SPATIAL AND TEMPORAL PATTERNS OF HERBACEOUS SPECIES AT MIDDLEBACK STATION, SOUTH AUSTRALIA.

by

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FRONTISPIECE

Dense ephemeral growth, predominantly *Stipa nitida* and *Danthonia caespitosa*, in October 1980 in Overland Paddock. Growth of this magnitude followed two consecutive years of well above average rainfall.

SUMMARY

The previously uninvestigated spatial and temporal patterns of annual and ephemeral species at Middleback station, South Australia were the subject of this study. The study area is in the semi-arid region of the state where the low rainfall is erratic and unpredictable and consequently the appearance of annual and ephemeral species is unreliable from year to year.

Investigations of seasonal patterns did not lead to the identification of distinct groups of summer and winter germinating annuals. There were a few species restricted to growing in the cooler months of the year but there were no species restricted to growing during the summer months. Most species could germinate with varying success from late summer through to spring. The time of appearance of annual plants varied from one year to the next, and consequently there were marked changes in the floristic composition, frequency and density of annuals over the period of the study. An unexpected observation was that there were changes in interspecific association, measured by X^2, from one growth event to the next.

The distribution and spatial pattern of annual plants were influenced by the perennial bushes. Some annual species are restricted to growing beneath the bushes, others avoid the bushes while a third group shows no preference. Some species could be found occupying different microhabitats at different times and at different sites. Many of the differences observed in the annual vegetation from one growth event to the next can be partially attributed to differences in the quantity and temporal distribution of rainfall events. The changes in

the spatial pattern of annual species may be due to the variation in rainfall interacting with edaphic factors to produce differences in the spatial arrangement of microhabitats from year to year. That is, habitats for annual plants may not be stable over time but may vary depending upon the prevailing climatic conditions.

The dispersal of seed from annual plants was investigated as a possible cause of spatial pattern. It was found that the dispersal of seed from annual plants is restricted. The great majority of seed is found within 1 m of the parent plant. For some species the dispersal distance is even less. The small stature of the annual plants means that the seed is released close to the ground so flight through the air is not the major component of dispersal. Movement across the ground surface largely determines dispersal distance. This is influenced by the size and shape of the seed, the presence of surface obstructions, the texture of the soil surface and the soil microtopography.

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Finally, I thank Clare Graham for her encouragement throughout this study and for the editing and typing of this thesis.

DECLARATION

This thesis contains no material which has been accepted for the award of any other degree or diploma in any University. To the best of my knowledge and belief this thesis contains no material previously published or written by any other person, except where due reference is made in the text.

I consent to the thesis being made available for photocopying and loan if accepted for the award of the degree.

8/11/1985

Kym P. Nicolson

TECHNICAL DEFINITIONS

Throughout this thesis there are a number of terms which are used repeatedly. It is considered useful to define these terms in this technical preface before the body of the thesis.

Two commonly used terms to descibe short lived plants are annual and ephemeral. An annual is defined for the purpose of this thesis as a plant that germinates and grows during periods of favourable moisture and completes its life cycle within one year. An ephemeral was defined by Crisp (1975) as a species which germinates and grows in response to sufficent rain but dies out at the onset of drought, leaving no aerial parts. Such growth periods are irregular and may not occur at all in a given year. The definition of an ephemeral includes species which may persist for two to three years when conditions are favourable. During the study it was found that some species generally behaved as annuals but survived for more than one year under very wet conditions. In this thesis the term annual is predominantly used, but when species showed a behaviour not covered by the above definition of an annual the term ephemeral is used.

The terms bush and shrub are used to discriminate between two components of the perennial vegetation. A bush is a woody perennial which grows upto 1.5 m high. The term shrub describes multibranched woody perennials greater than 1.5 m high.

A seed is used to refer to the matured ovule without accessory parts. In the studies on dispersal the term dispersal unit is used to describe the seed and any associated structures which are dispersed from the plant. For some species the seed is the dispersal unit.

The nomenclature for plant species occurring in the study area is according to the most recent list of species names for South Australia by Jessop,(1984). Author citations are not given in the text but can be found in Appendix I of this thesis.

MAJOR CHAPTER HEADINGS

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3 BROAD SCALE ANNUAL PATTERN

4 SEASONALITY OF ANNUALS

5 <u>STABILITY OF ANNUAL PATTERN</u>

6 THE INFLUENCE OF BUSHES UPON PATTERN IN ANNUAL VEGETATION

7 SEED DISPERSAL OF ANNUALS

1. INTRODUCTION

1.1 Introduction

A common feature of the hot arid regions of the world is the occurrence of numerous short lived herbaceous species after heavy rainfall events (Went,1948,1949; Shreve,1951; Beatley,1967,1974; Perry,1970a,b; Juhren et al.,1956). Hot arid environments are characterised by long periods of high temperatures and low moisture availability. Rainfall patterns are often erratic and unpredictable with drought conditions sometimes lasting for several consecutive years. When effective rainfalls occur they are followed by a period of germination and rapid growth of numerous herbaceous species which may be so abundant that they form a temporary dense cover on the usually bare ground. The desert environment is particularly suitable for short lived plants. Germination, rapid growth and reproduction during the brief moist periods enables the ephemeral plant to avoid the conditions of severe moisture stress which influence the growth and reproduction of other desert plants (Shreve,1951).

Went (1948) suggested that desert plants are particularly suitable as experimental material because they are subject to more extreme conditions than other plants and so their responses are geared to greater climatic differences. This is especially applicable to desert annuals.

During periods when conditions are unfavorable for growth, annuals exist only as dormant seeds in the soil. A response of this type to moisture stress has been referred to as drought evasion (Cloudsley-Thompson & Chadwick,1964) or drought escaping (Kozlowski,1964). This response differs from that of many other desert plants such as xerophytes which persist throughout periods of moisture stress. Xerophytes are non-succulent and non-halophytic plants of arid regions which maintain living above-ground organs throughout the year, and obtain their water from local precipitation or atmospheric moisture. Annual plants however are mesophytic because they only survive in the vegetative state during periods of abundant soil moisture. Annual plants of desert regions have developed a response to moisture stress that allows them to persist in the severe desert environment. Xerophytic plants have developed a different set of adaptive characteristics which enable them to remain in the vegetative state under the same conditions.

The persistence of annual plants in desert environments is closely linked to the seed. In many perennial species the importance of the seed has been reduced and in some species has been replaced by vegetative reproduction. The seed is of central importance to the survival of annuals. It represents a discrete phase in the life cycle of the annual plant and is the dormant phase that can survive high temperatures in a dehydrated state. Went (1979) regarded the seed of an annual plant more as a survival unit than a dispersal unit. The ability of the seeds of annual plants to survive in the soil for extended periods until favourable conditions for germination occur may be more important than the ability of the seed to move away from the parent plant.

This study, the aims of which are detailed in section 1.3, takes up the issue of arid zone annual flora and seeks, via studies in a previously uninvestigated locality, to throw further light on principal features of annual plants. In particular field patterns of annual plants were investigated, with a view to the identification of possible factors that may determine their distribution. This involved the study of temporal patterns as well as spatial patterns to determine the effects of variable environmental conditions on the annual populations and the stability of annual patterns.

1.2 Literature

There have been numerous studies of annuals from non-arid regions. The conditions under which these annuals exist are different to those of arid regions and consequently they often show different responses to environmental factors. The literature that is reviewed in the following sections refers predominantly to annual plants from arid regions, although reference is made to studies from temperate regions in later chapters, where appropriate.

1.2.1 Germination

The germination of annuals which usually coincides with the onset of favorable conditions for growth and survival has led to considerable interest in the factors that control germination (Soriano,1953; Wareing,1965; Koller,1969; Mott,1972a,b,1974a,b). Annual plants possess drought avoidance behaviour because they are present during periods of available soil moisture but are absent during periods of moisture stress. The mechanism however is far from self evident. Germination occurs after rainfall events and at a time of year that allows the plants to grow and complete their life cycles; in other words we do not observe the soil seed bank being depleted by a succession of germinations that are subsequently killed by drought. The seed is of major importance in the survival of annual plants as it is the only link between successive populations. Germination should therefore occur at a time which favours the survival of the plants to maturity so that there is a new input of seed into the seed store. If the plants die before producing seed then there would be a net loss of seed from the seed store. This behaviour contrasts with perennial plants where the failure of a seeding event is not usually critical to the maintenance of the population.

An important requirement for seed in the soil to germinate is available soil moisture (Harper & Benton,1966; Mayer & Poljakoff-Mayber,1978). The seeds often have mechanisms to prevent germination if only light falls of rain occur. These usually take the form of inhibitors which have to be leached from the seed before germination can occur. Another method of ensuring that mature populations develop from the germination of seed is to allow germination only during the seasons in which rainfall regularly occurs. The controls are often dormancies of the seed which do not allow germination to occur unless a certain set of conditions are fullfilled.

Two types of dormancy can be recognised. Primary dormancies are conditions required for germination, including the correct temperature, moisture and light conditions. Secondary dormancies are said to be present when the seed is given the correct conditions but germination does not occur. Secondary dormancy may be due to immaturity of the embryo, impermeability of the seed coat to water or gases, prevention of embryo development due to mechanical causes, special requirements of temperature and light, or the presence of substances inhibiting germination (Mayer & Poljakoff-Mayber,1978).

Another form of dormancy is called after-ripening. The seeds of many species will not germinate when released from the plant. These seeds will germinate under natural conditions if they are kept for a period of time. After-ripening can be defined as any changes that occur in the seeds as a result of storage which improve germination (Mayer & Poljakoff-Mayber,1978). This form of dormancy can be important in controlling the time of germination of desert annuals. Mott (1972a) found that the seed from the grass _Aristida_ _contorta_ was dormant when released from the plant but storage at high temperatures for a number of months improved germination. This storage condition was interpreted as the seeds requiring high summer temperatures to break dormancy. This particular dormancy restricted germination to after summer.

A second function of the germination controls is to ensure that only a small proportion of the seed in the soil germinates at any one time. The seed remaining in the soil is a reserve to guard against the possibility that the seeds which have germinated may not produce reproductive individuals due to adverse conditions. Without these rigid controls it is unlikely that annual plants could survive in arid environments.

A consequence of germination controls and dormancies is that germination is restricted to periods when a certain combination of temperature and rainfall conditions prevail. The times at which germination can occur will depend upon the local climatic conditions of an area. The differences in climate from one arid region to another (McGinnies,1979) will cause marked differences in the behaviour of the annuals and it is therefore difficult to generalise concerning the behaviour of annual populations from different localities.

1.2.2 Temporal patterns

The annual flora of an arid region can change markedly from one year to the next (Beatley,1974). A species may be dominant in one year, but entirely replaced in the same area by a different species the following year (Loria & Noy-meir,1980). The causes of temporal variability in the abundance of annual species are not completely understood, but shifts in species abundance are generally considered to be due to an interaction between the conditions required for germination and the environmental conditions at the time of the initiating rainfall event (Went,1948; Beatley,1974). It has also been suggested that annual floras may be influenced by the abundance of individual species in preceeding annual floras (Heady,1958).

In some regions more than one annual flora may occur in a year and these can be identified on the basis of the season in which they germinate and grow (Went,1948,1957; Shreve,1951). The species composition of these populations of annuals may be different. Went (1957) found that when soils from the Colorado Desert were moistened in the laboratory at low temperatures (10° C) chiefly winter annuals germinated. If they were moistened at higher temperatures (26° - 30° C) only summer annuals germinated, while at intermediate temperatures a third group of plants could be recognised. The groups of plants found corresponded well with the annual floras that could be observed under field conditions.

A similar observation was made on annuals in Western Australia by Mott (1972a) who noted that following summer rains there was a predominance of grass species in the annual vegetation, however following winter rains, dicotyledons were the most common. This observed field behaviour could be reproduced under controlled conditions. When topsoils containing seed were incubated under different conditions it was found that a combination of moisture and temperature was important in determining which annual species germinated.

The two most common seasonal groups of annuals recognised are summer and winter annuals. A summer annual was defined by Went (1948) as :

> " A species which germinates and completes its life cycle during the summer and early autumn months."

A winter annual was described as:

> " A species which germinates and completes its life cycle during the winter and spring months."

As well as these two groups, other categories have been defined. Beatley (1967,1974) described spring and autumn annuals from the Mojave

Desert.

The majority of the studies on annual plants of desert regions are from the American deserts (e.g. Went,1948,1949,1953,1955,1957; Went & Westergaard,1949; Juhren et al.,1956; Shreve,1951; Tevis,1958a,b; Beatley,1967,1969b,1974). Two studies from the Australian arid region (Mott,1972a; Crisp,1975) have shown differing results. As was previously mentioned, Mott (1972a) observed differences between summer and winter annual floras. In contrast, the study of Crisp (1975) in the north-east of South Australia, found that there were no distinct seasonal floras, rather one highly variable annual flora. Most species could be found after rainfall events but the relative abundance of the species varied depending upon the time of year that the rainfall event occurred.

Studies in the southern Mojave Desert (Went,1953,1955) have shown that desert annuals once germinated usually reach maturity even if only as small depauperate individuals that are barely reproductive. It has been suggested that the environmental conditions prevailing at the time of seed germination are more critical to the determination of the annual flora than the conditions that are encountered at later stages in the life cycle.

Juhren et al. (1956) who also conducted studies in the Mojave Desert supported this conclusion but reported a range of 9-71% survival to reproduction for the annual plants. This result suggests that the conditions subsequent to germination may be important in determining the density of plants at maturity. Tevis (1958a,b) and Beatley (1967,1974) also reported that annual plants in the Californian deserts may have survival values ranging from 0-70%. The conclusion they drew was that soil moisture was an important factor in determining the survival of annuals to reproduction.

In populations of plants grown at high density it has been shown that self thinning may occur, (Harper & McNaughton,1962; Yoda et al.,1963; Harper & Gajic,1961; Hiroi & Monsi,1966; White & Harper,1970; Kays & Harper,1974). When the log of mean plant weight of survivors is plotted againt the log of the density of survivors, the values of successive harvests were found to lie around a line of slope of approx. -1.5, (Yoda et al., 1963). It has not been investigated as to whether self thinning is a contributor to mortality in populations of arid annuals. In many instances it may not be expected to have a significant effect. Self thinning usually is observed in populations of plants grown at high density. However when populations are sown at a lower density there is a longer period before self thinning occurs, (Kays & Harper,1974). The plants must be larger in size before mortality occurs at lower densities. In the case of annual plants the density of the germinating population may be low (relative to that reported in the studies above) and the mature individuals may be small in stature. It may be that only under exceptional conditions for germination and growth of annual plants that self thinning occurs.

There obviously exists a degree of contradiction in these results with some workers recording minimal mortality while others have recorded near total mortality of the populations studied. The conclusion that can be drawn from this collection of different results is that it is not realistic to generalise on the behaviour of annuals. Annual plants are by nature opportunistic and are predominantly controlled by the prevailing environmental conditions. It is therefore not unexpected that under certain conditions there may be virtually no mortality but under a different set of conditions there may be death of the whole population before it reaches maturity.

In a study of an annual community in a more temperate region of California which was dominated by winter annuals, Heady (1958) also found that there were considerable differences in the total numbers of plants found from one year to the next. There were also differences in the proportions of the species present at maturity. He was not able to obtain any precise relationship between the numbers of plants and any meteorological data. The conclusion he drew was that the differences could have been the result of the seed production of the previous years or the loss of viable seed during the summer months.

Inouye et al. (1980) found that competition between annuals was an important factor affecting fecundity but that it did not cause mortality of individuals. They also found that seed predation by ants and rodents had a significant effect upon the density of the mature population and in some instances affected the species composition of the germinating annuals.

1.2.3 Spatial patterns

There have been few investigations of the spatial patterns of annual plants. Went (1948) observed differences in the annual flora between areas for which there was no obvious cause related to topography, vegetation or soils. He proposed that these differences were the consequence of uneven rainfall across the region causing differences in the species which germinated. A similar phenomenon was observed in Israel (Loria & Noy-Meir,1980) where great spatial heterogeneity in the density and composition of annuals was found. In this instance it was considered to be the result of local differences in the run-off and run-on relationships, and in soil salinity profiles.

