MEAN DAILY TEMP(°C)	LOWEST WATER POTENTIAL (MPa)
Trial 1 (1989/1990)	194.5	79.4	26.90	-6 to -7
Trial 2 (1990/1991)	166.0	50.0	28.11	-9 to -10

Gurevitch *et al.* (1990), however, suggest that competition intensity may decrease or increase as a consequence of diminishing resources. They believe that while perhaps the most obvious effect is that competition becomes more intense when resources are in short supply, it is also possible that competition may increase when resources become abundant as a result of competing neighbours becoming larger and therefore closer to each other. This latter situation may account for the observed yearly variations in competitive effects within bluebush populations if the higher water availability promoted root growth and hence increased competition. Given my results, it would seem that the maintenance of high soil water contents does increase root competition. Monthly results suggest increased competition in spring-early summer when higher amounts of water are available in the soil profile at depths of at least 25-40 cm (see Figures 3.9 and 3.10); this contrasts with other studies demonstrating an increase in competitive effects over summer (Fonteyn and Mahall, 1981; Manning and Barbour, 1988; D'Antonio and Mahall, 1991). More directed studies looking at root growth in response to water availability, particularly possible root-deciduous characteristics in drought, are required to confirm these suggestions.

Alternatively, the results may indicate that the removal of neighbouring shrubs becomes less detectable over the summer period. It is possible that neighbouring shrubs expand and take over the previously occupied root space soon after neighbour removal and that, as a consequence, the removal of shrubs would have less effect on target plants over time and competition would not be detected. A similar effect was found following the removal of the invasive species *Carpobrotus edulis* from a *Halopappus venetus* community (D'Antonio and Mahall, 1991). Here, the effect of removing shrubs became insignificant after an initial period, implying that the demand for water by increased leaf areas of remaining plants matched the enhanced water availability following the removal of *C.edulis* plants. A similar argument may be used to explain the results here, although it appears unlikely given the slow growth rate of bluebush. This could be tested by removing shrubs at several intervals over the spring-summer period to determine the presence of competition rather than just in late winter-spring.

Effects of Irrigation and Nutrient Addition

My results suggest that irrigation led to an improvement in the water status of target shrubs early in the season. After December, however, very little carry-over effect from one month to another was detected both in terms of plant water potential and also shoot water content. High soil-surface evaporation rates and a lack of water penetration to lower soil layers appeared to negate any improvement in soil water availability during most of the summer. As bluebush is a deep-rooted species, it appears unlikely that the water from irrigation reached down to the rooting layer at any time later in the summer. This hypothesis could be further tested by taking soil moisture and plant water potential measurements at much shorter time intervals following each watering (as in Manning and Barbour, 1988). Only in April, when rain had fallen and temperatures had decreased, did irrigation have a measurable, lasting effect on plant water potentials.

Similarly the addition of nutrients did not appear to influence the water status of target plants; on all but one occasion, there was no difference between the nutrient-only and control treatments. This is not surprising, given that nutrient addition has little effect on soil water availability. Likewise, previous studies have suggested that the addition of nutrients in semi-arid environments does not stimulate plant growth in perennial shrubs species.(Ludwig *et al.*, 1989). This latter hypothesis could not be tested for bluebush as the plastic tags attached to individual shoots for growth measurements could not be used to record shoot length and leaf number accurately; as a result, additional evidence to support or deny the existence of competition between neighbouring shrubs for soil nutrients could not be ascertained.

Relative Water Content of Shoots

The water content of bluebush shoots (RWC) decreased progressively over the summer, with only slight increases following rain in December and April. The loss of water from the leaves continued despite the ability to become drought-hardened. Hay (1991) demonstrated that water loss in bluebush can be reduced during dry conditions by several morphological changes in leaf structure and function. These adaptations include the reduction in leaf size and surface:area ratio, and the development of water storage tissue and extra leaf hairs.

Despite these seasonal trends, there were few measurable differences between the treatments. Although the analysis of variance indicated significant differences in December 1990, this result does not seem valid as the shoots from the control bluebushes had higher RWC than the treatment shoots. As there was an increase in the water status of many of the treatment target plants at this time, this outcome appears unlikely and may reflect sampling errors. Such inaccuracies may have resulted when re-hydrating the shoot to achieve turgidity or during weighing procedures. Overall, therefore, the lack of variation between treatments suggests that shoot RWC of bluebush is determined primarily by external conditions and not by the internal water status of the plant. As changes in leaf morphology can occur under droughting conditions (Hay, 1991), it is possible the extent of leaf hardening may control the level of water in individual shoots through direct responses to climatic conditions. More specific physiological experiments are needed to confirm these ideas.

ECOLOGICAL IMPLICATIONS OF COMPETITION

Although competition was clearly demonstrated during this study, it is difficult to ascertain the short and long-term ecological significance on bluebush populations and community structure. Such difficulties arise because competitive effects may occur inconsistently over time and at different stages of the life-cycle of plant species. It is known that competition may act during different phases of the life history of a plant (Grubb, 1977; Aarssen and Epp, 1990) influencing survival, growth and/or reproduction. Investigations have demonstrated most clearly that by reducing competitive effects through the removal of neighbouring plants, either of the same or different species, higher growth rates are often achieved. Specific examples of species demonstrating such an effect include desert annuals (Friedman *et al.*, 1977; Inouye *et al.*, 1980), *Hillaria rigida* (Robberecht *et al.*, 1983), *Stipa neomexicana* seedlings (Gurevitch, 1986) and seedlings of Douglas-fir and red alder (Shainsky and Radosevich, 1992). Additionally, studies have shown that reproductive output may be increased (*e.g. Encelia farinosa*: Ehleringer, 1984; desert annuals: Inouye *et al.*, 1980; the grass *Anthoxanthum odoratum*: Platenkamp and Foin, 1990) and seedling survival is improved (*e.g.* desert annuals: Friedman *et al.*, 1977; *Plantago*: Sagar and Harper, 1961; *Rumex*: Putwain and Harper, 1970). Furthermore, studies have demonstrated that competition may be variable in frequency and extent (Fowler, 1986), stressing that it is an effect which may vary in importance through time. It is likely that competitive effects may only be important during particular years and under certain conditions.

This study suggests that the frequency, extent and timing of competition at both an intraspecific and interspecific level may play a determining role in the many aspects of the population dynamics of bluebush. Results suggest that both the spatial distribution patterns and size of bluebush were altered by competitive effects. It is likely, however, that competitive effects influencing reproduction and seedling survival are most important in the long-term maintenance of bluebush populations. As bluebush recruits only rarely (Osborn *et al.*, 1935; Crisp, 1978), detrimental influences on the success of individuals during reproductive episodes may conceivably have long-lasting, and possibly irreversible, effects on population structure and function. Similarly, competitive effects influencing seedling survival may be crucially important especially if other disturbance effects such as grazing are taken into account. Although most information relevant to these effects and their relative importance is generated by studies conducted over several seasons, short-term observations regarding these aspects of bluebush population dynamics will be examined in subsequent chapters.

CONCLUSIONS

- Spatial distribution patterns of bluebush at Middleback Station are predominantly regular implying the presence of intraspecific competition between individual bluebushes. Random patterns appear to arise only when bluebush is less dominant such as in mixed species stands or when the abiotic environment is particularly spatially heterogeneous.

- Competition leads to density-dependent bluebush growth with larger shrubs possessing larger areas for potential resource acquisition.

- Competition for soil water does occur over the summer period primarily between neighbouring bluebushes.

- The ecological significance of competition in the maintenance of bluebush communities is difficult to determine. While competitive effects were shown to influence plant size and spatial distribution patterns, the effect on reproduction is likely to be more crucial in the long-term maintenance of populations.

CHAPTER 4

FACTORS INFLUENCING FLOWERING, FRUITING AND SEED DISPERSAL

INTRODUCTION

BACKGROUND

Reproduction in Arid-zone Perennial Plants

Flowering

In mesic environments, flowering is usually seasonal, with individual plants having a good chance of completing the reproductive cycle in every year. In more arid environments, however, erratic and unreliable rainfall events generally prevent a regular cycle in both annual and perennial plants, giving no general relationship between flowering and season. In perennial species in particular, reproduction can occur at most times of the year as seed production is not generally critical for survival (Fischer and Turner, 1978; Mott, 1979).

Although the onset of flowering is controlled by three major factors, photoperiod, temperature and moisture, it is the last of these which plays the critical role in determining flowering times in arid-zone plants (Mott, 1979). Many studies have shown the presence of rainfall-stimulated flowering; *e.g.* Beatley (1974) reported that flowering of perennial shrubs in the Mojave desert usually took place following rainfall in the autumn months, and Preece (1971) demonstrated experimentally that the tree species *Acacia aneura* (mulga) required large, consecutive summer and winter rainfall for successful reproduction. Other studies have suggested that decreases in soil water availability may delay flowering in perennial plants. Lags of up to a few days have been shown in *Urtica* (Stinging Nettle) and up to four weeks in *Artemisia pauciflora* (Boot *et al.*, 1986; Bykov, 1974 in Mott, 1979). In addition, complete failure of successful fruiting, or both flowering and fruiting, has been reported in very dry years in a range of species and life-forms (Davies, 1968; Davies, 1976; Beatley, 1974; Bykov, 1974 in Mott, 1979).

Seed Production

As reproduction is usually performed at a cost to growth, the amount of reproductive effort may be critical to both fitness and survival (Harper, 1977; Silvertown, 1987). Allocation to reproduction is variable in terms of both seed number and seed size; Harper (1977) suggests that these two factors are often alternatives in the strategy of reproduction.

Seed number is variable in many species and appears to be chiefly influenced by climate and resource availability (Mott, 1979; Marshall *et al.*, 1986; Coffin and Lauenroth, 1992). As may be expected, the number of fruit (seeds) produced is usually reduced under drought conditions (Mott, 1979), as energy is allocated to survival rather than reproduction. Spatial variations in seed production have also been reported following changes in soil texture and grazing by cattle (Coffin and Lauenroth, 1992). In a similar manner, decreases in seed number have been noted for plants that are under competitive stress from neighbouring plants (Silvertown, 1987).

Selective forces may also act on seed size and weight (Howe and Smallwood, 1982; Fenner, 1985). Previously, it was thought that the seed was one of the least plastic plant organs, varying little in size and weight; Harper (1977) stated that "plants respond to stress phenotypically by varying almost every other component before seed size is affected." More recently, however, seed size variations have been detected, particularly when the general availability of resources has been altered (Maun and Cavers, 1971; Stephenson, 1980; Willson and Price, 1980; Wulff, 1986a). General trends imply a decrease in seed size and weight with decreases in resource availability (Gutterman, 1980-1981; Fenner, 1985). For example, Willson and Price (1980) reported weight changes of *Asclepias* seeds following nutrient, leaf removal and shading modifications, while Marshall *et al.* (1986) observed seed weight reductions following mild water, nutrient and defoliation stress in the legume, *Sesbania macrocarpa.* It has also been suggested that species and species ecotypes from drier habitats produce larger seeds (Salisbury, 1942; Baker, 1972; Schimpf, 1977), possibly to favour seedlings which can quickly establish a root system by using their own food reserves (Fenner, 1985)[1].

Investigations into the effect that variations in seed number and size may have on life-cycle characteristics of individual species have only recently become popular (Winn, 1985; Wulff, 1986b; Ågren, 1989). As a consequence, the extent to which seed variations influence other important recruitment factors such as seed dispersal, germinability and seedling growth is not particularly well-documented (Schimpf, 1977; Wulff, 1986a). Although the consequences of reduced seed number seem evident, variations in seed size are more difficult to determine. Using the results of previous studies, Hendrix and Trapp (1992) recently summarised the effects of reduced seed size within individual species. They showed that smaller seeds generally resulted in reduced germination, decreased or delayed emergence from deeper sowing depths and more stringent requirements for emergence in litter and herbaceous cover. Additionally, seedlings from smaller seeds may be less competitive and more susceptible to grazing.

Seed Dispersal

Seed dispersal mechanisms play an important role in the demographic characteristics of individual species by sorting seeds non-randomly among the available micro-sites in any given environment. As a result, dispersal may cause the aggregation of seeds, rather than an even spread (Bullock, 1989). Dispersal may move seeds a varying distance way from the parent plant; this may or may not be advantageous to successful recruitment (Fenner, 1985).

Dispersal from parent plants occurs via three main agents, wind, water and animal (Howe and Smallwood, 1982; Nicholson, 1986) and in two main phases, dropping from the plant (Phase I

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[1] Although possibly still applicable to individual species variations, this hypothesis was recently falsified at a species level by Jurado and Westoby (1992) following a series of experiments examining seeds of many Central Australian species. Using seeds from 32 species, they were able to demonstrate that seedlings from heavier-seeded species did not allocate more resources to roots than light-seeded species.

dispersal) and subsequent movement along the ground (Phase II dispersal) (Watkinson, 1978). In dry environments, wind-dispersed plants are relatively common in number and proportion (Howe and Smallwood, 1982). Nicholson (1986) believed that there were three possible fates for seeds following Phase I dispersal:

(i) no further movement - incorporation into seed bank,
(ii) removal by predators (ants, birds and small mammals) and
(iii) movement as a result of wind or water, and then incorporation into the seed bank or removal by predators.

On many continents, particularly North America, the primary predators are birds and granivorous mammals. In Australia, these animals are less important seed gatherers (Morton, 1985; Wiens, 1991); instead, ants are the major post-dispersal seed predators (Andersen and Ashton, 1985). As they are prevalent in a variety of habitats (Wellington and Noble, 1985; Andersen, 1987; Gross *et al.*, 1991; Ireland, 1992), they must be taken into account when attempting to understand and manage Australian ecosystems (Andersen, 1991).

There has been considerable debate regarding the beneficial and detrimental effects of seed collection by ants; they vary according to whether the ants act as seed dispersers or as predators/harvesters. Some ants act as seed dispersers by removing seeds from the initial dispersal site. The ants are often attracted by a food appendage (eliasome), which may help the ant carry the seed and also provides an alternative food source to the actual seed. In this situation, the ants do not eat entire seeds; they are usually left intact, either in the nest or on the surface of the nest (Bennett and Krebs, 1987; Ireland, 1992). This procedure can be considered advantageous to the seed as it transports the seed away from the parent plant and may therefore reduce later competition from seedlings at the initial dispersal site or from the parent plant. Additionally, the movement of seed below ground may assist germination and seedling establishment, and may make the seeds unavailable to predators (*e.g.* seed harvesting ants, mammals and birds; Beattie, 1985 and Ireland, 1992). Although it has also been proposed that by carrying seeds to their nests ants facilitate dispersal to nutrient-rich micro-sites (Culver and Beattie, 1978, 1980; Davidson and Morton, 1981; Beattie, 1985), the legitimacy of this hypothesis has recently been questioned (see Rice and Westoby, 1986; Bond and Stock, 1989 and Westoby *et al.*, 1991). In contrast, ants may also have a detrimental effect by gathering seeds and subsequently eating them in their entirety; seeds are removed to nest sites and either eaten immediately or stored in chambers for later use (Mott and McKeon, 1977; Gross *et al.*, 1991). These procedures effectively remove the seed from the seed bank by either direct predation (*i.e.* the seeds are eaten) or by placing them at a soil depth sufficient to make germination impossible.

Observations of Bluebush Reproduction

Flowering and Seed Production

Reproductive episodes in bluebush are rare with flowering occurring very sparingly and irregularly (Osborn *et al.*, 1935; Ratcliffe, 1936; Wood, 1936; Jessup, 1951; Graetz and Wilson, 1984). It does not seed as heavily nor as frequently as other Australian chenopods, particularly saltbush and blackbush (Burbidge, 1946; Carrodus, 1962; Leigh and Mulham, 1965). Observations of flowering/fruiting events suggest that bluebush can reproduce at virtually any time of the year. Heavy rainfall events usually bring about the onset of flowering, although this is not always the case (Hall *et al.*, 1964; Perry, 1972). Burbidge (1946) observed seed production in 3 out of 4 years (1942-1945) despite the incidence of poor seasons. Also the presence of heavy rains does not imply the onset of flowering as this species does not set seed in every good season (Wilcox, 1974).

Seed Dispersal

Aggregation of seeds has been observed in the Australian arid-zone. Here, the seeds of many plant species, including several chenopods, have been reported accumulating in areas containing litter, twigs, dead branches and high amounts of ephemeral cover (Malik, 1970; Nicholson, 1986). High seed densities have also been reported around the bases of perennial plants (Hall *et al.*, 1964; Williams, 1979). Seed dispersal in chenopod species is generally localised, with longer-distance dispersal only occurring through whirlwinds which may disperse seeds over many kilometres (Williams, 1979).

Knowledge of seed and fruit dispersal in bluebush in particular is scant. Hall *et al.*(1964) suggested that the fine, papery nature of the wing assisted the seed to be disseminated from the parent plant by wind and, as a result, the seeds are blown across the ground and become trapped in litter, broken soil and other plants. In seed dispersal observations carried out at a re-vegetation site at Manna Hill, South Australia, Butler (1985) found seedlings were contained within 200 m of the seed source and concluded therefore that wind dispersal may only be of local importance. The role of ants in the dispersion of bluebush fruiting perianths is not well-discussed in the literature; anecdotal observations suggest that bluebush fruit is collected by seed-harvesting ants (Nicholson, 1986; C. Ireland, pers. comm.).

AIMS

Few quantitative studies have been carried out to examine the factors influencing flowering and fruiting of arid-zone perennial shrubs at either the population or individual shrub level. Despite the reported infrequency of reproduction, knowledge of flowering and fruiting in bluebush is particularly scant and is limited to anecdotal observations. This chapter investigates the fruiting characteristics of bluebush at Middleback Station during the years 1988-1992 to gain more specific information on reproductive events. Specific issues addressed in this chapter include;

(i) the influence of environmental factors on the timing of flowering/fruiting events and on seed production,

(ii) the spatial arrangement of fruiting bushes and the influence of plant size/available area, and

(iii) the mechanisms of fruit dispersal, particularly by ants.

METHODS

FIELD DATA COLLECTION

Flowering and Fruiting

General Observations

Bluebush flowering and fruiting characteristics were examined at Middleback Station during the period March 1988 to December 1991. During this time, observations of flowering across the station were conducted by myself, the Nicolson families and fellow research students; all positive sightings were recorded by date and location. As flowers of this species are inconspicious, all observations were based on the appearance of fruiting perianths. Fruits from each reproductive event were collected for later determination of size, oven-dry weight (100°C/24 hours) and germinability.

Observations Within Permanent Quadrats

To examine fruiting characteristics more specifically than could be achieved by casual observations, fruiting was also followed within the six permanent quadrats described in Chapter 3 and Appendix 2. Observations of fruiting within these areas were made on each trip to Middleback, at approximately monthly intervals, over the four year study period. On each occasion, the quadrats were examined for the presence of flowering or fruiting bushes, with reproductive plants tagged and located on computer-generated quadrat maps for correct identification. At this time, an estimate of the extent of flowering on each bush, expressed as a percentage of the bush bearing fruit, was also made.

Seed Dispersal Studies

Initial Dispersal Patterns

The dispersal patterns of bluebush were determined by following the movement of harvested fruiting perianths across the soil surface from pre-defined locations. This method was used as an alternative to tracking dispersal of fruits shed naturally, as previous attempts of following such perianths proved too difficult because of slow and unpredictable release.

Dispersal of bluebush fruits was examined in an area adjacent to the Field Centre in February 1990, using fruits collected during the previous fruiting episode (April 1989). Each fruit was lightly dotted on both sides with fluorescent dye applied with the tip of a fine paintbrush to allow easier observation. Fruit dissemination was followed from two sources; plates mounted on top of stakes approximately 60 cm from the soil surface (to imitate seed fall from adult plants) and flat plates secured to the ground (to examine fruit movement along the ground). Each plate was positioned on a mound previously occupied by a bluebush plant to emulate as much as possible the typical micro-environments surrounding adult bluebushes. Two replicates at each plate height were used. Wind speed was estimated half-hourly over the 36 hour experimental period using a portable anemometer mounted above bush height.

Fifty fruits were placed on each of the plates at 9 am on 22 February 1990. The position and orientation of fruits was subsequently recorded at regular intervals over the next four hours. A portable ultra-violet light was used the following night to determine further fruit dispersal. Patterns from one raised and one surface plate only were investigated; there was insufficient time to follow fruit from the other plates. At this time, distance from the plate and fruit orientation was again determined. The micro-environment in which the fruit was located was also recorded as one of the following; open spaces between adult shrubs, under bluebushes, under saltbushes, on mounds previously occupied by a mature shrub, amongst litter or in an area densely populated by the annual species, *Carrichtera annua*.

Seed Removal by Ants

Studies of bluebush fruit removal by ants were carried out adjacent to the Middleback Field Centre in March and June 1991. Foraging for seed was followed by examining the removal of fruits from depots located in different micro-environments: open areas between mature shrubs; under mature shrubs; amongst litter; and in areas densely populated by ephemeral species (particularly *C. annua*). Removal of fruit from mounds previously occupied by plants was not scored in this instance as few such mounds were present in the study area.

In an experimental set-up similar to Casper (1987), seed depots were constructed from foam drinking cups, the bottom of which had been cut to give a dish approximately 2 cm deep and 4 cm in diameter. A roofing nail was pushed through the bottom of the dish to secure it to the ground while a masking tape ramp was fixed to the bottom of each depot to allow access by ants. In addition, 'control' depots were produced without the ramps to determine fruit loss by wind, while 'protected' depots were surrounded by cages of 1 cm chicken wire to restrict predation of fruits by small mammals and birds. Twenty depots were placed along 8 transects at approximately 2 m apart, with 5 depots randomly placed in each of the four micro-environments considered. Additionally, two control and protected depots were randomly placed along each transect in a variety of micro-environments. Small depressions in which to place each depot were carefully dug before the depots were secured. Ten bluebush fruits were added to each depot prior to the commencement of observations, with fruit loss from the depots recorded after 2 days.

ANALYSIS METHODS

Flowering and Fruiting

General Observations

Normally, logistic regression procedures could be used to determine the climatic variables influencing flowering and fruiting patterns. This method was not chosen in this instance, however, as only a few occurrences of flowering occurred during the study period and as some events were site specific. General patterns, however, were determined by comparing graphs of climatic patterns with timing and extent of fruiting events. Climate data used in this analysis was obtained from Commonwealth Bureau of Meteorology (1984) sources. Similar comparisons were made for fruit size, weight and germinability.

Observations Within Permanent Quadrats

Fruiting statistics were compiled from the annotated quadrat maps and field notes. The percentage of plants in fruit was calculated for each site on each occasion. Chi-squared analysis via a 2 x 2 contingency table was used to determine whether the number of plants fruiting on successive occasions was significantly greater than expected. Spatial pattern analyses of flowering bushes were carried out as described in Chapter 3 using Batcheler's ratios (Batcheler, 1971) calculated using a FORTRAN program written by J. Pearce, Statistics Department, The University of Adelaide.

The likelihood of shrubs flowering was modelled by logistic regression as generalised linear models (GLIMS), using the presence and absence of fruits on individual plants. Models were constructed on an individual site basis and for all sites combined, using similar procedures to those used for species response models (Chapter 2). Variables included in the analysis include four plant size estimates (height, maximum horizontal diameter through the canopy, cover and volume) and five estimates of available area calculated during Dirichlet polygon analysis (area, perimeter and number of polygon sides and the area:perimeter and area:number of sides ratios) as derived in Chapter 3. Two models were constructed for all flowering data; one including location as a factor variable and the other not taking location into account. For the Two-Mile quadrat, polygon features were determined using the mixed bluebush and blackbush tessellations as this was shown to represent bluebush available area more closely than polygons constructed using only bluebush shrubs[1]. All models were constructed using the computer software package GENSTAT (Statistics Department - Rothamsted Experimental Station, 1987).

Seed Dispersal Studies

Data for seed dispersal characteristics were recorded in the form of counts. Trends were subsequently determined using raw percentages in addition to means and standard errors. .

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[1] See the spatial pattern analysis section of Chapter 3 for further discussion of this.

Analyses of variance on arc-sine transformed data were performed to determine if fruit loss could be attributed to ant removal and to investigate possible differences in removal rates between the nominated micro-environments. The computer software package SPSS-X (SPSS Inc., 1986) was used for all analyses.

RESULTS

FLOWERING AND FRUITING

General Observations

Fruiting of bluebush plants at Middleback Station was observed on various parts of the property on five separate occasions between 1988-1991 (Table 4.1). Of these reported sightings, the April 1989 fruiting event was the most extensive, with fruiting plants observed at many sites on Middleback and Roopena Stations. At this time a high percentage of plants flowered and fruited, with records also showing high numbers of fruits per plant. In comparison, the remaining flowering events were much less extensive. On three occasions (May 1988, November 1988 and April 1990) fruiting plants were observed in only one locality, with accompanying low numbers of fruiting bushes and numbers of fruit per plant. In May/June 1991, fruiting was observed at several locations although numbers of fruiting plants and fruits produced was low.

Table 4.1: Flowering events observed on Middleback and Roopena Stations between March 1988 and December 1992. The % of bushes in flower and the number of fruits per bush were estimated visually. Classes for % of bushes in flower are: low, <5%; medium, 5-20%; high, >20%. Classes for fruit number are: low, < 50 fruit per plant; medium, 50-250 fruit per plant; high, >250 fruit per plant.

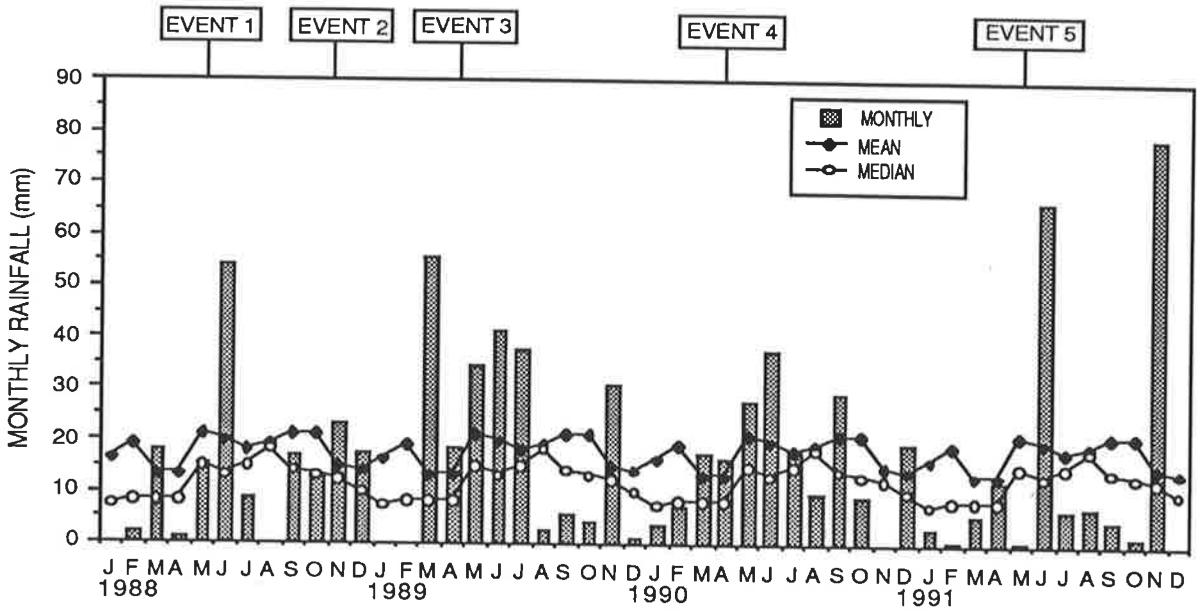
DATE	LOCATION	DISTRIBUTION	% FLOWERING	#FRUITS/BUSH
May 1988	Purpunda Paddock	Limited	Medium	Medium
November 1988	Field Centre	Limited	Low	Low
April 1989	Various Areas	Extensive	High	High
April 1990	Overland Paddock	Limited	Low	Low
May/June 1991	Various	Extensive	Low	Low

Seasonality of bluebush fruiting does exist, at least in part, with four of the five fruiting events reported during the autumn period (April-June), following the relatively hot and dry conditions of summer. Examination of the annotated climate graphs reveals that flowering/fruiting generally occurred in periods preceded by at least one month of above the recorded median rainfall in the 2-3 months before fruiting when maximum daily temperatures averaged 20-25°C (Figure 4.1). Fruiting events in May 1988, April 1989, April 1990 and May/June 1991 followed periods of above median rainfall for the months of March 1988, March 1989, March 1990 and April 1991 respectively. These results also show, however, that reproduction does not always occur following large rainfall events; no fruiting was observed after high rainfalls in November 1989, May/June 1990, September 1990 and June 1991.

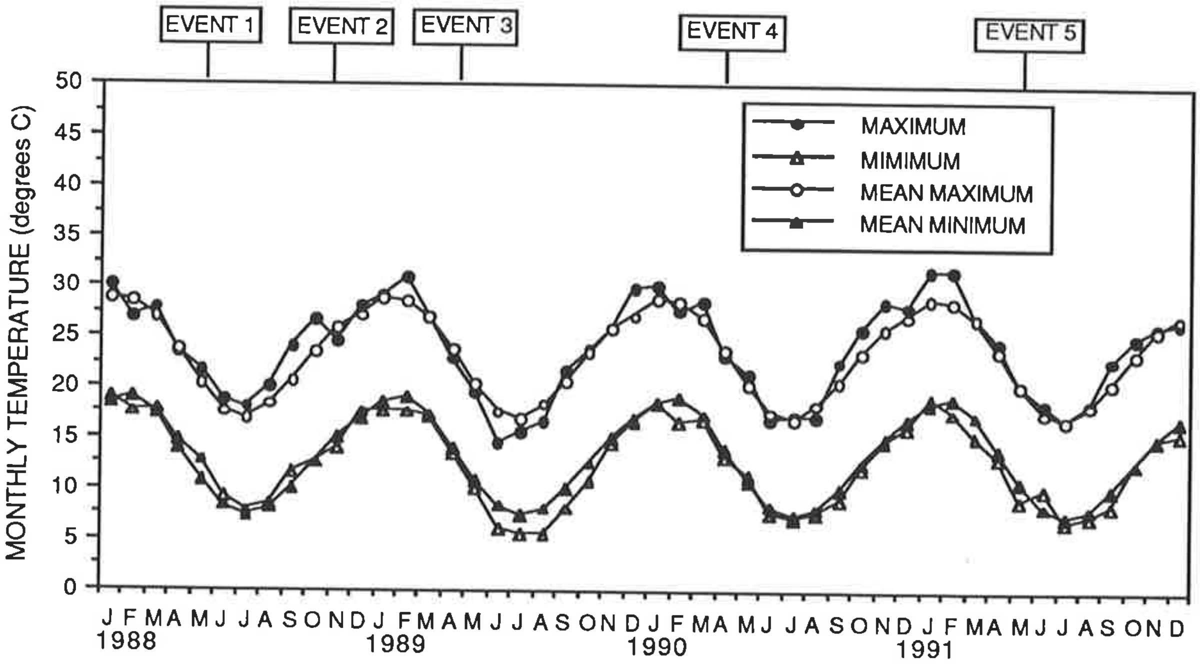
Similarly, the extent of fruiting (distribution around the region, numbers of bushes in flower and numbers of flowers on each bush) appears to be related to the amount of rain. Widespread, heavy fruiting was observed following rain in March 1989, where falls in excess of three times the monthly average rainfall (six times the median amount) were recorded (56 mm for the month, 52.6 mm of which fell over a period of six days). In contrast, fruiting events following less outstanding rainfalls was much more limited. Likewise, examination of fruit size and germinability reveals some variation in fruits produced at each from each flowering (Table 4.2). The largest and heaviest fruits were recorded from the April 1989 fruiting, although these were later shown to have the lowest percentage germination in laboratory trials.

Table 4.2: Characteristics of fruit collected from Middleback and Roopena Stations. Classes for fruit number as for Table 4.1. Fruit diameter represents the mean of 25 seeds and dry weight (oven dry, 100°C/24 hours) represents the mean of 20 seeds. Percentage germination was determined within two weeks of seed collection using standard germination trials (described in detail in Chapter 5).

DATE	#FRUIT/BUSH	FRUIT DIAMETER (mm)	DRY WEIGHT (g)	%GERM
May 1988	Med	7.47±0.20	0.0043±0.0007	80.0±6.3
November 1988	Low	6.72±0.26	0.0033±0.0005	-
April 1989	High	10.30±0.31	0.0058±0.0020	64.0±2.3
April 1990	Low	8.01±0.23	0.0049±0.0007	72.8±1.3
May/June 1991	Low	7.69±0.30	0.0046±0.0009	69.6±4.4



(a) Monthly Rainfall Totals at Middleback Homestead (means and medians from Roopena Homestead)



(b) Maximum and minimum monthly temperatures for Whyalla (means and medians also from Whyalla) (Bureau of Meterology, 1983).

Figure 4.1: The occurrence of fruiting events in relation to climatic conditions at Middleback and Roopena Stations during the period 1988-1991.

Observations Within Permanent Quadrats

Fruiting Percentages

The presence of fruiting bluebushes within the permanent quadrats was recorded twice during the four year observation period, in April 1989 and May/June 1991, when fruiting was detected in all six quadrats. The number of plants bearing fruit is shown in Table 4.3, where the number of plants observed to flower on both occasions is also indicated. These results show that overall numbers of fruiting plants was higher during the first observation (24.8% compared to 2.8%). Chi-square analysis indicated that a higher proportion of plants than expected had fruited on both 1989 and 1991 (χ^2=60.168, d.f.=1, p<0.001).

Table 4.3: Number of bluebushes fruiting in each of the permanent quadrats during the two observed fruiting periods.

(a) Observation 1: April 1989

SITE	# BLUEBUSH IN TOTAL	# FRUITING	% OF TOTAL
Field Centre	197	67	34.0
Two-Mile	115	26	22.6
Purpunda	180	14	7.8
North-east Overland	235	32	13.6
South-west Overland	234	106	45.0
Cooyerdoo	136	27	19.9
TOTAL	1097	272	24.8

(b) Observation 2: May/June 1991

SITE	# BUSH	FRUITING IN 1991		FRUITING IN 1989 &1991	
		NUMBER	%	NUMBER	% OF 1991
Field Centre	197	7	5.1	5	71.4
Two-Mile	115	6	5.2	2	33.3
Purpunda	180	7	3.9	3	42.8
North-east Overland	235	5	2.1	2	40.0
South-west Overland	234	3	1.3	1	33.3
Cooyerdoo	136	3	2.2	1	33.3
TOTAL	1097	31	2.8	14	45.2

There are many factors which may influence the propensity of any individual plant to flower/fruit including plant size/age, area available to the plant for resource acquisition (*i.e.* competition effects), environmental factors influencing the individual plant environment including variations in microtopography and soil type, and genetic controls. While an investigation into the latter two points was not included in this study, the influence of the first two of these factors were examined by collating the means for bluebush size and the area potentially available to each plant for resource acquisition (as defined by Dirichlet polygon analysis; Mead, 1966; Liddle, 1982; Kenkel, 1990) for each of the four classes of fruiting bushes at all sites (Table 4.4). General trends suggest that plants which flower more frequently are located in larger polygons, and are generally taller and larger in horizontal diameter.

Table 4.4: Size and Dirichlet polygon features (± S.E.) for bluebushes within each permanent quadrat grouped according to fruiting status.