Went (1942) found that groups of annuals could be separated on the basis of their behaviour in relation to the perennial plants of the area. The distributions of some annual species bore no relationship to any shrubs or other pre-existing vegetation and were predominantly found in the open spaces between the bushes. Another group of species could grow either under the shrubs or in the open spaces between the shrubs. In some instances preference was shown for certain species of shrubs. In general, for this group of species, there were no large size differences between the plants associated with the shrubs and those growing in the open spaces between the shrubs.

The third group of annuals recognized by Went (1942) consisted of those species that were almost always found near or under shrubs. If a plant of this group germinated away from the bushes then its development was poor and its size was much smaller than that of the individuals growing near the bushes. These observations led to the suggestion that there was a complex interaction between the annual plants and the shrubs, although the mechanism of this interaction was not known.

Based on these observations by Went (1942), further investigations were conducted by Muller (1953) and Muller & Muller (1956). These studies indicated that the response of the annual plants of this third group was partially due to the effect of toxins released from some of the perennial shrub species. These toxins could restrict the growth of some species of annuals. The situation was complicated when it was found that the toxins could be rendered inactive by microbial activity in the litter around the base of some of these shrubs species.

1.2.4 Physiological aspects of annuals

Desert annuals appear to have physiological and habit characteristics that may be correlated with the season in which they germinate and grow. Mulroy & Rundel (1977) examined 64 winter and 66 summer annuals from the Mojave and Sonoran Deserts. They found that the winter annuals showed C3 metabolism with few exceptions. In contrast, summer annuals predominantly possessed C4 metabolism.

There are four properties of C4 metabolism which are associated with providing specific ecological advantages to summer annuals. These are: (1) Optimal rates of carbon fixation occur at higher temperatures. (2) Optimal rates of carbon fixation occur at high light intensities. (3) Net productivity rates are high. (4) Relative water use efficency is high (Laetsch, 1947; Brown & Smith,1972; Black,1973; Black et al.,1973; Guterrez et al.,1974; Pearcy et al.,1974; Christie,1975,1981,1982; Johnson,1975; Christie & Detling,1982).

Winter annuals generally possess C3 or the Calvin photosynthetic pathway which is effective at moderate temperatures, the optima for most plants falling in the range 15-25° C and with net carbon assimilation falling off rapidly at temperatures above and below the species optima.

Mulroy & Rundel (1977) also found a number of habit characteristics that were associated with summer and winter growth. The majority of winter annuals commence growth as rosettes with the leaves closely appressed to the ground surface. This prostrate growth habit is interpreted as allowing the plant to occupy a micro-environment that is significantly warmer diurnally than is the air a few centimetres above the ground surface. As the temperatures increase during the spring months the rosette leaves die or lift away from the surface. At the same time the plant may use newly produced stem leaves or green stems for photosynthesis. Summer annuals, in contrast, tend to have a more erect habit.

1.2.5 Importance of annuals

Annual populations are of major importance in maintaining populations of native herbivores, as well as introduced herbivores in commercial enterprises (Davies,1968; Perry,1970b). Annual populations also stabilise the soil surface by reducing wind and water erosion. A number of studies have found that fluctuations in desert rodent populations are related to the seasonal success of annual plants (Fitch & Bentley,1949; Reynolds,1958; Beatley,1969a,1976). Beatley (1969a) found a direct relationship between the seasonal success of winter annuals and reproduction in desert rodents. When winter annuals failed to germinate in the autumn, rodent reproduction failed the following spring.

The main form of land use in the semi-arid and arid regions of Australia is the depasturing of introduced sheep and cattle upon the native vegetation. In years of above average rainfall annual growth is usually abundant and this may have the effect of increasing the productivity of these animals (A.D. Nicolson, pers. comm.). In many areas with a history of overgrazing, and in very dry areas, annual plants may be a major component of the vegetation, and animal production is heavily dependent on seasonal herbaceous growth. Studies on the diet of sheep have indicated there is a preference for annual and herbaceous material when it is present (Leigh & Mulham,1966a,b, 1967; Leigh et al.,1968,; Leigh,1974; Wilson et al.,1969; Robards et al.,1967; Griffith & Barker,1966; Storr,1968). A similar preference has also been found in the diet of Kangaroos, (Chippendale,1962,1968; Griffith & Barker,1966; Storr,1968; Bailey et al.,1971).

The abundance of undesirable herbivores such as the introduced European rabbit (Oryctolagus cuniculus L.) also depend heavily upon the annual vegetation. In the years when there is abundant annual growth there is a rapid population increase (B.Cooke, pers. comm.). In this instance the annual vegetation assists in maintaining the population of an unwanted herbivore which has been implicated in causing marked changes to the age structure of arid zone shrub species (Crisp & Lange,1976; Lange & Graham,1984).

1.3 Aims

My impression of the literature on annual plants from arid regions is that it deals more with temporal than spatial patterns of annual plants. The principle concern has been the investigation of the ability of annual plants to survive in an arid environment through controls which allow germination to occur only when conditions are favourable for growth. An aspect which has been considered in less detail is the spatial patterns of annual plants.

Two different scales of spatial pattern can be considered. The first is the broad scale relationships that exist between the annual and perennial communities. The second concerns spatial relationships between annual species. It is not known if annual species have distinct habitat requirements which may cause a patterned annual flora. Three hypotheses concerning annual pattern may be proposed.

The first is based upon the opportunistic nature of annual plants. If conditions are favourable, then germination occurs. The assumption here is that the only factors controlling annual pattern are the distribution of seed in the soil and that germination is largely independent of habitat. The strategy of an annual plant is to germinate, grow and then release seed back into the seed store, usually within a short time span. This is supported by Went (1948) who observed that most annuals which germinate survive to the reproductive stage. This suggests that the density of annual plants rarely is great enough for self thinning to occur.

The second hypothesis is that annual species do have specific habitat requirements in relation to soils and topography. The hypothesis predicts a stable distributional pattern of annual plants, dependent upon the distribution of the various habitats. If this hypothesis was true then the pattern of annuals would be expected to be stable from one year to the next. Differences in the annual flora may still occur if there are marked climatic differences from one year to the next.

A third possible hypothesis is that there is temporal heterogeneity in the habitats suitable for the germination, establishment and growth of annual plants. The variation in climatic conditions particularly rainfall from one year to the next may mean that a habitat or area that was suitable for the germination and growth of a species in one year may be unsuitable for that species the next year. The habitat may be suitable for the establishment of a different species in the second year.

These three hypotheses are not necessarily mutually exclusive. To some degree the hypotheses depend upon the scale at which the annuals are investigated. All three hypotheses are considered in relation to different investigations of annuals in this thesis.

1.4 Thesis plan

The plan of this thesis is shown in Figure 1.1. Chapters 3 and 4 describe the initial studies on the spatial and temporal pattern of annual plants in the study area at Middleback station. Chapter 3 details a study of broad scale annual patterns, investigating the relationships between the annual vegetation and some of the common perennial communities in the study region. Chapter 4 considers the seasonal pattern of annual plants in the field throughout 1979. Also included in this chapter are the results from laboratory studies designed to determine whether or not seasonal annual floras exist in the study area.

Chapter 5 follows from the results of the two previous chapters. It is an investigation of the patterns of annuals within a 0.5 ha area and how these patterns may change from one year to the next. This investigation also considers changes in the floristic composition of the annual vegetation over a 5 year period. An attempt is made to relate the behaviour of the annual plants to changing environmental conditions over the 5 year period. Small scale patterns of annual plants are also considered in Chapter 6. In this chapter the distribution of annual plants in the immediate vicinity of two species of perennial bush is considered.

Chapter 7 is not a study of pattern but a study of one of the possible causes of spatial pattern in annual plant distributions. This chapter describes investigations into the dispersal mechanisms of a variety of annual species and attempts to determine the distances seeds move from the parent plant. If annual plants are opportunistic and their distribution is not greatly influenced by habitat factors then their distribution will be determined largely by seed dispersal.

The final chapter attempts to draw conclusions on annual behaviour from the studies of spatial and temporal patterns and relate these conclusions to studies of annual plants from other arid regions of the world.

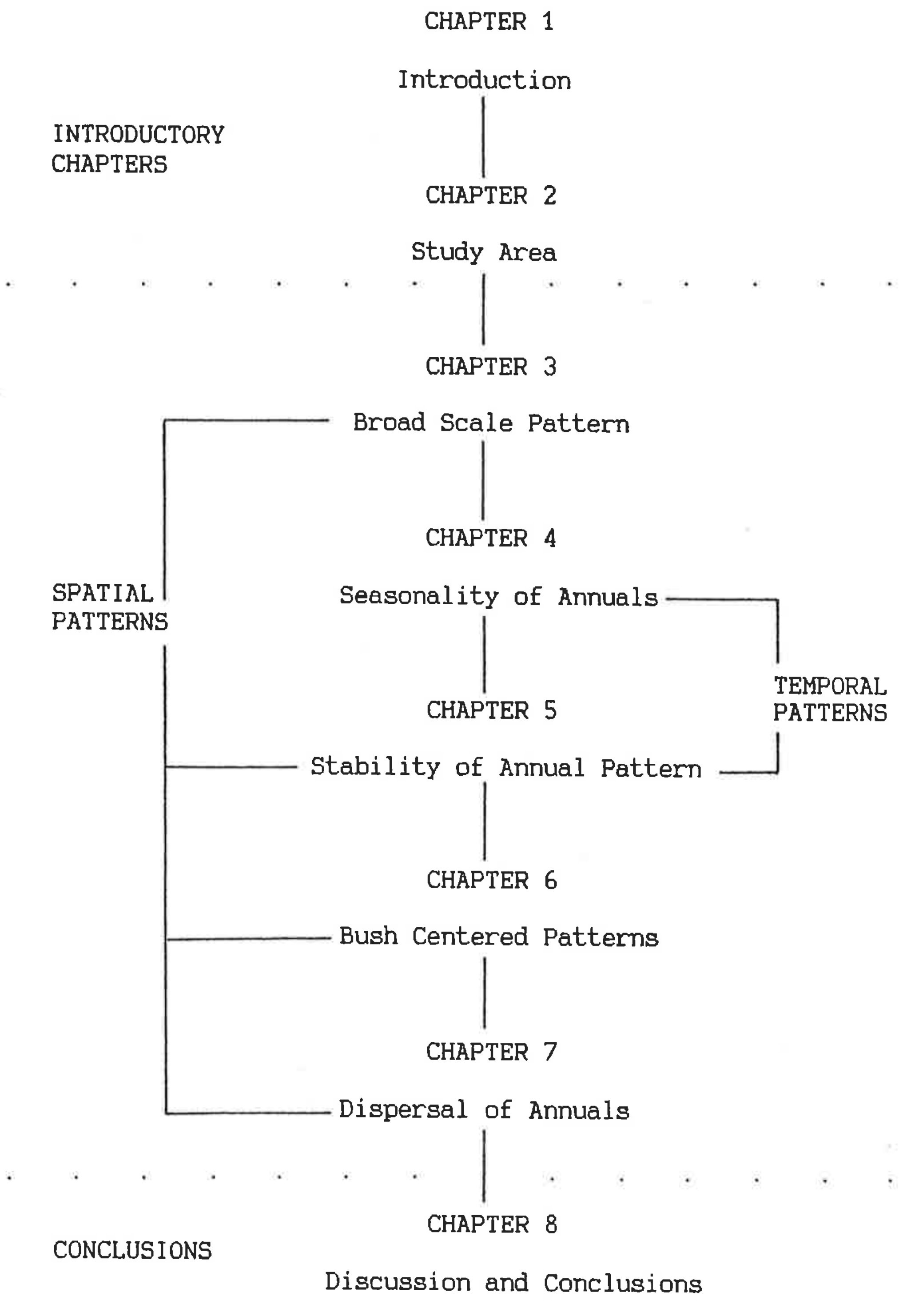

Figure 1.1 Schematic representation of thesis structure.

2. STUDY REGION

2.1 Introduction

The study was conducted in arid rangelands on Middleback Station (32° 57'S, 137° 24'E) which is a pastoral lease 20 km north-west of Whyalla, South Australia (Fig. 2.1). The main form of land use in the Whyalla region is the depasturing of sheep on the native vegetation. The history and management of the station by the current lessees is described by Lange et al. (1984). As well as sheep other herbivores in the area include the European rabbit and Kangaroos (Macropus spp). The numbers of these herbivores fluctuate from year to year depending upon whether favourable or drought conditions prevail, whereas the number of sheep on the station does not vary greatly from one year to the next.

This chapter describes the climate, vegetation and soils in the Whyalla region. Some of these are discussed in greater detail in later chapters in relation to particular studies.

2.2 Climate

2.2.1 Introduction

Temperatures in the study region are warm to hot in summer and cool in winter. The rainfall is low and unreliable and evaporation is high throughout the year (Laut et al. 1977). The dominant weather patterns are derived from pressure systems moving eastward over the Australian continent, and from cyclic seasonal fluctuations. A series of high pressure systems tend to be positioned over the region in winter and south of the Great Australian Bight in summer (Jensen & Wilson,1980)

The only long term weather records kept at Middleback Station are daily rainfall records. The information on temperature, humidity, evaporation, wind speed and direction has been obtained from surrounding centres for which these records were available. The temperature and wind data is taken from Whyalla where the Bureau of Meteorology has kept detailed records since 1953 at the Whyalla Post Office. The data on evaporation is taken from Jackson (1958) for Yudnapinna Station which is 100 km north of Middleback Station. This may seem a considerable distance away, however, in the arid region weather recording stations are usually much further away from a given point than this.

The position of Whyalla on the coast, while Middleback Station lies inland (Fig. 2.1) does cause slight differences in temperature and differences in wind speed and direction between the two centres. The data presented in this section from centres other than Middleback Station should be regarded as a regional description only.

2.2.2 Rainfall

Rainfall records have been kept continuously at Middleback Homestead since 1925 and although not an official Bureau of Meteorology recording station, the records have been accurately maintained for the whole period (A.D.Nicolson, pers. comm.). The mean annual precipitation is 209 mm but varies considerably from one year to the next with no clear cycle (Fig. 2.2). Since 1925 there have been four years of far above average rainfall. It is known that 1921 was also an above average year that caused flooding in the area, but no record of the actual rainfall is available. There have also been a number of exceedingly low rainfall years. During the period of this study a wet year (1979, 450 mm) and a drought year (1982, 100 mm) were experienced. Three very wet years in 1973,1974 and 1979 have had a marked effect upon the rainfall mean. The mean from 1925 to 1971 was 192.6 mm and the mean from 1925 to 1982 was 209.6 mm.

The number of days on which rain was recorded varied considerably from year to year. The lowest recorded number of wet days was 12 in 1939 (132 mm) and the highest was 60 in 1973 (511 mm). There is no simple relationship between the number of wet days and the total rainfall although there is a trend for wet years to have more wet days (Fig. 2.3). Neither parameter is a good measure of the effectiveness of rainfall (Jackson,1958).

The periodicity of the rainfall through the year shows little pattern and monthly averages do not vary greatly (Table 2.1). February has the highest mean monthly rainfall while March has the lowest. Winter months have almost twice as many wet days as the summer months. July has an average of 4.1 wet days per month while February has only 1.7 wet days per month. Summer rainfalls are usually few but heavy, while numerous light falls occur in winter. This aspect is considered in greater detail in Chapter 4. The number of days on which rainfall has been recorded at Middleback Station is lower than it would be by the strictest standards due to the fact that "trace" rainfall events are not recorded (Noble,1975).

Comparison of the Middleback Station and Whyalla rainfall data indicates that there are differences between the two centres. Whyalla has a higher rainfall in all months of the year. The distribution of the rainfall for Whyalla is also different with the highest monthly means recorded in May (27 mm) and October (27 mm). The number of wet days is greater for Whyalla although the distribution throughout the year is similar.