FRUITING	NO.	PLANT SIZE			POLYGON CHARACTERS		
		HEIGHT (cm)	COVER (m^2)	VOLUME (m^3)	#SIDES	AREA (m^2)	PERIMETER (m)
Fruited Twice	14	71.07±3.20	0.73±0.13	0.38±0.08	5.43±0.29	5.66±1.34	9.19±0.09
Apr 1989 Only	258	69.86±1.04	0.70±0.03	0.34±0.02	5.77±0.75	4.81±0.17	8.75±0.16
M/J 1991 Only	17	71.18±4.93	0.71±0.09	0.37±0.07	5.70±0.33	6.46±1.03	10.27±0.10
Did Not Fruit	808	60.59±0.72	0.47±0.01	0.22±0.01	5.72±0.04	4.87±1.13	8.76±0.09

Spatial Patterns of Fruiting Bushes

During April 1989, the distribution of fruiting bluebushes at each site was predominantly random despite differences in the shrubs in fruit. Non-random spatial pattern was detected only at the Cooyerdoo site where fruiting plants were clumped in distribution (Table 4.5). Due to the low numbers of fruiting bushes in May/June 1991, no pattern analysis was undertaken. The distribution of fruiting bushes in each quadrat for both fruitings is shown in Figures 4.2 a-f.

Table 4.5: Spatial pattern of fruiting bluebushes during the first observed fruiting event (April 1989). Pattern was determined by Batcheler's ratios with significance indicated as *, p<0.05.

SITE	# BUSHES	# BUSHES IN FRUIT	BATCHELER'S RATIO	SPATIAL PATTERN
Field Centre	197	67	0.7113	random
Two-Mile	115	26	0.5954	random
Purpunda	180	14	0.5484	random
North-east Overland	235	32	1.0212	random
South-west Overland	234	106	0.7451	random
Cooyerdoo	136	27	1.2985 *	clumped

Fruiting Models

The flowering/fruiting models constructed for the combined data sets and each site are shown in Tables 4.6 and 4.7, with a summary of significant variables given in Table 4.8. No significant model could be constructed for the Purpunda Paddock site due to the low numbers of fruiting bushes (only 7.8%). Both plant size estimates and polygon features were found to be useful predictors of bluebush flowering. Although many of the same variables were present in the models, between site variation was demonstrated by both differences in the individual site models themselves and also the inclusion of location as a significant factor in the combined sites model. Polygon area (used to estimate the area available to each plant for resource acquisition) was included in the combined sites model when location was not included as a factor and so it may account (at least partially) for between-site differences.

Figure 4.2: Spatial arrangement of fruiting bluebushes within the 50 x 20 m permanent quadrats.

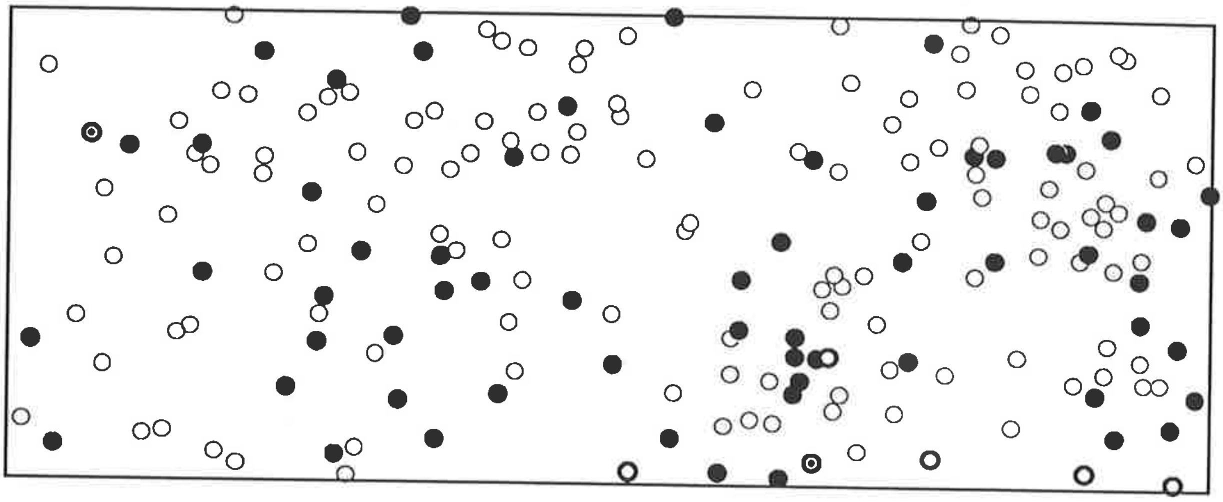
Legend:

● Fruited in 1989

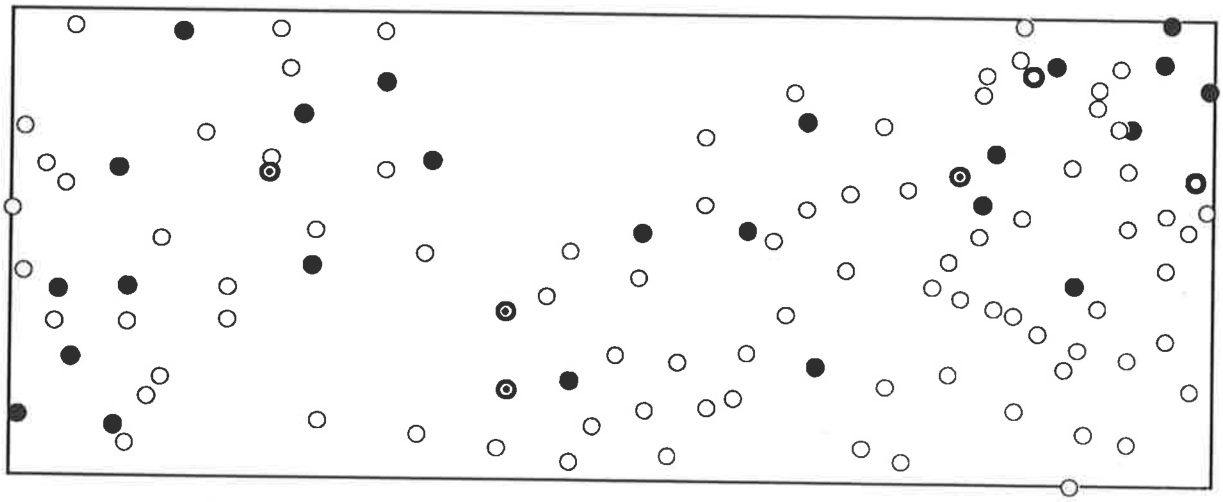
◉ Fruited in 1991

◯ Fruited in 1989 and 1991

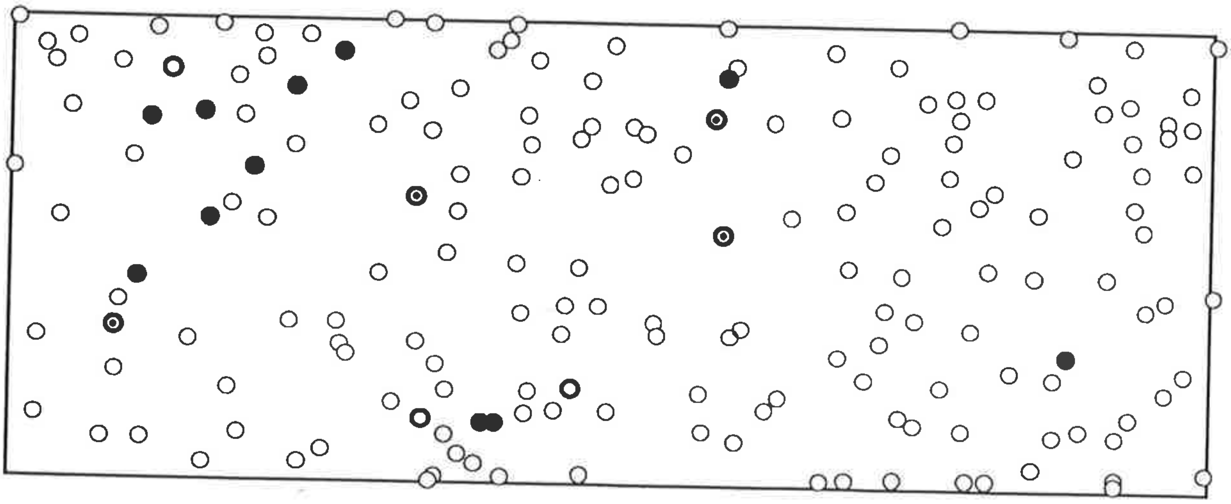
○ Did not fruit in the years 1988-1991



(a) Field Centre Site



(b) Two-Mile Site



(c) Purpunda Site

Figure 4.2 (cont): Spatial arrangement of fruiting bluebushes within the 50 x 20 m permanent quadrats.

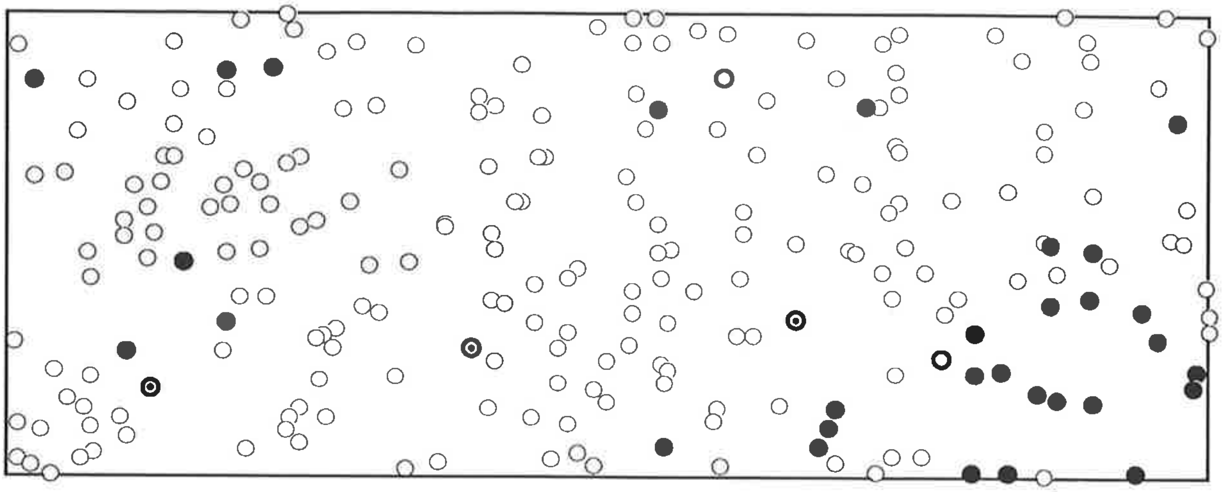
Legend:

● Fruited in 1989

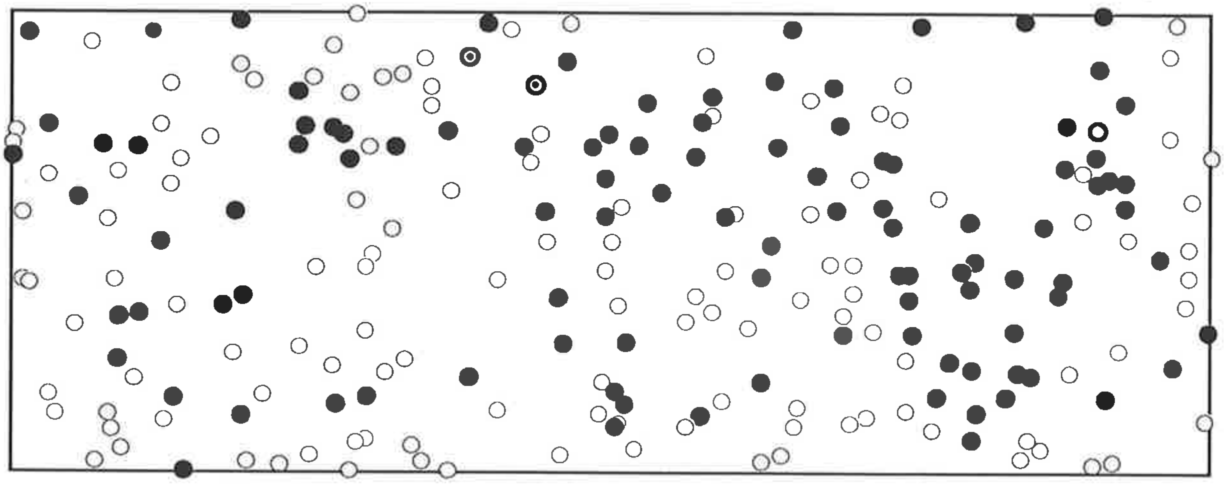
⊙ Fruited in 1991

○ Fruited in 1989 and 1991

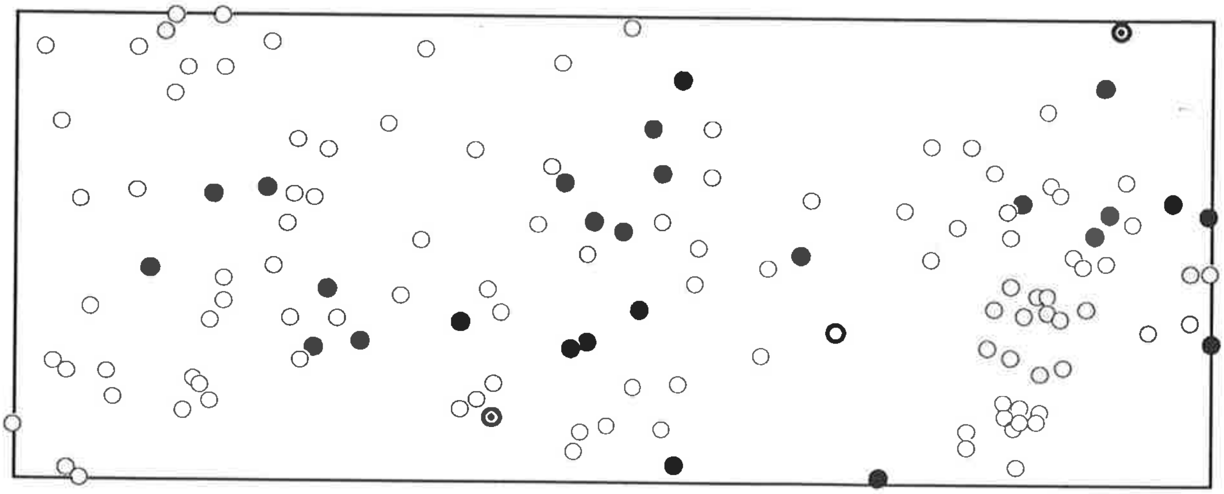
◯ Did not fruit in the years 1988-1991



(d) North-east Overland Site



(e) South-west Overland Site



(f) Cooyerdoo Site

Table 4.6: Logistic regression model for the presence of flowering in bluebush at all sites. Significance of variables is indicated as follows: *, $p<0.001$; *, $0.01<p<0.05$.**

(a) Location included as a factor

NULL MODEL 1192.28 D.F. 1071
FINAL MODEL 1020.95 D.F. 1063
DEVIANCE EXPLAINED (R^2) = 0.1437***

MAIN EFFECTS

VARIABLE	ESTIMATE	S. ERROR	RATIO	F VALUE
Constant	-3.987	0.507	-7.86	-
Location - Cooyerdoo	0.000	-	-	22.38 ***
Location - Two-Mile	0.111	0.323	0.34	
Location - Field Centre	0.592	0.279	2.12	
Location - Purpunda	-1.309	0.368	-3.55	
Location - NE Overland	-0.340	0.304	-1.12	
Location - SW Overland	1.271	0.267	4.75	
Plant Height	0.034	0.007	4.75	52.43 ***
Plant Cover	2.711	0.798	3.40	5.40 *
Plant Volume	-4.23	1.48	-2.85	8.67 **

(b) Location not included

NULL MODEL 1192.28 D.F. 1071
FINAL MODEL 1125.056 D.F. 1067
DEVIANCE EXPLAINED (R^2) = 0.0564***

MAIN EFFECTS

VARIABLE	ESTIMATE	S. ERROR	RATIO	F VALUE
Constant	-3.188	0.441	-7.23	-
Plant Height	0.028	0.007	4.18	41.13 ***
Plant Cover	2.859	0.753	3.80	9.55 **
Plant Volume	-3.99	1.40	-2.86	6.94 **
Polygon Area	-6.49E-06	2.62E-06	-2.47	6.13 *

Table 4.7: Logistic regression model for the presence of flowering in bluebush at five of the permanent quadrats. Significance of variables is indicated as follows: *, p<0.001; **, 0.001<p<0.01; *, 0.01<p<0.05. Note: no significant model could be constructed for the Purpunda site.**

(a) Field Centre Site

NULL MODEL	236.165	D.F. 186
FINAL MODEL	224.351	D.F. 185
DEVIANCE EXPLAINED (R^2) = 0.050**		

MAIN EFFECTS

VARIABLE	ESTIMATE	S. ERROR	RATIO	F VALUE
Constant	-1.494	0.286	-5.22	-
Plant Cover	1.180	0.355	3.32	9.74 **

(b) Two-Mile Site

NULL MODEL	120.844	D.F. 110
FINAL MODEL	108.660	D.F. 109
DEVIANCE EXPLAINED (R^2) = 0.101***		

MAIN EFFECTS

VARIABLE	ESTIMATE	S. ERROR	RATIO	F VALUE
Constant	-4.42	1.08	-4.08	-
Plant Height	0.0456	0.0143	3.20	12.22 ***

(c) North-east Overland Site

NULL MODEL	186.152	D.F. 231
FINAL MODEL	178.587	D.F. 230
DEVIANCE EXPLAINED (R^2) = 0.041**		

MAIN EFFECTS

VARIABLE	ESTIMATE	S. ERROR	RATIO	F VALUE
Constant	-4.088	0.893	-4.58	-
Polygon Perimeter	2.597E-03	9.630E-04	2.70	9.74 **

Table 4.7(Cont.): Logistic regression model for the presence of flowering in bluebush at five of the permanent quadrats. Significance of variables is indicated as follows: *, p<0.001; **, 0.001<p<0.01; *, 0.01<p<0.05.**

(d) South-west Overland Site

NULL MODEL 316.740	D.F. 229
FINAL MODEL 227.049	D.F. 226
DEVIANCE EXPLAINED (R^2) = 0.125***	

MAIN EFFECTS

VARIABLE	ESTIMATE	S. ERROR	RATIO	F VALUE
Constant	1.57	1.31	1.20	-
Plant Height	3.933E-02	8.07E-03	4.87	21.19 ***
Polygon Perimeter	-8.200E-03	2.72E-03	-3.01	6.16 *
Polygon Area	6.020E-05	2.51E-5	2.40	5.03 *

(e) Cooyerdoo Site

NULL MODEL 131.859	D.F. 133
FINAL MODEL 119.180	D.F. 132
DEVIANCE EXPLAINED (R^2) = 0.096***	

MAIN EFFECTS

VARIABLE	ESTIMATE	S. ERROR	RATIO	F VALUE
Constant	-3.746	0.794	-4.72	-
Plant Height	0.036	0.011	3.27	14.04 ***

Table 4.8: Summary of significant variables in the flowering models for the permanent quadrats. Estimates are shown as positive (+) or negative (-). Significance is indicated as: *, p<0.001; **, 0.001<p<0.01; *, 0.01<p<0.05. Note that no model for Purpunda paddock could be constructed.**

MODEL	PLANT SIZE ESTIMATES			POLYGON FEATURES		LOCATION
	HT	COVER	VOL.	AREA	PERI.	
ALL SITES						
No location	+***	+**	-**	-*		
With location	+***	+*	-**			***
INDIVIDUAL SITES						
Field Centre		+**				
Two-Mile	+***					
NE Overland					+**	
SW Overland	+***			+*	-*	
Cooyerdoo	+***					

Apart from location, plant size was the most significant factor influencing the likelihood of flowering. Height, in particular, was found to be significant in three of the models. Parameter estimates for height and for cover were positive indicating that taller plants, and those with large horizontal covers, had a greater probability of flowering than smaller plants. Plant volume was also included in the all-sites model, this time with a negative estimate, suggesting that very large plants had a lower probability of flowering than would be expected. As volume is directly calculated from estimates of height and cover (volume equates to 0.666 x height x cover), the inclusion of this variable into the model implies the presence of a negative interaction term between plant height and cover.

Only a few of the the 'available area' polygon variables considered were included in the flowering models. For plants at the North-east Overland site, polygon perimeter estimates were included, indicating an increased likelihood of flowering in plants with increased polygon perimeter. The inclusion of this factor in this instance is likely to indicate the strength of competition from surrounding plants . In comparison, perimeter was included in the South-west Overland site with a negative estimate, suggesting the opposite of the above. At this site, however, polygon area was also found to be significant, with plants positioned in larger polygons showing a higher probability of fruiting. As perimeter indirectly represents both polygon size and shape, a negative estimate may suggest that, for a given size, a circular polygon gives an increased probability of flowering compared with an oval-shaped polygon.

SEED DISPERSAL STUDIES

Initial Dispersal Patterns

Seed dispersal results are shown in Figures 4.3 and Table 4.9. It should be noted that many fruits went missing during these trials. This may be due to a several factors: the fruits travelling a greater distance than was examined (this is likely as more were lost from the raised plates), the fluorescent dye markings being too small and indistinct, or the fruits becoming hidden in twigs or litter. Measured wind speeds ranged from 0.5-3.8 ms^{-1} (average 2.4 ms^{-1}) over the first four hours and 0.5-5.8 ms^{-1} (average 3.6 ms^{-1}) over the 36 hours. Using the Beaufort scale, these wind speeds could be generally described as light to gentle breezes (Butler, 1991). Wind speeds at the soil surface would have been lower.

Measurements of distances from the fruit sources showed that fruit dispersal from the raised plates (used to simulate fruit dropping from an adult bush) occurred over a greater distance than those from the surface plates over the initial four hour period (Figure 4.3). At the end of this time, fruits had travelled over a metre from the raised plates but only around 11 cm from the surface plates. Later examination by U.V. light revealed that fruit dispersal had continued over a greater distance, with 7% of fruits travelling more than 10 m from the fruit source within the 36 hour trial period (Table 4.9). At this time, however, most fruit was still located within 1-5 m of the fruit sources. Similar differences between the raised and surface plates were also detected. Higher percentages of fruit were detected close to the surface plate (26% compared to 6% within 1 m) and at large distances from the raised plate (12% compared to 2% from 5-10 m).

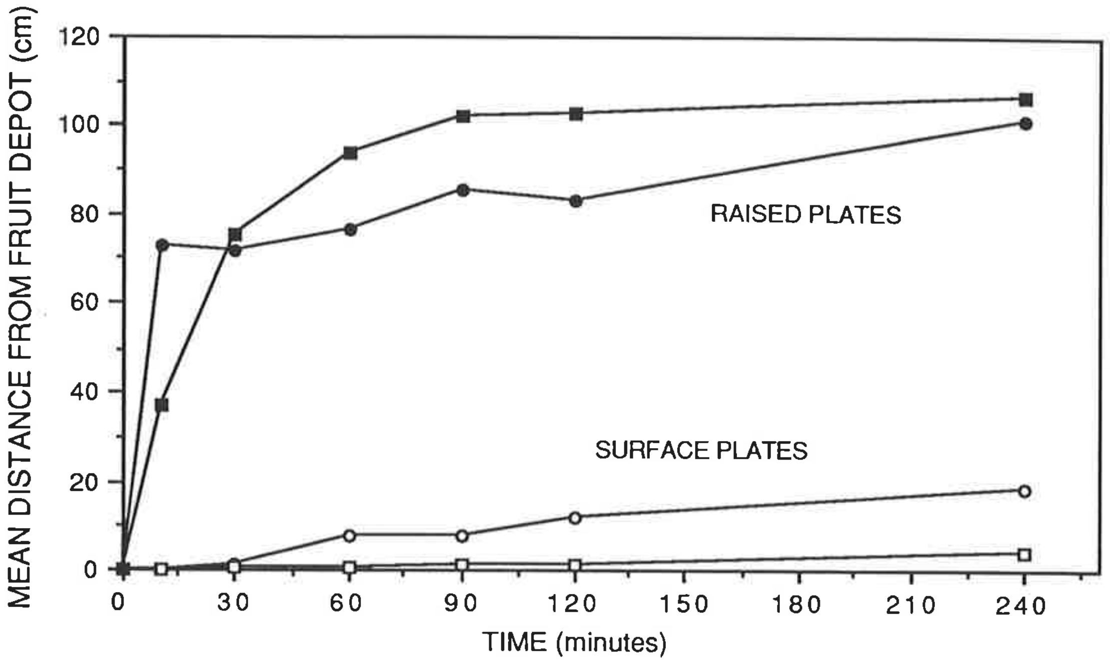


Figure 4.3: Observed movement of bluebush fruit from fruit depots located at ground level and raised on a plate 60 cm above the soil surface over the first 4 hours.

Table 4.9: Movement of bluebush fruit from depots located at ground level and raised on a plate 60 cm above the soil surface after a period of 36 hours. Values represent the fruit number (out of a possible 50) recorded within each distance interval.

PLATE	0-1 m	1-2 m	2-5 m	5-10 m	10+ m	NOT FOUND
Surface	13 (26%)	11 (22%)	6 (12%)	3 (6%)	1 (2%)	16 (32%)
Raised	3 (6%)	9 (18%)	7 (14%)	4 (8%)	6 (12%)	21 (42%)

Recordings of fruit micro-environment during the U.V. light study revealed that relatively high numbers of fruit were found both under bluebush, saltbush and amongst litter (Table 4.10). As these micro-environments are estimated to represent only 16, 7, and 3% of the total environment respectively, these results would suggest that fruits are preferentially accumulating in these areas. In comparison, lower fruit numbers were present in locations densely populated by the ephemeral species Ward's weed (*C. annua*) and on mounds previously occupied by adult plants. While these two micro-environments do encompass less overall area than adult perennial bushes, the low numbers recorded in this trial may indicate that these areas do not trap fruit under normal conditions. It should also be noted, however, that relatively high percentages of fruits were detected in open environments, suggesting that fruit movement was still proceeding and that larger dispersal distances and movement into different micro-environments was still possible .

Table 4.10: Micro-environment location of fruits following movement from seed depots positioned at ground level and raised on a plate 60 cm above the soil surface after 36 hours. Values in parentheses are the numbers of fruit located in each micro-environment as a percentage of fruit recovered. The proportions of each micro-environment are visual estimations.

PLATE POSITION	OPEN AREAS	UNDER BLUEBUSH	UNDER SALTBUSH	ON MOUNDS	DENSE LITTER	DENSE EPHEMERALS
Surface	13 (38%)	6 (18%)	5 (15%)	1 (3%)	6 (18%)	3 (9%)
Raised	9 (31%)	7 (24%)	3 (10%)	1 (3%)	9 (31%)	0 (0%)
Est. % of ground surface	50	16	7	6	3	18

Examination of fruit orientation after 36 hours suggests that wind dispersal does not favour either horizontal orientation of bluebush fruits (perianth tube upright or downwards); only slightly higher counts of fruits with the tube upright were achieved (Table 4.11). In most micro-environments, there was little difference in the orientation of fruits except amongst litter where the fruit were found more frequently in the perianth tube down position. Interestingly, two fruits were found in a perpendicular orientation with one fruit located down a crack in the soil while the other was lodged on a large mound previously occupied by an adult plant.

Table 4.11: Fruit orientation following movement from seed depots after 36 hours (surface and raised plates combined). Values in parentheses are the numbers of fruit located in each micro-environment as a percentage of fruit recovered.

FRUIT ORIENTATION	OPEN AREAS	UNDER BLUEBUSH	UNDER SALTBUSH	ON MOUNDS	DENSE LITTER	DENSE EPHEMERALS
Tube Up	12 (19%)	7 (11%)	5 (8%)	0	10 (16%)	1 (2%)
Tube Down	9 (14%)	6 (10%)	3 (5%)	1 (2%)	5 (8%)	2 (3%)
Vertical	1 (2%)	0	0	1 (2%)	0	0

Seed Removal by Ants

Removal studies show that ants do actively gather bluebush fruits, with significantly more fruits being removed from the open (ant and small forager access) and protected (ant access only) depots than from the control (wind and small forager access) depots (14% vs 3%, Table 4.12). There were also slight differences in removal rates between the four micro-environments (Table 4.13). Although no differences were detected in Trial 1 (March 1991), significantly less fruit was removed from areas densely populated by ephemerals, particularly *C. annua* during Trial 2 (June 1991).

Table 4.12: Number of fruit removed from depots (maximum of 10) with different levels of protection. Results of oneway ANOVA examining differences between treatments for each trial are indicated by the F-value where ***, $p<0.001$. Pairwise comparisons were examined by LSD tests; similar superscript letters indicate no significant difference between treatments at $p<0.05$.

TREATMENT	# FRUITS REMOVED (MEAN±S.E.)	
	TRIAL 1 (MARCH 1991)	TRIAL 2 (JUNE 1991)
Control	0.30 ± 0.11^{a}	0.25 ± 0.12^{a}
Protection	2.10 ± 0.33^{b}	2.50 ± 0.32^{b}
Open	1.45 ± 0.40^{b}	1.85 ± 0.25^{b}
F-VALUE	9.20***	15.26***

Table 4.13: Number of fruit removed from depots (maximum of 10) in various micro-environments. Results of oneway ANOVA examining differences between micro-environments for each trial are indicated by the F-value where **, $0.001<p<0.01$. Pairwise comparisons as for Table 4.12.

MICR0-ENVIRONMENT	# FRUITS REMOVED (MEAN±S.E.)	
	TRIAL 1 (MARCH 1991)	TRIAL 2 (JUNE 1991)
Open	2.33 ± 0.38^{a}	2.56 ± 0.36^{b}
Under Shrubs	2.03 ± 0.41^{a}	2.08 ± 0.32^{b}
Dense Ephemerals	1.38 ± 0.22^{a}	1.08 ± 0.17^{a}
Amongst Litter	1.77 ± 0.18^{a}	2.20 ± 0.35^{b}
F-VALUE	1.29	4.17**

DISCUSSION

FLOWERING AND FRUITING

Timing of Reproductive Episodes

Observations of bluebush fruiting at Middleback Station during 1988-1991 show that fruiting in this species is more common than the literature suggests. Although many authors have described bluebush as an infrequent seeder (Osborn *et al.*, 1935; Ratcliffe, 1936; Wood, 1936; Jessup, 1951; Graetz and Wilson, 1984), five fruiting events (albeit generally patchy and sparse) were reported in four years. Given the widely-accepted hypothesis that flowering in arid species is often rainfall-stimulated (Went, 1953; Beatley, 1974; Mott, 1979; Pitt and Wikeem, 1990), it is possible that this observed frequency of flowering in bluebush may be uncharacteristic, reflecting above-average rainfalls over the observation period. At first glance, this does not appear the case, with yearly rainfall totals average to below-average for 1987-1991, apart from 1989 where a 10% increase was noted (Table 4.14). Further examination of the rainfall records, however, indicate that several above-average monthly rainfalls were measured (18/48 months in excess of the mean monthly rainfall, 21/48 months above the median monthly rainfall), lending support to the above hypothesis.

Table 4.14: Yearly rainfall totals at Middleback Station for the years 1987-1991. The average annual rainfall is approximately 210 mm.

YEAR	RAINFALL (mm)
1987	217.8
1988	168.8
1989	230.1
1990	194.6
1991	190.0

Scrutiny of the raw data suggests that fruiting of bluebush at Middleback Station occurs following above-average rainfalls in the 1-4 months preceding flowering/fruiting. As a cautious estimate, it would appear that falls of at least 20 mm within 1-3 days are required to stimulate the onset of flowering. Although further experimentation is required to confirm this approximation, such a value may be deemed sensible. A similar amount of rain (> 25 mm) has been shown to be necessary for flowering in several north American perennial shrub species including *Larrea* and *Ambrosia* (Beatley, 1974). It is not possible to compare this value to those determined for other Australian chenopod species; previous studies of such species refer only to flowering following 'heavy', 'effective', 'sufficient' or 'adequate' rainfalls (Williams, 1961; Williams, 1979; Briese, 1982). Rather than just examining rainfall, it would also be interesting to predict both the level of soil moisture needed to promote fruiting and the time period over which this level needs to be maintained. However, because of the erratic weather conditions and sparse flowering/fruiting observations, such information could only be gained through much more extensive and long-term recordings The monthly soil water content measurements which were taken during this study were insufficient for this purpose; daily measurements taken over a significant period in many locations would be required for accurate estimates.

Evidence collected during this study also indicates that high rainfalls do not always stimulate the onset of flowering/fruiting; on several occasions rainfalls in excess of 20 mm were received but did not induce flowering. Similarly, none of the bluebushes which were irrigated during the neighbour removal trial (25 mm of water per month for 10 months - September 1990 to June 1991; see Chapter 3) were seen to flower/fruit by September 1991. There appear to be two main explanations for this. Firstly, the 'lack of fruiting' in some instances may be due to the length of time since previous reproductive episodes. It is possible that bluebushes need time to recover from the "effort of reproduction" (Fenner, 1985; Silvertown, 1987), particularly in the case of rainfalls in May/June 1990 and June 1991. This does, however, go against the observation that more shrubs flower in successive seasons than may be expected. Alternatively, flowering in bluebush may be seasonally controlled with factors including temperature and daylength also determining flowering times (Mott, 1979). This appears likely as observations indicate that flowering occurred primarily in autumn (April/June) when temperatures were moderate, day-length was relatively long and soil water availability had increased following rainfall. This latter hypothesis may also account for the the timing of flowering/fruiting in late 1988, the only observation of reproduction in the spring-summer period. On this occasion, above-average temperatures in August to October, in addition to higher than average rainfalls in September, may have stimulated the non-seasonal flowering of bluebush in November.

Variations in the Distribution and Numbers of Fruiting Shrubs

The distribution and number of fruiting plants appears strongly linked to rainfall characteristics. Firstly, the percentage of bushes which fruited was clearly higher following more substantial rainfalls *i.e.* with greater availability of water, a higher proportion of plants were stimulated to reproduce. This result would support similar studies which have shown an increase in the proportion of resources devoted to reproduction under less stressful conditions (e.g. the annual species *Polygonum cascadense*: Hickman, 1975; and *Chamaesyce hirta*: Snell, 1975 in Silvertown, 1987). Additionally, this study suggests that the distribution of flowering/fruiting bushes around Middleback Station is related to the distribution of rainfall, which is not only erratic but patchy. While the most widespread fruiting event (April 1989) followed heavy rainfalls which extended across most of the state, more restricted flowerings occurred following lower, more limited falls of rain. It is likely that these latter fruiting events occurred as a result of downpours which extended over a confined area.