2.2.3 Temperature and evaporation

Seasonal variations in temperatures of the region are predictable and cyclic. The summers are hot with temperatures of up to 50° C. Winters are cool with night temperatures falling to below zero (Table 2.2) and frosts may occur. January has the highest monthly mean maximum temperature and July the lowest. Temperatures in excess of 40° C have been recorded in the six months from October to March. Zero temperatures have been recorded in June, July and August. The mean monthly humidity shows little variation throughout the year.

Mean monthly pan evaporation at Yudnapinna station (Jackson,1958) indicates a maximum evaporation of 36.8 cm in January and a minimum of 6.6 cm in June (Table 2.1). The total yearly evaporation is 2.4 m which is more than ten times the average rainfall. The high evaporation rate causes many of the rainfall events to be ineffective, especially light falls in summer.

2.2.4 Wind speed and direction

The Bureau of Meteorology provides tables of percentage occurrence for wind speed and direction over a 27 year period for Whyalla. The readings are for both 9.00 am and 3.00 pm. Wind roses for the 3.00 pm reading (Fig. 2.4) show that during the summer months the winds are predominantly from the south and to a lesser degree the south-east. As the winter months approach, the percentage of winds from the north and north-west increases. Following winter, the winds swing back to the south and south-east.

2.3 Soils

The soils of the region are described as brown calcareous earths (GC 1.12 & GC 1.22, from Northcote,1960). The soils of the region are the subject of a number of publications. They are described in the Soils Data Handbook of the 9th International Congress of Soil Science (1968). The origin of the soils was described by Jessup & Wright (1968) and the soil surface cryptogams by Rogers (1970).

2.4 Vegetation

The perennial vegetation in the region is predominantly chenopod shrubland consisting of bushes up to 1.5 m high, belonging to the family Chenopodiaceae. In some areas the vegetation is a low scattered woodland with the chenopod bushes as understory (Wood et al.,1947; Jackson,1958). The main woodland species is <u>Acacia</u> <u>papyrocarpa</u> (Western

Myall, formerly A.sowdenii). Other prominent species are Heterodendrum oleaefolium (Bullock Bush), Casuarina cristata (Black Oak), Myoporum platycarpum (False Sandalwood) and Santalum acuminatum (Quandong).

The shrubland is dominated by two chenopod species, Atriplex vesicaria (Bladder Saltbush) and Maireana sedifolia (Bluebush) which often form a uniform-looking vegetation of evenly spaced bushes. The vegetation consists of various proportions of the two species ranging from only M.sedifolia to only A.vesicaria. Other bushes that occur in varying abundance are Rhagodia ulicina (formerly Chenopodium ulicinum), Maireana pyramidata (Blackbush), M.turbinata and Lycium australe (Native Boxthorn). There are scattered individuals of shrubs up to 3 m high the most common being Eremophila scoparia, Exocarpos aphyllus and Cassia nemophila.

A list of all the species, both ephemeral and perennial, that were encountered in the course of this study is in Appendix I. This list includes species which were present but may not be refered to in the text. Also in Appendix I there are brief descriptions of some of the ephemeral species which are frequently referred to throughout this thesis. Further details of the vegetation and soils can be found in Wood (1937), Crocker & Skewes (1941), Crocker (1946) and Specht (1972).

RAINFALL STATISTICS

	Mean RF(mm)	Mean Wet Days	Mean Evap(mm)
JAN	16.15	1.75	368
FEB	23.32	1.77	291
MAR	12.25	1.60	267
APR	15.39	2.17	169
MAY	19.17	3.46	108
JUN	17.32	3.81	66
JUL	17.29	4.10	74
AUG	17.63	3.68	103
SEP	19.31	3.32	163
OCT	20.27	2.96	226
NOV	15.32	2.03	283
DEC	14.13	1.67	336

Table 2.1 The mean monthly rainfall (RF) and wet days per month at Middleback Homestead, 1926-1983. The monthly evaporation data is from Jackson (1958) for Yudnapinna Station.

TEMPERATURE STATISTICS

	Mean		Mean	Extreme	
	max	min		max	min
JAN	28.6	18.1	23.3	49.5	8.0
FEB	28.3	18.9	23.6	44.4	7.8
MAR	25.7	17.2	21.5	44.3	6.7
APR	23.0	13.6	18.3	37.7	3.3
MAY	20.0	10.7	15.5	31.3	0.6
JUN	17.6	8.5	13.1	27.2	-2.2
JUL	16.4	7.4	11.9	29.5	-2.8
AUG	17.7	8.1	12.9	33.0	-0.6
SEP	20.2	9.9	15.1	38.0	0.0
OCT	22.4	12.6	17.5	40.3	0.9
NOV	25.5	14.7	20.1	45.6	5.5
DEC	26.7	16.6	21.7	44.9	6.7

Table 2.2 Temperature (° C) statistics for Whyalla, from tables provided by the Bureau of Meteorology, Adelaide, showing the mean maximum, mean minimum and daily mean temperature. The extreme maximum and minimum temperatures give an indication of the potential variation in temperature.

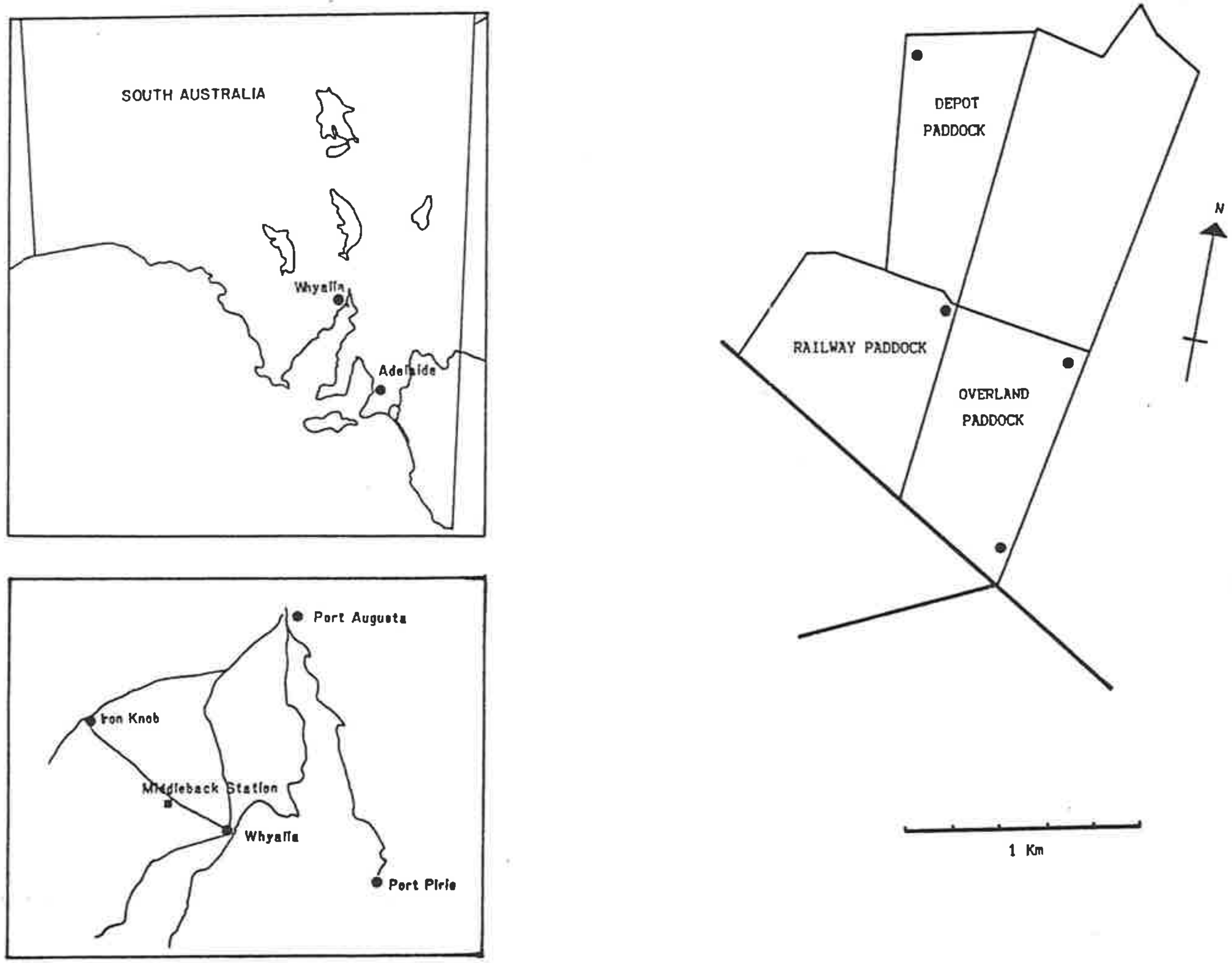

Figure 2.1 The location of Middleback Station and the location of paddocks in which the studies were conducted.

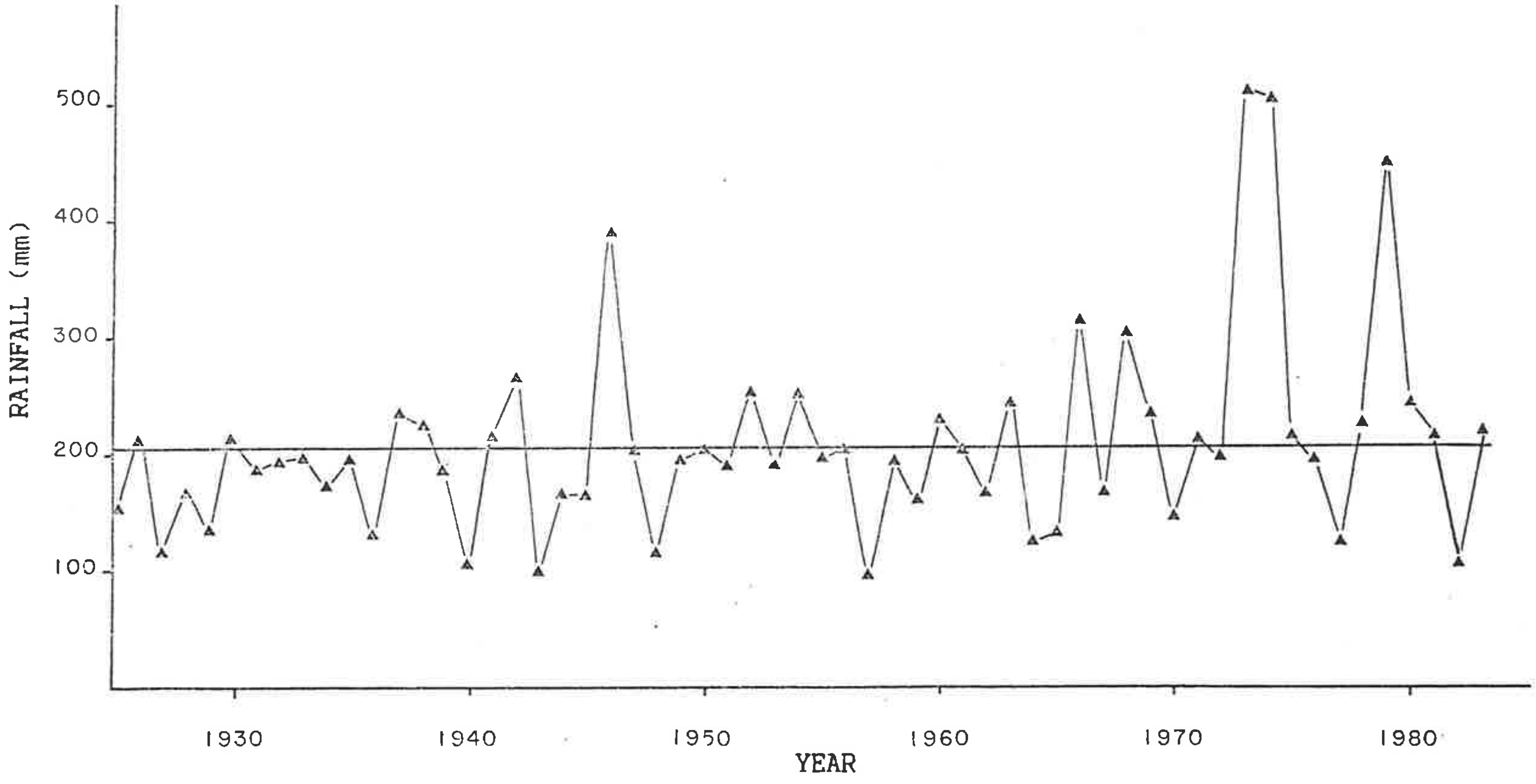

Figure 2.2 Annual precipitation recorded at Middleback homestead 1926-1983

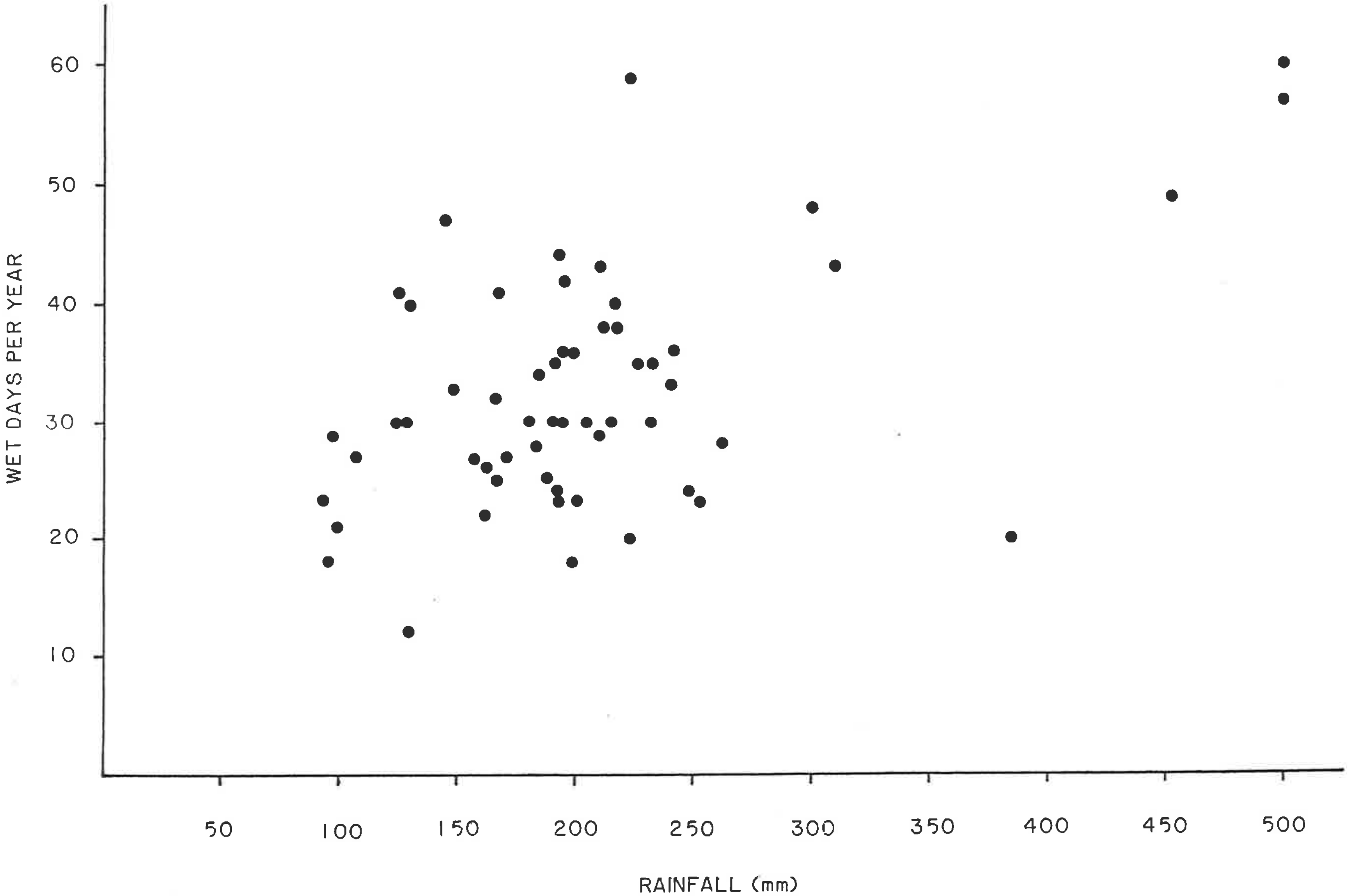

Figure 2.3 Scattergram of the number of wet days per year versus the annual precipitation at Middleback homestead

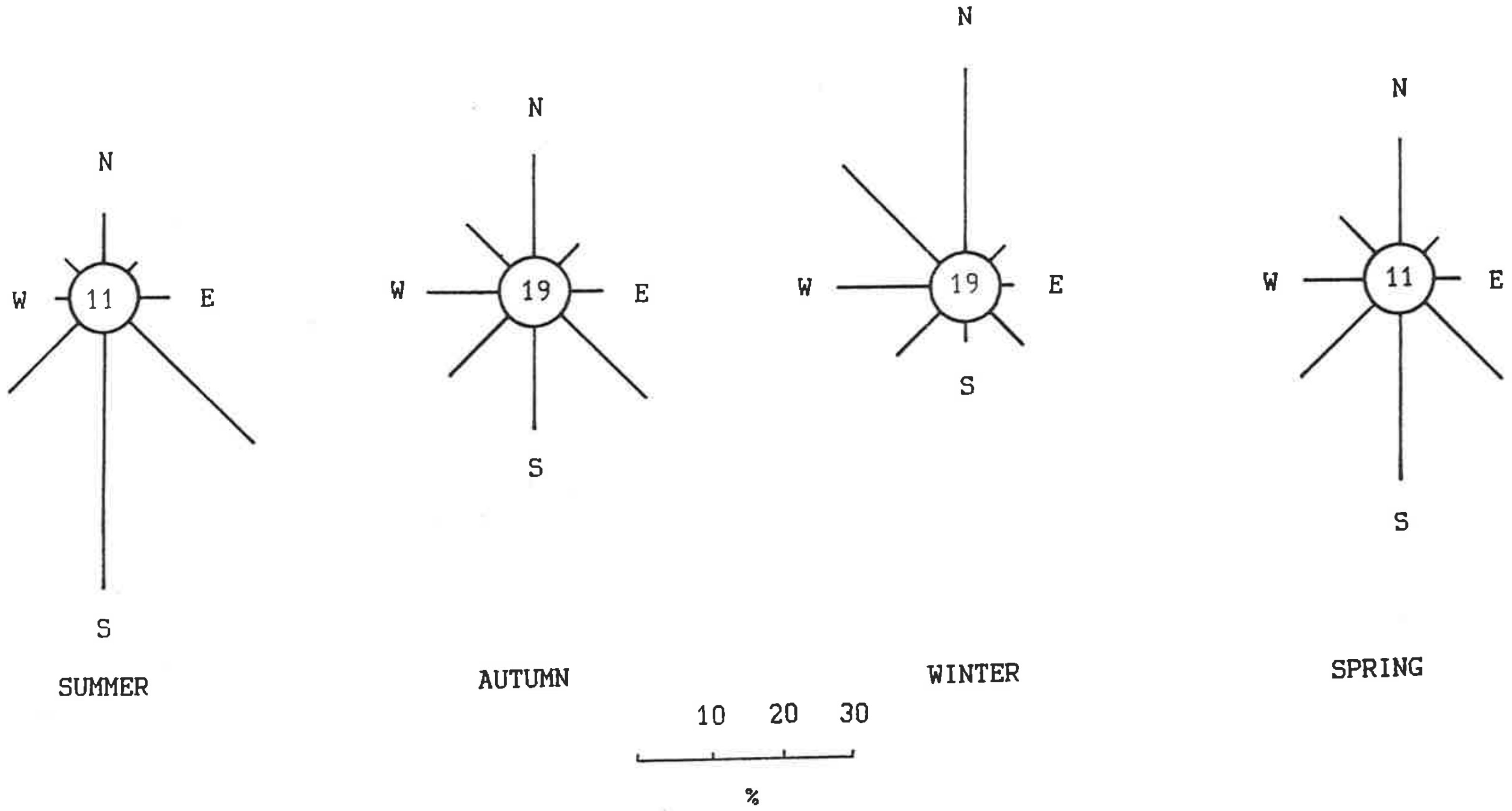

Figure 2.4 Wind roses for Whyalla, 3.00 pm recordings. The number in the centre of each rose is the percentage of calm days.

3. BROAD SCALE ANNUAL PATTERN

3.1 Introduction

Very little was known concerning the annual species of the Whyalla region before the commencement of this study. Previous botanical research undertaken in the region had been predominantly concerned with the perennial vegetation and the effects of sheep grazing (Barker,1972; Noble,1975; Andrew,1978). All these studies mentioned annual plants only briefly, so that details of the distribution and abundance of the annuals in the region were unknown. This chapter describes a study which was designed to examine the abundance of different annuals in the study area and their distribution in relation to the perennial communities. An experimental approach was adopted, which consisted of removing soil samples from the field and inducing germination of seeds in the soil under controlled conditions.

3.1.1 Vegetation classification

Classification of vegetation samples, as with ordinary classification in the general sense, attempts to group similar samples (Whittaker,1978). The similarity of the samples can be measured in terms of the floristic or structural characteristics of the vegetation. Classifications of this type are arbitrary to the extent that they depend largely upon the interpretation of the observer (Specht,1972) and the technique used (Lange et al. 1965). There is an underlying assumption to such classifications that the grouping of similar samples of plants reflects similarities in edaphic, topographic and climatic conditions. Plants are often considered to indicate particular habitat types. The relations of the plant or community to process and practice are direct corollaries of the basic principle that each is the best possible measure of the conditions under which it grows (Clements, 1928).

Many vegetation classifications are based upon the distribution of the perennial species and little consideration is given to annual species. In terms of vegetation classification, the emphasis upon the perennial component may be justified, but a consequence is that little is known about the distributional patterns of annual plants.

The perennial species of the study region show considerable spatial patterning in their occurrence. The differences in distribution are sufficiently pronounced that different vegetation types can be recognised. If the distribution of perennial plants indicates different habitats, then it may be suggested that the annual plants should show a pattern of distribution that is related to that of the perennial component. This can be stated as an hypothesis that: Annual species should show a pattern in their distribution which would be related to the different available habitats as indicated by the different perennial vegetation types of the study region.

3.2 Methods

3.2.1 Introduction

In the Whyalla region a considerable proportion of the annual precipitation can be attributed to thunderstorm activity. As annuals depend upon sufficient moisture for the initiation of a growth event, localised rainfall patterns can lead to marked differences in the annual flora over short distances (Went,1949). Field surveys of annual distribution over large areas may therefore not reflect the potential distribution and abundance of the species. The problem of heterogeneous rainfall distribution can be overcome by removing soil samples from the field and then initiating an annual growth event by controlled watering. The irrigation of areas in the field was not logistically practicable.

Controlled climatic conditions allow the temperature to be manipulated to initiate the germination of different annual species. It is not possible to predict in which years an annual flora will be present,so by removing soils from the field to the laboratory it was possible to determine the annual flora, despite the fact that annuals were not present in the field at the commencement of the study.

Ten replicate sites for each of six perennial vegetation types were selected in the southern part of Middleback Station. The area in which the sites were selected was approximately 10 km x 15 km.

3.2.2 Vegetation groups

Three main vegetation types based upon the dominant perennial chenopod species of the study area were recognised:

(1) Maireana pyramidata shrubland
(2) Atriplex vesicaria shrubland
(3) A.vesicaria : M.sedifolia

The mixed M.sedifolia - A.vesicaria vegetation type is the most common in the study region and is highly variable in the relative proportions of the two species. Due to the variability in the proportions of the two species, this vegetation type was divided into four groups based on the relative proportions of the two species, determined by counting the plants within a quadrat 100 m x 1.5 m. The proportions were:

(1) A.vesicaria : M.sedifolia 80:20 - 60:40
(2) A.vesicaria : M.sedifolia 60:40 - 40:60
(3) A.vesicaria : M.sedifolia 40:60 - 20:80
(4) M.sedifolia

The last group (4) was considered a part of the M.sedifolia - A.vesicaria vegetation type because it occupies a similar habitat and is possibly the result of grazing which has removed all the A.vesicaria.

3.2.3 Soil collection

Soil samples were collected[1] at each site. Seeds in the soil are usually located near the soil surface unless the soil has been severely disturbed as in agriculture (Harper,1977). The soil samples were taken from the surface to a depth of 2.5 cm. It was assumed that the majority of the seed would be in this sample and there would be no differences between sites due to depth of seed in the soil.

At each of the 60 sites, 10 subsamples of soil were taken from beneath the bushes and 10 subsamples were taken from between the bushes. The 20 subsamples were thoroughly mixed and two 500 g samples were taken and placed in aluminium trays. The two samples were considered as one replicate.

The trays of soil were placed in growth cabinets at the University of Adelaide. The 120 trays were placed in three growth cabinets in a random arrangement. It was thought that the majority of species would germinate in the cooler months and so a winter temperature regime of 14° C for a 14 hour day and 7° C for a 10 hour night was used (Whyalla temperatures, see section 2.2.3). Light was provided during the day period from a bank of fluorescent and incandescent lights.[2] Humidity was set to 70% to reduce moisture loss from the trays.

The field capacity of the soil was determined by watering a 500 g sample of soil until saturated. The sample was allowed to drain for 1 hour and then re-weighed. The weight of water retained was used to approximate the field capacity of the soil. The moisture loss from the trays was quite rapid and so they were watered to 90% of field capacity

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1. February 1979

2. 250-300 μeinsteins/m^2/sec in the 400 - 750 nm range

every third day. This ensured that trays were never waterlogged and that soil moisture was not a factor limiting germination and growth.[1]

The experiment was initially designed with replicated sites so that Analysis of Variance (ANOVA) could be used to test for significant differences between the vegetation groups either on the basis of density or biomass. The ANOVA test relies upon a number of assumptions, one of which is that the variances of the groups being tested are similar. ANOVA is relatively insensitive to minor deviations from this requirement but if the differences between group variances become too large, the test is invalid (Sokal & Rohlf,1969).

Homogeneity of variances may be tested by comparing the F-max ratio (the ratio of maximum to minimum variances) with critical values for the particular degrees of freedom. There are other, more accurate methods for testing for the homogeneity of variances but unlike the F-max test, many of these tests are sensitive to non-normality of the data (Sokal & Rohlf,1969).

3.3 Results

3.3.1 Species incidence and associations

Thirty four annual species germinated in the trays. The list of species and their frequencies is presented in Table 3.1. Five species were common, occuring in more than half the trays. These were _Schismus barbatus_, _Lophochloa pumila_, _Crassula colorata_, _Tetragonia eremaea_ and _Daucus glochidiatus_. A number of species were present only at very low

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[1] The experiment was terminated and the plants harvested after 13 weeks.

frequencies. These were Stellaria sp., Hypochoeris glabra, Omphalolappula concava, Chenopodium cristatum and Bulbine semibarbata.

The five species with the highest frequency listed above, were recorded for all vegetation types although not at all sites. Chenopodium cristatum and Medicago minima were found only in soils from Maireana pyramidata dominated sites, and Stellaria sp, Hypochoeris glabra and Omphalolappula concava were only found in soils taken from Atriplex vesicaria dominated sites. The remaining species occurred in more than one vegetation type.

All the species were tested for association using X^2 to determine whether there were patterns in species occurrence. It was found that 11 species showed significant association at $p < 0.001$ (Table 3.2). The associations could be divided into groups, or nodes of associated species (Lange,1968). Three nodes were recognized (Fig. 3.1). The first node (A) was an interaction between seven species. The remaining two nodes (B & C) were simple two-species interactions. Only one of these associations was related to the vegetation types. The association of Emex australis and Medicago minima was restricted to the Maireana pyramidata vegetation type.

3.3.2 Density and biomass of annuals

The significance of the F-max values for the density and biomass results are presented in Table 3.3. Of the 34 species recorded in the samples, 21 had highly significant differences in the variances associated with the density recorded across the vegetation groups.

Another seven species could not have an F-max calculated due to their low frequency of occurrence. The remaining six species had non-significant F-max values but were present only at very low density and were non significant ($p>.05$) across the vegetation types when tested with ANOVA.

The results of the F-max test on the biomass data showed a similar trend. The majority of species had highly significant differences in variances across the vegetation types. The species which did not show significant differences in their variances were generally of low frequency and were not distributed with significant differences between the vegetation types when tested with ANOVA. The ANOVA test in the study did not demonstrate any significant difference in either density or biomass of the annual species across the vegetation groups.

In situations where the assumption of homogeneity of variances is found to be untrue, it is common practice to apply a transformation to the data so that the transformed values conform to the assumptions of the analysis. The two transformations used here were a logarithmic and a square root transformation. When zero scores are present it is common to use log(Y+1) or square root(Y+0.5) (Sokal & Rohlf,1969). The result of these transformations was that in most instances the differences in variances was reduced, however, analysis of the transformed data by ANOVA did not demonstrate significant differences between the vegetation types. The ANOVA tables, although non significant, are presented in Appendix 2.

The small grass Schismus barbatus showed the highest density of all species with 331 individuals found in one sample from the A.vesicaria vegetation type (Table 3.4). This species also showed large maximum densities in samples from other vegetation types. Other species which showed high maximum densities were Crassula colorata, C.sieberana, Lophochloa pumila, Medicago minima, Emex australis, Tripogon loliiformis and Daucus glochidiatus.

The mean density (Table 3.5) and the standard deviations (Table 3.6) are also presented to demonstrate the high degree of variability in the occurrence of species across the vegetation groups. The species with the highest mean density was Schismus barbatus (48 per sample) for the A.vesicaria vegetation type. The standard deviation associated with this mean was 104. A similar result was observed for most species in that the standard deviation usually exceeded the mean value for a vegetation type. The variation in the numbers of plants was usually as great within a vegetation type as between the vegetation types.

Analysis of the biomass data showed the same result as the density data (Table 3.3). There were no significant differences in the biomass between the vegetation types for both the untransformed or transformed data. The total biomass for each species for the vegetation groups (Table 3.7) indicates the small stature of the annuals.

3.4 Discussion

The species that germinated in the soil samples represented a wide range of plant families. The occurrence and abundance of species was variable.

The association analysis indicated that a number of the species were positively associated. In some instances there were small groups of associated species (Fig. 3.1). The technique of using species association in vegetation classification has been used in numerous studies (Goodall,1953; Williams & Lambert,1959,1961; Lange,1968). Whenever species associations are found it is assumed that there is a cause, usually relating to environmental factors. The associations found in this study are important because they demonstrate pattern in the distribution of annual plants, although unrelated to the distribution proposed in the original hypothesis.

The conclusion drawn from these results was that the factors which control the distribution of perennials do not influence the annual population to the same degree. The hypothesis that the pattern of annual distribution would be related to the perennial vegetation types (Section 3.1) would therefore be rejected.

Two associated species, Emex australis and Medicago minima, did show a pattern and were restricted to the Maireana pyramidata vegetation type although they did not occur in all samples of this vegetation type. These species are a special case in that both are introduced species which have been able to survive in watercourses where M.pyramidata dominates. Other factors may also influence the distribution of E.australis and Medicago minima. The dispersal units of both species are large and may be readily moved along the wash areas by the movement of water. The soil surface is often disturbed in these areas by the increased grazing pressure and this may provide a surface suitable for colonisation by E.australis and M.minima.