Data collected during this trial also suggested that not all bluebush shrubs in a given area were equally likely to flower; within the permanent quadrats, a higher than expected number of bluebushes were reported to fruit in successive reproductive events (April 1989 and May/June 1991). Although previous studies have indicated that flowering/fruiting is more likely in those plants which have access to more resources (Harper, 1977; Silvertown, 1987), available area estimates were not shown to be the best predictors of bluebush fruiting in this instance. Instead, logistic regression analyses indicated that the probability of fruiting was more significantly related to plant size features; there was an increased probability of fruiting with increased plant size, in particular bluebush height. This relationship may reflect the increased likelihood of fruiting with age (growth), although as bluebush is slow-growing and long-lived species, this observation is unlikely to indicate the direct increasing age→increasing size→increasing likelihood of reproduction relationship which illustrated in most plant species (Silvertown, 1987). Instead, it is plausible that plant size factors, particularly height, represent indirect age effects, where the taller plants are medium-aged, actively-growing individuals and the shorter plants are older, senescencing individuals. Personal observation would support this idea, for shorter bushes were often seen to possess basal stems of greater diameter and old woody stems that had clearly died back. In this case, the lower probability of fruiting in shorter (*i.e.* older) plants would indicate a loss of reproductive capability/output with increasing age; this has been demonstrated in several agriculturally-important plants and is related to decreased photosynthesis and other metabolic/hormonal changes (Bidwell, 1979). Alternatively, the relationship between plant size and the probability of fruiting may reflect a relationship between plant density, resource availability and fruiting (as discussed by Silvertown, 1987). In Chapter 3, a positive correlation between bluebush size and density was found implying that larger plants occur more sparsely and have a larger area for potential resource acquisition. These larger plants often appear 'healthier' possessing densely-arranged leaves on many actively-growing stems. It may be hypothesised that these larger plants have reduced competitor influences, the ability to maintain higher energy levels and excess energy which can be allocated to reproduction. It would appear that both of these explanations could be used to account for differences in the likelihood of flowering and fruiting in bluebush, although neither hypothesis has truly been directly demonstrated here.

Some evidence, however, was presented to demonstrate that fruiting probabilities may be influenced by the area potentially available to each bluebush for resource acquisition. Polygon features were included in two of the logistic regression models used to predict fruiting in each permanent quadrat; at both the South-west Overland and North-east Overland sites fruiting occurred predominantly in those bluebushes with larger available areas or larger polygon perimeters.[1] Similarly, polygon area was included in the second all-sites model, replacing location. In contrast to what may have been expected, however, this variable was included into the model with a small but negative estimate. Although this result is somewhat difficult to interpret, it may indicate that at some locations the probability of fruiting was higher in smaller polygons (for a given shrub size). This may occur either as a consequence of changes in bluebush density between the sites or because of differences in resource levels which may result from variations in soil type or rainfall.

Additionally, despite the observed regularity in spatial distribution of bluebushes at several of the sites (Field Centre, Purpunda, North-east Overland and South-west Overland), fruiting shrubs were generally randomly positioned within the permanent quadrats *i.e.* larger bluebushes with a higher likelihood of fruiting are located randomly within the populations. At the Cooyerdoo site, however, fruiting bluebushes were clumped in distribution, suggesting that other external environmental factors may have influenced either bluebush size or fruiting at this location. The quadrat map indicates that the fruiting bushes were generally located away from the mallee trees. It is plausible that the increased competition for resources from mallee trees may have reduced bluebush size/available area and hence indirectly fruiting probability, for example, shading effects may have reduced flowering/fruiting in those bluebushes positioned under the mallee canopies by altering the light/temperature regime.

Variations in Fruit Number and Size

The number of fruit per bush, and mean fruit size and weight, also varied between fruiting events as a consequence of changes in rainfall/soil-water availability. The number of fruits produced on each plant was noticeably reduced following moderate rainfall; at these times only a few fruits (<50 fruits/bush) were usually present. In comparison, fruiting was much more prolific (>250 fruits/bush) following the heavier, widespread rainfalls in early 1989. Although this may be evidence for the decreasing of seed number in preference to size when under

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[1] This factor has previously been correlated to polygon area (see Chapter 3).

stress (Silvertown, 1987), the results also showed that there was a decrease in fruit weight and size with lower rainfalls. This latter observation seemingly contradicts the hypothesis that seed weight increases with decreasing water availability (Schimpf, 1977), and may imply that seedlings produced when conditions are just sufficient for establishment may not possess the competitive ability of seedlings produced when conditions are optimal (Baker, 1972; Salisbury, 1942; Hendrix, 1992; but see Jurado, 1992). Contrary to this, differences were also detected in the germinability of fruit, with those produced under seemingly optimal conditions having reduced germinability. This is a surprising result which I cannot explain; it may be an artifact of harvest maturity or pathogen attack of the seeds.

It has been suggested that the environmental conditions preceding flowering may have a discernible effect not only on fruiting output, but also on subsequent events *i.e.* germination, seedling growth and survival (Schimpf, 1977; Winn, 1985; Wulff, 1986, 1986; Hendrix and Trapp, 1992). Given the fruiting characteristics of bluebush determined here, it seems likely that the fruiting process during optimal seasons may be more likely to lead to successful seedling establishment (Table 4.15). To confirm and clarify these ideas, however, a more extensive, long-term study of bluebush fruiting is required to examine particularly;

(i) the relationships between fruit size/weight and corresponding seed size/weight,
(ii) seedling survival and growth rates from seeds of different size/weight, and
(iii) the effect of climate on seed germinability.

Table 4.15: Bluebush fruiting characteristics in average (moderate rainfall) and optimal (heavy rainfall) years. Those factors which appear advantageous for population maintenance are indicated with asterisks.

AVERAGE YEAR	OPTIMAL YEAR
Flowering/fruiting restricted	*Flowering/fruiting widespread
Lower fruit production	*Higher fruit production
Smaller fruit - seedlings less competitive?	*Larger fruit - seedlings more competitive?
*Higher seed germinability?	Lower seed germinability?

Further Work

Few previous studies have been carried out examining the factors influencing flowering and fruiting at an individual shrub level for arid-zone perennial shrubs. Although this study represents an initial examination of some of the factors for bluebush, further studies need to be carried out to confirm many of the hypotheses proposed. In particular, it would be helpful to carry out observations over a longer period of time and possibly over a greater area to clarify the ideas presented regarding the climatic, resource availability and plant age (size) controls on on fruiting. It would also be interesting to develop flowering models which could incorporate not only presence/absence of flowering but also some measure of fruit yield. Studies using other short-lived and longer-lived perennial species would also provide useful comparative information.

SEED DISPERSAL STUDIES

Initial Dispersal Patterns

Following seed production, successful recruitment relies on seed being transported to a location in which germination and seedling establishment is possible (*i.e.* a so-called safe-site). Many investigators have shown that fruit and seed morphology often indicates the general means of dispersal (Howe and Smallwood, 1982; Fenner, 1985). Previous studies have suggested that wind is the major medium for bluebush fruit dispersal, with the fine, papery perianth wing assisting in both the flight from the parent plant to the soil surface and its subsequent movement along the ground (Hall *et al.*, 1964). Although dispersal distances of bluebush fruit had never been specifically investigated prior to this study, Butler (1986) believed that fruit could travel at least 50 m, and possibly even 200 m from a seed source, depending on among other factors, the bluebush shrub density and wind velocity. My results, however, do not generally support these ideas; a majority of fruit did not move more than a few metres from the fruiting plant during the dispersal trials. Although early observations implied that the dispersal distances may be large, particularly from the raised plates, and that dispersal may not have been complete at the time of recordings, many of the fruits had already become lodged in various different micro-sites only a few metres from the fruit depots (75% of the recovered fruit was within 2 m). It must be remembered, however, a large number of fruiting perianths were not recovered during this study, and that while it is possible that they become lodged close to the plant and were not visible, it is also possible that they travelled a greater distance than was examined using the U.V. light. Nonetheless, the restricted pattern that was noted is similar to that previously reported for blackbush (*M. pyramidata*), where peak seed fall was 0.2-0.4 m from the fruiting plant and 90% of fruit was found within 2.0 m (Nicholson, 1986). In an evolutionary context, it has been hypothesised that seeds remain close to the parent plant where conditions are presumed to be favourable for growth and survival (Nicholson, 1986).

Bluebush fruits were seen to preferentially accumulate amongst other surface litter and around the base of perennial shrubs, confirming the observations of Burbidge (1946) and Hall *et al.* (1964). It has been suggested that these locations may be good sites for seed germination as they represent areas where surface mulch accumulates and rainfall infiltration is increased (Hall *et al.*, 1964), thereby supporting the hypothesis that restricted seed dispersal may maximise the chance that conditions will be favourable for growth and survival. Seedlings in this environment, however, may have a reduced chance of survival due to root competition with adult shrubs (Hall *et al.*, 1964). This problem would be encountered to a much lesser extent in seedlings growing from fruits which had become lodged in litter.

Both soil micro-environment and fruit orientation following dispersal may affect the probability of seed germination and the likelihood of seedling establishment, particularly through seed-soil contact (Harper *et al.*, 1965). Although in bluebush fruits better seed-soil contact may result if the fruiting perianth is positioned horizontally with the perianth tube upright, there was little evidence to suggest that this orientation occurred more often than horizontal placement with the perianth tube downwards. Additionally, the more favoured 'perianth-tube upright' orientation seen in the litter micro-environment is unlikely to produce better seed-soil contact and enhanced water uptake as the fruits would not generally be in close contact with the soil surface.

It would seem that those fruits which had become positioned vertically after dispersal by lodging in cracks in the soil surface may have the greatest ability for water uptake. Although the chance of vertical placement of fruits is low, such fruits may be favoured for germination. Since fruit orientation is likely to be important, it is explored in the next chapter.

Seed Removal by Ants

Ants appeared to gather bluebush fruits when they were available, thus supporting the anecdotal observations of Nicholson (1986), who recorded three genera of ants (*Melanopus* sp., *Pheidole* sp. and *Chelaner* sp.) collecting bluebush fruits during a study of annual species at Middleback Station, and C. Ireland (pers. comm.), who observed ants carrying individual bluebush fruits whilst undertaking a study of seed harvesting in the western myall (*Acacia papyrocarpa).* The harvesting of bluebush fruits by ants occurred at a much higher rate than the loss of seeds by other means (*e.g.* small mammal foragers, birds), confirming previous suggestions that ants are the major post-dispersal seed agents in Australian environments (Andersen and Ashton, 1985; Andersen, 1987; Gross *et al.*, 1991). These results contrast with those reported for North American deserts, where mammals and birds are the dominant seed foragers (Morton, 1985).

Although it has been demonstrated that ants do gather bluebush fruits, it remains difficult to compare the rate and extent of fruit collection with those observed for other species. While the rate of fruit removal was found to be above, below and roughly equivalent to that reported for other plants (*e.g.* Wellington, 1985; Andrew, 1986; Andersen, 1987; Gross, 1991; Ireland, 1992), none of these studies can be directly compared to the rate of bluebush seed harvesting recorded during this study; the importance of seed foraging varies significantly both temporally and spatially (Harmon and Stamp, 1992). Climatic and other environmental conditions influence not only which plant species will be present, but the suite of species which produce seed, the size and number of seeds available and the number and type of ants which are present. Previous studies have shown varying rates of seed removal from depots, with differences arising because of variations in seed size and weight (Mott and McKeon, 1977), sound/unsound seed (Andrew, 1986), the presence/absence of seed arils or eliasomes (seed appendages rich in food sources such as lipids and proteins) (Davidson and Morton, 1981; Ireland, 1992), the choice and number of seeds on offer (Mott and McKeon, 1977; Andersen, 1987), and the ant species examined (Gross *et al.*, 1991). Dietary specialisation by ants has been observed to the extent that only one seed type or species is gathered (Andrew, 1986; Gross *et al.*, 1991). Studies have suggested that seed-harvesting ants in the Middleback region do not show highly specialised dietary selection; Nicholson (1986) listed seeds/fruits of 21 species of annual and perennial plant species which were harvested by ants from three genera during 1979-1983 while Ireland (1992) found seeds of Wards weed and western myall within ant nests.

Little variation in seed gathering was exhibited by the ants in different micro-environments, implying that ants gather seeds widely. There was no evidence that ants forage predominantly around the base of possible fruiting plants or that they collect fruit from open spaces or amongst litter. There was, however, weak evidence to suggest that less bluebush fruit was collected from amongst dense ephemeral growth during Trial 2. This reduced rate may indicate that the ants found it difficult to remove and carry the large bluebush fruits across a soil surface containing many Wards weed (*C. annua*) stalks (500-800 stalks per m^2) or alternatively, that ants preferentially harvested the Wards weed seed (rather than bluebush fruits) in this area. While further tests would need to be carried out to confirm these ideas, it would also be interesting to examine seed foraging patterns in the vicinity of a shedding bluebush to determine if ants concentrate their foraging in this area.

I believe that the ants at Middleback Station act predominantly as predators of bluebush fruit rather than dispersers. Four points of evidence suggest this:

(i) Ants do remove bluebush fruit from seed depots;

(ii) Bluebush fruit do not contain an eliasome or aril which can be eaten by ants. As ants would be unlikely to carry seed which they do not consider to be a food source, it is likely that ants eat the entire seed;

(iii) The seed coat of bluebush is not hard and would seemingly be relatively easy for ants to break through;

(iv) Bluebush fruits have been tentatively reported as present within below-ground chambers of an ant-nest at Middleback Station (C. Ireland, pers. comm.). As this nest was occupied by ants of the genus *Pheidole*, a genus predominantly consisting of seed harvesters not dispersers (Van der Pijl, 1982; Andersen, 1990), it seems reasonable to conclude that these fruits were collected and stored as a food source.

Additional evidence also suggests that bluebush fruit which has been taken underground by ants but not eaten is effectively removed from the seed bank. While the burial of bluebush fruit is known to significantly decrease the probability of successful germination (Burbidge, 1946), Gross *et al.*(1991) also suggested that seeds stored in granaries may be lost to the seed bank through physical damage or through fungicidal secretions by the ants.

Ecological Implications of Seed Dispersal

Seed dispersal plays a critical role in the maintenance of existing populations and in the expanding of population sizes and ranges (Harper, 1977; Silvertown, 1987). The two major findings of this study (albeit a short-term study) imply that patterns of fruit dispersal do little but maintain current bluebush populations. The first investigation suggested that a majority of fruits are dispersed only a short distance (generally less than 5m) from the parent plant before they become lodged. Such restricted seed dispersal patterns, while perhaps exploiting any advantages which have promoted reproduction in the parent plant, are not always beneficial for subsequent germination and seedling establishment events. Localised dispersal may produce a high density of seeds in a given area, subsequently leading to dense seedlings and the possibly of seedling-seedling competition and parent-seedling competition. In contrast, there appears to be several major advantages in the more widespread dispersal of fruit away from the parent plant. These include the possibility of (i) avoiding a disproportionate seed and seedling mortality near the parent plant (escape hypothesis), (ii) colonising disturbed areas (colonisation hypothesis) and (iii) locating micro-habitats which are suitable for establishment and growth (directed dispersal hypothesis) (Howe and Smallwood, 1982). Similarly, little evidence was presented to demonstrate that ants had a beneficial impact on subsequent dispersal patterns; I concluded that ants reduced the number of seeds in the seed bank by predation from a number of micro-environments. While this may not have the direct detrimental effect on recruitment that was previously assumed[1], it suggests that ants do not play a significant role in the further dispersal of bluebush fruit.

Overall, it would appear that bluebush fruit dispersal strategies are unlikely to expand population ranges. Given the infrequency of flowering and fruit production and the dispersal patterns discussed above, it would appear that such strategies are primarily aimed at the maintenance of populations. The results of these trials do not provide evidence to suggest that plants have the capacity for widespread dispersal particularly into colonising disturbed areas. This has obvious implications for the natural re-establishment of bluebush in areas that have previously been subjected to heavy grazing, fire or mechanical disturbance.

CONCLUSIONS

- Flowering and fruiting occurs following rainfall, with the distribution and number of shrubs fruiting increasing with larger falls. It is suggested that falls in excess of 20 mm in the preceding 1-4 months are required to promote fruiting, although not all falls of this magnitude result in fruiting. Some seasonal control of reproduction may also occur; during the observation period fruiting was reported primarily in autumn.

- The number of fruit per shrub and the mean fruit size increased with increasing rainfall. However, germinability of the fruit produced following the heaviest rainfalls was decreased.

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[1] Recent findings of Andersen (1989) have demonstrated that in long-lived sclerophyllous plants, the availability of safe sites was a much more significant control of recruitment than seed supply. He concluded that in most years there was an oversupply of seed for the small number of safe sites, and that losses by ant predation did not prevent the establishment of large seed banks.

- Within populations, flowering and fruiting did not occur randomly with respect to shrub characteristics. On an individual shrub basis, fruiting appears related to plant size; larger shrubs were more likely to flower. This relationship may indicate either an age effect or a link between plant density, resource availability and fruiting. Fruiting shrubs were generally positioned randomly within the population.

- Preliminary fruit dispersal trials suggest a restricted dispersal strategy with most fruit becoming lodged within 5 m of the parent plant. Fruit preferentially accumulated within litter which had collected on the soil surface and around the base of perennial shrubs .

- Ants do gather bluebush fruits from a variety of micro-environments, acting predominantly as seed predators. They do not appear to aid in the further dispersal of bluebush seed.

CHAPTER 5

GERMINATION CHARACTERISTICS AND THE PROVISION OF SAFE-SITES

INTRODUCTION

BACKGROUND

Germination in Arid-zone Plants - the Concept of a Safe Site

In arid environments, germination is usually very sensitive to environmental stress. The germinating seed must contend with variation in conditions including temperature fluctuations often beyond germination limits, recurrent lack of moisture and soil nutrient deficiencies which may affect metabolism (El-Sharkawi *et al.*, 1989). As the events that determine the fate of individual plants frequently occur during germination and seedling establishment (Grubb, 1977; Harper, 1977), these fluctuations have an important influence on the dynamics of plant populations and composition of plant communities (Fowler, 1988).

Successful germination and establishment requires the presence of favourable micro-sites (Winkel *et al.*, 1991b; Eriksson and Ehrlén, 1992) which Harper *et al.* (1961) described as 'safe-sites'. They are dependent on the environment immediately surrounding the seed, and may be no more than a few centimetres in diameter (Fowler, 1988). Although they differ from species to species, many factors have been shown to play important roles in defining a safe-site. These include the texture, microtopography, compaction and salinity of the soil, temperature, photoperiod, and the presence of neighbouring seedlings and shrubs (Harper *et al.*, 1965; Sheldon, 1974; Mutz and Scifres, 1975; Gutterman and Agami, 1987; Fowler, 1988; Winkel *et al.*, 1991a).

From studies conducted in the mesic environments of Great Britain, Harper *et al.* (1965) concluded that one of the most important characteristics of a micro-site was its ability to maintain high humidity and soil moisture. In the more extreme environment of arid and semi-arid rangelands, this idea is maintained; although the soil does dry out quickly, sites with increased humidity and soil moisture do show increased seedling emergence. Several studies have suggested that cracks and depressions in the soil surface and sites where gravel and plant litter have accumulated provide common natural safe-sites (Winkel *et al.*, 1991b). For example, Eckert *et al.* (1986), showed increased seedlings of Wyoming big sagebrush (*Artemisia tridentata wyomingensis*), perennial grasses and annual forbs emerging from cracks and trenches rather than unprotected surfaces. Similarly, Evans and Young (1970); (1972) reported increased emergence of grass species under plant litter due to moderation in maximum/minimum temperatures, decreased light and increased relative humidity. Most recently, Winkel *et al.* (1991b).demonstrated the effect of micro-environment on germination. They found emergence of warm season grasses was highest in gravel micro-sites, followed by litter, soil-surface cracks and finally bare soil.

Inherent seed characteristics including seed size, shape, structure and composition can also determine germination behaviour (Elberse and Breman, 1989; Mayer and Poljakoff-Mayber, 1989). In particular, it has been shown that seed morphology can affect the rate of water uptake or *imbibition* (Hegarty, 1978). This may have a dramatic influence on both the speed and success of germination, given that water is the first and most important requirement (Bidwell, 1979). Various features of the seed have been shown to influence water uptake. While the effect of seed coat permeability is obvious, several studies have demonstrated that size, shape and orientation control imbibition by influencing the degree of contact between the seed and the soil surface. Sheldon (1974) illustrated that germination response varied with seed position in the family Compositae; the uptake of water was influenced by the angle of the pappus, and hence the achene, relative to the soil surface. Similarly, Winkel *et al.* (1991a) reported that smaller grass seeds were often buried to a greater depth by rain or trampling, thereby increasing seed-soil contact and water uptake rate.

In unpredictable environments, dormancy mechanisms also influence germination behaviour. Here, the ability to delay germination until suitable conditions are present has obvious advantages. Harper (1977) concluded that there were three basic types of dormancy mechanisms:

(i) Innate Dormancy - includes seeds which are either immature on dispersal or which possess an impenetrable seed coat that requires scarification. Effects are temporary and may be broken by favourable seasons, light, moisture and temperature;

(ii) Induced Dormancy - seeds which have acquired a dormancy after release from the plant; and

(iii) Enforced Dormancy - seeds which are capable of germinating but are not exposed to adequate levels of light, oxygen, moisture or temperature.

The maintenance of seed viability may also be crucial in arid environments, where the seed must often wait for favourable germination conditions (*i.e.* enforced dormancy). The time period over which seeds retain their ability to germinate is generally genetically determined, although environmental factors and storage conditions may have a notable effect. Viability is highly variable between species with seeds remaining viable anywhere from 1 week to many years (Mayer and Poljakoff-Mayber, 1989). Most seeds, however, last for only one to a few years (Bidwell, 1979), with viability retained best under conditions where the metabolic activity of the seeds is reduced. Unless destroyed by pathogens, the loss of viability is not an abrupt event; usually the percentage of seeds which will germinate slowly decreases over time. Studies have shown that decreases in seed viability may be due to several factors including lesions and fragmentation of DNA, chemical changes which are enzymic in nature and seed desiccation (Mayer and Poljakoff-Mayber, 1989).

Germination Characteristics of Bluebush

Laboratory Trials

Germination characteristics of Australian perennial chenopods are generally not well-understood. Most of the known information was gathered during a series of experiments conducted during the 1940's by Nancy Burbidge (Burbidge, 1945; 1946). While these studies did provide important details on the recruitment of chenopods, they were preliminary, concentrating on germination characteristics under conditions of varying temperature, soil saturation and soil depth for four Australian chenopod species; bluebush, saltbush (*A. vesicaria*), blackbush (*M. pyramidata*) and satiny bluebush (*M. georgei*). They were solely laboratory-based, and as such, were restricted in their application to the natural environment. Burbidge (1945) was aware of this inherent difficulty, clearly stating; "Studies of germination...have been mainly concerned with viability tests, overcoming dormancy or increasing the rate of germination under incubator or field conditions. There is a definite gap in the knowledge of the behaviour of seed in its natural habitat".

Burbidge (1946) demonstrated that germination in bluebush is rapid and usually complete within three days. It occurred over a wide range of temperatures (6.0°-36.0°C) with maximum germination percentages achieved at 16.8°C. While germination did appear inhibited at both the maximum and minimum temperatures tested, there was little difference in the final germination percentages observed in trials conducted between 9.0° and 30.5°C. These results are similar to those reported for the other *Maireana* species but are different to saltbush results; in this latter species germination occurs over a more restricted temperature range (5.5°-24.0°C except for a single occurrence at 36.5°C) with a lower optimal temperature (10.5°C). At optimal temperature, germination occurs more rapidly in bluebush than saltbush; Burbidge reported that 50% of maximum germination occurred after 4 days for bluebush and 16 days for saltbush.

Germination was also observed over a wide range of soil saturation levels for all four species examined. This, Burbidge (1946) suggested, represents the adaptability of these chenopod species to exist in environments where both the intensity and incidence of rainfall is highly variable. A higher reduction in bluebush germination percentages was noted at the lowest saturation level (20%), especially when compared to the other *Maireana* species. It was concluded, however, that germination of bluebush should be possible after rains in almost any month of the year, although in January the likelihood of successful germination was reduced because of the rapidity with which the soil dries out.

Burbidge (1945, 1946) also examined the influence of planting depth on germination percentages. Results demonstrated a reduced response in all *Maireana* species if the seeds were covered to any extent; bluebush germination decreased from 33.3% to 16.0% following burial of 1.25 cm sand, and to no germination if covered by 2.50 cm sand. These results imply that these species would not be useful as colonising species in areas of sand drift. Saltbush, on the other hand, showed an enhanced germination percentage if the seeds were covered by 1.25-2.50 cm of sand, which led Burbidge (1945) to suggest that germination of this species may be favoured over bluebush in disturbed environments. However, Burbidge (1946) stressed that under field conditions these results may be very different. She believed that surface seeds were almost certainly favoured in this series of experiments due to the humid environment of the temperature-controlled cabinets. Under field conditions, burial would provide less variable moisture conditions and hence, a more suitable germination environment .

Longevity of bluebush seed was also studied by Burbidge (1946). She found that seed could be stored in air-tight containers for up to two years without significant loss of viability. In comparison, studies have shown that saltbush seed remains viable for at least seven years and *M. pyramidata* remains viable for up to three years (Burbidge 1945, 1946; Beadle, 1948).

Field Observations

Reports on bluebush germination in the field are very scarce and anecdotal, with few observations of germination events. As the only evidence of germination in the field is generally the appearance of seedlings, it is not known whether this obvious lack of information suggests that germination events are rare or that germination has a low degree of success. Hall *et al.* (1964) suggest that germination may only be possible in environments where rainfall penetration is high, such as where surface mulch has accumulated or disturbance has occurred. Such hypotheses have been recently supported by Butler (1985), who observed germination of bluebush during revegetation trials at Manna Hill, South Australia. He reported a germination rate of approximately 60% along ploughed furrows in August, following above-average rainfalls in July. It was concluded that germination took place because of high levels of soil moisture, low evaporation levels and moderate relative humidity (40-70%). Butler also observed that emergence occurred primarily on the sides on the furrow, with only limited emergence of seedlings in the furrow trough.

Bluebush seed remains viable for only a few months in the field (Burbidge, 1946; Hall *et al.*, 1964; Leigh and Mulham, 1965; Perry, 1967; Cunningham *et al.*, 1981). Observations have shown a rapid decrease in germination percentages in fruit remaining *in situ* for even short periods of time, particularly following periods of heavy rain. An example of such viability loss was recorded by Burbidge (1946). While initial germination percentages of 40-50% were recorded for fresh fruit harvested in March 1945, subsequent germination trials using fruit collected from the same location three months later (after a 45 mm rain event) showed much lower germination. Only 2% of the seed remaining on the bushes was viable at this time, while all seed on the ground was not viable. Similar studies have generally shown that both blackbush and saltbush seed viability is also limited to only a few months in the field, particularly following summer rainfalls (Burbidge, 1945; Knowles, 1951). This was disputed by French (1975), however, who demonstrated 75% germination in one year old blackbush seed collected from beneath adult bushes.

AIMS

Many studies have been carried out on a vast number of species to determine the optimal conditions for germination. Few, however, have considered germination behaviour under more likely 'sub-optimal' conditions or from a 'safe-site' perspective. In particular, it has been noted that there is a lack of studies demonstrating the types of micro-sites that are favourable for the germination and establishment of range plants (Winkel *et al.*, 1991b). Recent debate has also taken place regarding the extent to which recruitment is limited by the availability of micro-sites or seeds (Eriksson and Ehrlén, 1992).

Although many people have reported that bluebush germination and establishment is rare, very little work has been undertaken examining why this may be the case. This chapter aims to extend the work of Burbidge (1946) and provide insight into possible factors which may reduce the natural germination rate of bluebush. A combination of laboratory and field-based trials were used to investigate:

- (i) the water availability (soil moisture) conditions required for germination. In particular:
    - a. the time period required for sufficient water uptake by fruits, and how quickly water may be lost from fruits when not exposed to water.
    - b. the extent to which germination may be reduced when under moisture stress or when exposed to high salinity and intermittent wetting and drying cycles.
- (ii) the influence of fruit orientation on germination speed and success.
- (iii) the influence of the soil surface micro-environment on germination speed and success, and therefore, the most likely safe-sites for germination.
- (iv) the longevity of bluebush fruits, and whether a shortage of viable seed may be a crucial limiting factor in bluebush germination.

METHODS

LABORATORY TRIALS

Seed Collection and Storage

Bluebush fruits were collected for germination trials following the widespread flowering event in March-April 1989. Fruits were selected from bushes around Middleback Station homestead on 27 April 1989. Whole branches containing mostly mature fruits were sampled from as many bushes as was practical. At this time, the fruits were partially dry and were green to light-brown in colour.

The branches as a whole were transported back to Adelaide, where they were air-dried. Fruits were gently removed and sorted to remove all stem and leaf material, and were subsequently stored in glass jars under three storage regimes:

(i) Airtight (sealed metal lid on jar), room temperature
(ii) In air (paper top on jar), room temperature
(iii) In air (paper top on jar), 5°C.

The air-tight containers were opened only to remove fruits for germination trials.

Further fruits were collected from the same bushes on 23 June 1989, at which time the fruits had become much drier and darker in colour. They were harvested as indicated above. In addition, fruits which had accumulated around the base of adult plants were also collected at this time and again in September 1989. All fruits were subsequently stored in glass jars in air at room temperature until required.

Standard Methods

Germination trials were conducted in either of two Warren Sherer growth cabinets set at 22°C and 80% humidity unless otherwise stated. A daylength of 12 hours was standard with both incandescent (400 μEinsteins m^{-2} sec^{-1}) and fluorescent (520 μEinsteins m^{-2} sec^{-1}) lights on during the day periods. Other conditions which vary during these studies are indicated in the relevant sections.

Trials were carried out in 9 cm diameter plastic petri dishes (Johns Medical Plastics, Sydney), using a filter paper substrate. In this method, a standard bleached white paper tissue (Kleenex Brand) was folded to the size of the petri dish over which a filter paper (Whatman #1) was placed. 25 ml of de-ionised water was then added. Filter papers, tissues and solutions were replaced every 3-4 days throughout the trials. In each trial, 25 fruits which had been air-stored were added to each petri dish, with 5 replicate dishes per treatment. Dishes were placed in a randomised design in the growth cabinets. Trials were run over a period of 14 days, with newly-germinated fruits removed on the first day of detectable radicle emergence to avoid possible recounts. Care was taken to ensure that true germination had occurred (*i.e.* radicle was > 1 mm in length).

Water Availability Trials

The influence of water availability on the germination behaviour of bluebush fruits was examined using four experiments, the methods for which are described below. All experiments used fruits collected in April 1989 and stored in air at room temperature.

Water Uptake and Loss

Fruits used in these studies were stored over silica gel in a desiccator for 7 days prior to experimentation. For water uptake studies, fruits and individual seeds which had been removed from their outer perianth coverings were imbibed by immersing in vigorously aerated water at 25°C. Three replicates of 25 seeds were used. Moisture content (expressed as % oven-dry weight ; 24 hours/100°C) was determined by removing fruits, blotting off the excess water and weighing at regular intervals for 12 hours. Conversely, for water loss measurements, fruits were fully imbibed in vigorously aerated water at 25°C for 24 hours. Moisture content of fruit (again expressed as % oven-dry weight) was determined by first weighing the fully imbibed fruits, and then recording moisture loss from fruits placed on open petri dishes left out on the laboratory bench. Fruits were reweighed at regular intervals over the following 24 hours.

Soil Saturation

Standard germination trials to test the effect of moisture availability on germination were carried out using top-soil collected at Middleback Station. 25 g of oven-dry soil was added to each petri dish along with 25 air-stored fruits. The required amount of water was then added by weight. Trials were conducted at 5 water availability levels (Table 5.1). Each petri dish was reweighed every 2-3 days during the trials and extra water was added as necessary.

Table 5.1: Soil saturation levels used during the moisture availability trials. Soil water potentials were estimated from soil moisture characteristic curves determined from Middleback top-soil (see Appendix 3).

SATURATION LEVEL (% of full saturation)	GRAVIMETRIC WATER CONTENT (g water/g soil as %)	SOIL WATER POTENTIAL (MPa)
20	6.7	-2.239
40	13.3	-0.079
60	20.0	-0.010
80	26.6	-0.006
100	33.3	-0.004

Wetting and Drying Cycles

These trials were designed to detect the effects of prior exposure to moisture on germination behaviour. In the first experiment, fruits were exposed to free water for a constant of time, such as may be experienced during rainstorms. Fruits were placed in vigorously aerated water at 25°C and were removed at regular intervals up to 36 hours (Table 5.2). In the second experiment, fruits were subjected to wetting and drying cycles (Table 5.3). Fruits were again placed in vigorously aerated water during wetting cycles and were positioned on open petri-dishes in the growth cabinet during drying cycles. Subsequently, all fruits were air-dried for a period of 7 days before standard germination trials were carried out. Three replicates per treatment were used.

Table 5.2: Exposure times of bluebush fruit to vigorously aerated water during the experiment 1.

REGIME	TIME OF EXPOSURE (HOURS)
1	1
2	3
3	6
4	12
5	24
6	36

Table 5.3: Wetting and drying cycles used during experiment 2. Fruits were exposed to vigorously-aerated water during wetting cycles, and were placed on open petri dishes during drying cycles.

REGIME	CYCLES
1	12 hr Wet / 12 hr Dry / 12 hr Wet
2	12 hr Wet / 24 hr Dry / 12 hr Wet
3	24 hr Wet /1 2 hr Dry / 12 hr Wet
4	24 hr Wet / 24 hr Dry / 12 hr Wet
5	24 hr Wet / 12 hr Dry / 24 hr Wet
6	24 hr Wet / 24 hr Dry / 24 hr Wet

Moisture Stress and Salinity

The effect of moisture stress was investigated by replacing the petri dish solutions, normally de-ionised water, with aqueous solutions of either polyethylene glycol (PEG) (mol. wt. 6000; BDH Laboratory Reagents, Poole) or sodium chloride (Unilab Laboratory Reagents, Sydney) in standard germination trials. The concentrations of PEG and NaCl used during the trials are listed in Tables 5.4 and 5.5. Osmotic potential was determined using a Wescor 5100B vapor pressure osmometer. Trials were conducted over 21 days to allow for the increased time lag which might have been present for effective water uptake by the seeds.

Table 5.4: Concentrations of aqueous poly-ethylene glycol (mol wt 6000) used during moisture stress studies.

PEG (g/100 ml)	OSMOTIC POTENTIAL (MPa)
15	-0.289
21.2	-0.560
25.2	-0.756
31.0	-1.094

Table 5.5: Concentrations of sodium chloride solutions used during moisture stress studies.

NaCl (g/100 ml)	OSMOTIC POTENTIAL (MPa)	CONCENTRATION (mM)
0.35	-0.217	59
0.70	-0.565	120
1.40	-1.036	240
2.10	-1.498	359

Fruit Orientation

The influence of fruit orientation on germination was investigated using standard trials with a soil substrate (as for the soil saturation experiments). Three orientations were considered; horizontal fruit with the perianth tube upward, horizontal fruit with the tube downward and fruit with the wing vertical (as may occur if the fruit is lodged in a crack or against debris). Fruit was placed on the soil surface or in 'cracks' which were made in the soil by a knife. In this latter case, the fruits were positioned so that the perianth tube was approximately at soil surface. Trials were carried out over 14 days using two soil saturation levels (80 and 100%). Five replicates of each treatment were used.

Seed Longevity

The germination of bluebush seed was tested over a period of 12 months following the collection of seed in April 1989. Fruits stored under three regimes (air, airtight and cold) were tested using a series of standard germination trials staggered over the study period. Additionally, the germination characteristics of fruits from the same fruiting event, but collected later (June 1989), were also determined and compared to results for similarly-aged, laboratory-stored fruits. Both fruits collected whilst still attached to mature plants and those gathered from around the base of plants were used. These same fruits were then air-stored in laboratory and re-tested at 30 weeks. In September 1989, 30 fruits were again collected from around the base of these plants. These were tested for germinability on return to the laboratory.