There was considerable variation in the numbers of a single species between sites in the one vegetation type. There are two possible explanations for this: (1) The annual flora differs between sites vegetated with the same perennial species, due to subtle environmental differences which do not influence the bush component. (2) The composition of the annual flora is locally very patchy. Sites in the one vegetation type differed as much as between vegetation types. The annuals may be responding to subtle differences in the microhabitats and microclimatic variation to produce a highly patterned seed store in the soil. In an experiment of this type where small samples of soil were used the result could be markedly influenced by within-site variability.

3.5 Conclusions

The use of controlled conditions removed the problem of non-homogeneous rainfall that occurs in the field situation. The results did not support the hypothesis that the distribution of annual plants would be related to the perennial communities. Patterns of annual distribution were detected by association analysis but most of the pattern did not coincide with perennial distribution. The experiment also demonstrated variability in the occurrence and density of annuals, so great as to preclude statistical analysis according to models requiring homogeneity of sample variances.

The distribution of annual plants may be influenced by different factors to perennials. The survival of annual plants may largely be independant of habitat at the scale studied in this experiment. The scale that may be important for the germination and establishment of annuals could be that of microsites which would be independant of the factors influencing the perennial vegetation.

If annual species are opportunistic and depend upon the interaction of temperature and rainfall to determine which species germinate, then there is no guarantee that the same species associations will be observed from one year to the next. In fact it has been reported that there may be marked changes in the annual flora from one year to the next (Loria & Noy-Meir,1980). This is persued further in Chapter 5.

The suggestion of Heady (1958) that annual populations may be largely the consequence of previous annual populations, also bears consideration. If the seed released from one population can markedly influence subsequent annual populations then the species composition, the quantity of seed released and the fate of the seed will be important. In respect of the experiment described in this chapter the distribution and density of annuals observed may be the consequence of what seed were released from previous annual populations, how much seed was produced and where the seeds were transported to.

The results presented in this chapter do not explain the patterns of the annual plants, but rather raise a number of interesting questions which will be addressed in later chapters.

		VEGETATION GROUPS					
	F	1	2	3	4	5	6
Actinobole uliginosum	3	1	0	1	0	0	1
Atriplex spongiosa	11	2	2	2	1	0	4
Brachycome lineariloba	5	1	2	0	0	2	0
Bulbine semibarbata	2	0	0	1	0	0	1
Calandrinia eremaea	3	1	1	1	0	0	0
Calotis hispidula	9	2	3	1	0	1	2
Chenopodium cristatum	1	0	1	0	0	0	0
Crassula colorata	43	6	7	9	9	5	7
Crassula sieberana	9	4	3	1	0	1	0
Danthonia caespitosa	4	0	1	0	0	3	0
Daucus glochidiatus	32	6	5	8	4	3	6
Emex australis	5	0	4	1	0	0	0
Erodium cygnorum	11	2	2	4	0	3	0
Gnephosis burkittii	3	1	0	2	0	0	0
Goodenia pusilliflora	10	3	2	1	0	4	0
Helipterum pygmaeum	4	1	0	3	0	0	0
Hernaria hirsuta	7	1	3	2	0	0	1
Hordeum leporinum	3	0	0	2	0	0	1
Hypochoeris glabra	1	1	0	0	0	0	0
Isoetopsis graminifolia	3	0	0	1	0	0	2
Lophochloa pumila	44	7	9	8	9	6	5
Medicago minima	5	0	5	0	0	0	0
Omphalolappula concava	2	2	0	0	0	0	0
Oxalis corniculata	3	2	0	1	0	0	0
Plantago drummondii	7	2	0	1	2	0	2
Schismus barbatus	49	7	10	9	9	5	9
Sclerolaena sp.	15	2	0	2	3	6	2
Senecio quadridentatus	11	3	0	4	1	0	3
Sonchus oleraceus	3	2	0	0	0	0	1
Stellaria sp.	1	1	0	0	0	0	0
Stipa nitida	4	2	1	0	0	1	0
Tetragonia eremaea	33	5	4	8	6	6	4
Tripogon loliiformis	4	0	2	0	0	0	2
Vittadinia cuneata	8	1	0	1	2	1	3

Table 3.1 The number of trays (max 60) in which the annual species occurred. The total number (F) and the number for each vegetation group (max 10 per vegetation type). 1; *A.vesicaria* 2; *M.pyramidata* 3; *A.vesicaria* = *M.sedifolia* 4; *A.vesicaria* < *M.sedifolia* 5; *M.sedifolia* 6;*A.vesicaria* > *M.sedifolia*

SPECIES

	2	3	4	5	6	7	8	9	10	11
1	***	ns	ns	***	**	*	*	ns	ns	ns
2		ns	ns	***	***	***	*	ns	ns	***
3			***	ns	ns	ns	ns	ns	ns	ns
4				ns	ns	ns	ns	ns	ns	ns
5					***	**	***	ns	ns	*
6						*	***	ns	ns	*
7							ns	ns	ns	**
8								ns	ns	ns
9									***	ns
10										ns

Table 3.2 The significance of X^2. *** $p<0.001$; ** $0.01> p >0.001$; * $0.05> p >0.01$;ns non significant. The species are 1 Daucus glochidiatus, 2 Crassula colorata, 3 Brachycome lineariloba, 4 Crassula sieberana, 5 Senecio quadridentatus, 6 Tetragonia eremaea, 7 Schismus barbatus, 8 Vittadinia cuneata, 9 Medicago minima, 10 Emex australis, 11 Calotis hispidula

	DENSITY F-max		BIOMASS F-max	
Actinobole uliginosum	9.0	*	157.7	**
Atriplex spongiosa	4.5	ns	150.1	**
Brachycome leariloba	10.6	*	72.5	**
Bulbine semibarbata	0	-	0	-
Calandrinia eremaea	1.0	ns	61.1	**
Calotis hispidula	11.6	*	7.1	ns
Chenopodium cristatum	0	-	0	-
Crassula colorata	20.9	**	66.5	**
Crassula sieberana	21.1	**	341.1	**
Danthonia caespitosa	82.6	**	3.1	ns
Daucus glochidiatus	210.7	**	222.9	**
Erodium cygnorum	5.3	ns	191.6	**
Emex australis	1089.3	**	9.4	*
Gnephosis burkittii	1.8	ns	14.3	**
Goodenia pusilliflora	19.7	**	73.8	**
Helipterum pygmaeum	7.2	ns	4.1	ns
Hernaria hirsuta	100.5	**	77.9	**
Hordeum leporinum	14.1	**	5.8	ns
Hypochoeris glabra	0	-	0	-
Isoetopsis graminifolia	0	-	0	-
Lophochloa pumila	71.3	**	41.6	**
Medicago minima	0	-	0	-
Omphalolappula concava	0	-	0	-
Oxalis corniculata	1.8	ns	5.1	ns
Plantago drummondii	435.6	**	26.6	**
Schismus barbatus	810.5	**	1106.5	**
Sclerolaena sp	20.0	**	42.1	**
Senecio quadridentatus	8.5	*	21.3	**
Sonchus oleraceus	16.1	**	210.3	**
Stellaria sp	0	-	0	-
Stipa nitida	20.3	**	3.4	ns
Tetragonia eremaea	21.9	**	31.0	**
Tripogon loliiformis	178.3	**	200.5	**
Vittadinia cuneata	470.6	**	1075.8	**

Table 3.3 F-max ratio and its significance for both density and biomass values, testing for homogeneity of variances between the six vegetation groups. * 0.05> p >0.01 ; ** p<0.01 ; ns non significant. - indicates insufficent values for a valid calculation.

	VEGETATION GROUPS					
	1	2	3	4	5	6
Actinoble uliginosum	1	0	3	0	0	1
Atriplex spongiosa	2	2	1	1	0	1
Brachycome lineariloba	6	2	0	0	7	0
Bulbine semibarbata	0	0	0	0	0	1
Calandrinia eremaea	1	1	1	0	0	0
Calotis hispidula	3	3	1	0	1	1
Chenopodium cristatum	0	1	0	0	0	0
Crassula colorata	22	18	41	24	60	54
Crassula sieberana	86	64	19	0	27	0
Danthonia caespitosa	0	1	0	0	9	0
Daucus glochidiatus	25	4	32	2	22	13
Erodium cygnorum	1	1	2	0	2	0
Emex australis	0	33	1	0	0	0
Gnephosis burkittii	1	0	1	0	0	0
Goodenia pusilliflora	5	1	2	0	5	0
Helipterum pygmaeum	1	0	2	0	0	0
Hernaria hirsuta	2	10	2	0	0	1
Hordeum leporinum	0	0	2	0	0	8
Hypochoeris glabra	17	0	0	0	0	0
Isoetopsis graminifolia	0	0	4	0	0	0
Lophochloa pumila	25	14	77	58	137	21
Medicago minima	0	68	0	0	0	0
Omphalolappula concava	4	0	0	0	0	0
Oxalis corniculata	1	0	1	0	0	0
Plantago drummondii	21	0	1	3	0	6
Senecio quadridentatus	4	0	2	2	0	5
Schismus barbatus	331	109	33	88	10	48
Sclerolaena sp	3	0	1	5	6	2
Sonchus oleraceus	4	0	0	0	0	1
Stellaria sp.	2	0	0	0	0	0
Stipa nitida	1	2	0	0	6	0
Tetragonia eremaea	12	4	23	7	9	6
Tripogon loliiformis	3	0	0	0	0	45
Vittadinia cuneata	1	0	8	1	2	21

Table 3.4 The maximum densities (no./tray) recorded for the annual species in each vegetation type. Vegetation groups are 1;A.vesicaria 2; M.pyramidata 3; A.vesicaria = M.sedifolia 4; A.vesicaria < M.sedifolia 5; M.sedifolia 6; A.vesicaria > M.sedifolia

	VEGETATION GROUPS					
	1	2	3	4	5	6
Actinoble uliginosum	0.1	0	0.3	0	0	0.1
Atriplex spongiosa	0.3	0.3	0.2	0.1	0	0.4
Brachycome lineariloba	0.6	0.3	0	0	0.8	0
Bulbine semibarbata	0	0	0	0	0	0.1
Calandrinia eremaea	0.1	0.1	0.1	0	0	0
Calotis hispidula	0.5	0.5	0.1	0	0.1	0.2
Chenopodium cristatum	0	0.1	0	0	0	0
Crassula colorata	7.7	3.1	19.7	7.2	16.4	17.7
Crassula sieberana	14.6	9.4	1.9	0	2.7	0
Danthonia caespitosa	0	0.1	0	0	1.4	0
Daucus glochidiatus	10.6	1.1	7.9	0.5	2.8	4.4
Erodium cygnorum	0.2	0.2	0.5	0	0.6	0
Emex australis	0	4.5	0.1	0	0	0
Gnephosis burkittii	0.1	0	0.2	0	0	0
Goodenia pusilliflora	0.9	0.2	0.2	0	1.2	0
Helipterum pygmaeum	0.1	0	0.5	0	0	0
Hernaria hirsuta	0.2	1.5	0.4	0	0	0.1
Hordeum leporinum	0	0	0.3	0	0	0.8
Hypochoeris glabra	1.7	0	0	0	0	0
Isoetopsis graminifolia	0	0	0.4	0	0	0.3
Lophochloa pumila	6.1	6.6	14.7	14.5	20.0	4.4
Medicago minima	0	7.1	0	0	0	0
Omphalolappula concava	0.5	0	0	0	0	0
Oxalis corniculata	0.2	0	0.1	0	0	0
Plantago drummondii	2.3	0.1	0.5	0	0.7	0
Schismus barbatus	48.6	38.9	7.6	16.7	2.2	11.8
Sclerolaena sp.	0.5	0	0.2	1.0	1.4	0.3
Senecio quadridentatus	0.9	0	0.6	0.2	0	1.1
Sonchus oleraceus	0.5	0	0	0	0	0.1
Stellaria sp.	0.2	0	0	0	0	0
Stipa nitida	0.2	0.2	0	0	0.6	0
Tetragonia eremaea	2.1	1.0	4.5	2.1	1.8	1.2
Tripogon loliiformis	0.5	0	0	0	0	5.9
Vittadinia cuneata	0.1	0	0.8	0.2	0.2	3.2

Table 3.5 The mean density (no./tray) of the species germinated in the trays for the 6 vegetation groups. The vegetation groups are 1; A.vesicaria 2; M.pyramidata 3; A.vesicaria = M.sedifolia 4; A.vesicaria < M.sedifolia 5; M.sedifolia 6; A.vesicaria > M.sedifolia

	VEGETATION GROUPS					
	1	2	3	4	5	6
Actinobole uliginosum	0.3	0	0.9	0	0	0
Atriplex spongiosa	0.7	0.7	0.4	0.3	0	0.5
Brachycome lineariloba	1.9	0.7	0	0	2.0	0
Bulbine semibarbata	0	0	0	0	0	0.3
Calandrinia eremaea	0.3	0.3	0.3	0	0	0
Calotis hispidula	1.1	1.0	0.3	0	0.3	0.4
Chenopodium cristatum	0	0.3	0	0	0	0
Crassula colorata	8.2	5.4	14.5	8.3	24.9	18.4
Crassula sieberana	7.6	20.3	6.0	0	8.5	0
Danthonia caespitosa	0	0.3	0	0	2.9	0
Daucus glochidiatus	10.2	1.4	10.0	0.7	6.8	4.7
Erodium cygnorum	0.4	0.4	0.7	0	0.9	0
Emex australis	0	10.5	0.3	0	0	0
Gnephosis burkittii	0.3	0	0.4	0	0	0
Goodenia pusilliflora	0.7	0.4	0.6	0	1.9	0
Helipterum pygmaeum	0.3	0	0.8	0	0	0
Hernaria hirsuta	0.6	3.2	0.8	0	0	0.3
Hordeum leporinum	0	0	0.7	0	0	2.5
Hypochoeris glabra	5.4	0	0	0	0	0
Isoetopsis graminifolia	0	0	0.9	0	0	0.7
Lophochloa pumila	7.7	4.9	22.9	19.4	41.9	6.9
Medicago minima	0	21.4	0	0	0	0
Omphalolappula concava	1.3	0	0	0	0	0
Oxalis corniculata	0.4	0	0.3	0	0	0
Plantago drummondii	6.6	0.3	1.1	0	1.8	0
Schismus barbatus	104.6	42.3	9.6	26.0	3.6	14.7
Sclerolaena sp.	1.1	0	0.4	1.9	1.8	0.6
Senecio quadridentatus	1.5	0	0.8	0.6	0	1.8
Sonchus oleraceus	1.3	0	0	0	0	0.3
Stellaria sp.	0.6	0	0	0	0	0
Stipa nitida	0.4	0.6	0	0	1.9	0
Tetragonia eremaea	3.7	1.5	7.0	2.6	2.7	2.0
Tripogon loliiformis	1.1	0	0	0	0	14.4
Vittadinia cuneata	0.3	0	2.5	0.4	0.6	6.8

Table 3.6 The standard deviations associated with the mean densities presented in table 3.5 for the vegetation groups. The vegetation groups are 1; A.vesicaria 2; M.pyramidata 3; A.vesicaria = M.sedifolia 4; A.vesicaria < M.sedifolia 5; M.sedifolia 6; A.vesicaria > M.sedifolia