FIELD TRIALS

Definition of Micro-Sites

Several environmental variables (other than direct climatic factors) were considered as possible influences on small-scale germination in the Middleback Station area. These include:

(i) soil type - sand, loam, clay etc.,

(ii) lichen cover - type and extent of cryptogamic crust,

(iii) litter - including leaf fall, dead twigs and branches,

(iv) surface disturbance - including that caused by sheep or small burrowing animals (rabbits, lizards etc.) as well as human disturbance,

(v) soil microtopography - unevenness of the soil surface (including small pebbles),

(vi) presence of perennial shrubs - including many chenopod and *Cassia* species,

(vii) presence of trees - including western myall (*Acacia papyrocarpa*) and black oak (*Casuarina cristata*),

(viii) presence of ephemeral species and perennial grasses - including Ward's Weed (*Carrichtera annua*), *Danthonia* spp. and *Stipa* spp.,

(ix) presence of predators - especially ants and birds.

These variables, however, are not independent. Considering this, four major micro-environments were delineated using combinations of the above factors: open areas, scalds, bluebush mounds, and mounds formerly occupied by perennial shrubs (defined in Table 5.6). Other minor environmental factors were incorporated to modify these micro-environments including the presence of litter, pebbles, ephemerals and disturbance. Two other different micro-environments were used: mounds containing ant nests and positions under myall trees.

Experimental Procedure

The field germination trial was carried out at Middleback Station during April 1990, in an area adjacent to the Field Centre. The location was selected on the basis of proximity to water, freedom from sheep grazing and the presence of the soil surface micro-environments defined above.

Twenty five different micro-environment and irrigation combinations were tested in this trial (Table 5.6); each treatment included four replicates. Treatments were randomly assigned to a position along one of six parallel east-west transects set 10 m apart, with the test plot located in the correct micro-environment as near as possible to the predetermined transect position. Circular plots, consisting of 2.5 cm deep plastic rings, 30 cm in diameter, were used to define each micro-environment and to enable the scattered fruits to be relocated for germination counts. Rings were placed at least 1.5 m apart and were carefully pushed into the soil surface to a depth of approximately 1 cm. Rings delineating the 'bluebush mound' micro-environments were placed under the shrub canopy and on the southern shaded side. Manual disturbance treatments were carried out in the appropriate rings to a depth of 5-7 cm using a garden hoe.

After the installation of all rings, 25 fruits were added to each plot. The fruits used were those collected in April 1989 and had been stored in air at room temperature since this date. Approximately 60% germination was achieved in laboratory tests with a sample of these fruits prior to field trials.

Table 5.6: Micro-environments located within the area used for the field germination trial.

Note: The four major micro-environments can be defined as follows:
Open - Flat land, lichen crust, no litter, pebbles or ephemerals, undisturbed by animal or vehicular tracks, no perennial shrubs or trees within 1.5 m;
Scald - Flat land, no lichen crust, no litter, pebbles or ephemerals, undisturbed by animal or vehicular tracks, no perennial shrubs or trees within 1.5 m;
Bluebush Mound - Mound of earth containing a mature bluebush plant, generally a lichen crust, no litter, pebbles or ephemerals, undisturbed by animal or vehicular tracks, no other perennial shrubs or trees within 1.5 m; and
Old Mound - Mound of earth formerly containing a mature perennial plant, generally a lichen crust, no litter, pebbles or ephemerals, undisturbed by animal or vehicular tracks, no other perennial shrubs or trees within 1.5 m.

TREATMENT NUMBER	MICRO-ENVIRONMENT
General Treatments	
O	Open
OL	Open + Litter
OP	Open + Pebbles
OE	Open + Ephemerals
OD	Open + Disturbance
S	Scald
SL	Scald + Litter
SP	Scald + Pebbles
SD	Scald + Disturbance
B	Bluebush Mound
BL	Bluebush Mound + Litter
BD	Bluebush Mound + Disturbance
M	Old Mound
ML	Old Mound + Litter
MD	Old Mound + Disturbance
A	Ant Mound
T	Under Myall Tree Canopy
Irrigation Treatments	
OW1	Open + Water 1
OW2	Open + Water 2
SW1	Scald + Water 1
SW2	Scald + Water 2
BW1	Bluebush Mound + Water 1
BW2	Bluebush Mound + Water 2
MW1	Old Mound + Water 1
MW2	Old Mound + Water 2

Two levels of irrigation were applied to plots in each of the four major micro-environments (Tables 5.6 and 5.7). These watering amounts were increased during the course of the experiment because germination percentages were low. At each watering time, the designated amount of dam water was applied slowly to the plot from a small bucket. The plastic rings defining the plots restricted any overflow at this time, allowing the applied water to be concentrated directly on the plot.

Table 5.7: Irrigation regimes used during the field trial. The amounts of water added to each plot have been converted from litres/plot to mm to represent simulated amounts of rainfall.

DAYS	TIME	REGIME 1	REGIME 2
1-6	a.m.	-	10 mm
	p.m.	10 mm	10 mm
7-14	a.m.	-	20 mm
	p.m.	20 mm	20 mm

Daily germination counts were made prior to the morning watering treatments for the following 14 days. During this time an automatic weather station on loan from the South Australian Department of Agriculture was used to monitor rainfall, humidity, air temperature and soil surface temperature in both sun and shade.

ANALYSIS METHODS

Laboratory Trials

Many methods have been devised to express germination in mathematical terms, in an attempt to provide a complete and concise description of the process. Ideally, an analysis should include information about when germination began, how quickly it progressed once started, and its final extent. Total germination after a certain period of time is the most frequently used statistic, although no information about either the start or the rate of germination is implicit in this measure (Brown and Mayer, 1988). Single germination indices have also been widely used as they do consider important factors such as rate and total germination. All indices, however, have been found to be ambiguous and insensitive to time and extent of germination (Brown, 1984). Brown and Mayer (1988) found that of all the published indices only one (Timson's method) was better than total germination.

In this study, information regarding both the extent of germination and germination speed was collated for each of the trials. Final germination percentages (usually Day 14 results) were used as a guide to the success of germination, where treatment samples were compared to standard controls carried out with similarly-aged fruits. Germination speed was measured as days to 10% and 50% of the total germination percentage. Differences in the final number of seeds germinating at day 14 (day 21 for the moisture stress trials) and in times for 10 and 50% germination were generally investigated using analysis of variance; non-parametric Kruskal-Wallis tests were used when the data were non-normal. Arc-sine transformations were carried out on all percentage data prior to analysis. LSD tests were used in all ANOVAs to detect pair-wise differences between treatments. Analyses were carried out using the software packages SPSS-X (SPSS Inc., 1986) and Statview (Abacus Concepts, 1988).

Field Trials

The numbers of fruit shown to germinate during this trial were very low, with no germination observed in many of the plots. Chi-square tests were used to test differences between treatments using the computer software package Statview (Abacus Concepts, 1988).

RESULTS

LABORATORY GERMINATION TRIALS

Water Availability Trials

Water Uptake and Loss

The uptake of free water by bluebush fruits and seeds is rapid, particularly over the initial 5 hour period; further observations suggest this process is complete within 8-10 hours (Figure 5.1). Much more water is taken up by the fruits than by the seeds, particularly over the first hour. During this time, fruits increased in weight by almost 100%, while seeds increased by less than 2%. In 24 hours, fruits and seeds increased in weight by 165 and 50% respectively.

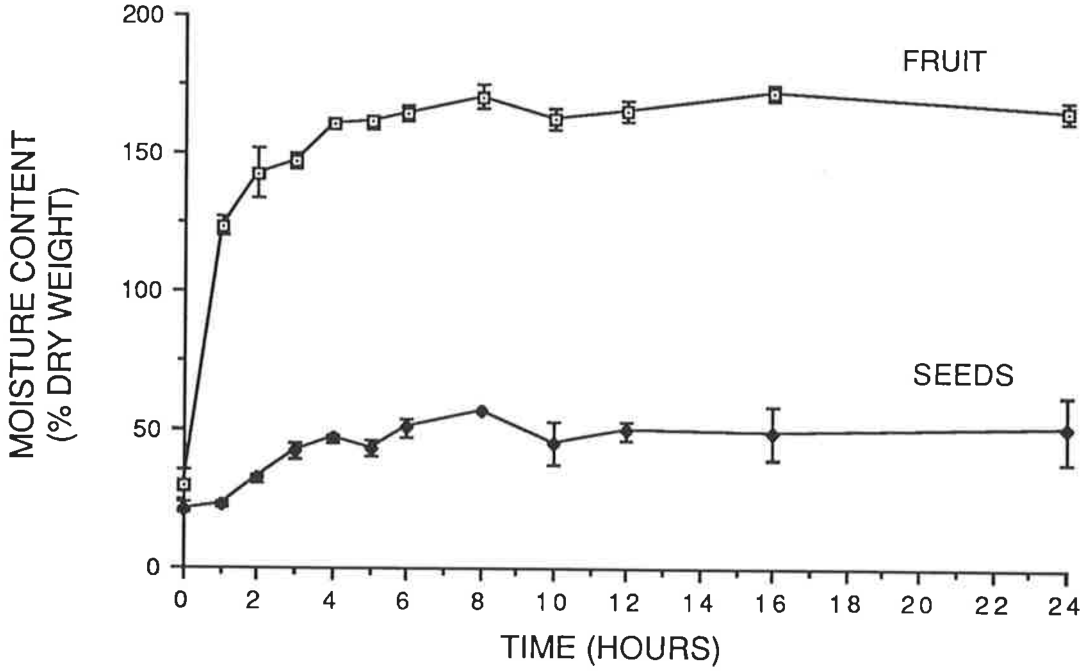

Figure 5.1: Uptake of water by bluebush fruits and excised seeds over a 24 hour period. Results are expressed as percent oven-dry weight of seeds (means ± S.E.).

Loss of water from fruits was also shown to be rapid (Figure 5.2). During the first 2 hours, fruits decreased in weight from 180 to 80%, and then decreased further from 80% to 32% in the next 22 hours. Similar trends were detected in the excised seeds. After 24 hours, both the fruits and seeds had dried to within 3% of their initial moisture content.

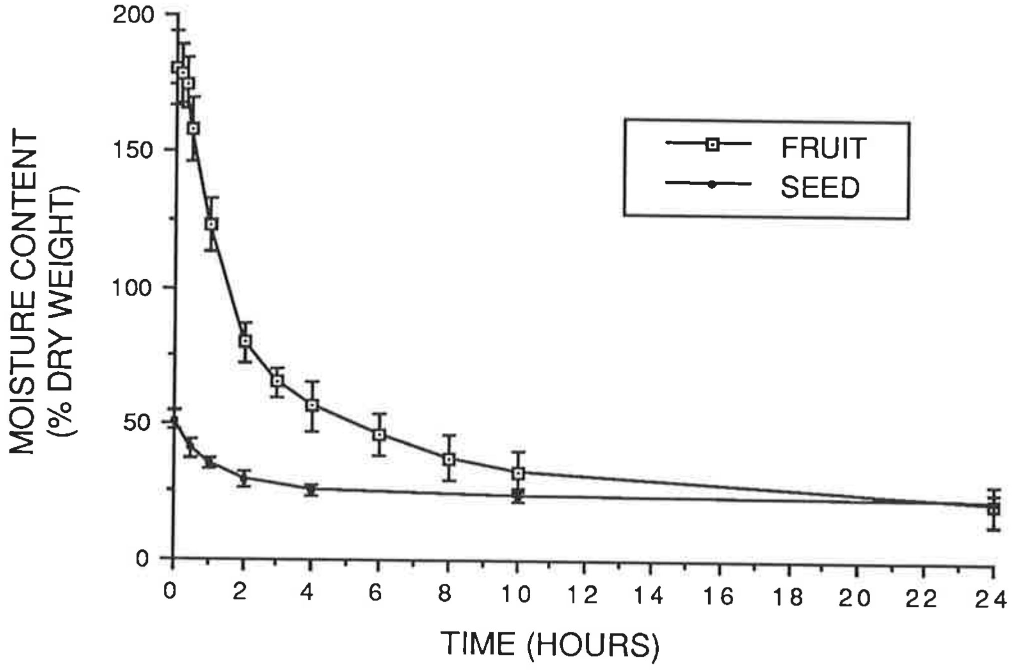

Figure 5.2: Loss of water from fully-imbibed bluebush fruits and excised seeds over 24 hours. Results expressed as percent of oven-dry weight (means ± S.E.).

Soil Saturation

Moisture content of the sand influenced the germination of bluebush seeds (Figure 5.3). Both the number of seeds observed to germinate and the speed of germination increased with increasing water availability. Higher germination percentages were generally observed in the high moisture treatments with more than 90% of seeds germinating on fully saturated soils (~ -0.004 MPa, 33.3% gravimetric water content ; Table 5.8). Lower germination percentages were noted for the remaining treatments, with no successful germination detected at 20% saturation level (~ -2.239 MPa, 6.7% g.w.c.). There was little difference in the number of seeds germinating at the two temperatures. Germination generally took longer to commence under drier conditions, particularly at the cooler temperature (Table 5.9).

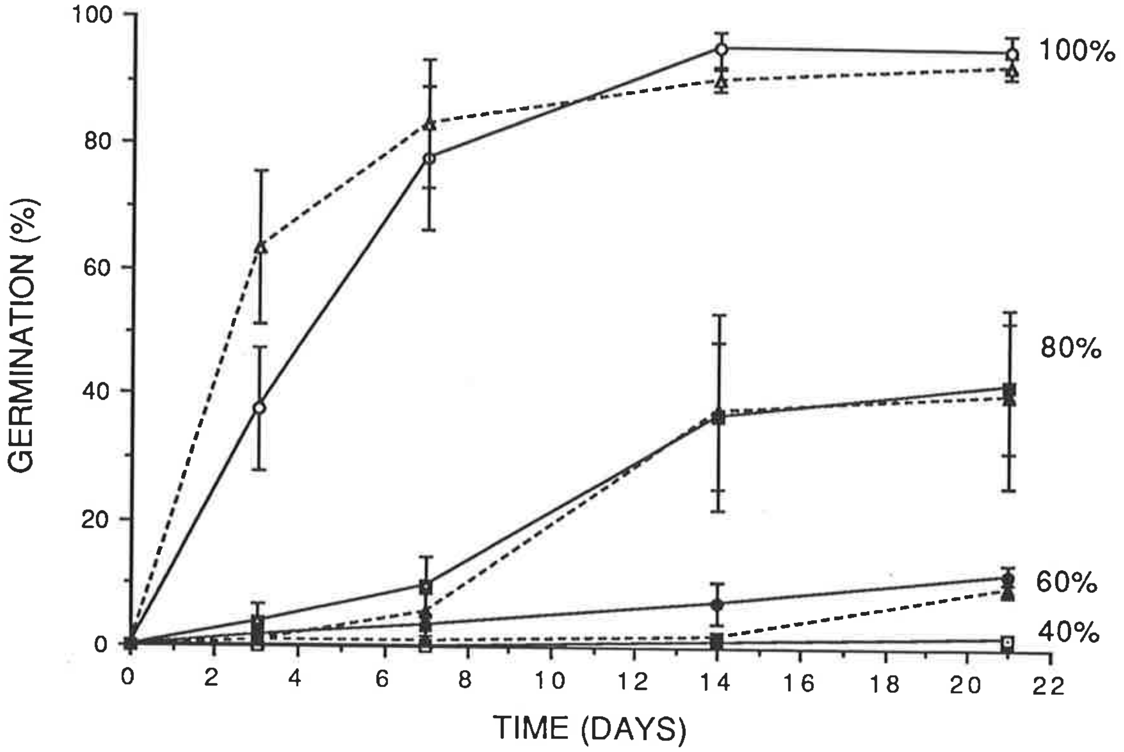

Figure 5.3: Germination of bluebush fruits (means ± S.E.) under different levels of soil saturation (40, 60 and 80%) and two temperatures (15°C, dashed lines; 25°C, closed lines). Values are means of 5 replicates ± S.E.

Table 5.8: Final (Day 21) germination percentages of bluebush fruits under different levels of soil saturation and two temperatures. Significance of one-way ANOVA used to detect differences between saturation levels (using the transformed data) is shown by the given F-value (*, $p<0.001$). Means followed by similar superscript letters within each row are not significantly different at $p<0.05$ as indicated by LSD tests. Soil saturation levels correspond to the following soil water potentials (in MPa): 20%, -2.239; 40%, -0.08; 60%, -0.01; 80%, -0.006; 100%(field capacity), -0.004.**

TIME	SATURATION LEVEL (%)					F-VALUE
	20	40	60	80	100	
15°C	0	0	9.6^a	40.0^b	92.8^c	43.77***
25°C	0	0.8^a	7.2^b	36.8^c	95.2^d	60.82***

Table 5.9: Times required (in days) to achieve 10 and 50% germination under different levels of soil saturation and two temperatures. Significance of one-way Kruskal Wallis test is shown by the given H-value (**, $0.001<p<0.01$; *, $0.01<p<0.05$; n.s. $p>0.05$). Values represent the mean of 5 replicates except for 40% saturation/25°C values (mean of 2 replicates - no germination was detected in the other 3 replicates). Soil saturation levels correspond to the soil water potentials listed in Table 5.8.

	SATURATION LEVEL (%)				H-VALUE
	40	60	80	100	
10 % Germination					
15°C	∞	11.76	6.06	1.01	7.05*
25°C	11.3	5.33	4.34	1.69	5.79 n.s.
50% Germination					
15°C	∞	16.61	10.29	2.05	12.51**
25°C	14.05	12.48	10.24	3.56	10.15*

Wetting and Drying Cycles

Prior exposure to free water for a single length of time increased germination speed in subsequent trials (Figure 5.4; Table 5.10). Furthermore, times taken to achieve both 10% and 50% germination suggest that these increases are correlated to the length of soaking. 50% germination occurred after 3.68 days in the control (not previously exposed), after 2.78 days following 12 hours soaking and after 1.95 days following 36 hours soaking. Prior exposure to water also decreased the time for 10% germination from 2.76 days in the control samples to almost half this time (1.41 days) when exposed to water for 12 hours. These single exposures to water, however, did not affect final germination percentages (Table 5.11). Results indicate no difference in the number of seeds germinating between treatments at 14 days, with all samples showing a final germination percentage of between 58.7 and 69.3%.

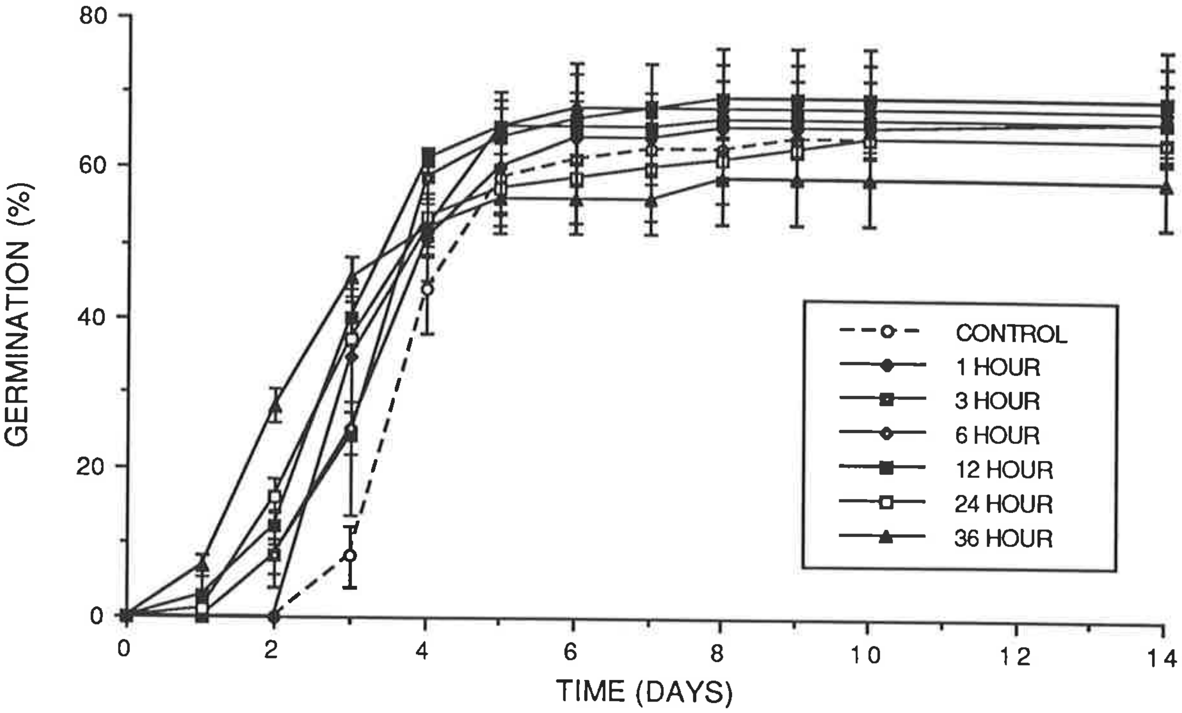

Figure 5.4: Germination of bluebush fruits following pre-exposure to water. Seven exposure times of between 0 (control) and 48 hours were used.

Table 5.10: Times (in days) required to achieve 10 and 50% germination with different times of pre-exposure to water. Significance of one-way ANOVA used to detect differences between treatments is shown by the given F-value (*, $p<0.001$). Means followed by similar superscript letters within each row are not significantly different at $p<0.05$ as indicated by LSD tests.**

	SOAKING TIME (HOURS)							F-VALUE
	CON	1	3	6	12	24	36	
10 %	2.76^{a}	2.23^{ab}	1.99^{bc}	1.91^{bc}	1.41^{cd}	1.38^{cd}	0.84^{d}	8.86***
50 %	3.68^{a}	3.01^{b}	3.29^{ab}	3.28^{ab}	2.78^{b}	2.70^{b}	1.95^{c}	9.28***

Table 5.11: Final germination percentages of bluebush fruits with different times of pre-exposure to water. Significance of one-way ANOVA used to detect differences between treatments (using the transformed data) is shown by the given F-value (*, $p<0.001$). Means followed by similar superscript letters are not significantly different at $p<0.05$ as indicated by LSD tests.**

TIME	SOAKING TIME (HOURS)							F-VALUE
	CON	1	3	6	12	24	36	
Day 14	64.0^{a}	68.0^{a}	69.3^{a}	66.8^{a}	66.7^{a}	64.3^{a}	58.7^{a}	0.46 n.s.

Exposure of bluebush fruits to wetting and drying cycles also affected germination speed in subsequent trials (Figure 5.5). Significant differences between the control and treated samples are revealed in times taken to achieve both 10% and 50% germination (Tables 5.12). Prior exposure to water decreased times for successful germination; 10% germination decreased from 2.76 days in the control to 0.34 days following Regime 6 (24Wet/24Dry/24Wet), while 50% of germination occurred after 3.68 days in the control and 1.77 days with Regime 6. Long exposure times intermitted with short drying times promoted the largest increases in germination speed, with fruits subjected to Regimes 5 (24Wet/12Dry/24Wet) and 6 observed to show 10% germination after less than 0.5 days.

Final germination percentages were also affected by wetting and drying cycles (Table 5.13). Although little difference was observed between the control and several of the treatments, significant differences in the total number of seeds germinating at day 14 were observed for Regime 1 (12Wet/12Dry/12Wet) and Regime 5 (24Wet/12DryD/24Wet). Lower percentages (32.9%) were detected following Regime 5, seeds previously subjected to a long exposure/short drying regime, while germination appeared to be stimulated by Regime 1 (12Wet/12Dry/12Wet) (81.6% germination).

Table 5.12: Times (in days) required to achieve 10 and 50% germination under different wetting and drying cycles (regimes defined in Table 5.3). Significance of one-way ANOVA used to detect differences between treatments is shown by the F-value (*, $p<0.001$; **, $0.001<p<0.01$). Means followed by similar superscript letters within each row are not significantly different at $p<0.05$ as indicated by LSD tests.**

GERM	WETTING/DRYING REGIME							F-VALUE
	CON	1	2	3	4	5	6	
10 %	2.76^{a}	0.74^{bc}	1.14^{b}	0.39^{c}	0.95^{bc}	0.48^{c}	0.34^{c}	7.58***
50 %	3.68^{a}	2.35^{b}	2.34^{b}	1.77^{b}	2.01^{b}	2.17^{b}	1.77^{b}	6.76**

Table 5.13: Final germination percentages of bluebush fruits subjected to various wetting and drying cycles (regimes defined in Table 5.3). Significance of one-way ANOVA used to detect differences between treatments (using the transformed data) is shown by the F-value (*, $p<0.001$). Means followed by similar superscript letters are not significantly different at $p<0.05$ as indicated by LSD tests.**

TIME	WETTING/DRYING REGIME							F-VALUE
	CON	1	2	3	4	5	6	
Day 14	64.0^{b}	81.6^{c}	68.2^{b}	66.9^{b}	66.7^{b}	32.9^{a}	62.8^{b}	9.40***

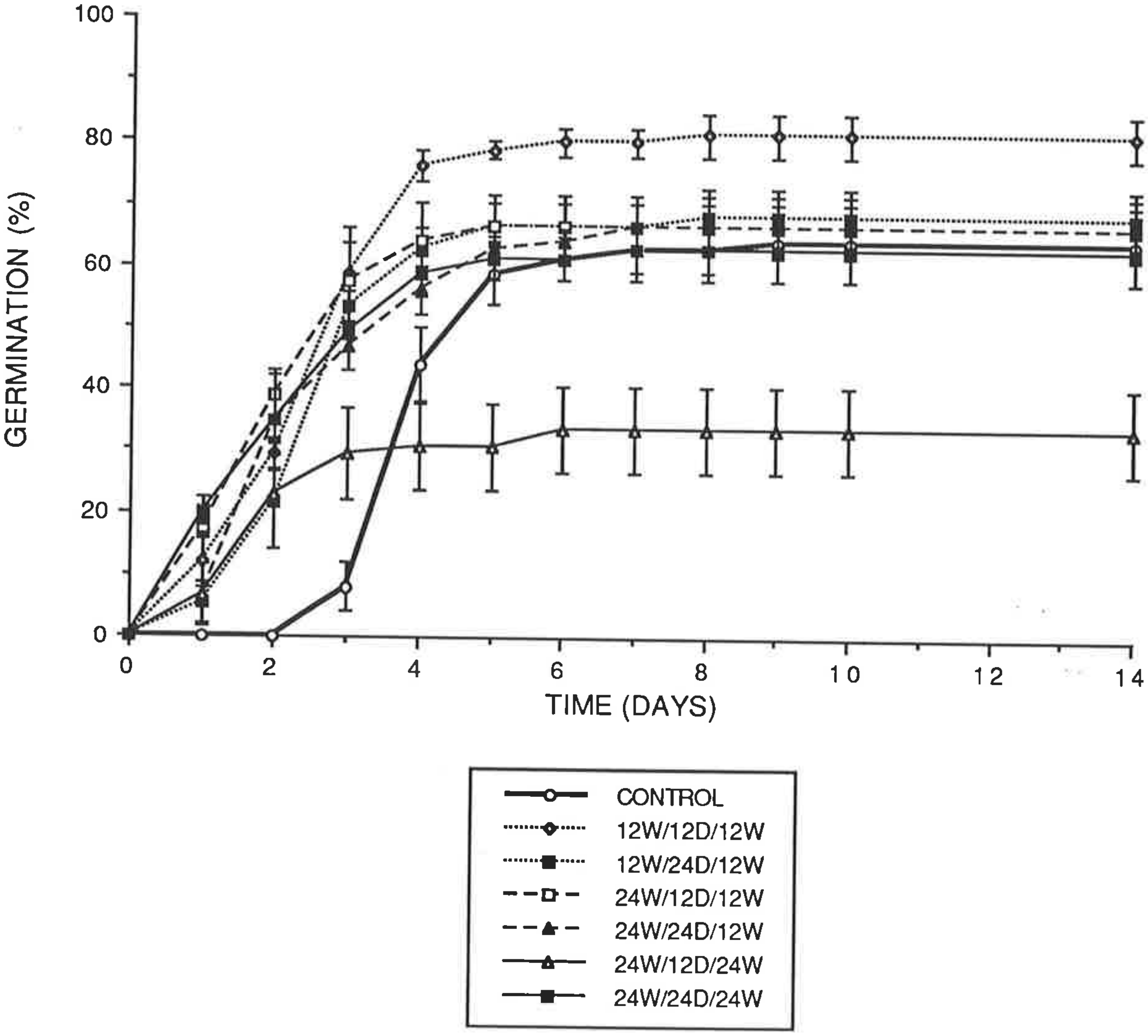

Figure 5.5: Germination of bluebush fruits (means ± S.E) following pre-exposure to water. Seven exposure times of between 0 (control) and 48 hours were used.

Moisture Stress

Increasing osmotic potential decreased both the speed and extent of germination. Salinity and polyethylene glycol results (PEG) are shown in Tables 5.14-17 and Figure 5.6.

Germination speed was retarded in all salinity treatments, particularly with solutions with concentrations of 1.4% NaCl (-1.036 MPa) and above. At this concentration, 10% germination was achieved after 5.39 days (compared to 1.30 days in the control) while 50 % germination was recorded in 8.65 days (2.46 days in the control) (Table 5.14). Germination did not occur at this concentration until day 5, and was even more delayed in the most concentrated solution, where the first evidence of germination was observed on day 10. Although final percentages of germinating seeds were lower in the most saline treatment (20.5% germination), percentages similar to the control were achieved using the less-concentrated solutions (Table 5.15). In the -0.565 MPa solution, final germination numbers were nearly 10% higher than in the control.

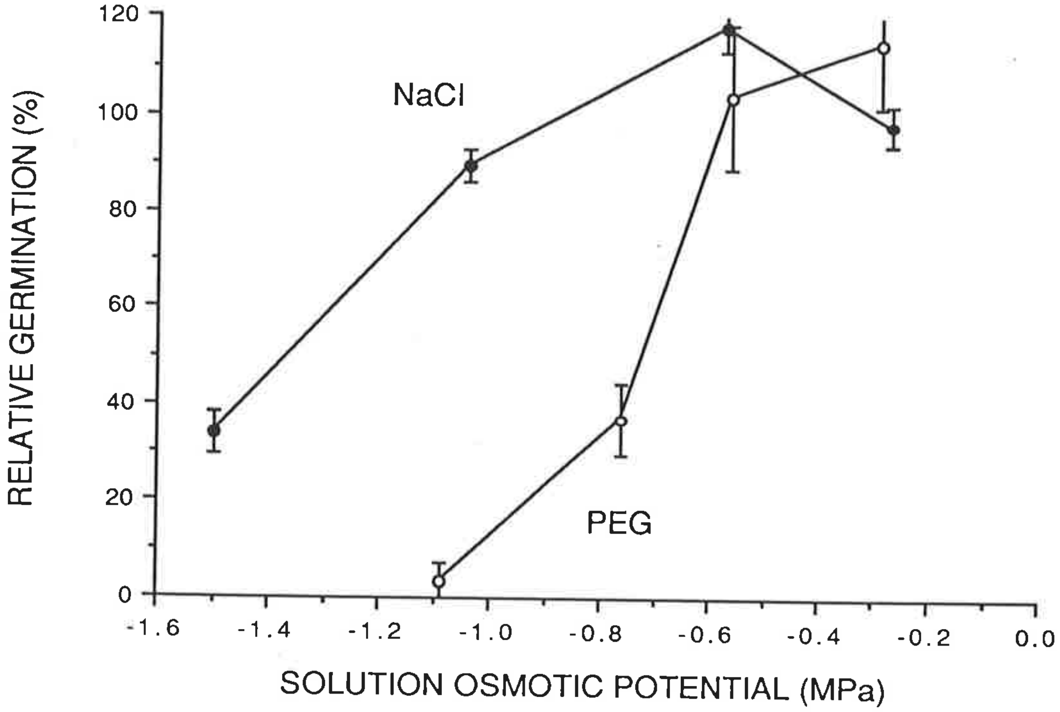

Figure 5.6: Germination of bluebush fruits under varying levels of moisture stress (induced by sodium chloride and PEG solutions). Values are expressed as the percentage of control (de-ionised water) solutions (means ± S.E.).

Table 5.14:Times (in days) required for 10 and 50% germination when placed in NaCl solutions of different osmotic potential. Significance of one-way ANOVA used to detect differences between treatments (using the transformed data) is shown by the F-value (*, p<0.001). Means followed by similar superscript letters within each row are not significantly different at p<0.05 as indicated by LSD tests.**

GERM %	OSMOTIC POTENTIALS (MPa)					F-VALUE
	CON	-0.277	-0.565	-1.036	-1.498	
10 %	1.30^{a}	2.25^{b}	2.89^{b}	5.39^{c}	8.70^{d}	123.32***
50 %	2.46^{a}	3.73^{b}	4.73^{c}	8.65^{d}	10.73^{e}	192.63***

Table 5.15: Final germination percentages of bluebush fruits when placed in NaCl solutions of different osmotic potential. Significance of one-way ANOVA used to detect differences between treatments (using the transformed data) is shown by the F-value (*, p<0.001). Means followed by similar superscript letters are not significantly different at p<0.05 as indicated by LSD tests.**

TIME	OSMOTIC POTENTIALS (MPa)					F-VALUE
	CON	-0.277	-0.565	-1.036	-1.498	
Day 21	60.8^{b}	60.1^{b}	72.4^{c}	55.2^{b}	20.5^{a}	31.64***

Similar results were reported for the PEG trials; osmotic stress clearly inhibited the number of seeds germinating in solutions of -0.56 MPa and above (Table 5.16). In comparison, little difference was detected in germination percentages recorded for the control and less-concentrated solutions; slightly enhanced germination percentage were noted in the less-concentrated solutions compared to the control (Figure 5.6). Germination speed was also slower in the more concentrated solutions (Table 5.17). First observations of germination at each concentration took place on days 2, 4, 6 and 20 respectively. Times required for 10% germination increased from 1.43 days in the control to 5.53 days under treatment 3, and for 50% germination, from 3.36 days to 9.67 days.

Table 5.16: Final germination percentages of fruits when placed in PEG solutions of different osmotic potential. Significance of one-way ANOVA (using transformed data) is shown by the F-value (*, $p<0.001$). Means followed by similar superscript letters are not significantly different at $p<0.05$ as indicated by LSD tests.**

TIME	OSMOTIC POTENTIALS (MPa)					F-VALUE
	CON	-0.289	-0.560	-0.756	-1.094	
Day 21	36.0^{c}	41.2^{c}	37.2^{c}	13.1^{b}	4.5^{a}	29.07***

Table 5.17:Times (in days) required to achieve 10 and 50% germination when placed in PEG solutions of different osmotic potential. Significance of one-way ANOVA used to detect differences between treatments (using the transformed data) is shown by the given F-value (, $0.001<p<0.01$; *, $0.01<p<0.05$). Means followed by similar superscript letters within each row are not significantly different at $p<0.05$ as indicated by LSD tests.**

GERM.	OSMOTIC POTENTIALS (MPa)					F-VALUE
	CON	-0.289	-0.560	-0.756	-1.094	
10 %	1.43^{a}	2.89^{a}	3.63^{ab}	5.53^{b}	∞	6.82*
50 %	3.36^{a}	5.87^{a}	6.17^{a}	9.67^{b}	∞	8.13**

Influence of Fruit Orientation

Orientation of bluebush fruit on the soil surface had a variable influence on germination speed and success under different moisture availability levels (Figure 5.7; Table 5.18). With high moisture availability (100% soil saturation), orientation of the fruit had little effect on germination success; no differences between orientations were obtained on Day 14 (Table 5.19). Under drier conditions, however, fruits placed vertically showed almost double the germination success of horizontal fruits early in the trial (up to Day 9). By Day 14, fruit placed horizontally with the perianth tube in the upright position showed a reduced germination percentage.

Examination of times taken for 10 and 50% germination not only reinforce the expected difference between saturation levels (times were much faster at the higher saturation level), but also show differences between orientation treatments (Table 5.20). At 80% saturation, fruits placed vertically germinated more quickly than the horizontal fruits; 10% germination occurred in

0.60 days, compared to 2.28 and 3.2 days in the horizontal fruits. Similarly, 50% of maximum germination occurred in 2.55 days in the vertical fruits, and between 6.25 and 7.15 days in the horizontal fruits. At full soil saturation, no differences in the speed of germination were detected for different fruit orientations.

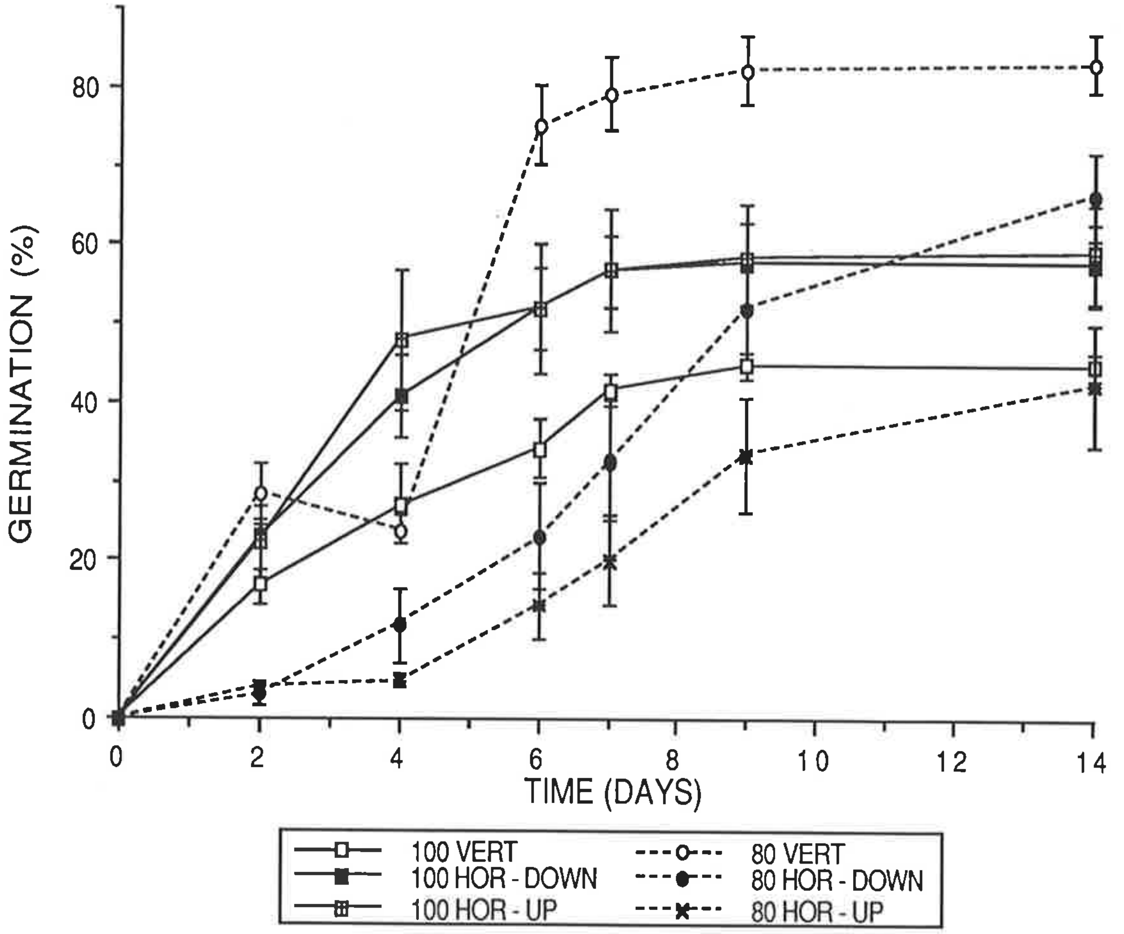

Figure 5.7: Germination of bluebush fruits placed in three orientations (vert - wing vertical; hor- down, wing horizontal and perianth tube downwards, hor - up, wing horizontal and perianth tube upwards) on the soil surface and at two soil saturation levels (100% and 80%). Values are means ± S.E.

Table 5.18: Two-way analyses of variance showing the effect of orientation and soil saturation on final germination percentages. Significance of factors is indicated as follows: ***, $p<0.001$; n.s., $p<0.05$.

VARIATION	TERMS	DF	SS	MS	F VALUE
Main Effects	Orientation	2	498.067	249.034	2.702 n.s
	Saturation	1	291.595	291.595.	3.164 n.s.
Interaction	Orient. x Saturation	2	1376.543	688.272	7.469***
Explained		5	2166.206	433.241	4.704***
Residual		24	2211.686		

Table 5.19: Final germination percentages of fruits placed in various orientations at the soil surface. Significance of one-way ANOVA (using the transformed data) is shown by the given F-value (, $0.001<p<0.01$; n.s., $p>0.05$). Means followed by similar superscript letters within each row are not significantly different at $p<0.05$ as indicated by LSD tests.**

SATURATION	ORIENTATION			F-VALUE
	VERTICAL	TUBE DOWN	TUBE UP	
80 %	84.2^{a}	67.2^{a}	41.7^{b}	10.87**
100%	47.6^{a}	57.0^{a}	59.5^{a}	0.62 n.s.

Table 5.20: Times (in days) required to achieve 10 and 50% germination when fruits are placed in different orientations. Significance of one-way ANOVA (using the transformed data) is shown by the given F-value (*, $p<0.001$; *, $0.01<P<0.05$; n.s., $p>0.05$). Means followed by similar superscript letters within each row are not significantly different at $p<0.05$ as indicated by LSD tests.**

TREATMENT	ORIENTATION			F-VALUE
	VERTICAL	TUBE DOWN	TUBE UP	
80 % SATURATION				
10% Germination	0.60^{a}	3.20^{b}	2.28^{ab}	4.14*
50% Germination	2.55^{a}	6.25^{b}	7.15^{b}	34.85***
100 % SATURATION				
10% Germination	0.57^{a}	0.48^{a}	0.61^{a}	0.62 n.s.
50% Germination	3.44^{a}	2.61a	2.79^{a}	1.14 n.s.

Seed Longevity

Laboratory-stored Fruit

All treatments showed a significant decline in total germination over the 52 weeks of observations (Figure 5.8; Table 5.21). Little difference was noted, however, between fruits stored in air at room temperature and those at 5°C (Tables 5.22). In these two treatments, final germination percentages fell only slightly with over 70% relative germination reported at the end of the experiment. Decreases in germination between dates were observed between 15, 23 and 30 weeks in the air-stored fruits, whilst fruits stored in the cold showed a decrease over the first four weeks and then again between weeks 23 and 30. Fruits stored in air-tight jars showed similar trends to the air-stored and cold treatments for the first 15 weeks, although slightly less germination was noted at week 10. Between 15 and 23 weeks, however, these fruits showed a dramatic decrease in germination percentage, with no germination occurring after this time. As fruits were re-tested in each following experiment, such results may suggest total loss of seed viability, possibly as a result of fungal infections.

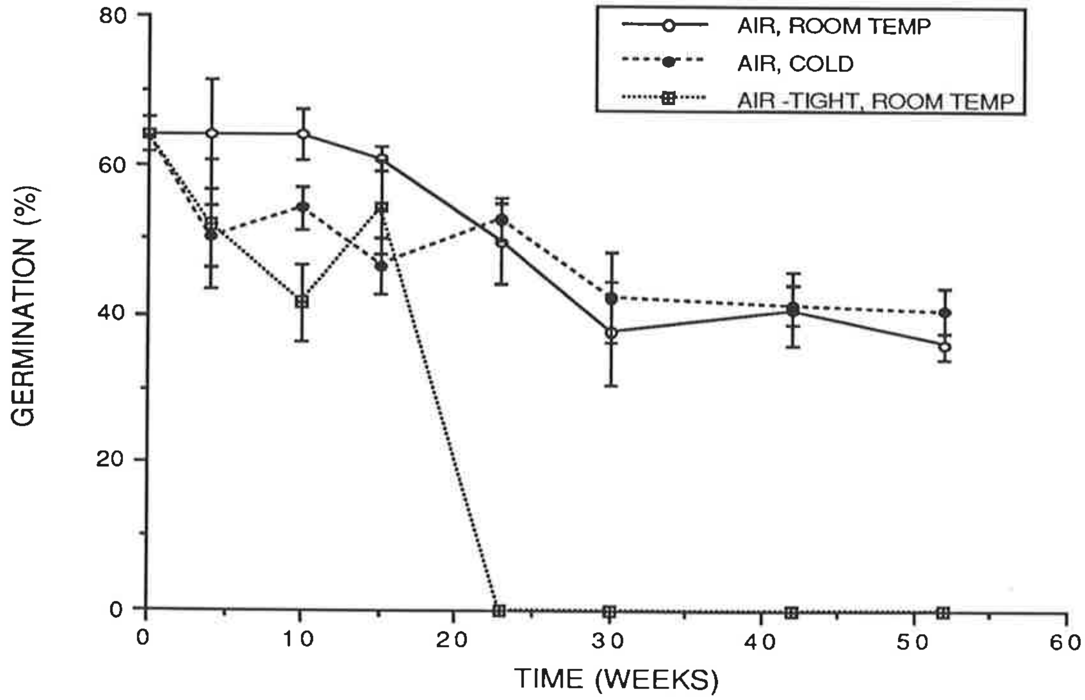

Figure 5.8: Longevity of bluebush fruits stored in the laboratory under three storage regimes. Values are means ± S.E.

Table 5.21: Time series analysis (repeated measures ANOVA) used to examine differences in final germination percentages according to storage regime. Significance of factors is indicated as: ***, $p<0.001$.

VARIABLE	D.F.	F-VALUE	SIGNIFICANCE
BETWEEN SUBJECT EFFECTS			
Storage Regime	2	221.21	0.000***
WITHIN SUBJECT EFFECTS			
Time	7	67.82	0.000***
Storage Regime x Time	14	23.16	0.000***

Table 5.22: Final germination percentages of bluebush fruit over time. Significance of one-way ANOVA used to detect differences between treatments (using the transformed data) is shown by the given F-value (*, $p<0.001$; **, $0.001<p<0.01$; n.s., $p>0.05$). Means followed by similar superscript letters within each row are not significantly different at $p<0.05$ as indicated by LSD tests.**

WEEKS OF	STORAGE CONDITIONS			F-VALUE
STORAGE	CONTROL	COLD	AIRTIGHT	
4	64.7^{a}	50.4^{a}	52.0^{a}	1.15 n.s.
10	64.2^{b}	54.4^{b}	41.4^{a}	8.05**
15	60.8^{a}	54.5^{a}	54.5^{a}	0.60 n.s.
23	49.7^{b}	52.8^{b}	0^{a}	161.65***
30	40.0^{b}	42.0^{b}	0^{a}	48.25***
42	40.7^{b}	40.8^{b}	0^{a}	146.27***
52	39.9^{b}	38.3^{b}	0^{a}	188.60***

Fruit Collected from the Field At Later Dates

Seeds remaining *in-situ* after the initial harvesting in April 1989 and collected in June 1989 (Harvest 2), showed a significantly lower rate of germination compared to the control sample (air-stored in the laboratory) during trials carried out at 10 weeks.(Table 5.23). Germination of the ground-harvested seed was approximately half that of the control, with seeds that had remained on the plant after maturity showing an even lower germination percentage. Subsequent storage of these fruit in the laboratory for 20 weeks showed a further decrease in overall germination percentages and similar differences between treatments. Ground-harvested seeds had decreased to a greater extent than the control, with less than 25% of seeds germinating under standard conditions. In addition, none of the seeds that had remained on the plant after maturity successfully germinated at this time. Trials carried out on fruits collected around the base of plants in September 1989 (Harvest 3 - approximately 22 weeks after the initial harvesting of fruits) showed no successful germination.

Table 5.23: Germination percentages (±S.E.) of field harvested fruits. Significance of one-way ANOVA used to detect differences between seed sources (using the transformed data) is shown by the given F-value (*, $p<0.001$). Means followed by similar superscript letters within each column are not significantly different at the $p<0.05$ level as indicated by LSD tests.**

SEED SOURCE	HARVEST 1 April 1989 - Week 1	HARVEST 2 June 1989 - Week 10	STORAGE - Week 30
Fresh	64.0 ± 1.38	64.2 ± 2.05^{a}	36.68 ± 4.21^{a}
Attached	–	1.9 ± 3.35^{b}	0^{b}
Ground	–	19.9 ± 4.78^{c}	1.9 ± 3.35^{b}
F-VALUE		42.842***	40.044***

FIELD GERMINATION TRIALS

A very low rate of germination was observed during field trials in all micro-environments despite rainfall and mild temperatures during the experiment; only 72 of a possible 2500 fruits (2.88%) germinated. The weather station records show that over the first 3 days of the trial, 14.0 mm of rain fell, mostly at night. Furthermore, temperatures during this period were mild with average soil surface temperatures of 16.0°C at night and 18.7°C during the day. Although rainfall was not recorded after day 3, temperatures remained cool (mean daily air temperature 18.9°C, night temperature 14.1°C). Average soil surface temperature was 17.9°.

Germination of the bluebush fruits was similar in the four main micro-environments although fruits placed in the manually-disturbed plots showed a higher rate of germination (8.5% of fruits; Table 5.24). For the other treatments, very few seeds germinated (0.364%), with the presence of pebbles and litter having little effect on germination rates. Additionally, germination under bluebush shrubs was similar to that observed in the open environment, despite this micro-environment being, on average, 1.3°C cooler than in the open. No fruit were observed to germinate under the canopy of myall trees or near ant nests. Irrigation of bluebush fruits, particularly the higher level, significantly increased germination rates in two of the four micro-environments, the scald and the bluebush mounds (Table 5.25). With low level watering, numbers of seeds germinating was greatest in the 'old mound' environment where 5% germinated was observed. In comparison, fruits added to plots in the 'scald' micro-environment had the highest germination success under watering regime 2 (13% germination).

Table 5.24: Numbers of fruit germinating (out of a possible 100) in each micro-environment; each value represents the sum of four replicates. Significance of Chi-square tests are shown by the χ^2-value (*, p<0.001;**, 0.001<p<0.01). The - symbol represents an unobserved and untested variable combination.**

ENVIRONMENT	CONTROL	+ EPHEMS	+ LITTER	+ PEBBLES	+ DISTURBED	χ^2 VALUE
Open	0	0	0	1	11	39.79 ***
Scald	1	–	0	0	6	14.40 ***
Bluebush Mound	0	–	1	–	8	13.06 **
Old Mound	0	–	1	–	9	15.10 ***
Ant Mound	0	–	–	–	–	-
Under Myall Tree	0	–	–	–	–	-

Table 5.25: Numbers of fruit germinating (out of a possible 100) in each micro-environment under watering treatment. Each value represents the sum of four replicates with regimes explained in Table 5.6. Significance of Chi-square tests are shown by the χ^2-value (*, p<0.01;*, 0.01<p<0.05).**

MICRO-ENVIRONMENT	NO WATER	REGIME 1	REGIME 2	χ^2 VALUE
Open	0	1	3	3.54 n.s.
Scald	1	3	13	15.46 ***
Bluebush Mounds	0	0	3	6.06 *
Old Mounds	0	5	5	5.18 n.s.

DISCUSSION

GENERAL DISCUSSION OF RESULTS

Influence of Water Availability

Water Uptake and Loss From Fruits

The rate of uptake and the amount of water that is required for completion of germination is highly variable between and within individual species (Hegarty, 1978); it is determined by the composition of the seeds, the permeability of the seed coat/fruit and the availability of water in the environment (Mayer and Poljakoff-Mayber, 1989). In bluebush, rapid uptake of water was observed, suggesting that when water is particularly prevalent, exposure for only a short time (possibly 8-10 hours) is required for sufficient imbibition to initiate germination. While uptake by fruit was initially more rapid than excised seeds, after only a short time rates were comparable. This suggests that while the bluebush fruiting perianth itself absorbed some water during imbibition, this did not appear to influence water uptake into the seed to any great extent. The imbibition characteristics of bluebush fruits and seeds may indicate an adaptation to semi-arid/arid conditions, where uptake is maximised at times water is available. It should be noted, however, that under more usual circumstances, longer uptake times than those quoted would be required for germination; it is expected that the uptake of water from the soil would occur more slowly than observed here due to reduced water availability and osmotic effects.

Water loss experiments indicate that both seeds and fruits of bluebush dehydrate rapidly on removal from a moist environment; most moisture was lost within 2 hours. Although early studies suggested that the retention of absorbed water by seeds may be an adaptation to xeric conditions (Yamamoto, 1964 in Hegarty, 1978), more recent studies have disputed this claim. Current theories propose that rapid dehydration of seeds may be advantageous in an arid environment, preventing the germination of seeds into high moisture stress environments (Mott, 1974; Hegarty, 1978). Results from this trial suggest that bluebush seeds are not among those seed-types which are unable to gauge uncertain water availability conditions and germinate irrespective of the chance of subsequent seedling survival (Mayer and Poljakoff-Mayber, 1989).

The failure of bluebush seeds to germinate under field conditions demonstrates the need for extended periods of high soil moisture to promote bluebush germination. Despite rainfall, cool conditions and irrigation, germination percentages were very low, with the number of seeds germinating far below that expected following laboratory trials. I believe that these low percentages can be directly attributed to the low availability of moisture in the surface layers of the soil; fruits were clearly unable to imbibe and maintain sufficient water for germination because of rapid soil surface drying. Observations showed that even with the application of 20 mm of water twice a day, the soil surface within the plots quickly dried, causing the fruits to lose the water they had previously taken up.

Effect of Moisture Stress

The germination of bluebush fruit was correlated with water availability; laboratory trials showed that both the speed and extent of germination was reduced with decreasing soil saturation levels. As seen in other studies on desert species, optimum germination occurred when soils were at field capacity (100% saturation, -0.004 MPa) (Hadas, 1977; Agami, 1986; Meidan, 1990). The level of moisture stress at which bluebush germination was still possible was shown to be comparatively low during the soil saturation trials, with little if any germination occurring at 40% soil saturation (-0.08 MPa). These results contrast with those of Burbidge (1946), who reported that significant germination in bluebush could occur over a large soil saturation range (40-100%) and also with the PEG-induced moisture stress trials, where significant germination was observed at potentials of -0.756 MPa (~ 40% saturation). The lower germination percentages observed during my soil saturation trials may have resulted from incorrect measurement of soil saturation levels; growth cabinet conditions may have induced rapid soil dehydration and much lower soil water availability levels than were suggested for each treatment. Alternatively, contrasting results may have been observed because of differences in the matrix potential of the soils used in the germination trials. I used a clay loam medium which, at a given soil saturation level, may have a more negative matrix potential than Burbidge's sand medium (Jeffrey, 1987); as a consequence, in my trials water may have been more difficult to remove from the soil and less uptake by bluebush fruits may have occurred.

The level of moisture stress at which bluebush germination can still occur is similar, and in some instances less than, the levels published for other species; germination has been observed (albeit at decreasing percentages) until water potentials reach -1.0 to -1.2 MPa (Dasberg and Mendel, 1971; McWilliam and Phillips, 1971; Mott, 1974; Khan *et al.*, 1987; El-Sharkawi *et al.*, 1989). Hegarty (1978) and Romo *et al.* (1991) suggest that the failure of seeds to germinate under moisture stress represents a positive response to environmental conditions and is a form of induced (secondary) dormancy which ensures that germination will only occur during low stress conditions (*i.e.* soils must be near to field capacity for high germination percentages). This is advantageous in arid climates where the surface of the soil dries out quickly following rainfall. If germination is only possible when rainfalls of sufficient intensity occur on consecutive days to maintain high moisture levels at the soil surface, seedling losses will generally be reduced (McWilliam and Phillips, 1971; Mott, 1974; Mott and Groves, 1981). However, Bewley and Black (1982) point out that the ability to germinate under conditions of water stress may confer certain ecological advantages. They suggest that it may allow species to become established in areas where more drought-sensitive species cannot establish.

The interaction between moisture availability and temperature has also been noted as an important controlling influence of germination in arid species (Mott and Groves, 1981; El-Sharkawi *et al.*, 1989); studies have shown that reductions in germination at low and high temperatures are often more noticeable at low water potentials (Sharma, 1973). In this study, however, little difference in germination of bluebush fruits was noted at the two temperatures (15° and 25°C) for each of the soil saturation levels. Given that significant decreases in bluebush germination do occur at higher (>30°C) and lower (<10°C) temperatures, I believe that a temperature x moisture interaction may be an important influence on bluebush germination, but only at the extremes of temperature. Additional studies examining germination over a range of water potentials at temperature extremes may confirm this hypothesis.

Effect of Salinity

Results show both decreased germination speeds and percentages with high salinities, suggesting that increasing osmotic potentials significantly slowed water imbibition at these concentrations. The NaCl ions themselves, however, did not appear to be produce toxic effects at these concentrations as germination percentages were actually greater in the salinity trials than those measured at equivalent osmotic potentials using the PEG solutions (a supposedly inert chemical) (Mayer and Poljakoff-Mayber, 1989).

Although germination is almost always reduced in increasingly saline solutions, non-halophytic species have a variable salinity-tolerance (Bewley and Black, 1982). Comparisons with other species suggests that bluebush germination is more tolerant of salinity than some semi-arid/arid species (*e.g. Chrysothamnus*, Khan *et al.*, 1987; *Zygophyllum dumosum*, Agami, 1986; *Z. qatarense*, Ismail, 1990) while it also exhibits similar responses to others (*e.g. Atriplex halimus*; Mayer and Poljakoff-Mayber, 1989). As expected, tolerance is not as high as that reported for many halophytic species (Khan and Ungar, 1984). Such levels of tolerance may suggest that bluebush germination would generally not be significantly limited by soil salinities, although its use as a coloniser species on highly salinised land would be doubtful.

Effect of Wetting and Drying Cycles

Although hydration treatments may affect germination in a wide variety of ways (see review by Hegarty, 1978), bluebush germination was generally enhanced by wetting and drying. Increased germination speeds suggested that the physiological development of the embryo during hydration was not lost during dehydration while the general similarity in final germination percentages indicates little embryo damage resulted from this development and subsequent dehydration (Griswold, 1936; Hegarty, 1978). Germination percentages were only observed to decrease following the longest soaking regime; here it is likely that germination had passed the critical stage where subsequent dehydration results in severe injury to the embryo. Increased germination percentages were also noted for seeds subjected to the shortest soaking regime. The reasons for this apparent increase are not clear; they may relate to changes in seed coat permeability or solute loss from the seed or the synthesis of seed proteins (Hegarty, 1978).

The ability of bluebush fruits to survive wetting and drying cycles may be advantageous in semi-arid and arid environments for two main reasons. Mott (1974) noted that seeds which can withstand short periods of wetting and drying without viability loss would be favoured in environments with frequent showers, as the amount of germinable seed would not be reduced. Similarly, the stimulation of germination rates may result in a more rapid germination following substantial rainfalls, therefore implying a survival advantage to seedlings (Wilson, 1971 and Wilson *et al.*, 1974).

Influence of Fruit Orientation

The position of seeds or fruits relative to the soil surface may have a considerable effect on germination, primarily through changes to the amount of seed:soil contact (Harper *et al.*, 1965; Harper and Benton, 1966; Sheldon, 1974; Mayer and Poljakoff-Mayber, 1989; Winkel *et al.*, 1991b). In bluebush, orientation was found to have a significant effect on germination of fruit when water was not freely available (*i.e.* soil saturation was less than 100%). Possibly as a result of the fruit becoming partially buried in the soil, vertically-orientated fruits were seen to germinate more rapidly than seeds horizontally placed on the soil surface. Winkel *et al.* (1991a) suggested that seed burial may increase seedling emergence by increasing seed:soil contact and water flow to the seed. Following this reasoning, vertical fruits may have been able to imbibe and retain more moisture than those fruits which were fully exposed, a factor which may be particularly important in the drying atmosphere of the growth cabinet. In the field, however, much of this effect would be expected to be lost; vertically-orientated fruits are rare[1], usually

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[1] Only 3.2% of recovered fruits were located in a vertical orientation after the dispersal trials outlined in Chapter 4.

observed only when fruits become lodged against litter or pebbles. In this position, the fruits would have reduced seed:soil contact and hence are likely to show reduced germination. Additionally, studies revealed a decrease in the germination percentage of fruits placed horizontally with the perianth tube in the upright position. This is a surprising observation, as fruit morphology would suggest that this horizontal orientation would give better seed:soil contact than if the fruit was positioned with perianth tube downward. Such results may suggest that water uptake does not take place equally through all parts of the fruit; more water may be imbibed through the perianth tube.

Influence of Micro-environment

Manual disturbance of the soil surface promoted the germination of bluebush seeds. High numbers of germinated seeds were recorded in all four disturbed micro-environments, supporting previous observations that soil disturbance can enhance field germination of chenopod seeds, particularly bluebush. Although several reasons for this have previously been proposed including trapping seed, improving moisture storage and infiltration, ameliorating ground temperature fluctuations and providing a seed bed (Cunningham, 1976; Cunningham *et al.*, 1976; Butler, 1985), I believe that at this time disturbance of the soil surface was particularly advantageous because it broke-up the soil surface. This promoted rainfall infiltration rather than evaporation and provided better seed:soil contact by allowing fruit to settle within the surface layer of the soil rather than on top of the soil crust.

During the irrigation trials, the 'scald' micro-environments, areas of flat, compacted soil which were devoid of a lichen crust, provided the best locations for bluebush germination. Enhanced germination percentages were most likely achieved at these locations for three main reasons:

(i) These areas represented the only micro-environment in which the water from irrigation did not quickly infiltrate the soil. With the aid of the circular plastic rings used to define the plots, water 'ponded' on the surface for up to 60 minutes following irrigation in these treatments, allowing water imbibition for longer than in the other micro-environments. Much of this difference may be due to variation in soil texture; the sandier soils on shrub mounds infiltrated rapidly and would be expected to hold little water near the surface (Walter and Stadelmann, 1974).

(ii) The scalds also possessed a large amount of surface dust which coated the seed during the irrigation and may have helped to retain moisture within the fruit once the surface water had disappeared.

(iii) The soil surface of the scalds was flat, favouring good soil-seed contact.

Despite reports to the contrary in other species (*e.g.* Evans and Young, 1970 and 1972; Eckert *et al.*, 1986; Winkel *et al.*, 1991b), no evidence was collected during this study to suggest that the presence of ephemerals, litter and pebbles influenced the germination of bluebush seeds. Similarly, the presence of adult shrubs was not linked with higher germination percentages. Such observations would suggest that fine-scale changes in micro-climate (*e.g.* shading, increased humidity and soil moisture, decreased temperatures) that result from the presence of these features were not sufficient to produce a detectable effect at this time. I believe, however, that it is still possible that these micro-environmental modifications are important during natural germination events (*i.e.* large rainfall events). Because of the erratic and unpredictable nature of bluebush field germination, this hypothesis would be difficult to test.

Seed Longevity Studies

Observations carried out during this study support previous reports examining bluebush seed viability (Burbidge, 1946; Hall *et al.*, 1964; Leigh and Mulham, 1965; Perry, 1967; Cunningham *et al.*, 1981). Clearly, there was a loss of viability after only a few months in the field. Fruits remaining both on adult plants and collected beneath plants clearly showed much lower rates of germination than fruits collected when fresh and air-stored in the laboratory. Although the length of time a seed remains viable is primarily genetically determined, several other factors may be of influence following dispersal of the seed (Mayer, 1989); moisture, temperature and the chemical composition of the soil are the most significant of these. Previous studies carried out by Burbidge (1946) and Hall *et al.* (1964) suggested that rainfall and high humidity levels may lead to a decrease in bluebush seed viability. These factors may also account for some germination loss in this study, as large amounts of rain did fall between Harvests 1 and 2 (~ 70 mm) and again between Harvests 2 and 3 (~ 40 mm). Exposure to rainfalls may have decreased fruit germinability in three major ways:

(i) Some viable seeds may have germinated and then died between the harvest times, leading to a proportional reduction in the number of viable seeds remaining in the seed population. This is not likely, however, given the total absence of newly-germinated seedlings observed in the area during the later harvests.

(ii) Intermittent rain and long wetting/drying cycles during the period between Harvest 1 and Harvests 2 and 3 may have led to water imbibition but unsuccessful germination, which led to embryo damage on dehydration. This latter factor was suggested in earlier laboratory trials, where a reduction in germination was detected following wetting and drying cycles of 24 hours wetting/ 24 hours drying/ 24 hours wetting.

(iii) Fungal Attack - Fruits remaining exposed for an extended period of time in the field may be subject to attack by several species of 'field fungi'. These may cause embryo death or lead to the production of toxic substances, and are usually more prevalent in high moisture conditions (Bewley and Black, 1982).

Other factors may have also contributed to the decrease in germination of field-collected fruits over time. Firstly, it is possible that fruits remaining on plants at Harvests 2 and 3 were inherently different to those which were dispersed after Harvest 1. Fruits left on plants may represent late-developing or malformed fruits; such factors have been show to produce variations in subsequent seed viabilities in various species (Mayer and Poljakoff-Mayber, 1989). Secondly, seed-harvesting ants may have preferentially removed some of the viable fruit during foraging[1]. Ants have been shown to take bluebush fruit from traps during dispersal trials (see Chapter 4). Some fruit-sorting may have occurred during this harvesting process; previous studies by (Andrew, 1986) have reported differences in the predation rates of sound

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[1] The removal of fruit by birds and small foraging mammals is not likely given the general paucity of these species in the Australian rangelands (see Morton,1985 and Wiens,1991).

and unsound *Sorghum* seed by the harvester ant *Meranoplus*, although no estimate of numbers of viable seeds within the sound category was made. If ants did select sound bluebush fruit over unsound or malformed fruit, a larger proportion of unsound (and maybe unviable) fruits may be left. Ant-harvesting trials incorporating seed viability are required to confirm this hypothesis.

In comparison to those fruits collected from the field, laboratory-stored fruit retained high levels of viability over the 12 month test period. Trials showed that 70% relative germination was possible after the maximum storage time. Differences detected between storage treatments indicate that cool to mild temperature differences (from 5° to approximately 20-25°) had little influence on seed viability during storage. Observations did suggest, however, that air-storage of fruits may be more appropriate than storage of fruits in air-tight containers due to the possible susceptibility of fungal attack. These results demonstrate that bluebush fruit can be air-stored for later use, such as revegetation trials.

The characteristics of bluebush seed longevity shown here are not necessarily consistent from one fruiting event to another as seed viability has been linked secondarily to the environmental factors experienced by the parent plant during seed formation, particularly water supply, temperature, mineral nutrition and light (Waller *et al.*, 1983; Mayer and Poljakoff-Mayber, 1989). Being an arid species, bluebush plants are likely to be exposed to considerable environmental variation, especially in moisture availability. Differences in the germination of fresh fruit collected following each flowering event observed at Middleback during 1988-1991 (see Chapter 4) clearly imply that both seed numbers and germinability are highly changeable. Unfortunately the amount of fruit available for harvest on each occasion did not allow seed storage/viability analysis to determine exact effects. I believe, however, that while the actual germination percentages quoted in this study are likely to vary, trends in the patterns of seed viability loss would remain essentially the same.

FACTORS LIMITING THE GERMINATION OF BLUEBUSH

Water and the Availability of Safe-Sites

Water is a key element restricting the germination of bluebush. Germination is delayed during times of moisture stress; surface soil saturation levels of at least 40-60% (-0.08 to -0.01 MPa) are required for minimal germination (> 10%) to occur, while for more significant germination (> 40%) saturations levels in excess of 80 % (-0.006 MPa) almost certainly need to be maintained. Evidence also suggests that when water is limiting, imbibition by the seed is decreased and the germination process is slowed. For successful germination to occur, therefore, a longer exposure to moisture would be needed than was estimated during water imbibition trials. Where soil moisture is less than field capacity (< 100% saturation), levels need to be maintained for several days (at least 3-4) for germination to occur.

In semi-arid environments, high moisture levels in the top layer of soil occur only rarely and for short periods of time. At Middleback Station, monthly records of soil water contents kept during period 1988-1991 as part of the soil water competition studies show that the moisture content of the soil at 10 cm from the surface varies between 20-48% saturation (estimated to be -2.25 to -0.03 MPa) in winter and 4-18% saturation (estimated to < -2.25 MPa) in summer (see Figures 3.9 and 3.10 and Appendix 3 for more specific data). Given the rate of evaporation, the amount of water present in the surface soil (< 0.5 mm from the surface) would generally be less than this for most of the year. Germination must occur, therefore, directly following periods of rainfall. Although single large rainfall events (such as late summer thunderstorms) would increase the moisture content of the soil to a sufficient level for imbibition, rapid soil surface drying would also occur. An irrigation experiment clearly illustrates the rapidity with which drying occurs (Figure 5.9), further suggesting that a single rainfall would not produce suitable surface soil moisture levels over a sufficient time period for germination to occur. Germination of bluebush seed is more likely when rain falls over a period of several days, during which time high humidity, low evaporation and high soil moistures are maintained. Given that at the very least 40-60 mm of rainfall would be required to fall over a 3-4 day period for successful germination, daily rainfall records suggest that there have only been 4 or 5 possible times for bluebush germination in the four years of observation at Middleback Station.

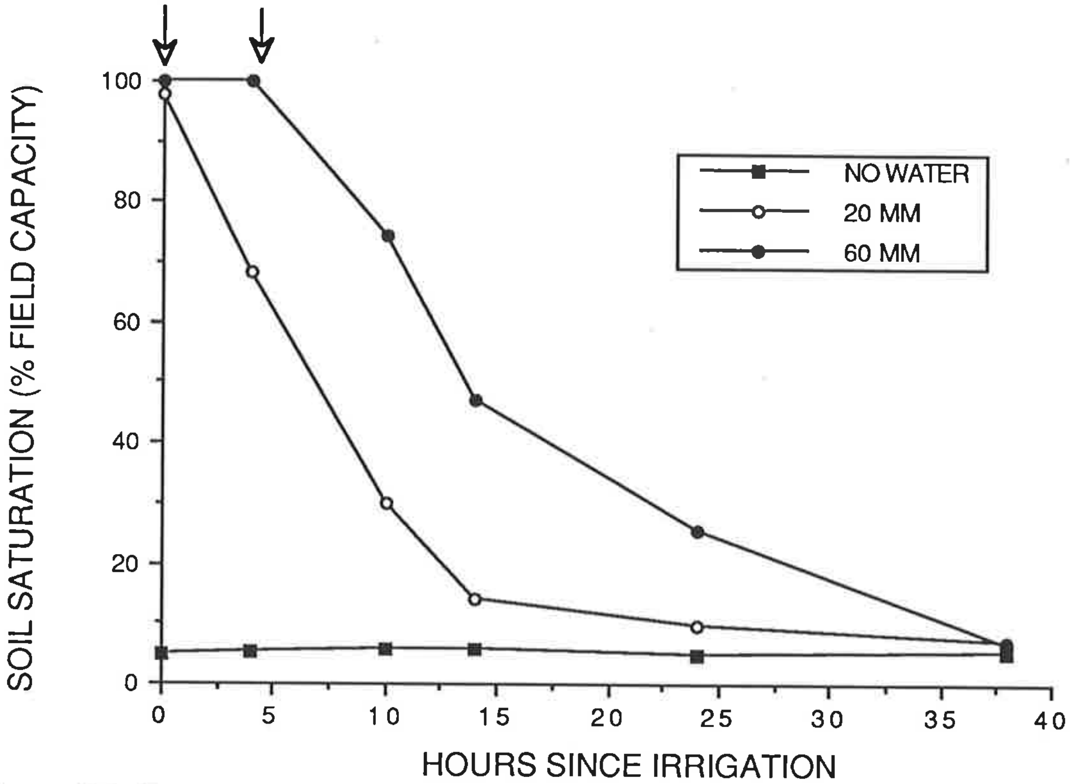


Figure 5.9: Rate of drying of the surface soil (<5 mm depth) following irrigation of 20 mm and 60 mm within a 30 cm circular plot. Irrigation was carried out in the evening, 21 February, 1990, maximum and minimum temperatures for 22 February were 31° and 19°C. Arrows indicate times where water ponded on the soil surface and infiltration was not complete.