	VEGETATION GROUPS					
	1	2	3	4	5	6
Actinoble uliginosum	0.005	0	0.628	0	0	0.043
Atriplex spongiosa	1.026	0.212	0.115	0.110	0	0.144
Brachycome lineariloba	0.387	0.266	0	0	0.631	0
Bulbine semibarbata	0	0	0	0	0	0.176
Calandrinia eremaea	0.172	0.022	0.054	0	0	0
Calotis hispidula	0.201	0.111	0.072	0	0.169	0.056
Chenopodium cristatum	0	0.005	0	0	0	0
Crassula colorata	1.622	0.409	3.374	0.381	1.032	1.301
Crassula sieberana	2.030	0.806	0.511	0	0.154	0
Danthonia caespitosa	0	0.192	0	0	0.379	0
Daucus glochidiatus	11.780	0.754	7.573	0.501	2.263	2.357
Emex australis	0	7.494	2.076	0	0	0
Erodium cygnorum	0.926	0.540	1.147	0	1.134	0
Gnephosis burkittii	0.163	0	0.043	0	0	0
Goodenia pusilliflora	0.158	0.078	0.110	0	1.045	0
Helipterum pygmaeum	0.077	0	0.451	0	0	0
Hernaria hirsuta	0.014	0.816	0.172	0	0	0.087
Hordeum leporinum	0	0	3.411	0	0	4.755
Hypochoeris glabra	0.191	0	0	0	0	0
Isoetopsis graminifolia	0	0	0.245	0	0	0
Lophochloa pumila	8.943	9.293	17.316	4.240	14.575	6.045
Medicago minima	0	7.677	0	0	0	0
Omphalolappula concava	0.128	0	0	0	0	0
Oxalis corniculata	0.036	0	0.015	0	0	0
Plantago drummondii	0.135	0	0.068	0.364	0	0.351
Schismus barbatus	24.713	23.240	4.736	2.975	0.637	10.647
Sclerolaena sp.	0.466	0	0.137	0.289	0.765	0.113
Sonchus oleraceus	4.109	0	0	0	0	0.279
Stellaria sp.	0.185	0	0	0	0	0
Stipa nitida	0.891	1.444	0	0	0.775	0
Tetragonia eremaea	1.998	1.089	2.332	0.644	0.792	0.693
Tripogon loliiformis	4.103	0	0	0	0	19.419
Vittadinia cuneata	0.068	0	0.227	2.258	0.223	0.290

Table 3.7 Total biomass (g dry wt) for each species for the vegetation groups. The vegetation groups are 1; *A.vesicaria* 2; *M.pyramidata* 3; *A.vesicaria* = *M.sedifolia* 4; *A.vesicaria* < *M.sedifolia* 5; *M.sedifolia* 6;*A.vesicaria* > *M.sedifolia*

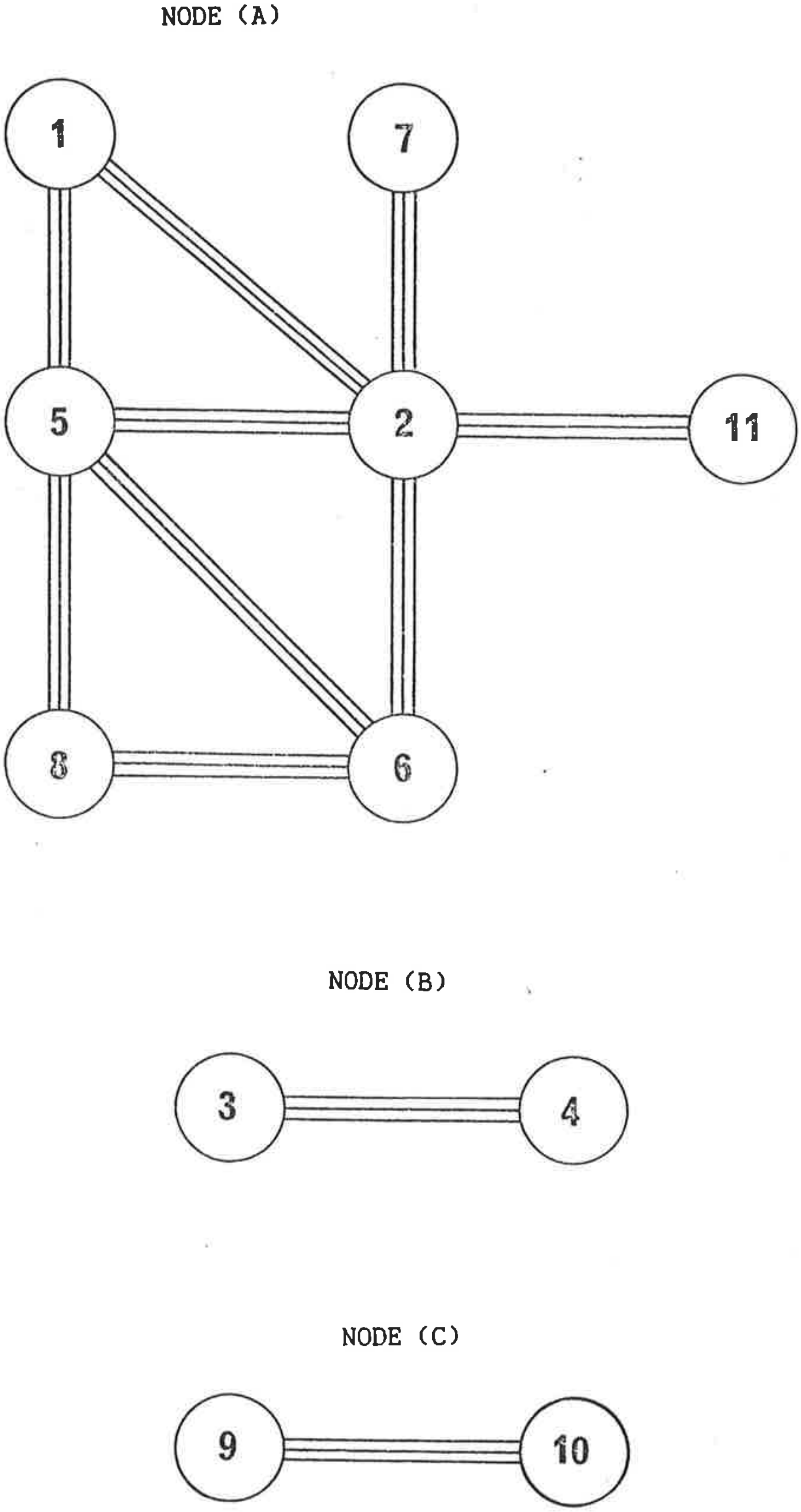


Figure 3.1 Nodes of associated species. Only associations of $p < 0.001$ are shown. Species (1) Daucus glochidiatus (2) Crassula colorata (3) Brachycome lineariloba (4) Crassula sieberana (5) Senecio quadridentatus (6) Tetragonia eremaea (7) Schismus barbatus (8) Vittadinia cuneata (9) Medicago minima (10) Emex australis (11) Calotis hispidula

4. SEASONALITY OF ANNUALS

4.1 Introduction

In this chapter a number of aspects concerning the seasonal occurrence of annuals in the Middleback region are investigated. The first part of the chapter contains an analysis of the Middleback rainfall patterns to determine when annuals are most likely to occur. This is then followed by field data on the seasonal occurrence of annuals and laboratory germination of seeds in topsoils. The final section discusses the physiological and morphological differences of summer and winter annuals and how this relates to the Middleback annual flora.

4.2 Rainfall patterns

4.2.1 Introduction

The germination of annual plants is controlled by available moisture for imbibition. It should be possible therefore to speculate upon the seasons of the year when annual plants are most likely to germinate in any given area by an inspection of the long term rainfall records. If rain consistently fell in a single season, then it might be expected that germination and growth of annuals would be restricted to that time of the year. If there were two wet seasons at different times of the year, two separate annual floras might be expected. Also the greater the temperature contrast between the seasons in which rainfall events occur, the more likely it would be that annual floras of different floristic composition would occur. This is probably the situation which gave rise to the summer and winter annuals observed by Went (1957) and also by Mott (1972a). If the temperature conditions are similar then the annual floras may also be similar.

In a region where the rainfall is erratic and unpredictable the chance of obtaining distinct annual floras would decrease. The annual species in this situation are more likely to have a broad range of temperatures at which they can germinate which would allow them to utilise the significant rainfall events regardless of the time of year at which the rainfall occurred.

Analysis of the rainfall data available for Middleback Station, based upon the probability of rainfalls of different magnitude occurring throughout the year, may allow the prediction of which seasons annual plants are most likely to germinate and grow. The rainfall characteristics of the study region were described in general terms (Chapter 2), however in this section it is proposed to speculate upon the potential for seasonal floras to germinate in the Middleback area based on an analysis of the long term rainfall records.

4.2.2 Rainfall analysis

The brief description of the Middleback rainfall (section 2.2.2) does not indicate the effectiveness of the rainfall or the consequences for the population dynamics of annual plants. The summer months, on average, have falls of greater magnitude than the winter months. The mean rainfall event (Fig. 4.1) for each month indicates that the average fall is greatest in February (13 mm) while the average fall in July is only 4.2 mm.

Figure 4.2 shows the frequency distribution for falls of different magnitudes. The figures show that there is a low frequency of light falls (< 1 mm) during the summer months, the majority of the falls are in the range 1 mm to 5 mm and 5 mm to 10 mm. In February there were five falls in the range 50 mm to 75 mm and one fall of between 150 mm and 200 mm (not shown). The winter months have a much larger number of falls but the distribution of the falls is in the range of <1 mm, 1-5 mm and 5-10 mm with the greatest number of falls occurring in the range 1-5 mm. There has never been a fall greater than 35 mm recorded in June or July. As annual growth events are initiated by heavy rainfall events it would appear that initiating rains are more likely to occur in the summer months.

4.2.3 Discussion

There is pattern in the seasonal distribution of rainfall at Middleback Station. The records indicate a slight dominance of summer rainfall but the summer events are not predictable. The summer peak is caused by infrequent, heavy rainfall events whereas the winter rainfall is composed of frequent and predictable light rains. The high evaporative loss over the year with exceptionally high rates found during the summer months (Table 2.1) will markedly reduce the effectivenss of the summer rains.

The effectiveness of rainfall also depends on the intensity and duration of falls. The summer falls are often of high intensity and short duration which can result in considerable runoff. In contrast, the light winter rains are usually of low intensity and so do not produce runoff to the same degree. These rains are effective for annuals because the frequent low intensity falls keep the soil surface moist. The lower evaporation rates during the winter months increase the effectiveness of the these falls.

The most important single requirement for annual germination is the presence of sufficient moisture in the soil for imbibition to occur. Heavy summer rains saturate the surface for only a short period of time due to rapid evaporation and the long interval between falls. The winter rainfall of lower intensity but higher frequency may be as effective as the heavy summer rainfall events. The absence of predictable trends in the rainfall pattern from one year to the next (Fig. 2.2 & Table 4.1) suggests that the germination and growth of annual plants may not be restricted to a specific season.

The temperature immediately following a rainfall event will also be important in determining which annual species germinate. This aspect is considered in Chapter 5 in relation to changes in the annual vegetation from one year to the next.

In conclusion, due to the unpredictability of the rainfall events required to initiate the germination of the annual plants, it is unlikely that distinct summer and winter floras would be found in the study region.

4.3 Field studies

4.3.1 Introduction

The opportunity arose in early 1979 to study the changes in a population of annuals which germinated in late summer. In late February 1979, 71.4 mm of rain fell on one day followed by a further 13.6 mm the next day. It was expected that following a rainfall event of this magnitude there would be germination of annuals. It was proposed to determine the species of annuals which germinated following this rainfall event and to monitor the annual flora to determine if any seasonal changes occurred throughout the year. Although the rainfall of the region is unpredictable (Sect. 4.2) it was hoped that subsequent rainfall events would occur in the year, and that these events would also cause germination of annuals. I was fortunate in that following February, there were four heavy falls of rain which occurred in May, September, November and December. The calender year of 1979 ended as the third wettest year on record (Figs. 2.2 & 5.29).

4.3.2 Methods

Three sites dominated by different perennial species representing a range of potential habitats were chosen in February 1979. All sites were chosen away from trees as there is evidence to suggest that trees influence the abundance of annuals (Johnson, 1978).

Site 1 *Atriplex vesicaria* - *Maireana sedifolia*

The first site was located in the north-east of Railway Paddock (Fig. 2.1). The vegetation in this area consisted of *Atriplex vesicaria*

- Maireana sedifolia with some Rhagodia ulicina and Zygophyllum aurantiacum and occasional Lycium australe. The soil was covered by a well developed lichen crust which indicated that the area had not been heavily grazed by sheep.

Site 2 Atriplex vesicaria

The second site was located in the north-east corner of Overland Paddock (Fig. 2.1) in a shallow drainage line dominated by Atriplex vesicaria. The site was a considerable distance from the nearest water (approx. 3 km) and although sheep were observed in the area on occasions, the site was not heavily grazed.

Site 3 Maireana pyramidata

The third site was located east of Coco Dam, halfway along the western boundary of Depot Paddock (Fig. 2.1). The vegetation in this area was predominantly Maireana pyramidata. Unlike the previous two sites this site was heavily grazed due to the proximity of the dam. The soil surface had been badly broken by the movement of sheep to and from the dam.

At each site, 10 quadrats were located at 2 m intevals along a transect. In some arid regions the perennial bushes influence the distribution of annual plants (Chapter 5). To avoid the possible effects of bushes a quadrat size was chosen which could be placed between the bushes. The quadrat size used was 50 cm x 50 cm. The corners of each quadrat were marked with small pins and a wire frame was used to accurately define the quadrat. The numbers of individuals of each species were recorded on 12 occasions during the period March

1979 to November 1979.

4.3.3 Results

Site 1 *Atriplex vesicaria*-*Maireana sedifolia*

At the *Atriplex vesicaria* - *Maireana sedifolia* site, a total of 13 species germinated as a result of the February 1979 rainfall event. The mean density of selected species is shown in Figure 4.3. The means and standard deviations for *Actinobole uliginosum*, *Daucus glochidiatus*, *Plantago drummondii*, *Senecio quadridentatus* and *Swainsona oliveri* were omitted due to the low occurrence of these species. *Daucus glochidiatus* and *Actinobole uliginosum* were present on one occasion only, and only one individual of each was present. *Plantago drummondii* was recorded on two occasions at low density. *Senecio quadridentatus* was present at low density from July to September. *Swainsona oliveri* was present at low density from April to July.

The majority of the remaining species germinated following the February rains and then persisted until the onset of the drier months. The exception was *Tetragonia eremaea* which was only recorded from late April to September.

Not all the species could be regarded as true annuals. *Danthonia caespitosa*, *Maireana sclerolaenoides* and *Sclerolaena obliquicuspis* responded to the December rainfall (Fig. 5.29). Their response was not new germination but revitalization of the existing individuals, many of which appeared dead.

Species exhibited a wide range of densities. The most common species was *Erodium cygnorum* which was present at high density for much of the year. Extensive germination of *E.cygnorum* followed the February rains and the population was maintained until June. Thereafter, *E.cygnorum* declined in density and no individuals were recorded in November. The species germinated following heavy rain in December (Chapter 5), but rapid loss of soil moisture due to high summer temperatures killed the individuals before they reached maturity.

The other species showed a similar trend to *E.cygnorum* although they occurred in lower densities. *Danthonia caespitosa* was the only species to show a steady increase in the population throughout the year with the highest density recorded in September.

The standard deviations for most species were greater than the means (coefficient of variation > 1) indicating a high degree of variability in the density of the species on individual quadrats. *Erodium cygnorum* was the only species where the standard deviations were considerably less than the mean densities throughout the study.

Site 2 *Atriplex vesicaria*

The trends in density of annuals at the *Atriplex vesicaria* site (Fig. 4.4 & 4.5) were similar to those for the *A.vesicaria*-*Maireana sedifolia* site although some species exhibited different patterns. The species present in highest density were *Danthonia caespitosa*, *Helipterum floribundum*, *Daucus glochidiatus* and *Sonchus oleraceus*.

Brachycome lineariloba and *Daucus glochidiatus* were recorded from June to September. Neither species germinated following the

February rains. The interpretation of this behaviour is that these two species represent winter annuals and can only germinate in the cooler months. Another species which was recorded in the cooler months was Emex australis.

Tetragonia eremaea did not appear in the quadrats until late April but then persisted throughout the year to September as it did at the previous site. Plantago drummondii showed differences in abundance between the two sites. It was uncommon at the A.vesicaria-M.sedifolia site but at the A.vesicaria site it was more abundant and persisted for a greater length of time. Two populations were observed. The first germinated following the February rains but had died by late June. This species again germinated in July and a small proportion of this population persisted until September.

Individuals of Erodium cygnorum, Euphorbia drummondii and Hypochoeris glabra had all died by August whereas the first two species persisted to September at the previous site. The numbers of Erodium cygnorum were lower than at the previous site.