It is also possible, however, that limited germination may occur outside these times of continuous heavy rainfall in micro-environments which show an improved soil water availability (*i.e.* disturbed areas or cracks in the soil surface). These germination events would still be preceded by rainfall, albeit less than that indicated above, but would be highly-localised (these particular micro-environments represent only a small percentage of the soil surface). I believe that this type of recruitment is particularly fortuitous and does not generally account for a significant proportion of the recruitments into stable populations.

Seed Viability

The availability of a suitable seed source is the other major factor which may limit the germination of bluebush (Eriksson and Ehrlén, 1992). Evidence collected in this study strongly suggests that the supply of viable seed is not an infinite resource available whenever conditions are suitable for germination. Instead, it has been demonstrated that bluebush plants flower only after sufficient rainfall (see Chapter 4) and, even then, seed viability is quickly lost in the field environment. The supply of seed is therefore likely to restrict bluebush germination. During this study, of the five possible opportunities for germination suggested earlier, only one fell at a time when a viable seed supply may have been available (*i.e.* within three months of seed set).

Co-occurrence of Fortuitous Episodic Events

Noble (1979) suggested that episodic climatic events are extremely important components of the life-histories of many perennial plant species which grow in semi-arid and arid environments. This study would support this hypothesis as it applies to bluebush.

The successful germination of bluebush seed is clearly reliant on the co-occurrence of rare episodic rainfall events. In most years, there is no germination of bluebush fruit due to either;

(i) insufficient rainfall in autumn for flowering, and hence a lack of available viable seed,
(ii) insufficient continuous and heavy rainfall for the maintenance of high soil moisture levels required for germination soon after seed set, or
(iii) a combination of these factors.

In occasional years, however, sufficient rain will fall within the necessary time-frame to both promote flowering and seed production, and allow for bluebush germination. It is these rare years that are crucial to the continued maintenance of bluebush populations.

CONCLUSIONS

- The uptake of water by bluebush fruits and seeds is similar to that seen in other semi-arid and arid species. Bluebush fruits imbibe water quickly, maximising uptake when water is most prevalent, but also rapidly lose water on dehydration. This latter characteristic may help to prevent the germination of seeds into environments of high moisture stress.

- Bluebush germination shows other characteristics which have been previously considered advantageous in semi-arid and arid plant species. Germination is delayed when soil moisture levels are decreased; the requirement for high intensity rainfall over consecutive days may represent an adaptation which guards against later seedling losses. Additionally, seeds can generally withstand wetting and drying cycles and are able to germinate under moderately saline conditions. The orientation of fruit with respect to the soil surface may also influence germination at reduced soil moisture levels by altering the amount of seed:soil contact.

- Under field conditions, it is difficult to achieve the high germination percentages achieved in laboratory trials. In this study, these lower percentages relate directly to the inability to maintain high moisture levels at the soil surface.

- Soil disturbance is beneficial to germination, most likely as a result of improved water infiltration. The presence of litter, ephemerals, pebbles and adult shrubs did not favour germination.

- Viability of bluebush fruits was significantly decreased after only a few months in the field. In comparison, fruit air-stored in the laboratory maintained viability for the 12 month trial period.

- The availability of both water and a viable seed source restricts germination in most years. In occasional years, however, the co-occurrence of rare episodic rainfall events will promote flowering and seed production, and allow for bluebush germination.

CHAPTER 6

PATTERNS OF SEEDLING ESTABLISHMENT, GROWTH AND SURVIVAL

INTRODUCTION

BACKGROUND

Seedling Establishment in Arid-zone Perennial Plants

In long-lived perennial plants, seedling survival rates are generally low (Harper, 1977; Krannitz and Carey, 1988; Owens and Norton, 1989), with successful establishment in some species only in certain favourable years (Grubb, 1977; Jordan and Nobel, 1981). Most often increased seedling emergence and survival is observed following periods of high rainfall (Beatley, 1974). As a consequence, many of the present-day plant communities containing long-lived perennials are believed to have recruited during runs of years of favourable conditions (Williams, 1982). Seedling desiccation is believed to the primary cause of death in arid-zone seedlings (Harper, 1977; Hennessy *et al.*, 1984; Harrington, 1991).

In addition to the episodic nature of recruitment in arid areas, seedling establishment may also be influenced by spatial variability. Many factors including micro-environmental variation (*e.g.* light availability, subsurface moisture and surface microtopography) and biotic influences (*e.g.* competition and herbivory) have been shown to play a significant role in the success of recruitment in many ecosystems (Harper, 1977). In the Australian semi-arid rangelands, it is likely that herbivory and other disturbances (Noy-Meir, 1973), neighbouring plants and individual species tolerances significantly affect the recruitment of perennial shrubs.

Effect of Neighbouring Plants

Some studies have suggested that the canopies of shrub and tree species may represent the most favourable environments for seedling establishment in arid environments, offering higher soil moisture levels, lower temperatures and more abundant food sources. Soil nutrients, particularly nitrogen, concentrate around the base of adult plants due to decomposition of accumulated litter (Charley and West, 1975; Malik *et al.*, 1976; West, 1982). Similarly, these higher organic levels have been shown to decrease evaporation and increase the ability of the soil to retain moisture after rainfall (Evans and Young, 1970; West, 1982); thus the areas around plants are sometimes known as 'fertile islands' (Romney *et al.*, 1978; Garner and Steinberger, 1989). The 'shading' effects of adult plants may also favour seedling establishment through micro-climate amelioration (Turner *et al.*, 1966). West (1982) and Franco and Nobel (1989) reported decreases in irradiance and soil surface temperatures and increases in relative humidity under plant canopies. Additional advantages of seedling establishment next to adult shrubs may be that the adults offer protection to the seedlings against grazing (Eldridge *et al.*, 1991) and that the site is known to support previous seedling establishment (Fowler, 1988).

Other investigations, however, have indicated that seedlings may be disadvantaged if positioned next to adult shrubs (Friedman, 1971; Fowler, 1986; Gurevitch, 1986). Seedling survival and growth may be reduced by root competition with the adult shrubs (Friedman and Orshan, 1975; Hunter, 1989; Reichenberger and Pyke, 1990), primarily for soil water (as directly demonstrated by Robberecht *et al.* (1983), Ehleringer (1984) and Nobel and Franco (1986) in neighbour removal experiments). Alternatively, seedling survival may be hampered by allelopathic effects. This idea was used to account for increased seedling mortality under *Larrea* canopies by Sheps (1973) (but see Barbour *et al.*, 1977). It has also been suggested that establishment may be decreased in the vicinity of adult plants as a consequence of the accumulated litter layers. These layers may reduce germination by decreasing soil-seed contact (Fowler, 1988), or by burying seed beyond depths at which germination can occur. As pointed out by Eldridge *et al.* (1991), however, seedling survival will not be affected in this situation.

It would appear, therefore, that the effects of neighbouring shrubs are not straight-forward, with variation occurring spatially, temporally and between species (Fowler,1988). A study carried out by Owens and Norton (1989) demonstrated that while *Artemisia* seedling survival was linked to the distance to adult shrubs, it was also related to the area available to each seedling for resource acquisition. They concluded that the added protection of shelter could only be considered advantageous to seedlings if they possessed sufficiently large available areas, implying that competition for resources was the primary control of seedling survival. Similar studies by Franco and Nobel (1989) have revealed that the influence of adult 'nurse plants' on the survival and growth of cactus seedlings may vary over time: nurse plants facilitate seedling establishment by reducing temperatures and providing a nutrient-enhanced microsite, but later reduce seedling growth because of shading and competition for soil water. Studies of saltbush (*A.vesicaria*) seedling establishment revealed that although survival varied with proximity to adult shrubs, no consistent relationship could be determined (Eldridge *et al.*, 1991). At some locations, seedlings found near to live shrubs were less likely to survive than those seedlings near dead shrubs or in the open, while at other sites the reverse was true. Such results support Fowler's (1988) hypothesis that micro-site favourably varies over time.

Influence of Disturbance

Soil disturbance has been shown to affect seedling establishment in a variety of habitats in alpine, temperate and arid/semi-arid ecosystems (Harper, 1977; Hunter, 1989; Chambers *et al.*, 1990; Dean and Milton, 1991; Hobbs and Huenneke, 1992). Most often disturbance is beneficial to recruitment; in fact many species require local disturbance for successful establishment in mature communities (Grubb, 1977; Pierson and Mack, 1990). Chambers (1990) summarised the soil properties which may be affected by disturbance; they include physical soil characteristics, nutrient and mineralization rates, soil water potentials and temperature. In arid areas, one of the main advantages of disturbance to seedlings is that it may help to accumulate water and increase infiltration (Hall *et al.*, 1964; Dean and Milton, 1991). For example, revegetation experiments carried out in semi-arid New South Wales reported moisture penetration in pitted areas up to three times that of undisturbed soil (Young, 1969).

Disturbance may also reduce root competition from neighbours (Hall *et al.*, 1964; Pierson and Mack, 1990); Hunter (1989) used this hypothesis to explain *Artemisia* seedling density increases on a denuded area in the northern Mojave Desert. Finally, mechanical disturbance treatments can also be beneficial as they protect seedlings from sand-blasting and desiccation by hot dry winds (Butler, 1985).

In contrast to the above, the effects of herbivory have been shown to be detrimental to the establishment of some native species; a number of studies examining the effects of introduced herbivores (mainly sheep and rabbits) on Australian arid-zone perennial species confirm this (Crisp and Lange, 1976; Lange and Purdie, 1976; Crisp, 1978; Fatchen, 1978; Lange and Graham, 1983). Similar responses to herbivory, from both native and introduced species, have been noted elsewhere (Eckert *et al.*, 1986; Frazer and Davis, 1988), although to a lesser extent. These studies suggest that seedling death may occur either as a direct consequence of grazing or as a result of trampling by stock. For completeness, it should be noted that the establishment of some species can be favoured following herbivory. It is those species which are relatively unpalatable to herbivores and resistant to trampling which are advantaged, usually by the removal of potentially-competitive neighbouring plants. This world-wide phenomenon has been reported for many native trees and shrubs in wooded grasslands, where grazing has reduced the perennial grass layer (Walker *et al.*, 1981; Harrington, 1991)

Physiological and Morphological Aspects of Seedling Establishment

It has been widely demonstrated that the likelihood of establishment also depends on the physiological and morphological characteristics of seedlings of individual species, many of which may be related to seed morphology and mass (Wood and Morris, 1990; Jurado and Westoby, 1992). In arid and semi-arid regions , seedling growth and survival has been linked to the general sensitivity of tissue to water stress (Frazer and Davis, 1988), the above-ground surface area:volume ratios (Jordan and Nobel, 1981), root:shoot ratios (Noy-Meir, 1973) and rooting depth of seedlings (Franco and Nobel, 1989). The speed of vertical root development may also be significant, as successful establishment requires roots to have reached sufficient depth to gain moisture once the topsoil begins to dry (Williams, 1979). Those seedlings requiring less time for roots to reach the wetting front following germination may have a better chance of establishment in arid environments.

Observations of Bluebush Seedling Establishment

Bluebush seedling establishment is comparatively rare; it has been estimated to occur at infrequent intervals of between 25 years (Wilson *et al.*, 1984a) and 50 years (Graetz and Wilson, 1984) although few actual observations of successful establishment have been recorded. At the T.G.B. Osborn Vegetation Reserve at Koonamore, S.A., seedlings were recorded only seven times in 35 years, and of these none survived for more than 2 years (Hall et al., 1964). Hall and her co-workers speculated that establishment of bluebush requires a sequence of years of good rainfall and is more likely in areas where the soil has been disturbed leading to increased rainfall infiltration and decreased root competition from other plants. Although litter that has collected around the base of plants may increase the likelihood of germination, they suggested that seedlings in this position often die as they are too close to vigorous roots of adults plants. Most bluebush seedlings appear to perish due to insufficient moisture (Hall *et al.*, 1964; Perry, 1972).

In addition to these anecdotal observations, the only successful seedling establishment events which have been documented for bluebush are for re-vegetation trials which have been carried out using mechanical disturbance. Trials using contour furrowing have shown seedling densities as high as 10 seedlings per metre of furrow one year after germination (Butler, 1985). In this instance, the enhanced establishment rates were directly attributable to the presence of the furrows, which acted to trap seeds, improve moisture infiltration and storage, lessen ground temperature fluctuations, and protect seedlings from strong and drying winds.

Similarly, there is little published literature on the growth of bluebush seedlings. Only one study to date (Butler, 1985) has examined the growth of bluebush seedlings quantitatively.

On average, seedlings grew in height at a rate of 7.26 cm a year and increased by 5.03 cm in canopy width, leading Butler (1985) to calculate that it would take approximately 10 years to reach a canopy biomass of 100 grams. However, as these observations were made during a revegetation trial using furrowing, it cannot be ascertained whether these rates were unnaturally high due to the mechanical disturbance of the ground.

AIMS

Seedling recruitment strategies are an important element in the overall maintenance of plant populations. For bluebush, these strategies may be particularly important given the low rates of recruitment which have been noted and the additional pressure of grazing from introduced herbivores over much of its distribution (Crisp, 1978). Although an understanding of such strategies would provide an important basis from which to propose management regimes, it must be acknowledged that such information is difficult to collect because of the episodic nature of reproductive episodes. During the course of this project, it was not possible to complete a comprehensive, field-based study examining the climatic and environmental requirements for successful establishment. Likewise, it was not possible to determine accurately when and how often seedling recruitment occurs. Instead, investigations reported in this chapter were centred on other important aspects of bluebush seedling recruitment.

The primary aims of this study were to examine the patterns of seedling establishment within field populations of bluebush and to assess the likely influence of neighbouring shrubs, disturbance and introduced herbivores on seedling survival and growth. Further studies were also carried out to examine the role of soil water availability on seedling growth, survival and morphology. Three different investigative strategies were implemented: following the fate of seeds which had germinated during the field germination trial (described in chapter 5); examining three 'in situ' populations of seedlings; and using pot trials. Information collected during the broad-scale survey (see Chapter 2) was used to supplement these studies.

METHODS

STUDIES OF NATURAL SEEDLING COHORTS

General Observations of Bluebush Seedlings

Observations of bluebush seedlings were also made whilst conducting the broad-scale survey (described in Chapter 3). At these times, the presence or absence of bluebush seedlings was noted at each of the sampling locations, along with estimates of mean height. The micro-environment of each seedling was classified into one of five categories: under bluebush, under other shrubs or trees, open flat areas, on vacant mounds or amongst litter. Kruskal-Wallis tests were used to detect differences between micro-environmental preferences using the software package Statview (Abacus Concepts, 1988).

Seedling Cohorts in the Middleback Area

Experimental Methods

Three populations of bluebush seedlings were discovered during four years of observation in the Middleback area. These populations, first observed in the spring of 1990, include:

(i) Honeymoon Cohort - This seedling population was found in September 1990, in Honeymoon Paddock, north-east of Roopena homestead. Here, seedlings were found in a holding paddock extending over an area of approximately 16 m infrequently. The seedlings were located in an area free of trees; isolated adult bluebushes and *Lycium australe* shrubs the only perennial species present. Seedlings were approximately 5-20 cm in height when first observed; this is believed to be the oldest of the seedling cohorts.

(ii) Myola 1 Cohort - This is the first of two cohorts of bluebush seedlings which were observed within a single paddock on Myola Station, west of Middleback Station. This area is periodically lightly grazed by sheep. This seedling population was located in a slight run-on area with bluebush, saltbush and

Acacia oswaldii trees the dominant perennials. Seedlings, ranging in height from 2-10 cm, extended over an area of approximately 20 m x 20 m.

(iii) Myola 2 Cohort - The second cohort was observed 75 m away from the previous cohort, alongside the vehicle track running through the paddock. Seedlings were restricted to the narrow disturbed fringe adjacent to the track and did not extend into the 'undisturbed' paddock environment. This site was on a slight hill and was dominated by adult bluebush and saltbush. Seedlings were 2-20 cm high.

In order to assess spatial distribution patterns and determine growth and survival rates it was necessary to map the locations of all seedlings at each site. To do this, a quadrat was first positioned within the general area of each seedling cohort. The size of each seedling quadrat was chosen on the basis of the spread of seedlings and nearby vegetation; quadrats were made large enough to encompass all tree and shrub species which may have been of influence. The location of all bluebush seedlings within each of these quadrats was mapped to the nearest 5 cm, as was the location of other seedlings and adult shrub and tree species. The height and horizontal diameters of all plants were recorded. Over the following twelve months, three subsequent measurements of seedling height and survival were made.

Analysis Methods

The spatial distribution of bluebush seedlings (and saltbush seedlings, if present) was examined for all three cohorts using standard Batcheler's ratio analysis (Batcheler, 1971) as outlined in Chapter 3. A series of modified Batcheler's ratio analyses were also performed to investigate the position of seedlings with respect to the adult plants at the Myola 1 and 2 sites (the Honeymoon quadrat was not analysed due to the very low numbers of adult shrubs and trees in the near vicinity). This analysis was carried out to determine if seedlings preferentially establish near to adult shrubs (as has been suggested by Hall *et al*, 1964). Using the computer program RSRP2 (A. Sparrow, Botany Department, The University of Adelaide), modified ratios were determined taking into account the horizontal cover of each adult plant. As suggested by Chapin *et al.* (1989), ratios were calculated as the distance from each seedling to the canopy outline of the nearest adult shrub compared to the distance from a random point to the nearest adult shrub. Significance was determined using a t-test .

Seedling survival in Myola 1 quadrat was modelled by logistic regression as a generalised linear model (GLIM), using seedling data collected during the first (October 1990) and last observations (September 1991). Models were constructed using similar procedures to those used for species response and flowering models (Chapters 2 and 4). Variables considered in the analyses were microtography (on or off mounds), position with respect to trees (under canopy or in the open), position with respect to neighbouring shrubs (under bluebush, under other shrubs or in the open) and initial seedling height. As microtopography and position with respect to neighbouring shrubs were considered to be potentially auto-correlated, two series of models for each species were obtained. The first of these models examined the relationship between microtopography and trees on seedling survival, while the second used shrubs as a replacement variable for microtography. Models were constructed using the computer software package GENSTAT (Statistics Department - Rothamsted Experimental Station, 1987).

SEEDLING ESTABLISHMENT AFTER FIELD GERMINATION TRIALS

Growth and survivorship of seedlings which germinated during the field germination trial (see Chapter 5) was recorded on six occasions over the 11 months following the completion of the trial (April 1990 - March 1991). On each occasion, recordings of survival, seedling height and leaf number were made. Visual trends in the data were examined to determine the influences of micro-environment and earlier irrigation on seedling characteristics.

LABORATORY POT TRIALS

A pot trial was carried out to determine seedling growth and survival rates under varying levels of soil water availability. This experiment was carried out under controlled conditions in a Warren Sherer growth cabinet preset at 22°C / 80% humidity / 12 hours dark and light. Trials were conducted in 11 cm plastic pots without drainage holes which were filled with 800 g of top-soil collected from Middleback Station. A small amount of building sand (5%) had been added to this soil before potting to prevent the soil from forming a solid block in the pot. A newly-germinated seed was planted in each pot, and all pots were watered to 80% soil saturation (measured by weight) for 7 days to ensure successful early establishment. In a few cases seedlings did not survive; these were replaced by other germinated seeds at the first opportunity. Each pot was then subjected to one of six soil saturation levels for a period of three months (Table 6.1) with twelve replicates per treatment. Pots were re-weighed, and watered if appropriate, every three days to maintain the correct soil saturation level. Seedling survival and height were measured weekly during the course of the experiment. After three months, the seedlings were harvested to determine root:shoot ratios. Seedlings were removed from the pots and excess soil was removed from roots by gentle washing. After carefully blotting the seedlings with paper towel, roots were removed from the shoots of plants and both were weighed. These were then dried (80°C/24 hours) before re-weighing.

Table 6.1: Soil water contents maintained within plastic pots during the three month seedling trials. Soil water potentials were estimated from soil moisture characteristic curves determined from Middleback top-soil (see Appendix 3).

SOIL SATURATION (% field capacity)	GRAVIMETRIC WATER CONTENT (g water/ g soil as %)	SOIL WATER POTENTIAL (MPa)
15	4.7	-6.310
25	8.2	-1.096
35	11.6	-0.125
50	16.6	-0.032
65	21.7	-0.008
80	26.7	-0.006

Time series analysis (repeated measures analyses of variance) was used to examine differences in seedling height and leaf number between treatments. Differences in root:shoot ratios were investigated using oneway ANOVA. Analyses were carried out using the software packages Statview (Abacus Concepts, 1988) and SPSS-X (SPSS Inc., 1986).

RESULTS

STUDIES OF NATURAL SEEDLING COHORTS

General Observations of Bluebush Seedlings

Bluebush seedlings less than 25 cm in height were observed at 10 of the 124 sampling sites during the broad-scale survey. Five cohorts were reported in the north-west region , four in the eastern section and one to the east of Port Augusta (Figure 6.1). At these sites, around half the seedlings occurred in open areas between shrubs and trees, while the other half were located under tree or shrub canopies (Table 6.2). In the latter case, seedlings were predominantly found under the canopies of the tree species mulga (*Acacia aneura*) and blackoak (*Casuarina cristata*), or under adult bluebush canopies. At two sites in the northwest, recruits were found amongst litter and dead mulga branches. There was no difference in the number of seedlings present in each micro-environment (Kruskal-Wallis test; H=9.085, d.f.=5, p=0.106).

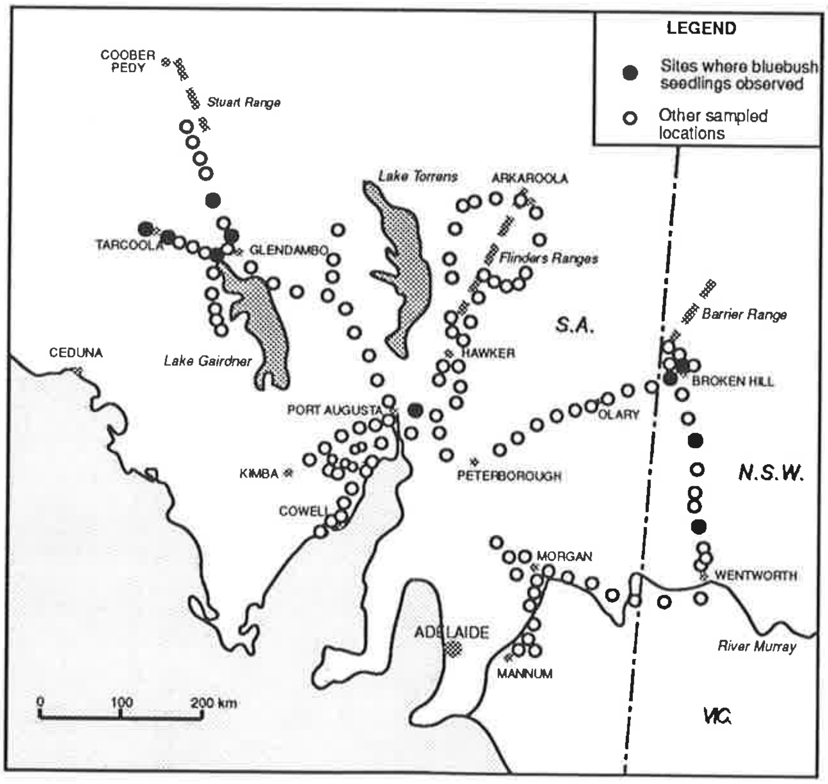


Figure 6.1: Location of seedlings observed during the broad-scale survey. Field work for this study was carried out during 1989 and 1990.

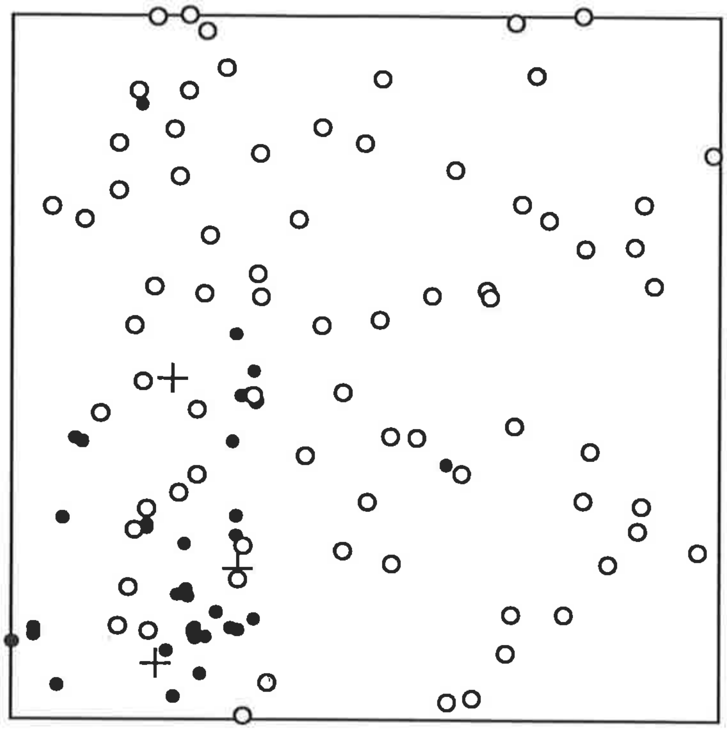
Table 6.2: Location and micro-environment description for the seedling populations observed during the broad-scale survey. Under BB refers to recruits positioned under the canopy of adult bluebush shrubs, Under 0S those under the canopy of other shrubs, while Under tree indicates seedlings under the tree canopy but not under any shrubs.

SITE	NUMBER	MICRO-ENVIRONMENT					
LOCATION	PRESENT	UNDER BB	UNDER OS	UNDER TREE	OPEN	MOUNDS	LITTER
North of Wentworth	47	18	0	22 (blackoak)	5	2	0
Wentworth-Broken Hill	9	0	0	0	5	4	0
North of Broken Hill	9	0	0	0	5	4	0
West of Broken Hill	2	0	1 (blackbush)	0	1	0	0
East of Port Augusta	3	2	0	0	0	1	0
West of Glendambo	1	0	0	0	0	1	0
East of Tarcoola	37	0	3 (saltbush)	2 (mulga)	13	3	16
West of Tarcoola	21	0	0	11 (mulga)	2	1	7
North of Glendambo	1	0	0	0	1	0	0
North of Bulgunnia	26	12	0	12 (mulga)	2	0	0
TOTALS	156	32 (20.5%)	4 (2.6%)	47 (30.1%)	34 (21.8%)	16 (10.3%)	23 (14.7%)

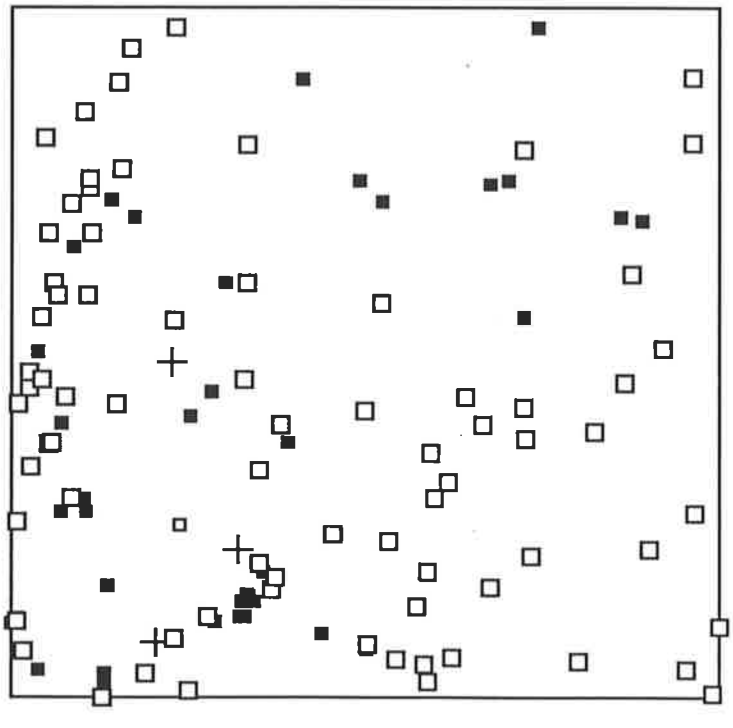
Seedling Cohorts in the Middleback Area

Spatial Distribution Patterns

The initial spatial distribution of bluebush and saltbush seedlings at each of the three sites was variable (Figures 6.2-6.4). At the Myola 2 (disturbed) and Honeymoon sites, bluebush seedlings were randomly positioned with respect to each other (Table 6.3). At the undisturbed Myola 1 site, both bluebush and saltbush seedlings were clumped when first measured in 1990, with saltbush seedlings randomly distributed the following year.

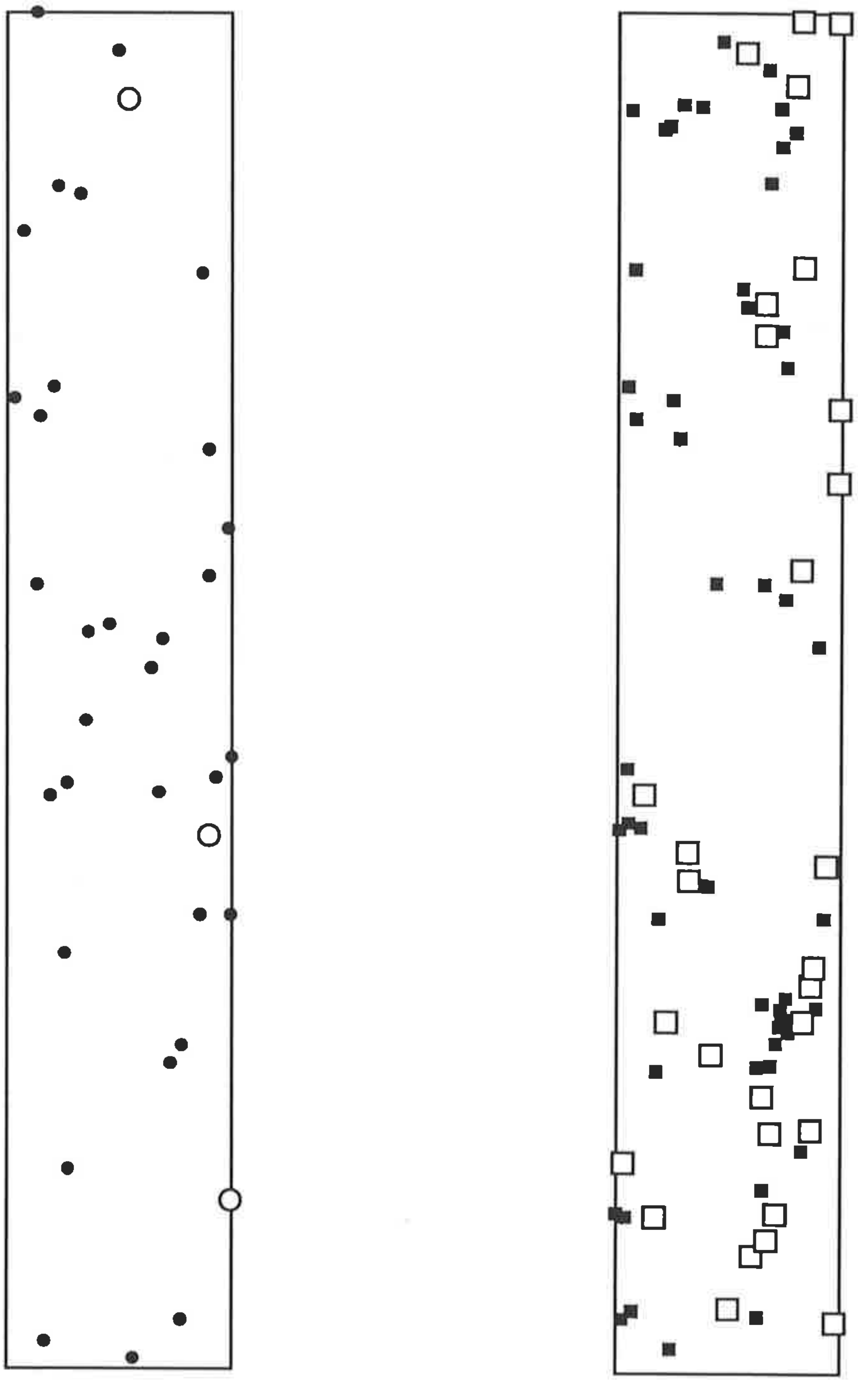


(a) Bluebush shrubs and seedlings



(b) Saltbush shrubs and seedlings

Figure 6.2: Distribution of seedlings and shrubs within the Myola 1 quadrat (20 x 20 m) in October 1990. The various shapes are coded as follows; large open shapes, adult shrubs; smaller closed shapes, seedlings and large crosses, *Acacia oswaldii* trees.



(a) Bluebush shrubs and seedlings

(b) Saltbush shrubs and seedlings

Figure 6.2: Distribution of seedlings and shrubs within the Myola 2 quadrat (12 x 2 m) in October 1990. The various shapes are coded as follows; large open shapes, adult shrubs; smaller closed shapes, seedlings.