Site 3 Maireana pyramidata

A total of 23 herbaceous species were recorded, of which 15 were uncommon. The remaining 8 species are referred to in Figure 4.6. A number of the species recorded at the Maireana pyramidata site were not recorded at the previous two sites. As with the previous sites a number of species germinated following the February rains and a second group germinated in the winter months. This second group comprised Tetragonia eremaea, Helipterum pygmaeum, Actinobole uliginosum, Brachycome lineariloba, Isoetopsis graminifolia, Hernaria hirsuta, Lophocloa pumila, Schismus barbatus and Goodenia pusilliflora. Three species of low abundance, namely Medicago minima, Hordeum leporinum and Hypochoeris glabra were also present.

The species present in highest density at this site, Gnephosis burkittii, Calotis hispidula, Actinobole uliginosum, Omphalolappula concava and Sclerolaena obliquicuspis, were different to the dominant species at the other sites.

The changes in the annual vegetation on one of the quadrats at this site are shown in Plate 1.

4.3.4 Discussion

The majority of species germinated following the February rains and were recorded throughout the year. Although distinct seasonal floras could not be identified, a few species did not germinate until later in the year (Fig. 4.2). Tetragonia eremaea did not germinate at any site following the February rains, but germinated in April when temperatures were considerably cooler. Two other species, Daucus glochidiatus and Brachycome lineariloba only germinated in the winter months.

Once germinated, the majority of species persisted throughout the year, although some species showed marked fluctuations in abundance. The changes in density were the result of mortality, grazing and germination of new individuals. Increases in the density of species between readings indicated that many of the annual species have the ability to respond to rainfall at different times of the year and were not restricted to germination at one time of the year only. Differences in the species abundance between sites may be the result of the quantity of rainfall at each site, site characteristics and individual species characteristics.

Many studies of annuals from different regions of the world (Went 1948,1949; Beatley 1974; Tevis 1958; Mott 1972a) have classified annual communities into summer and winter floras. A classification of this nature is not appropriate for the annual communities described here. Middleback annuals are ephemeral or opportunistic in the sense that they may utilise rainfall events for germination at different times of the year when the temperature conditions are different.

The weather conditions during 1979 were not necessarily typical for the Middleback area. The year of 1979 was the third wettest on record with a number of heavy rainfall events occurring during the year. The temporal patterns in the distribution of annual plants observed in this study may be the consequence of the unusually wet conditions. Frequent falls of rain may have allowed the populations of many species to survive for a longer period than normal. In drier years there may be a greater separation of species into seasonal floras.

The temperature at the time of the initiating rain would determine which species germinated. As well as seasonal fluctuations in temperature (section 2.2.3) marked differences may occur within a period of days. The rainfall event in February 1979 which initiated germination was followed by average temperatures for that month. If the period immediately following had been hotter or colder a quite different result may have been obtained. A 20° C difference in daily maximum temperatures can occur in February and temperature differences of this magnitude would markedly influence the germination of the annual plants. The seasonal abundance of annual plants may be different from one year to the next depending upon the month in which the rainfalls occur and the daily temperature following rainfall.

4.4 Laboratory germination

4.4.1 Introduction

A constraint on the interpretation of the field study was that it relied upon the particular 1979 sequence of rainfall events to trigger the germination of annuals described in the previous section. The results may have been different with an alternative rainfall pattern. To investigate this possibility the annual flora was studied under simulated summer and winter conditions in the laboratory.

4.4.2 Methods

In order to maximise the number of species of seed in the soil samples for this study, samples were collected from a number of sites[1] and were thoroughly mixed. Samples were taken from the top 2.5 cm of the soil surface, both from beneath bushes and between bushes. Thirty samples of 500 g were placed in small aluminium trays. Fifteen samples were placed in the growth cabinet and watered under a summer temperature regime (28° C[2], 18° C night) and the remainder under a winter temperature regime (15° C, 8° C night). The field capacity of the soil was determined as in Section 3.2.3 and the soils were

[1] Collected in January 1981

[2] Light intensity of 250-300 μeinsteins/m^2/sec in the 400 - 750 nm range

watered to 90% field capacity every third day for the winter regime and every second day for the summer regime. When the plants had grown sufficiently to enable them to be identified[1] the experiment was terminated and the number of individuals of the different species were counted.

4.4.3 Results

Sixteen species germinated under the summer temperature regime and 23 under the winter regime (Table 4.3). Seven were unique to the winter temperature regime, including Brachycome lineariloba and Daucus glochidiatus. No species germinated only in response to summer temperature conditions.

The abundance of the species across the two temperature regimes differed markedly. Crassula colorata, Tetragonia eremaea, Lophochloa pumila and Schismus barbatus were more abundant in respose to the winter temperature regime. Erodium cygnorum, Euphorbia drummondii and Danthonia caespitosa were more abundant in response to summer temperatures than winter temperatures.

4.4.4 Discussion

The annual flora appears to be opportunistic with many species germinating over a wide range of temperatures. A number of species germinated under cool conditions, however these represented only a small subset of the total annual flora of the area. Marked differences were found in the abundance of some species depending upon the

[1] Seven weeks

temperature regime used.

Studies of the germination requirements of annuals (Mott 1972a) have shown that many annuals can germinate within a range of temperatures. Maximum germination for a species usually occurs within a narrow band of temperatures. The situation described here may represent a group of species which have a wide range of temperatures within which they can germinate as opposed to a narrow band. The species which were restricted to winter germination possibly represent a group with a narrow range of temperatures within which they can germinate. It is interesting to note that a number of these species which were found to germinate in the cooler months were not native species.

4.5 Physiological and habit characteristics

4.5.1 Introduction

The previous sections indicated that few species of annuals in the study area germinated and grew in only one season of the year. No species were identified as summer annuals. The annual species found at Middleback are unlikely to possess the characteristics of summer annuals that were found for the Sonoran and Mojave Desert annuals by Mulroy & Rundel (1977). In this section the annuals are categorised on the basis of the physiological and habit characteristics recorded by Mulroy & Rundel (1977).

4.5.2 Methods

The photosynthetic pathway in plants can be identified from leaf anatomy with which it correlates (Esau,1977). In C3 plants the chloroplasts are scattered throughout the pallisade and spongy mesophyll cells. In C4 plants a dense concentration of chloroplasts in the cells surrounding the vascular bundles can usually be seen and is referred to as Krantz anatomy. It can be seen following hand sectioning of leaves.

The study was not intended as a detailed study of the leaf anatomy of herbaceous species but simply to determine if Krantz anatomy was present. For this reason hand sectioning of live material with immediate inspection under a compound microscope was the method used. The habit of the species was also recorded. The plants were classified as erect, prostrate, radial and cauline.

To ensure that there was no confusion in the recognition of Krantz anatomy a section of Atriplex vesicaria, a known C4 plant, was used as a reference species. For the standard reference species Krantz anatomy was obvious with inspection at low magnifications. Some of the herbaceous species were difficult to hand section due to the small size of leaves and the soft nature of the leaf tissue. The species which were difficult to section have been excluded from the results.

4.5.3 Results

The results of the dissection and inspection of the leaves for Krantz anatomy and classification of the different herbaceous species are presented in Table 4.4. Krantz anatomy was not observed in any of the annual species sectioned indicating that all possessed C3 photosynthesis.

The species showed a range of habits with the majority of the species being erect. Tetragonia eremaea, Euphorbia drummondii, Actinobole uliginosum and Gnephosis burkittii were prostrate.

4.5.4 Discussion

Mulroy & Rundel (1977) found physiological and habit differences between summer and winter annuals. The differences were explained in terms of the conditions to which summer and winter annuals are subject during their growing period. The one period of the year in which annual plants do not commonly appear is in mid-summer. Annuals may germinate following heavy rains in late summer but there are no species for which the growing season coincides with the summer season.

Groups of annuals could not be recognised on the basis of their physiology. If C4 photosynthsis is an adaptation to growth during the summer season then it would not provide any advantage to the species described in this chapter.

4.6 Conclusions

The three studies described in this chapter indicate that mutually exclusive summer and winter annual floras do not occur at Middleback station. The study area shows an irregular and unpredictable rainfall pattern which would be unlikely to lead to the development of seasonal floras. As rainfall is unpredictable the most successful strategy for annual species is to germinate over a wide range of temperatures. This ensures that at least some germination occurs after rain irrespective of season, which may lead to reproduction. There would be little advantage for annual species to have a narrow set of conditions under which they could germinate in such an unpredictable environment unless they were able to persist as dormant seed in the seed bank for some years. The annual flora may be best described as ephemeral or opportunistic in that it utilises favourable conditions whenever they occur.

	Rainfall event (mm)				
	>50	>40	>30	>20	>10
JANUARY	1	4	6	11	27
FEBURARY	6	9	12	19	32
MARCH	0	1	3	10	26
APRIL	1	2	4	10	25
MAY	0	1	4	7	31
JUNE	0	0	1	8	27
JULY	0	0	1	5	21
AUGUST	0	0	2	4	21
SEPTEMBER	1	2	3	7	24
OCTOBER	1	1	8	11	34
NOVEMBER	1	1	3	10	27
DECEMBER	1	1	5	11	27

Table 4.1. The frequency with which falls of rain greater than the indicated amount have fallen at Middleback homestead (1925-1983).

Atriplex vesicaria - Maireana sedifolia site	Reading no 1	2	3	4	5	6	7	8	9	10	11	12
Actinobole uliginosum			+									
Calotis hispidula		+	+	+	+	+	+	+	+	+	+	
Danthonia caespitosa		+	+	+	+	+	+	+	+	+	+	+
Daucus glochidiatus							+					
Erodium cygnorum		+	+	+	+	+	+	+	+	+	+	
Euphorbia drummondii		+	+	+	+	+	+	+	+	+	+	
Maireana sclerolaenoides		+	+	+	+	+	+	+	+	+	+	+
Plantago drummondii		+					+					
Sclerolaena obliquicuspis		+	+	+	+	+	+	+	+	+	+	
Senecio quadridentatus									+	+	+	
Swainsona oliveri			+	+	+	+	+	+	+			
Tetragonia eremaea				+	+	+	+	+	+	+	+	
Zygophyllum crenatum		+	+	+	+	+	+	+	+	+	+	

A.vesicaria site	1	2	3	4	5	6	7	8	9	10	11	12
Actinobole uliginosum					+	+	+	+	+	+		
Brachycome lineariloba						+	+	+	+	+	+	
Calotis hispidula		+	+	+	+	+	+	+	+	+		
Chenopodium cristatum			+	+	+							
Danthonia caespitosa		+	+	+	+	+	+	+	+	+	+	+
Daucus glochidiatus						+	+	+	+	+	+	
Emex australis					+	+	+					
Erodium cicutarium		+	+	+	+	+	+	+	+	+	+	
Erodium cygnorum		+	+	+	+	+	+	+	+			
Euphorbia drummondii		+	+	+	+	+	+		+			
Helipterum floribundum		+	+	+	+	+	+	+	+	+	+	
Hypochoeris glabra		+	+	+	+	+	+	+	+			
Medicago minima			+	+	+	+	+	+	+	+	+	
Plantago drummondii		+	+	+	+	+			+	+	+	
Sclerolaena obliquicuspis		+	+	+	+	+	+	+	+	+	+	
Sonchus oleraceus		+	+	+	+	+	+	+	+	+	+	
Tetragonia eremaea				+	+	+	+	+	+	+	+	
Vittadinia cuneata				+	+	+	+	+	+	+	+	

Maireana pyramidata site	1	2	3	4	5	6	7	8	9	10	11	12
Brachycome lineariloba			+	+	+	+	+	+	+	+	+	
Calotis hispidula		+	+	+	+	+	+	+	+	+		
Chenopodium cristatum			+	+	+	+	+	+				
Crassula colorata							+	+	+	+		
Emex australis			+	+	+	+	+	+	+	+	+	
Erodium cicutarium			+	+	+	+	+	+	+	+	+	
Erodium cygnorum			+	+	+	+			+			
Eragrostis dielsii		+	+	+	+	+	+	+	+	+	+	
Euphorbia drummondii		+	+	+	+	+	+	+	+	+	+	
Goodenia pusilliflora							+	+	+	+	+	
Gnephosis burkitii		+	+	+	+	+	+	+	+			
Helipterum pygmaeum					+	+	+	+	+	+	+	
Hernaria hirsuta							+	+	+	+	+	
Hordeum leporinum									+	+	+	
Hypochoeris glabra						+	+					
Isoetopsis graminifolia							+	+	+	+		
Lophochloa pumila						+	+	+	+	+	+	
Medicago minima		+										
Schismus barbatus						+	+	+	+	+	+	
Sclerolaena obliquicuspis		+	+	+	+	+	+	+	+	+	+	
Tripogon loliiformis		+	+	+	+	+	+	+	+	+	+	
Tetragonia eremaea					+	+	+	+	+	+	+	

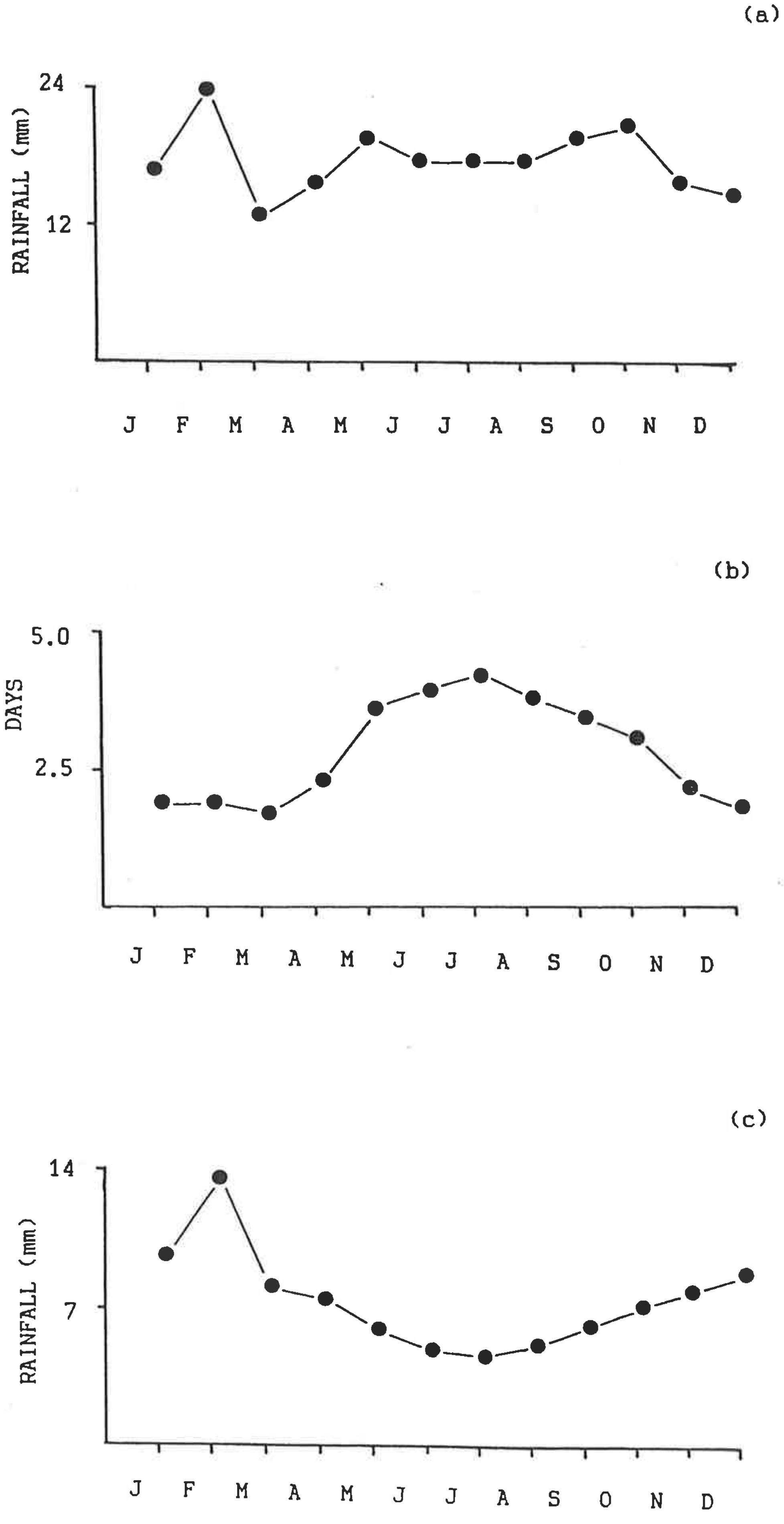
Table 4.2. Summary of occurrance (indicated by +) of annual species at the three sites. Dates of the readings are 1. 25/Feb. 2. 25/Mar. 3. 7/Apr. 4. 21/Apr. 5. 7/May 6. 7/Jun. 7. 21/Jun. 8. 7/Jul. 9. 21/Jul. 10. 7/Aug. 11. 15/Sep. 12. 15/Nov.