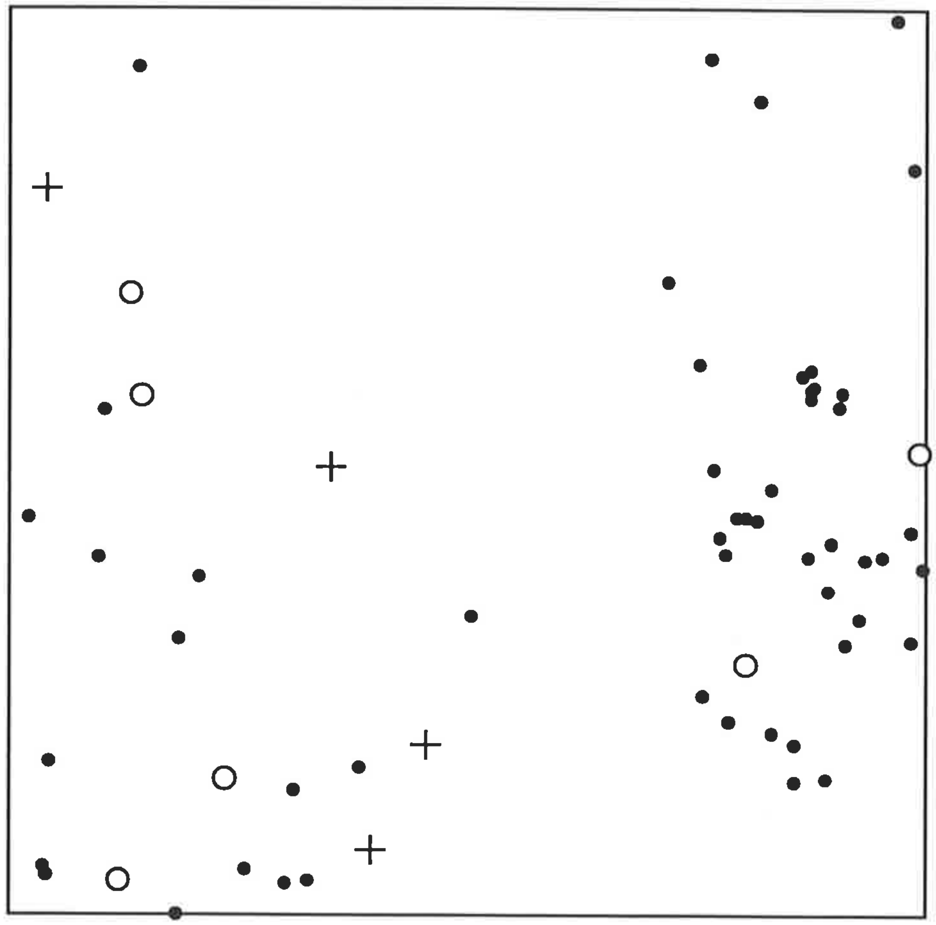


Figure 6.4: Distribution of bluebush seedlings and shrubs within the Honeymoon quadrat (16 x 16 m) in September 1990. The various shapes are coded as follows; large open shapes, adult shrubs; smaller closed shapes, seedlings and large crosses, *Lycium australe* (Australian boxthorn) shrubs.

Table 6.3: Batcheler's ratios for bluebush (BB) and saltbush (SB) adults and seedlings at each of the three seedling quadrats. Ratios were calculated using co-ordinates from each of the quadrats, with significance indicated as follows: * , $p<0.05$.

SITE	PLANTS	1990		1991	
	INCLUDED	RATIO	PATTERN	RATIO	PATTERN
Myola 1	BB Adults	0.9500	random	0.9500	random
	BB Adults & Seedlings	0.8909	random	0.8899	random
	BB Seedlings	4.2249*	clumped	5.5023*	clumped
	SB Adults	0.6705	random	0.6705	random
	SB Adults & Seedlings	0.7269	random	0.7294	random
	SB Seedlings	1.2425*	clumped	1.1553	random
Myola 2	BB Adults	-	-	-	-
	BB Adults & Seedlings	0.6344	random	0.6834	random
	BB Seedlings	0.7821	random	0.8740	random
	SB Adults	1.3172	random	1.3172	random
	SB Adults & Seedlings	1.0866	random	1.0902	random
	SB Seedlings	1.0228	random	1.0731	random
Honeymoon	BB Adults	1.6346*	clumped	1.6346*	clumped
	BB Adults & Seedlings	1.2609*	clumped	1.2593*	clumped
	BB Seedlings	1.0408	random	0.9723	random

At the Myola 1 site, further analysis demonstrated that bluebush and saltbush seedlings were not 'randomly' positioned within the quadrats with respect to other shrubs and trees (Table 6.4). Seedlings of both species were closely associated with *Acacia oswaldii* (Umbrella Wattle, Miljee), with many juveniles located under the canopy of this 3-4 m tall tree. Bluebush seedlings were also closely associated with adult shrubs, most often saltbush, and with dead bushes and vacant mounds. Bluebush recruits were also closely associated with saltbush recruits. At the disturbed Myola 2 site, contrasting patterns were observed (Table 6.5). Bluebush seedlings had not preferentially established near to adult bluebushes or saltbushes, and did not occur near to saltbush seedlings. Saltbush seedlings were found to occur near to adult saltbushes (as ratio was <1) but away from adult bluebushes (as ratio was >1). No tree species or vacant mounds/dead bushes were present in this quadrat. Analyses were carried out on the 1990 data only as low mortality rates were recorded in this quadrat between 1990 and 1991.

Table 6.4: Modified Batcheler's ratios indicating seedling pattern with respect to other plants at the Myola 1 (Undisturbed) quadrat. Ratios were calculated using the co-ordinate quadrat data and cover estimates for each plant. Ratios indicate association if less than 1, dissociation if greater than 1. Significance is determined by t-test and has been indicated as: *, 0.01<p<0.05; **, 0.001<p<0.01; ***, p<0.001.

SEEDLING SPECIES	PLANT SPECIES	1990 RATIO	1991 RATIO
Bluebush	Bluebush Adults	0.8713	1.0280
	Saltbush Adults	0.6600*	0.5243**
	Saltbush Seedlings	0.5118***	0.4667**
	Bluebush & Saltbush Adults	0.6294**	0.6798
	All Shrubs	0.6317**	0.7290
	Acacia oswaldii	0.1792***	0.3859***
	Vacant Mounds & Dead Bushes	0.3014***	0.3938**
Saltbush	Bluebush Adults	1.0268	1.0160
	Saltbush Adults	0.7602	0.7779
	Bluebush & Saltbush Adults	0.7982	0.7947
	All Shrubs	0.8367	0.8055
	Acacia oswaldii	0.5181***	0.6332**
	Vacant Mounds & Dead Bushes	0.7294	0.7603

Table 6.5: Modified Batcheler's ratios indicating seedling pattern with respect to other plants at the Myola 2 (Disturbed) site. Ratios and significance as for Table 6.4.

SEEDLING SPECIES	PLANT SPECIES	1990 RATIO
Bluebush	Bluebush Adults	0.9924
	Saltbush Adults	0.9870
	Saltbush Seedlings	0.9251
	Bluebush & Saltbush Adults	1.1551
Saltbush	Bluebush Adults	1.2094*
	Saltbush Adults	0.7199*
	Bluebush Seedlings	1.1936
	Bluebush & Saltbush Adults	0.7816

Survival Rates

Survival of seedlings in all three quadrats was reasonably high over the year of observation (Figure 6.5). As may be expected, the highest mortality occurred between the December (early summer) and April (autumn) readings when the weather was predominantly hot and dry. Over the year, bluebush seedling mortality was greater at the undisturbed site (60%) than at the disturbed site (6%) on Myola Station. In contrast, saltbush seedling survival was the same in the disturbed and undisturbed environments (76%). More than half of the seedlings survived within the Honeymoon quadrat despite heavy sheep grazing at some time during December 1990 and April 1991.

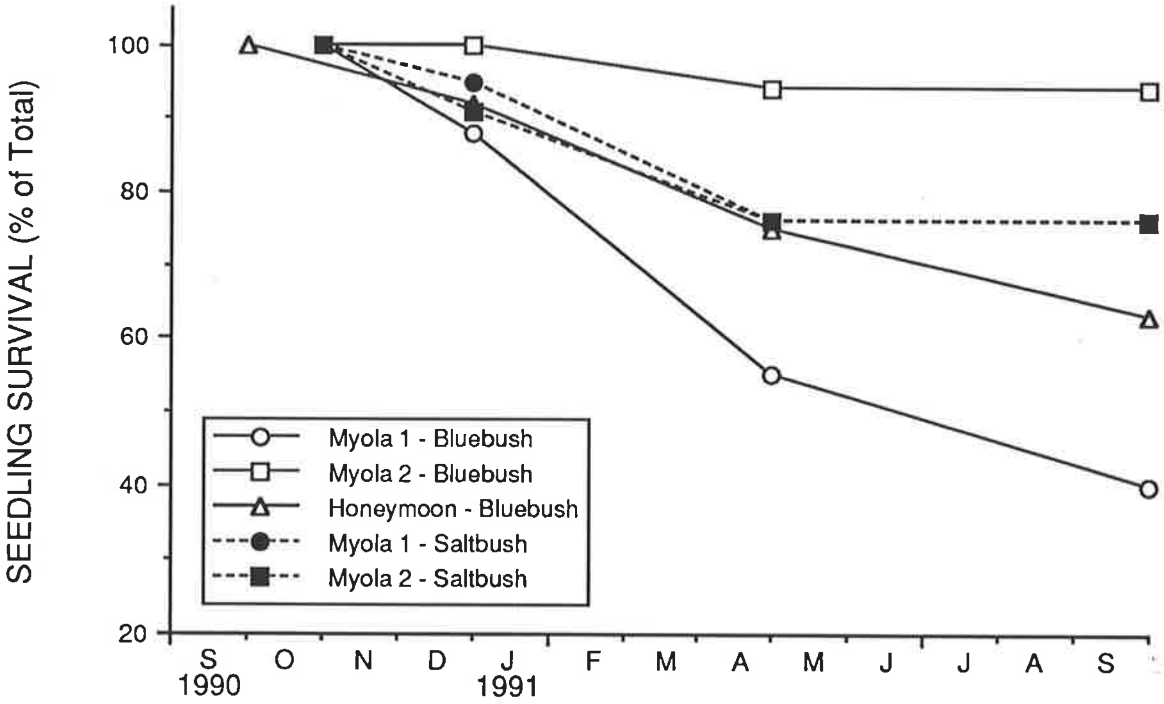


Figure 6.5: Survival rates of bluebush and saltbush seedlings at the three observed locations. The Myola 1 and Honeymoon cohorts are present in areas not subject to mechanical disturbance, while the Myola 2 cohort had previously been disturbed. The Honeymoon quadrat was grazed by sheep between December 1990 and April 1991.

The logistic regression models of bluebush seedling survival in the Myola 1 quadrat show that seedlings which are present on soil mounds (either those supporting shrubs or currently vacant) had higher survival rates (Table 6.6a). The presence of trees (in this case *Acacia* *oswaldii*), however, was also seen to be detrimental to bluebush seedling survival when neighbouring shrubs were considered in place of microtopography (Table 6.6b). In contrast, saltbush seedling mortality was not found to be influenced by any of the factors considered (*i.e.* no significant model could be constructed).

Table 6.6: Logistic regression model constructed to predict the likelihood of seedling survival from 1990 until 1991 using the variables: microtopography (on or off mounds), position with respect to trees (under canopy or in the open), position with respect to shrubs (included as a three level factor: under bluebush, under other shrubs or in the open) and initial seedling height. Significance of variables is indicated as; * $0.01<p<0.05$; **, $0.001<p<0.01$; ***,$p<0.001$.

(a) Model constructed using position on/off mounds and under/not under tree canopy, and initial seedling height as variables.

NULL MODEL 53.841 D.F. 39
FINAL MODEL 38.257 D.F. 36
DEVIANCE EXPLAINED (R^2) = 0.289***

VARIABLE	ESTIMATE	S. ERROR	RATIO	F VALUE
Constant	-0.500	1.410	-0.35	
Mounds	2.399	0.907	2.64	11.71**
Trees	-1.542	0.899	-1.72	2.84
Seedling Height	-0.076	0.217	-0.35	0.12

(b) Model constructed using position under/not under tree canopy and under/not under shrubs, and initial seedling height as variables.

NULL MODEL 53.841 D.F. 39
FINAL MODEL 45.739 D.F. 36
DEVIANCE EXPLAINED (R^2) = 0.150**

VARIABLE	ESTIMATE	S. ERROR	RATIO	F VALUE
Constant	0.740	1.200	0.62	
Trees	-2.119	0.842	-2.51	5.48*
Shrubs (1) Bluebush	0	0	0	0.48
(2) Other	0.71	1.02	0.70	
(3) Open	0.952	0.883	1.078	
Seedling Height	-0.055	0.192	-0.28	0.04

Growth Rates

Growth rates of seedlings were slow in all three quadrats (Figure 6.6). Little difference in growth of bluebush and saltbush seedlings was evident at the undisturbed Myola 1 site, where mean increases in height of 2.45 cm/year (bluebush) and 2.18 cm/year (saltbush) were recorded. The rates were slightly higher in the disturbed Myola 2 quadrat; bluebush height increased by 2.91 cm/year and saltbush height by 3.34 cm/year. In comparison, little overall increase in bluebush seedling height was recorded at the Honeymoon site (height increase of 0.03 cm/year). This lower rate is a result of sheep grazing and trampling between the December and April measurements, where the mean height of plants fell by nearly 2 cm.

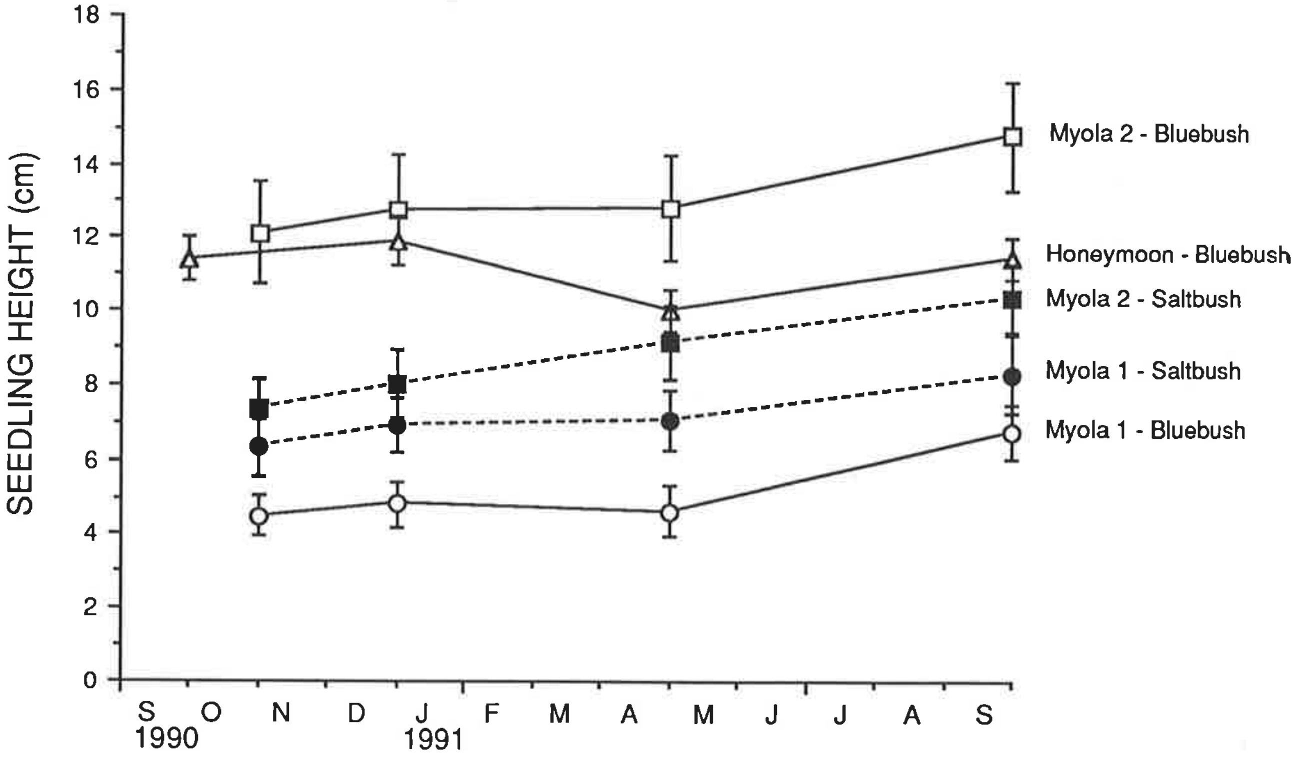


Figure 6.6: Growth rates of of bluebush and saltbush seedlings at three locations. Myola 1 and Honeymoon cohorts were present in areas not subjected to mechanical disturbance whereas the vicinity of the Myola 2 cohort had been disturbed. The Honeymoon quadrat was grazed by sheep between December 1990 and April 1991.

SEEDLING ESTABLISHMENT AFTER FIELD GERMINATION TRIALS

Survival Rates

Survival rates of seedlings which germinated during the field trial were very low, with a rapid decrease in the numbers of seedlings after 4 months and no seedling survival after 11 months. Seedling mortality did not appear to be related to climate conditions, as many of the seedlings died during the winter months when above-average rain fell. The highest survival rates were observed for seedlings on vacant mounds, particularly over the early months (Figure 6.7). Many of the seedlings contributing to these higher survival rates were found on mounds which had been manually disturbed to a depth of 5-7 cm using a garden hoe prior to the germination trial (Figure 6.8).

Growth Rates

Seedlings were observed to grow little during the study period. Most recruits obtained a height of only 1.5-2.0 cm; the maximum height of 2.5 cm was reached by a single seedling on a disturbed mound. No seedling possessed more than four leaves at any time.

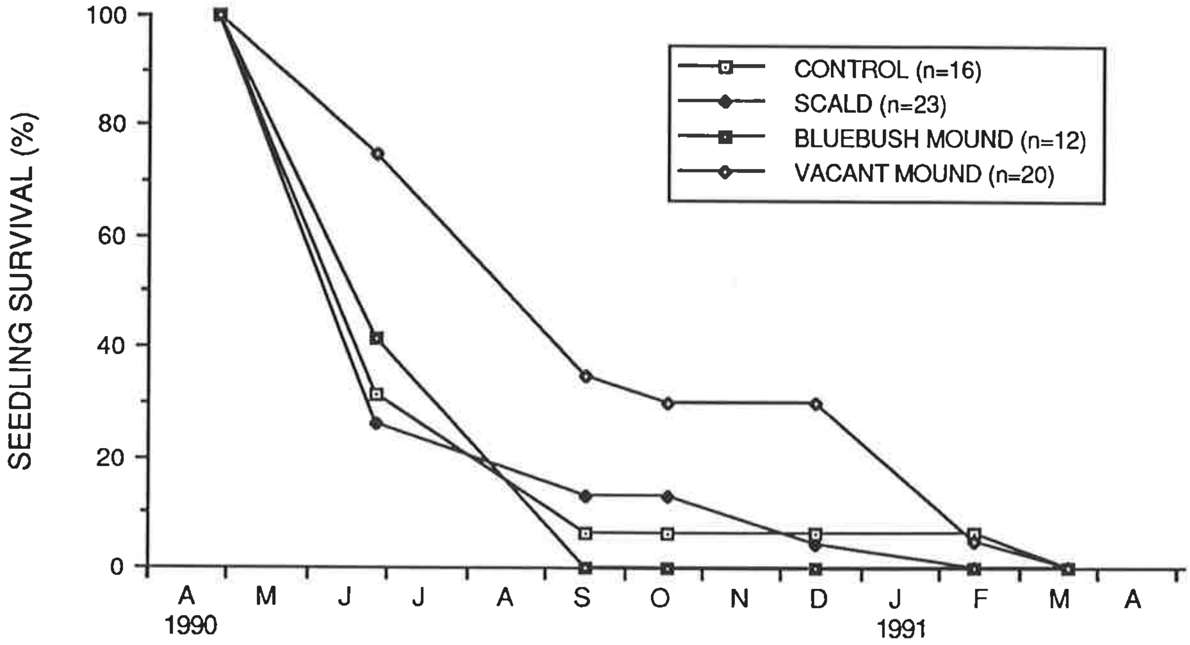


Figure 6.7: Seedling survival in four different micro-environments (see Table 5.6 for further description of each micro-environment type). The number of seedlings initially observed in each micro-environment is indicated in the legend.

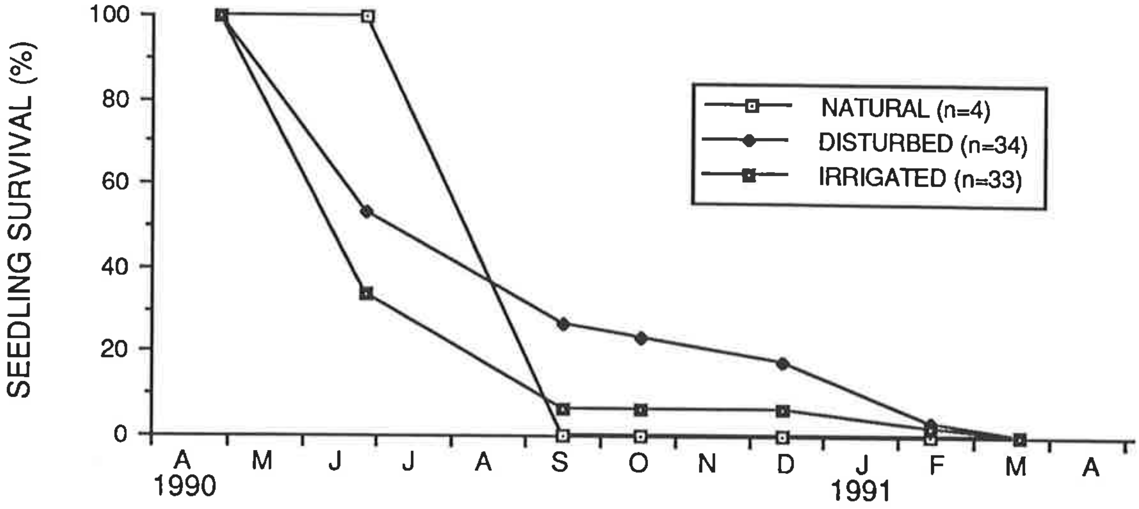


Figure 6.8: Seedling survival following soil treatments prior to and during germination. Irrigated plots received 10-20 mm of rainfall per day for 14 days, disturbed plots were manually disturbed to a depth of 5-7 cm and natural plots received no treatment. The number of seedlings initially observed for each treatment is indicated in the legend.

LABORATORY POT TRIALS

Seedling Survival

Seedling death was highest in the driest soil moisture treatment (15% soil saturation, -6.3MPa soil water potential), where less than 50% of seedlings survived over the three month period (Figure 6.9). High mortality was, however, also observed in the wettest treatment (80% saturation, -0.006 MPa). Little difference in survival was detected between the other treatments; survival rates of greater than 80% were achieved for these treatments.

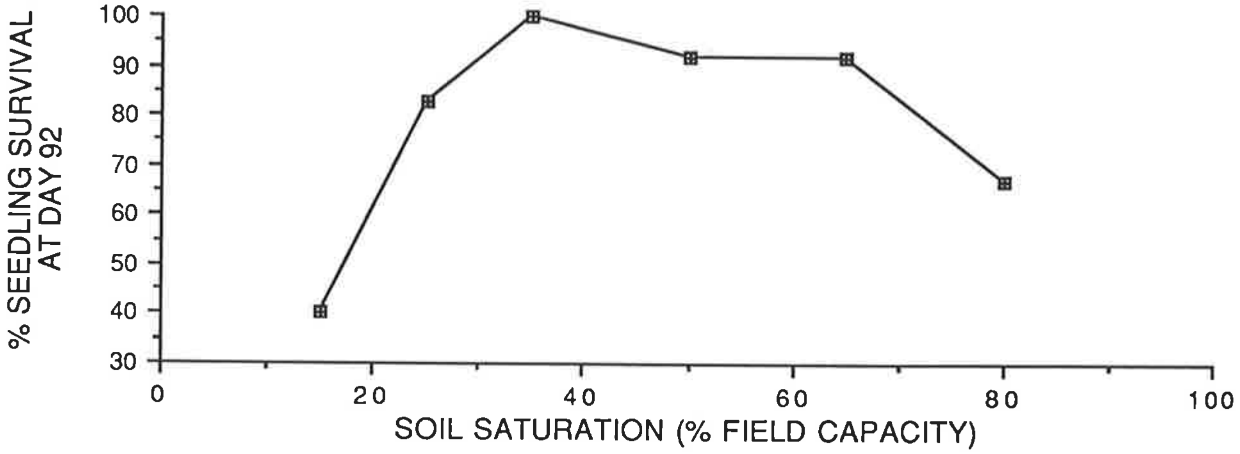


Figure 6.9: Survival of bluebush seedlings grown in pots maintained at six soil saturation levels for three months.

Seedling Growth

Differences in seedling height were reported during this trial (Table 6.7). However, clear trends relating growth to water availability were not observed (Table 6.8); there was little evidence of a bell-shaped growth response to water availability as indicated in the survival results. Final yield data revealed a detectable difference in the root:shoot ratio between treatments. In the drier pots, the root:shoot ratio was more than one (*i.e.* there was more root than shoot) while in the wetter pots the root:shoot ratio decreased to less than one.

Table 6.7: Time series analysis (repeated measures ANOVA) used to examine differences in seedling height according to soil saturation level during growth. Significance of factors is indicated as: **, $0.001<p<0.01$; ***, $p<0.001$.

VARIABLE	D.F.	M.S.	F-VALUE
BETWEEN SUBJECT EFFECTS			
Soil Saturation Level	5	2652.949	4.072**
WITHIN SUBJECT EFFECTS			
Time	11	1802.757	105.663***
Soil Saturation Level x Time	55	41.553	2.436***

Table 6.8: Final measurements of bluebush seedlings grown at six saturation levels for three months. Significance of one-way ANOVA used to detect differences between treatments is shown by the given F-value (, $0.001<p<0.01$; ***, $p<0.001$). Means followed by similar superscript letters are not significantly different at $p<0.05$ as indicated by LSD tests.**

SEEDLING	SOIL MOISTURE LEVEL (% Saturation)						F-VALUE
CHARACTER	15	25	35	50	65	80	
Height (mm)	34.0^{ab}	35.9^{ab}	42.8^{b}	27.1^{a}	30.2^{a}	42.5^{b}	3.87**
Root:Shoot Ratio	1.53^{a}	1.02^{b}	1.28^{a}	0.97^{bc}	0.77^{c}	0.84^{bc}	10.30***

DISCUSSION

BROAD-SCALE DISTRIBUTION OF SEEDLING COHORTS

Previous studies have suggested that bluebush seedlings occur only rarely (Hall *et al.*, 1964; Crisp, 1975) with successful establishment only once every 25 to 50 years (Graetz and Wilson, 1984; Wilson *et al.*, 1984a). My observations revealed a similar frequency of seedling cohorts; juveniles were reported at 17% of the survey sites where adult bluebush were present and at three locations in the Middleback region. The presence of these juveniles suggests that runs of several years of good rainfall must have occurred within the last few years (probably 5-10 years) in the vicinity of these populations. Unfortunately, the uncertainty in determining the age of each cohort, and the spatial variability in rainfall over the semi-arid and arid regions of this state, makes it virtually impossible to determine from rainfall records which particular rain events may have promoted these recruitment episodes. Thus, little information can be gained regarding the rainfall and other climate requirements for establishment. It is presumed that rare heavy rains must have fallen over several seasons to allow for adequate viable seed production, the availability of safe-sites for germination and the additional presence of favourable conditions for seedling establishment and continued growth.

Although several bluebush seedling cohorts were reported during the broadscale survey, my personal observations suggest that bluebush seedlings occur less often than seedlings of some other perennial chenopod shrub species. For example, juvenile saltbushes were reported at more than 50% of sites where saltbush adults were present, commonly occurring in extensive numbers over large areas (up to several hundred square metres). Some other less common species also appeared to show higher rates of recruitment; several seedling populations of *Maireana appressa* and *Atriplex stipitata* seedlings were recorded. The comparatively low rate of bluebush recruitment compared to other chenopod species has been reported previously (Ratcliffe, 1936; Wood, 1936; Beadle, 1948; Graetz and Wilson, 1984). These observations may indicate that the requirements for bluebush establishment are more strict than those of many other chenopod species.

SPECIFIC OBSERVATIONS OF SEEDLING POPULATIONS

General Trends

Seedling Mortality

Significant seedling mortality was observed during the experiment; many of the bluebush (and saltbush) seedlings apparently died from dehydration as a result of insufficient available soil water as has been observed for other arid-zone species (Harper, 1977; Hennessy *et al.*, 1984; Harrington, 1991). In undisturbed environments, bluebush seedling survival was generally lower than that observed for saltbush, a factor that may partially account for the commonly-acknowledged lower relative frequency of bluebush seedlings (Ratcliffe, 1936; Wood, 1936; Beadle, 1948; Graetz and Wilson, 1984). The ability to tolerate low water levels is known to be highly variable between species and may be related to above-ground tissue surface:volume ratios, root:shoot ratios and the growth rate and depth of seedling roots (Noy-Meir, 1973; Williams, 1979; Jordan and Nobel, 1981; Franco and Nobel, 1989); specific comparative tests are required to determine which of these factors are important in the drought strategies of bluebush and saltbush seedlings. It would also be interesting to contrast bluebush seedling survival rates with other arid perennial species. However, such comparisons are problematic because of a general lack of comparable published data, age differences in seedlings and the high variability in survival that would be expected due to climatic fluctuations (Gardiner, 1986; Eldridge *et al.*, 1991).

Bluebush seedling growth was slow in all field observations. Rates were well below those observed at all moisture levels during the pot experiments. Increased water loss as a result of drying winds and increased transpiration in the field (high humidities were maintained in the growth cabinets during pot trials) probably reduced growth. Growth was also slower than that recorded by Butler (1985) during revegetation trials (rates during this trial averaged 4.5-7.2 cm/year); increased water availability following soil disturbance (see below) may account for much of this difference . The similarity in the growth rates of bluebush and saltbush seedlings is somewhat surprising given the difference in survivorship demonstrated above; additional studies are required to confirm these trends and seek possible explanations. Comparisons with other species would also provide important information regarding the relative growth rates of bluebush seedlings (useful when considering species for revegetation trials and for determining possible competitive effects between seedling species). Again, this is not possible for the reasons outlined above.

Patterns in Seedling Establishment

The initial pattern of bluebush seedlings was different to that generally observed for adult shrubs. While regularity in pattern has been reported among a majority of adult populations in the area (Chapter 3), the distribution patterns of the smallest seedlings were found to be clumped, tending toward randomness. Clumping of seedlings in preferred sites is not surprising for, within a heterogeneous arid environment, only certain sites may be favourable for establishment (*i.e.* those areas providing sufficient water and other resources for recruitment, see Harper, 1977). Additionally, these clumps of juveniles may occur as a result of the non-random distribution of seeds within the environment; previous trials have shown that bluebush fruits accumulate under shrubs and amongst litter (Chapter 4).

Changes in bluebush seedling distribution patterns may be detected over time (*i.e.* following seedling deaths), although not all trends conformed to the expected change from initial clumped distributions to random patterning commonly associated with self-thinning in high density areas (Anderson *et al.*, 1969; Harper, 1977). Circumstantial evidence supports this hypothesis; in non-mechanically disturbed environments, small bluebush seedlings were significantly clumped (Myola 1 quadrat) while larger and presumably older seedlings were randomly distributed (Honeymoon quadrat). However, not all of the bluebush seedling cohorts in the mapped quadrats could be characterised by these simple pattern changes. Results showed that seedling pattern within the Myola 1 quadrat intensified (*i.e.* seedlings became more clumped) over the year of observation (1990 to 1991), while the seedlings in the disturbed Myola 2 quadrat were clearly randomly positioned within the quadrat, although individuals were small and similar in size to those in the undisturbed Myola 1 quadrat. Both of these observations contradict the hypothesis that the pattern of all bluebush seedlings change over time from clumped to random, and suggest that factors other than intraspecific competition may affect bluebush seedling pattern and survival. Environmental heterogeneity (*i.e.* patterned variation in microtopography, and water and nutrient availability) also appears to be an important influence (Anderson *et al.*, 1969; Anderson, 1970; Anderson, 1971); much of this variability may be due to the presence of trees, shrubs and soil mounds, and also soil disturbance.

Environmental Factors Influencing the Pattern, Survival and Growth of Seedlings

Shrubs and Mounds

Juvenile bluebush occurred more frequently in the vicinity of living shrubs or on mounds which were either vacant or occupied by dead shrubs than in open areas. This association has been noted previously for bluebush (Hall *et al.*, 1964) and other arid-zone species (Boyd and Brum, 1983; Fowler, 1986; Franco and Nobel, 1989; Aguiar *et al.*, 1992), and the physiological explanation for such patterning has been well-discussed in the literature. In arid ecosystems, the advantages for seedling establishment in canopy and mound environments (*c.f.* open, flat areas) are numerous; they may include increased soil moisture and nutrient availability (Evans and Young, 1970; Charley and West, 1975; Malik *et al.*, 1976; West, 1982), micro-climate amelioration through shading (Turner *et al.*, 1966; West, 1982; Franco and Nobel, 1989) and protection from grazing (Eldridge *et al.*, 1991). In this instance, it appears that bluebush seedlings are most likely favoured by the increased moisture status of the soil mounds, rather than by direct shading effects of neighbouring plants; evidence from both the pattern analysis and logistic regression models predicting survival supports this hypothesis. I also believe, however, that at least some of bluebush seedling pattern may be a consequence of seed dispersal patterns (in addition to the availability of favourable sites for seedling establishment). Bluebush fruit dispersal is not random - fruit commonly accumulates amongst surface litter and around the bases of nearby shrubs (see Chapter 4) - while germination rates are similar in all these environments (Chapter 5). As more seed would be present in these areas to begin with, it is logical to assume there may be a increased likelihood of seedling establishment in this environment. Finally, it is interesting to note that although similar relationships between saltbush seedlings and shrubs/mounds has been reported on a number of previous occasions (Anderson, 1967; Williams *et al.*, 1978; Eldridge *et al.*, 1991), data collected here did not confirm this hypothesis.

Bluebush seedlings (and also saltbush seedlings) were not generally found near to adult bluebush shrubs in the Myola 1 quadrat. Although this may be a somewhat surprising finding in light of the above, at least two hypothesis can be provided in explanation. Firstly, the decreased occurrence of bluebush seedlings may be caused through root competition with adult bluebushes; Hall *et al.*(1964) claimed that seedlings which were located at the base of adult plants near the concentrated vigorous root systems were at a severe disadvantage and usually died. Such a scenario does not seem appropriate here, however, as seedlings located around the base of all plants, particularly the shallow-rooted saltbush, would be similarly affected. A more likely explanation in this case implicates the influence of bush morphology. In the vicinity of the Myola 1 quadrat, many of the bluebush plants were large, with heavy procumbent branches that lay for quite a distance on the soil surface. It is possible that these branches provided an environment unsuitable for seedling establishment because of reduced light levels and the increased probability of physical seedling damage by the branches themselves. Furthermore, this hypothesis still allows for bluebush seedling establishment under adult shrubs of a more upright growth habit, such as saltbush and erect bluebushes. An examination of the growth morphology data for bluebushes with seedlings under the canopy (*i.e.* the three sites in the broadscale survey) revealed shrubs which were smaller than those at Myola and more upright in shape.

Trees

The role of trees in the establishment, survival and growth of bluebush seedlings is not clear from observations made during this study. Initial observations suggested that tree canopies provide a favourable micro-environment for establishment; nearly one third of bluebush seedlings encountered during the broadscale survey were positioned under mulga (*Acacia aneura*) and blackoak (*Casuarina cristata*) trees whilst 73% of juveniles at the undisturbed Myola 1 site were found under the canopies of *Acacia oswaldii* trees. Although this observation has not previously been documented for bluebush, it is not unexpected as the tree canopy environment may offer similar advantages for seedling establishment to that of neighbouring shrubs and mounds. Nonetheless, it seems reasonable to suggest that bluebush recruitment is not dependent on the availability of these micro-sites under trees, as trees are generally sparse to non-existent in most bluebush communities.

Further observations indicated that more of the bluebush seedlings located under tree canopies subsequently perished over the year of recordings. While it is possible that competition from the *Acacia oswaldii* trees may have reduced seedling survival at this site, it is also possible that the mortality of seedlings may be related to the relative size and distribution of shrubs and mounds under trees and out in the open. More specific analyses, perhaps using root exclusion tubes similar to those employed to test for seedling-shrub competition by Reichenberger and Pyke (1990), would be required to confirm this hypothesis.

Soil Disturbance

Following mechanical soil disturbance, bluebush seedling patterns were random, with no preference for locations near to neighbouring adult shrubs. This 'lack' of pattern suggests that disturbance of the soil has increased the availability of sites suitable for seedling establishment. More specifically, disturbance may have led to increased accumulation of water and infiltration (Hall *et al.*, 1964; Dean and Milton, 1991) and also increased nutrient availability (Chambers *et al.*, 1990) across the whole quadrat; as a consequence, the advantages previously conferred by neighbouring mounds (and shrubs) would no longer be apply and establishment should be equally likely throughout the quadrat.

Soil disturbance also increased bluebush seedling survival and subsequent growth, primarily through increasing water availability (by reduced runoff and greater infiltration) and enhancing root development (through soil break-up). Williams (1979) proposed that this latter factor played a particularly important role in the successful establishment of seedlings in the Australian arid-zone. He suggested that seedlings with rapid root development would be more likely to survive and develop as less time would lapse before roots had reached the lower soil layers where more moisture is available. Given this information, it is interesting that soil disturbance did not increase saltbush seedling survivorship at the Myola 2 site. However, this trend may indicate that saltbush seedlings are generally more resilient than bluebush seedlings and are able persist in less favourable conditions (*i.e.* in undisturbed environments).

Grazing

The effects of grazing on bluebush seedlings could not be accurately determined from this study for two main reasons. Firstly, although the Honeymoon population was noticeably grazed by sheep, comparisons with Myola cohorts (considered to be ungrazed due to the lack of sheep egesta) were difficult as they were located some distance away (over 30 km) and also appeared to be younger in age. Secondly, the grazing history of the Honeymoon site was not accurately recorded. The only conclusion that may be drawn is that the presence of sheep led to the detected decrease in seedling height; insufficient data were collected to ascertain any effects on seedling survival.

ECOLOGICAL IMPLICATIONS

Although bluebush recruitment is fundamentally dependent on rare and unpredictable climatic events (*i.e.* runs of years of heavy rainfall), it is also influenced by other 'environmental' factors. The following guidelines indicate ways in which I believe the establishment and survival of bluebush seedlings may be enhanced (given the appropriate climatic conditions). In existing bluebush communities, it is important that the microsites most favourable for establishment are retained; in particular, the integrity of soil mounds (either supporting live and dead shrubs or vacant) should be preserved. This may best be achieved by conservative stocking regimes; heavy livestock grazing may damage the soil surface structure directly by soil compaction and surface pulverization (this may reduce microtopography and lead to the formation of soil crusts), or indirectly by decreasing plant density and therefore increasing the likelihood of wind and water erosion (Marshall, 1974; Johns *et al.*, 1984). In some areas, the presence of trees and surface litter may also encourage bluebush seedling recruitment by providing a suitable environment for germination and protection of seedlings. This hypothesis, however, requires further testing. Of course, the maintenance of healthy, mature bluebushes is also necessary to ensure a good supply of viable seed; shrubs should be in the near vicinity as fruit dispersal is generally restricted to a few metres from the parent plant (Chapter 4). Once seedlings are present, a substantial period of time (at least 5-10 years) must be allowed for seedlings to become fully established and tolerant of climatic extremes and grazing pressures. In degraded environments, the best chance for bluebush recruitment relies on mechanical soil disturbance to enhance soil water availability and root growth. In these regions an external supply of seed would also be required.

However, it seems reasonable to hypothesize that bluebush recruitment rates fluctuate in response to shrub loss; the sites left vacant by bush death appear to offer the best environment for the continued survival and growth of young bluebush juveniles. These 'vacant soil mounds' provide a good site for initial establishment (due to the increased water availability of the mound) and also for continued growth (here competition from neighbouring adult bluebushes would be expected to be less than at other locations). I believe that recruitment follows a pattern similar to that which has been suggested for other arid shrub species, where the death of adults shrubs creates windows of opportunity for the recruitment of juveniles. As Gutterman and Agami (1987) state: "Only once in several years is there mass germination which fills in the gaps left by individuals that have not survived".

FURTHER WORK

Much of the work discussed in this chapter describes a short-term picture of bluebush seedling establishment. Although I was quite fortunate to locate the three seedling cohorts on

Middleback station, and those on the broadscale survey, the unknown age of each cohort and the variation in disturbance history have made comparisons and generalisations difficult. Furthermore, the single year of observations has made it impossible to test the applicability of these generalisations, particularly in relation to seeding survival and growth; previous seedling studies have shown that establishment, survival and growth patterns are highly variable between years, cohorts and species (Fowler, 1988; Eldridge *et al.*, 1991). Other studies are certainly required to confirm the tentative trends that have been suggested here. In particular, studies examining very early establishment characteristics (0-12 weeks) and long-term seedling growth and survival (1-25 years) would certainly help to fill gaps in current knowledge. Further investigations into the spatial patterns of bluebush seedlings, and the influence of mounds, shrubs and trees on seedling growth and survival are crucial, especially in regard to seedling-shrub/tree competition. The rare and erratic occurrence of bluebush cohorts will, however, make these studies difficult to accomplish.

CONCLUSIONS

- Although several cohorts of bluebush seedlings were seen, they appeared to occur less frequently than seedlings of other perennial chenopod shrub species, particularly saltbush.

- Mortality rates of bluebush seedlings were higher than those observed for saltbush seedlings, implying that bluebush may be less tolerant to low levels of water availability. Growth rates of bluebush and saltbush seedlings were similar.

- Bluebush seedlings were initially clumped to random in distribution. Subsequent seedling mortality led to variable spatial patterns rather than the expected change from clumped to random distributions; much of this variation appeared a result of environmental heterogeneity.

- Seedlings were more frequently located near to living shrubs and mounds (*c.f.* open, flat areas), possibly because of the increased water availability associated with mounds.

- The influence of trees on seedling establishment was not clear; initial observations suggested trees provide a favourable microenvironment while later studies revealed higher mortalities under tree canopies. Likewise, the influence of grazing could not be accurately determined.

- Further studies of bluebush seedling establishment are required to confirm the trends suggested here.

CHAPTER 7

CONCLUDING DISCUSSION

INTRODUCTION

The pearl bluebush, *Maireana sedifolia*, is a key species in the Australian rangelands, covering the largest area of any of the perennial chenopod shrubs (Leigh, 1972). Although it is a widespread and well-known species, little information has previously been documented regarding its basic biology and population dynamics. As has been pointed out by several prominent researchers (Walker, 1988; Westoby *et al.*, 1989; Call and Roundy, 1991; Provenza, 1991), such information is crucial to the development of appropriate programs which ensure the maintenance of viable and productive plant communities. This study has provided details of the autecology of the bluebush which can be utilised by researchers and pastoralists in the construction of future management regimes.

REVIEW OF STUDY

This study encompassed many aspects of autecology of bluebush. As these have been discussed in detail in the preceding chapters, they will only be briefly reviewed here. Summaries have been included under the auspices of the three main research areas: broad-scale distribution patterns, small-scale spatial patterns and recruitment characteristics.

BROAD-SCALE DISTRIBUTION PATTERNS

As with many of the Australian chenopod shrubs (Eldridge, 1988), the distribution of bluebush is controlled by soil water availability (Chapter 2). Its presence is linked not only to rainfall, but also to soil texture and related features. It is the predominant chenopod species on soils containing calcium carbonate (limestone) either as a layer or as nodules; it appears to dominate in these areas because it possesses deep tap-roots which can penetrate through the calcium carbonate to obtain water stored deeper in the soil profile (*c.f.* saltbush which has shallow roots which do not penetrate limestone). Similarly, it dominates on lighter-textured soil where a majority of the water is maintained deep in the soil profile and is therefore unavailable to shallow-rooted species. Increases in bluebush density and individual shrub size are also associated with increased soil water availability as seen by correlations with rainfall. At sites where a limestone layer was present, bluebush shrubs are smaller and less dense implying a tolerance of limestone rather than a resource requirement.

Bluebush is a major component of many vegetation communities, occurring with western myall (*Acacia papyrocarpa*), mulga (*Acacia aneura)*, mallee (*Eucalyptus* spp.), blackbush (*Maireana pyramidata*) and in almost monospecific stands. These delineated communities, as well as others not containing bluebush, result from differences in soil water availability along a rainfall/soil texture gradient which has been modified by factors including presence of a limestone layer, soil depth, pH and elevation.

SMALL-SCALE DISTRIBUTION PATTERNS

Individual bluebush shrubs are predominantly regular in distribution, with random patterns occurring only when bluebush is a less dominant species in the plant community or when the immediate environment is highly spatially heterogeneous (Chapter 3). The size of each bluebush is also correlated to the distance to neighbouring shrubs, further suggesting the presence of competition and density-dependent bluebush growth; bluebush possessing larger "available areas" for potential resource acquisition (*i.e.* those in less-dense stands) are generally larger in cover and volume than those with smaller available areas (*i.e.* those in dense stands). Although these patterns arise primarily as a result of intraspecific competition for soil water over the summer months (as directly demonstrated by neighbour removal experiments), the extent of competition appears to be variable both within and between years. The lack of detected interspecific competition may indicate that successful niche separation processes have evolved between bluebush and other common shrub species (Fowler, 1986).

RECRUITMENT CHARACTERISTICS

Importance of Episodic Events

Episodic climatic events are very important components in the life-histories of many semi-arid and arid plant species (Noble, 1979; Harrington *et al.*, 1984a). Likewise, these events are crucial in the recruitment of bluebush. Flowering, fruiting, germination and seedling establishment are all primarily influenced by soil water availability (which is mainly attributable to rainfall), with a successful progression from the production of sufficient viable seed to germination and then to establishment of juveniles only possible following several seasons of increased soil moisture (Chapters 4-6). These runs of good years occur infrequently and erratically, leading to recruitment phases which are well-appreciated to be rare (Osborn *et al.*, 1935; Ratcliffe, 1936; Wood, 1936; Jessup, 1951; Graetz and Wilson, 1984).

Other Factors of Influence

In addition to this fundamental dependence on rare and unpredictable climatic events, bluebush recruitment is clearly influenced by other biotic and abiotic factors (Chapters 4-6). Of these, soil disturbance has the most positive effect. The availability of safe-sites for germination, establishment and growth is increased following disturbance, primarily because of improved seed:soil contact, and enhanced water availability and root development.

The presence, pattern and size of adult shrubs (bluebush and other species) is also important in the recruitment patterns of bluebush. Firstly, the size of individual bluebush shrubs may affect the supply of viable seed; larger shrubs within populations are more likely to flower. Secondly, the distribution of these shrubs influences fruit dispersal patterns as fruit are rarely dispersed more than 5 m from the parent plant and often accumulate around the base of shrubs. Additionally, shrubs and associated soil mounds may provide more favourable environments for early seedling establishment and survival because of the increased soil moisture of the soil mounds. The longer-term (competitive) effects of neighbouring shrubs may also be important; however the short term nature of this study prevented further investigation.

Three other factors considered in this study appear to be influential at various stages of bluebush reproduction:

(i) the number of fruit dispersed may be decreased through predation by ants - this loss, however, is unlikely to have a large influence in climatically-favourable years when fruit production is high;

(ii) the presence of litter on the soil surface may alter the pattern of fruit dispersal and hence seedling establishment - fruit commonly becomes lodged amongst twigs and fallen tree branches; and

(iii) herbivores, although not examined in detail during this study, may possibly increase the availability of safe-sites for germination by trampling and disturbing the soil surface, thereby increasing seed:soil contact. Later, stock may have a detrimental effect on the survival and growth of seedlings through both grazing and trampling.

MANAGEMENT STRATEGIES

The management of rangeland areas may be considered to be a "complex optimization process" which should concentrate on improving the establishment of desirable species (Walker, 1988). In bluebush communities, shrub loss is not accompanied by the emergence of robust and reliable grasslands, as has been reported for the Riverine Plain (see Moore, 1952). Instead, loss has been associated with wind-drift of soils, the invasion of undesirable species and the loss of sustainable carrying capacity (Jessup, 1948; Lange *et al.*, 1984). Therefore, the fundamental aim of management in bluebush communities must be to retain the chenopod shrub cover by maximising the survival of mature plants and maintaining seedling recruitment levels.

Are bluebush populations surviving under current management regimes?

It is very difficult to foretell the continued persistence of the bluebush populations examined during this study. Despite many populations including juveniles (17% of those bluebush locations visited), it is not known whether the observed rates of recruitment are sufficient to maintain population numbers, primarily because both the long-term survival of seedlings and the rate of adult shrub mortality vary with climatic conditions, grazing and disturbance. However, using previously reported levels of adult bluebush mortality, it is possible to speculate as to whether bluebush recruitment does occur at rates similar to those of bush death. Crisp (1975) estimated adult bluebush mortality rates in ungrazed areas to be in the vicinity of 0.35% per year and up to 1.85% per year under intermittent grazing (Koonamore Vegetation Reserve data, averages over the period 1931-1972). So, with a once in twenty years recruitment pattern, an average of around 7% of the shrubs (and up to 37% in the grazed areas) would need replacing by juveniles at each establishment event to maintain the number of shrubs in the population. While these numbers are high, observations carried out during this study reveal that bluebush seedling inputs of this magnitude do occur; at four of the ten sites where seedlings were recorded, they composed over 25% of the population. Such results may indicate, therefore, that sufficient recruitment is occurring at some locations to maintain population numbers; in contrast, the results may also suggest that other populations are in decline. More specific predictions regarding the current status of bluebush populations would only be possible if adult mortality and juvenile survival rates were known for particular regions.

What management strategies could be adopted to ensure the continued existence of healthy bluebush populations, particularly in grazed areas?

Climate is the over-riding control of bluebush recruitment (and that of many other chenopod shrub species) and hence, in nearly all years, little can be done to directly increase bluebush seedling recruitment. In these normal years, however, there is a need to protect mature shrubs from over-grazing; this would not only enhance the survival of existing plants, but also ensure that fitness is maintained for flowering and subsequent seed production when the climatic conditions are suitable. During these times it is also necessary to maintain the integrity of soil mounds as these sites to provide favourable micro-environments for the initial establishment of seedlings and also help to trap seeds. Likewise, fallen dead trees and other litter should not be removed from the soil surface as these may also help to encourage establishment by trapping seed and providing a favourable environment for seedlings. In some degraded areas, soil disturbance may be needed for seed germination and subsequent seedling establishment; however, the cost of such rehabilitation work must be recoverable by increases in stock production.

Following periods of recruitment (*i.e.* seasons of good rainfall), the opportunistic spelling of paddocks (Graetz and Wilson, 1984) may enhance the continued growth and survival of bluebush seedlings. However, few pastoralists (particularly those running small holdings) would be able to consider this a viable option at a paddock-scale. Alternative strategies may be to reduce stock numbers in paddocks where recruitment has occurred, and possibly fence-off small sections of paddocks to allow establishment in well-used areas.

What appears to be the value of bluebush in the reclamation of degraded land?

Bluebush is a species which has only limited application in revegetation programs. Although it has been shown to respond favourably during trials (*e.g* contour furrowing study; Butler, 1985), its usefulness may be less than that of other perennial chenopod species because of:

(i) A more specific requirement for co-occurring high rainfall events for seed production, germination and seedling establishment (more so than other chenopod shrub species such as saltbush). In most years little viable seed will be available and insufficient rain will fall for germination and seedling establishment.

(ii) Restricted seed dispersal patterns from existing plants. This may prevent recruitment in areas away from the immediate vicinity of established bluebush shrubs.

(iii) Slow growth rates. Seedlings may require many years of careful maintenance before they are fully established and able to tolerate drought and grazing pressure.

In addition, soil disturbance which would help to trap seed, improve seed:soil contact and increase water availability is almost certainly required before high seedling establishment rates could be expected.

Nonetheless, bluebush does show some characteristics which may favour its use in revegetation trials under some circumstances. Firstly, it is a long-lived species which, once established, will persist for a long time unless disturbed. It is also drought-tolerant, able to persist (once established) in areas which other chenopods may find too arid. In particular bluebush possesses a competitive advantage over many other common chenopod shrubs on soils where a limestone layer is present because of its deep and extensive root system. Being less palatable to sheep than many other chenopods shrubs, it use may be considered in the revegetation of degraded areas around water points and other well-used areas (fencing off would be required during initial establishment). Finally, the attractive and characteristic blue appearance of this species may also encourage its use for purely aesthetic reasons.

DIRECTIONS FOR FUTURE RESEARCH

This study represents a short-term "snap-shot" examination of a long-lived plant species existing in a system which is erratic, unpredictable and subject to forces of disturbance and long-term ecological change. Consequently, the observations and hypotheses that have been reported and suggested here may not necessarily represent consistent and regular trends (Fowler, 1986; Eldridge *et al.*, 1991) nor can they be expected to encompass all aspects of bluebush behaviour. Further research is still required to confirm many of the stated hypotheses and ascertain variability and potential uses in predictive applications.

Particular areas requiring additional investigation have been suggested at the end of individual results chapters; they include aspects such as the patterns of flowering and seedling establishment, and the extent and timing of intra- and inter-specific competition.

Similarly, there are several long-term studies that could be undertaken to increase our understanding of bluebush biology. These include quantitative examinations of the soil moisture (rainfall) levels required for flowering and the abiotic and biotic factors influencing the quantity and quality of seed production. Studies of seedling recruitment emphasizing how both short and longer-term (up to 25 years) establishment patterns are influenced by climate, grazing and competition with neighbouring plants (both bluebush and other species) would also be useful, particularly if strategies likely to increase seedling growth and survival could be developed. Likewise, a more detailed knowledge of the influences of similar factors on adult growth may also help to maximizing the survival of mature plants and enhance the continued existence of bluebush populations.

For comparative purposes, it would also be interesting to investigate the physiological and morphological differences between bluebush and other morphologically-similar *Maireana* species such as the little-studied low bluebush (*M. astrotricha*) and blackbush (*M. pyramidata*). A combination of laboratory (pot) and field experiments could be used to more accurately determine tolerances and competitive abilities of each species (*i.e.* potential and realised niches) and the life-stages at which selective pressures may operate.

Although not included in this study, I believe that the effect of fire on bluebush population dynamics also warrants further investigation. Earlier studies have suggested that wildfires may have a significant effect in this vegetation type (so much so that Hodgkinson *et al.* (1984) suggests a fire exclusion policy), although they only occur in rare years when high levels of herbage have been produced following heavy rainfalls (generally wildfires do not occur because of low herbage levels, often due to the pressure of domestic stock, and the low intrinsic flammability of the chenopods). As a consequence of fire, it has been suggested that adult bluebush populations may be thinned out and post-fire regeneration may be significantly retarded (Lay, 1976; Graetz and Wilson, 1984; Hodgkinson *et al.*, 1984). Little quantitative evidence has been presented to confirm these trends; more research examining the more specific consequences of fire on bluebush populations needs to be undertaken, particularly concentrating on shrub mortality following fire, the patterns of seedling recruitment and the impact of grazing on regenerating areas.

Ultimately, however, the biggest challenge following this study is to further incorporate the information gained through the short-term experimentation and observations of bluebush into an appreciation of the processes operating at greater spatial and temporal scales (Provenza, 1991; S. Archer, pers. comm.). This knowledge would lead to an improved understanding of the structure and function of semi-arid chenopod shrub communities and would enhance the ability of pastoralists and other land managers to anticipate future change. As consequence, desirable transitions could be maximised during the infrequent "windows of opportunity" that occur in these environments, while undesirable changes could be prevented or avoided.

APPENDIX 1: SPECIES LIST FOR BROADSCALE SURVEY

AIZOACEAE
Mesembryanthemum sp.

AMARANTHACEAE
Ptilotus obovatus

APOCYNACEAE
Alyxia buxifolia

BORAGINACEAE
Halgania andromedifolia

CASUARINACEAE
Casuarina cristata

CHENOPODIACEAE
Atriplex acutibractea
Atriplex nummularia
Atriplex pseudocampanulata
Atriplex stipitata
Atriplex vesicaria
Chenopodium curvispicatum
Chenopodium desertorum
Chenopodium nitrariaceum
Dissocarpus biflorus
Dissocarpus paradoxa
Einadia nutans
Enchylaena tomentosa
Eriochiton sclerolaenoides
Maireana aphylla
Maireana appressa
Maireana astrotricha
Maireana brevifolia
Maireana erioclada
Maireana georgeii
Maireana pentatropis
Maireana pyramidata
Maireana radiata
Maireana sedifolia
Maireana turbinata
Rhagodia crassifolia
Rhagodia parabolica
Rhagodia spinescens
Rhagodia ulicina
Salsola kali
Sclerochlamys brachyptera
Sclerolaena diacantha
Sclerolaena divaricata
Sclerolaena intricata
Sclerolaena lanicuspis
Sclerolaena limbata
Sclerolaena obliquicuspis
Sclerolaena patenticuspis
Sclerolaena tricuspis
Sclerolaena uniflora

COMPOSITAE
Cassinia arcuata
Cassinia laevis
Cratystylis conocephala
Olearia calcarea
Olearia decurrens
Olearia muelleri
Olearia pimeliodies

CONVULVULACEAE
Convulvulus erubescens

CRUCIFERAE
Carrichtera annua
Lepidium leptopetalum

CUPRESSACEAE
Callitris columellaris

EUPHORBIACEAE
Beyeria lechnaultii
Beyeria opaca

GOODENIACEAE
Scaevola spinescens

GRAMINAE
Aristida contorta
Avena sp.
Danthonia caespitosa
Enneapogon avenaceus
Eragrostis sp.
Hordeum leporinum
Stipa elegantissima
Stipa nitida
Stipa petraea
Triodia irritans

LABIATAE
Westringia rigida
Prostanthera striatiflora

LAMIACEAE
Marrubium vulgare

LEGUMINOSAE
Acacia aneura
Acacia calamifolia
Acacia continua
Acacia jennerae
Acacia ligulata
Acacia notabilis
Acacia papyrocarpa
Acacia paradoxa
Acacia sclerophylla
Acacia sp.
Acacia tetragonophylla
Acacia victoriae
Cassia arcuata
Cassia artemisioides
Cassia nemophila var coriaceas
Cassia nemophila var nemophila
Cassia nemophila var platypoda
Cassia phyllodinea
Cassia sp. (?)
Cassia pruinosa

LILIACEAE
Asphodelus fistulosus
Dianella revoluta
Lomandra effusa

MALVACEAE
Abutilon otocarpum/calliphyllum
Selenothamnus squamatus
Sida ammophila
Sida calyxhymenia
Sida corrugata

MYOPORACEAE
Eremophila alternifolia
Eremophila desertii
Eremophila duttonii
Eremophila freelingii
Eremophila glabra
Eremophila oppositifolia
Eremophila scoparia
Eremophila sturtii
Myoporum parvifolium
Myoporum platycarpum

MYRTACEAE
Eucalyptus brachycalyx
Eucalyptus camaldulensis
Eucalyptus gillii
Eucalyptus gracilis
Eucalyptus intertexta
Eucalyptus largiflorens
Eucalyptus odorata
Eucalyptus oleosa
Eucalyptus porosa
Eucalyptus socialis
Melaleuca lanceolata

PITTOSPORACEAE
Pittosporum phylliraeoides

PROTEACEAE
Grevillea huegelii
Hakea eyreana/ednieana
Hakea francisiana
Hakea leucoptera

RUTACEAE
Geijera linearifolia
Microcybe multiflora

SANTALACEAE
Exocarpos aphyllus
Santalum acuminatum
Santalum murrayanum

SAPINDACEAE
Dodonaea bauerii
Dodonaea bursarifolia
Dodonaea lobulata
Dodonaea microzyga
Dodonaea viscosa var angustissima
Heterodendrum oleifolium

SOLANACEAE
Lycium australe
Lycium ferocissium
Solanum ellipticum
Solanum petrophilum

ZYGOPHYLLACEAE
Zygophyllum ammophilum
Zygophyllum apiculatum
Zygophyllum aurantiacum

APPENDIX 2: DESCRIPTION OF PERMANENT QUADRATS

FIELD CENTRE SITE

SITE DESCRIPTION: Gentle slope (<1.5°) with an easterly aspect. Area excluded from herbivore (sheep, kangaroos and rabbits) grazing.

COMMON PLANT SPECIES PRESENT:

OVERSTOREY: Scattered western myall (*Acacia papyrocarpa*) and punty bush (*Cassia nemophila var coriacea*)

UNDERSTOREY: Bluebush (*Maireana sedifolia*), *Rhagodia ulicina* and occasional dense patches of Ward's weed (*Carrichtera annua*)

SOILS AND SURFACE FEATURES: Orange-brown desert clay-loam (pH=8.5) with sheet limestone at 50 cm depth. Cryptogamic crust between shrubs, some pebbles on the soil surface.

Plate 3: Field Centre site (looking southwards)

TWO-MILE SITE

SITE DESCRIPTION: Relatively flat wash (run-on) area. Open to herbivore (sheep, kangaroos and rabbits) grazing and close to watering point (<100 m).

COMMON PLANT SPECIES PRESENT:

OVERSTOREY: Scattered western myall (*Acacia papyrocarpa*)

UNDERSTOREY: Blackbush (*Maireana pyramidata*), bluebush (*M.sedifolia*) and occasional patches of Ward's weed (*C. annua*)

SOILS AND SURFACE FEATURES: Orange-brown desert sandy-clay-loam (pH=8.3) with sheet limestone at 40 cm depth. Cryptogamic crust between some shrubs, some pebbles on the soil surface.

Plate 4: Two-Mile site (looking southwards)

PURPUNDA SITE

SITE DESCRIPTION: Gently sloping (1°) plain with easterly aspect. Open to herbivore (sheep, kangaroos and rabbits) grazing.

COMMON PLANT SPECIES PRESENT:

OVERSTOREY: None in the near vicinity

UNDERSTOREY: Bluebush (*M. sedifolia*), saltbush (*Atriplex vesicaria*) and *Maireana turbinata*

SOILS AND SURFACE FEATURES: Orange-brown desert clay-loam (pH=8.4) with sheet limestone at 45 cm depth. Cryptogamic crust between most shrubs, some pebbles on the soil surface.

Plate 5: Purpunda site (looking north-easterly)

NORTH-EAST OVERLAND SITE

SITE DESCRIPTION: Gentle slope (2°) with south-easterly aspect. Open to herbivore (sheep, kangaroos and rabbits) grazing.

COMMON PLANT SPECIES PRESENT:

OVERSTOREY: Bullock bush (*Heterodendrum oleifolium*) grove in the near vicinity

UNDERSTOREY: Bluebush (*M. sedifolia*), saltbush (*A. vesicaria*) and silver mulla mulla (*Ptilotus obovatus*)

SOILS AND SURFACE FEATURES: Orange-brown desert clay-loam (pH=7.8) with sheet limestone at 25 cm depth. Cryptogamic crust between most shrubs, some pebbles on the soil surface.

Plate 6: North-east Overland site (looking eastwards)

SOUTH-WEST OVERLAND SITE

SITE DESCRIPTION: Relatively flat plain (<1° of slope) Open to herbivore (sheep, kangaroos and rabbits) grazing and within 150 m of watering point.

COMMON PLANT SPECIES PRESENT:

OVERSTOREY: Scattered western myall (*A. papyrocarpa*)

UNDERSTOREY: Bluebush (*M. sedifolia*), spiny goosefoot (*Rhagodia ulicina*), Australian box-thorn (*Lycium australe*) and patches of Ward's weed (*C. annua*)

SOILS AND SURFACE FEATURES: Red-brown desert clay-loam (pH=8.5) with sheet limestone at 45 cm depth. Cryptogamic crust between most shrubs, some pebbles on the soil surface.

Plate 7: South-west Overland site (looking south-easterly)

COOYERDOO SITE

SITE DESCRIPTION: Relatively flat plain (<1° of slope) on the western side of the North Middleback Ranges. Open to herbivore (sheep, kangaroos and rabbits) grazing.

COMMON PLANT SPECIES PRESENT:

OVERSTOREY: Red mallee (*Eucalyptus socialis*)

UNDERSTOREY: Bluebush (*M. sedifolia*), broom emubush (*Eremophila scoparia*), fleshy saltbush (*Rhagodia crassifolia*) and *Maireana appressa*

SOILS AND SURFACE FEATURES: Orange-red loamy-loam (pH=8.0) with sheet limestone at 40 cm depth. Cryptogamic crust between most shrubs, many small ironstone pebbles on the soil surface.

Plate 8: Cooyerdoo site (looking southwards)

APPENDIX 3: DETERMINATION OF SOIL MOISTURE CHARACTERISTICS FOR SOILS IN THE MIDDLEBACK AREA

Soil moisture characteristics were determined for soil samples taken at two locations; (i) on Middleback Station, adjacent to the Field Centre permanent quadrat, and (ii) on Cooyerdoo Station, adjacent to the Cooyerdoo permanent quadrat. Samples collected from depths of 0-2, 10 and 25 cm were analysed separately.

The relationship between soil water content and soil matric potential was determined using suction plates and gas pressure plates.as described in Marshall and Holmes (1988). Ceramic pressure plates were used for all tests rather than pressure membranes. To construct the soil moisture characteristic curves, the gravimetric water content corresponding to six pre-selected soil moisture potential levels was determined for each of the samples (Table A3.1); the soil moisture potential levels were chosen to represent those expected in a field situation. All analyses were carried out by the Department of Soil Science, The University of Adelaide.

Soil moisture characteristic curves for the two sites were subsequently plotted (Figures A3.1 and A3.2), allowing soil water potentials to be estimated from previously-determined gravimetric soil water contents.

Table A3.1: Gravimetric soil water contents corresponding to pre-assigned soil moisture potentials for soils collected at Middleback (M) and Cooyerdoo (C).

SOIL MOISTURE	GRAVIMETRIC SOIL WATER CONTENT (g water/g soil)					
POTENTIAL (MPa)	M 0-2	M 10	M 25	C 0-2	C 10	C 25
-0.003	0.298	0.278	0.387	0.122	0.303	0.303
-0.01	0.212	0.160	0.199	0.056	0.137	0.156
-0.03	0.172	0.140	0.158	0.043	0.103	0.121
-0.10	0.132	0.104	0.120	0.035	0.099	0.103
-0.50	0.097	0.077	0.092	0.033	0.080	0.080
-1.50	0.082	0.072	0.074	0.027	0.069	0.067

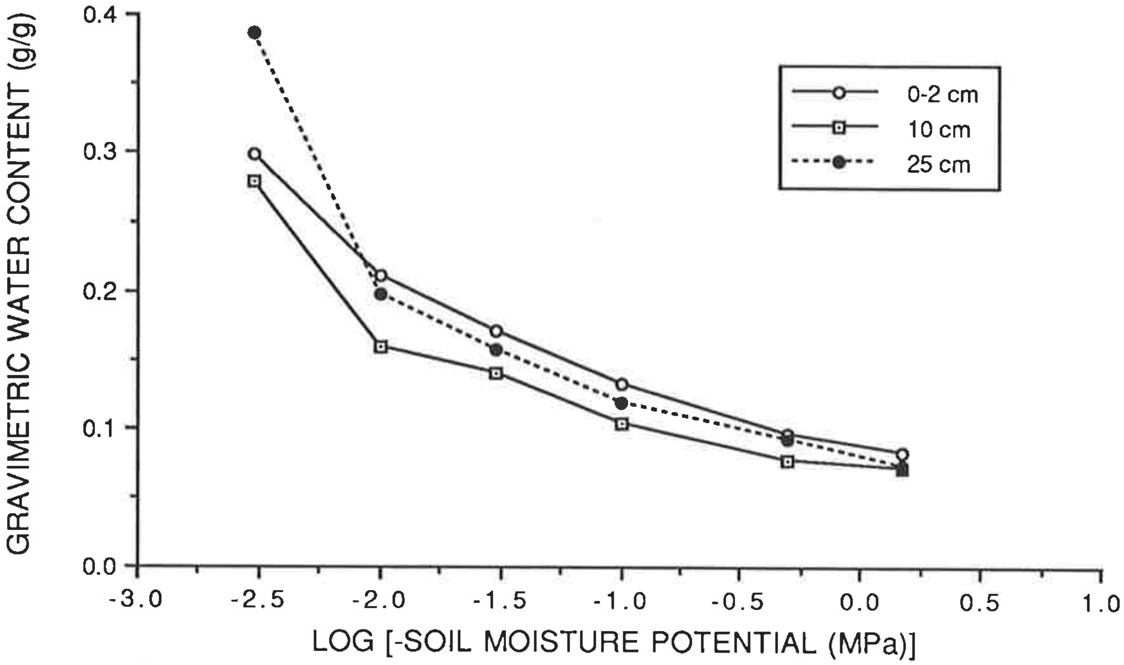


Figure A3.1: Soil moisture characteristic curves for soils collected from three depths at the Field Centre site.

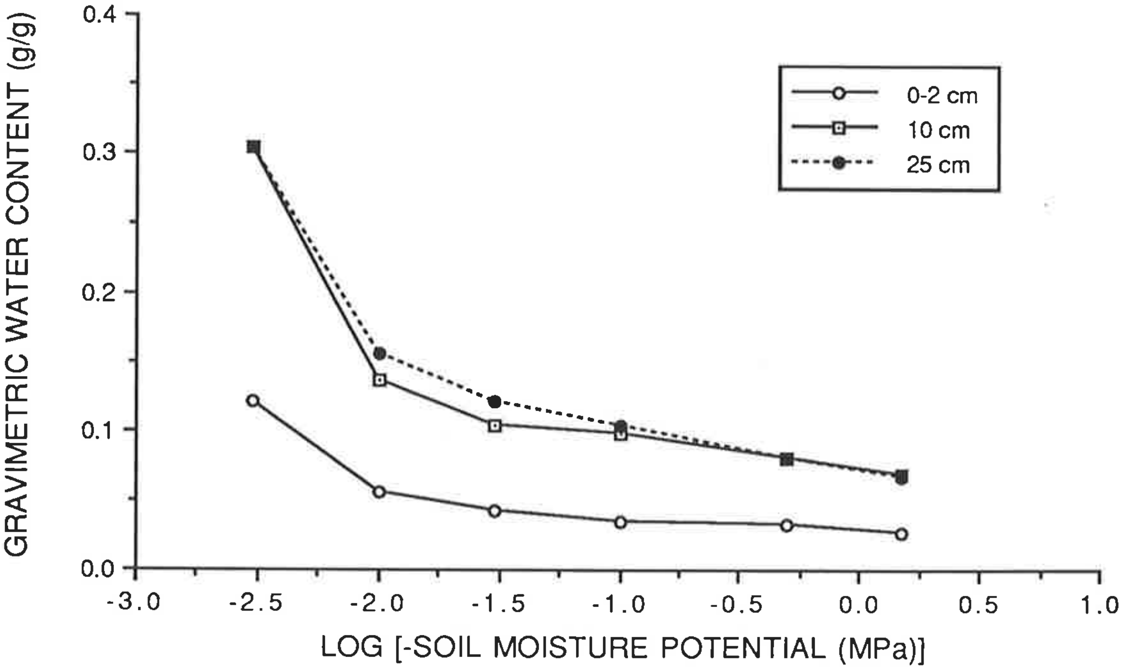


Figure A3.2: Soil moisture characteristic curves for soils collected from three depths at the Cooyerdoo site.

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