	Temperature regime	
	Summer	Winter
Brachycome lineariloba	0	15
Calotis hispidula	3	3
Crassula colorata	14	69
Danthonia caespitosa	21	5
Daucus glochidiatus	0	12
Erodium cicutarium	2	1
Erodium cygnorum	51	6
Euphorbia drummondii	10	1
Helipterum pygmaeum	1	4
Hernaria hirsuta	0	6
Isoetopsis graminifolia	0	6
Lophochloa pumila	7	102
Omphalolappula concava	1	5
Plantago drummondii	5	3
Schismus barbatus	5	177
Senecio quadridentatus	0	6
Sonchus oleraceus	2	1
Spergularia rubra	0	18
Stipa nitida	5	1
Swainsona oliveri	2	1
Tetragonia eremaea	23	171
Wahlenbergia gracilentia	0	4
Zygophyllum crenatum	3	6

Table 4.3. The number of annual species germinated under summer and winter temperature regimes in the laboratory. The numbers are the totals germinated in 15 replicate trays for each temperature regime. The temperatures used were for summer 28° / 18° C and for winter 15° / 8° C.

	C3/C4	Habit
Actinobole uliginosum	C3	P
Alyssum linifolium	C3	E
Brachycome lineariloba	C3	R
Calotis hispidula	C3	E
Crassula colorata	-	E
Danthonia caespitosa	-	E
Daucus glochidiatus	C3	E
Erodium cicutarium	C3	R
Erodium cygnorum	C3	R
Euphorbia drummondii	C3	P
Gnephosis burkittii	C3	P
Goodenia pusilliflora	C3	R
Helipterum floribundum	C3	E
Helipterum pygmaeum	C3	E
Hypochoeris glabra	C3	R
Isoetopsis graminifolia	C3	R
Lopochloa pumila	-	E
Medicago minima	C3	P
Oxalis corniculata	C3	E
Plantago drummondii	C3	R
Podocoma nana	C3	R
Schismus barbatus	-	E
Sonchus oleraceus	C3	C
Spergularia rubra	C3	E
Stipa nitida	-	E
Tetragonia eremaea	C3	P
Tripogon loliiformis	-	E
Zygophyllum crenatum	C3	E
Zygophyllum sp	C3	E

Table 4.4. Inferred photosynthetic pathway and habit for selected annual species. The species for which no photosynthetic type is stated are those which could not be confidently determined from hand sections. P= prostrate, R= radial, E= erect, C= cauline.



<u>Figure 4.1</u> Rainfall statistics for Middleback homestead for the period 1926 - 1983 (a) Mean monthly precipitation. (b) Mean wet days per month. (c) Mean size (mm) of a rainfall event.

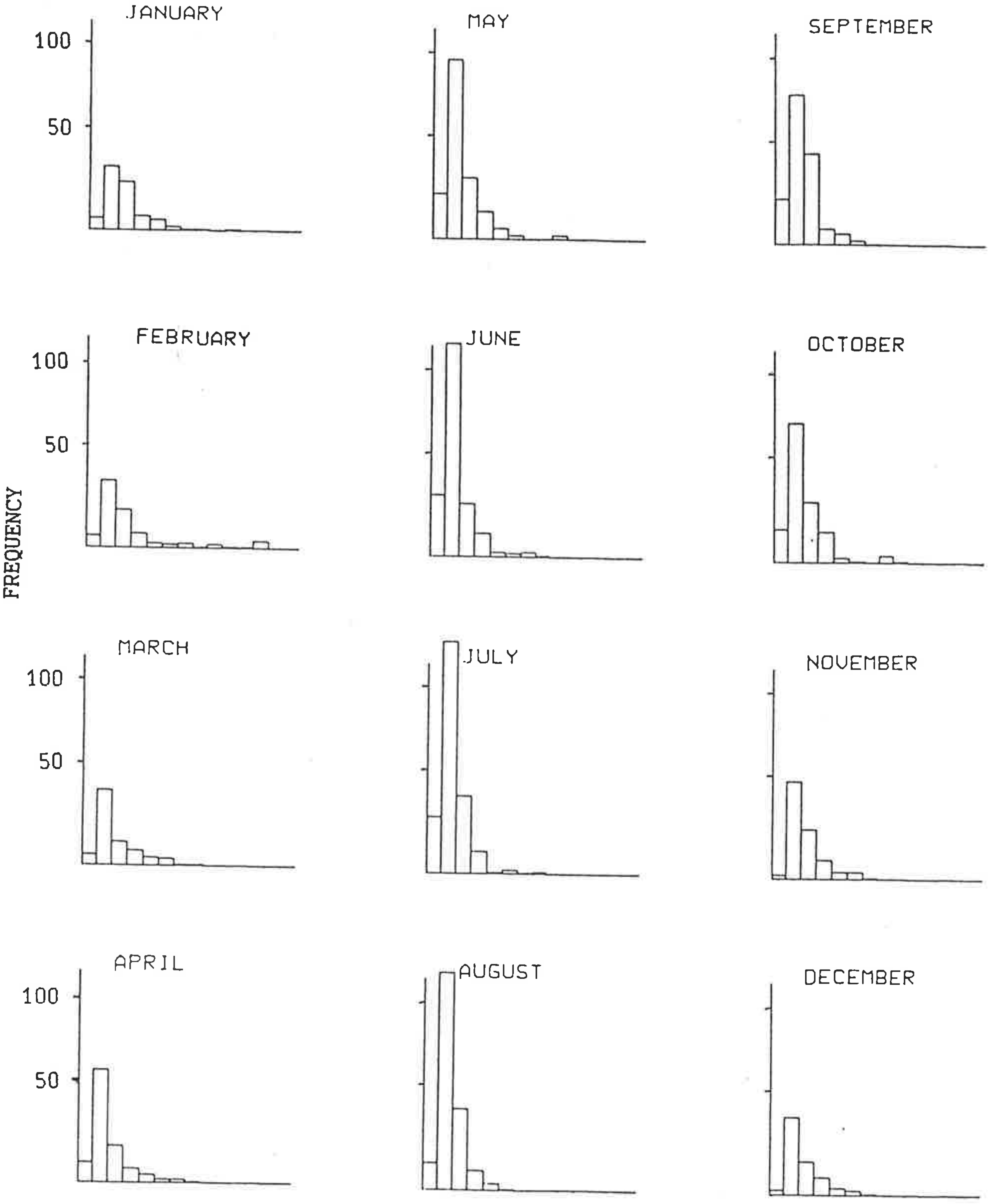


Figure 4.2 Frequency distribution of rainfalls of different magnitude, Middleback homestead 1926-1983. Intervals are 1. < 1 mm 2. 1-5 mm 3. 5-10 mm 4. 10-15 mm 5. 15-20 mm 6. 20-25 mm 7. 25-30 mm 8. 30-35 mm 9. 35-40 mm 10. 40-45 mm 11. 45-50 mm 12. 50-75 mm 13. 75-100 mm 14. 100-150 mm 15. 150-200 mm

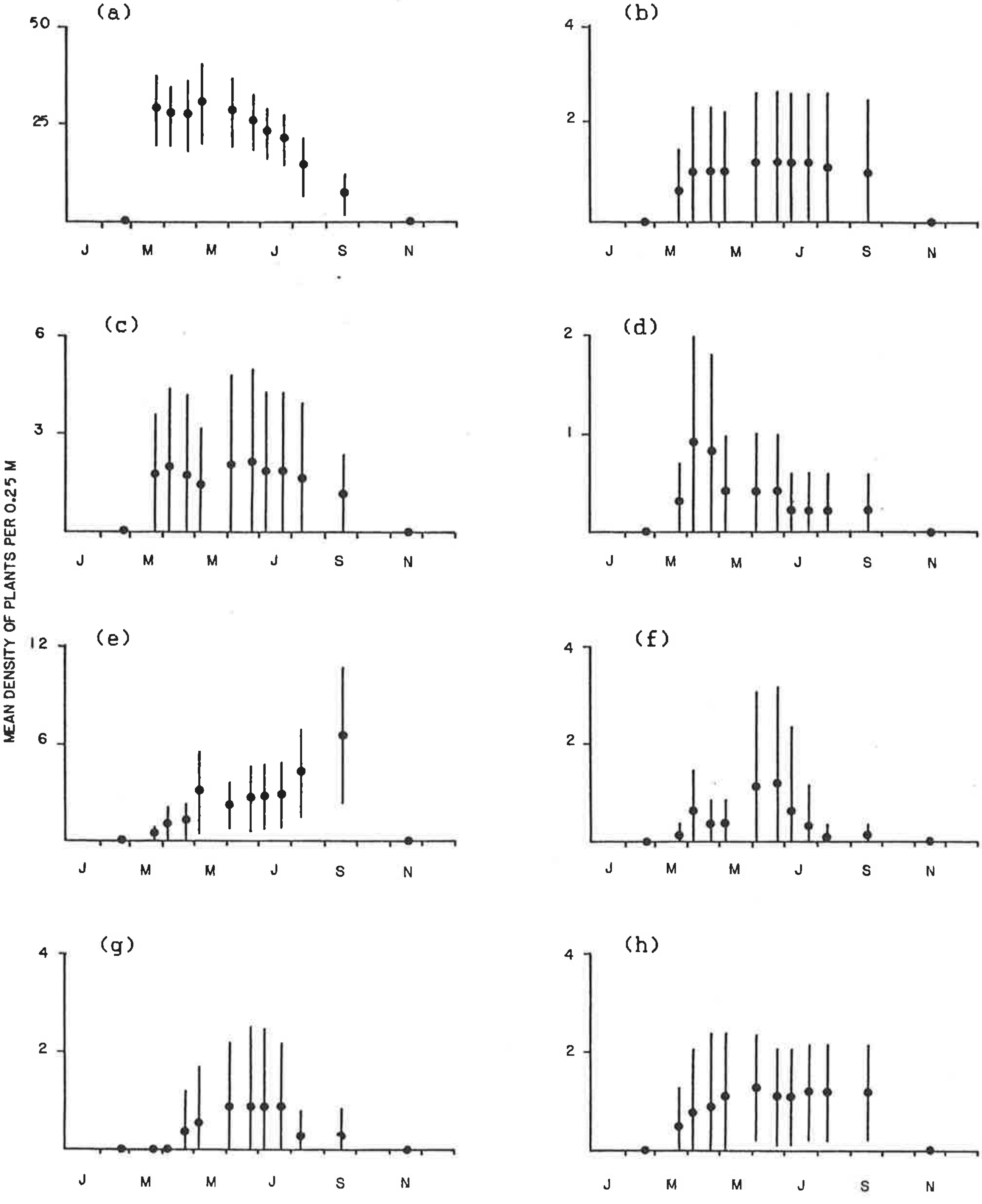


Figure 4.3 Mean density of annual plants at the Atriplex vesicaria - Maireana sedifolia site; February 1979 - November 1979, Quadrat size 0.5m X 0.5m. (a) Erodium cygnorum (b) Euphorbia drummondii (c) Zygophyllum crenatum (d) Sclerolaena obliquicuspis (e) Danthonia caespitosa (f) Calotis hispidula (g) Tetragonia eremaea (h) Maireana sclerolaenoides.

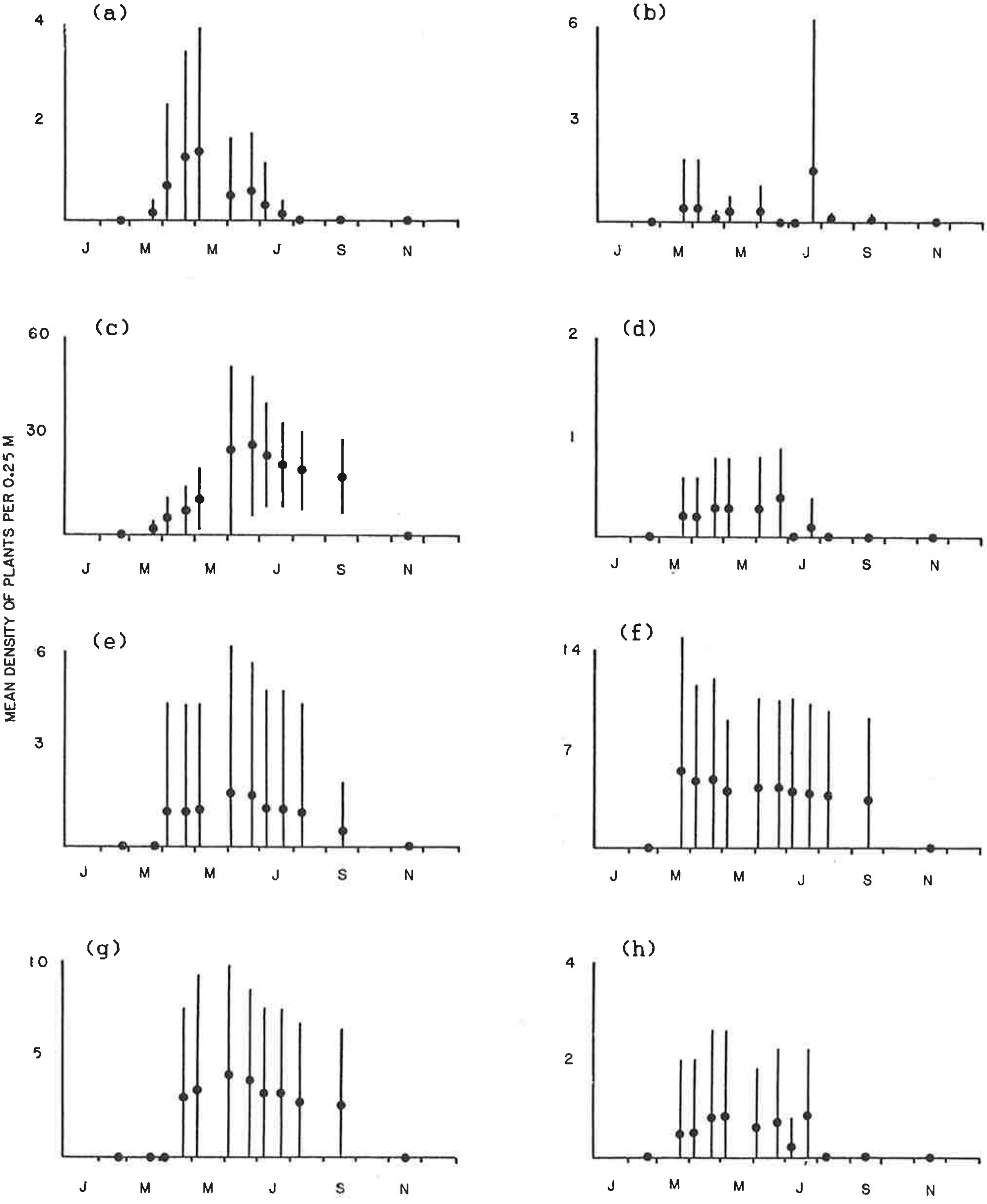
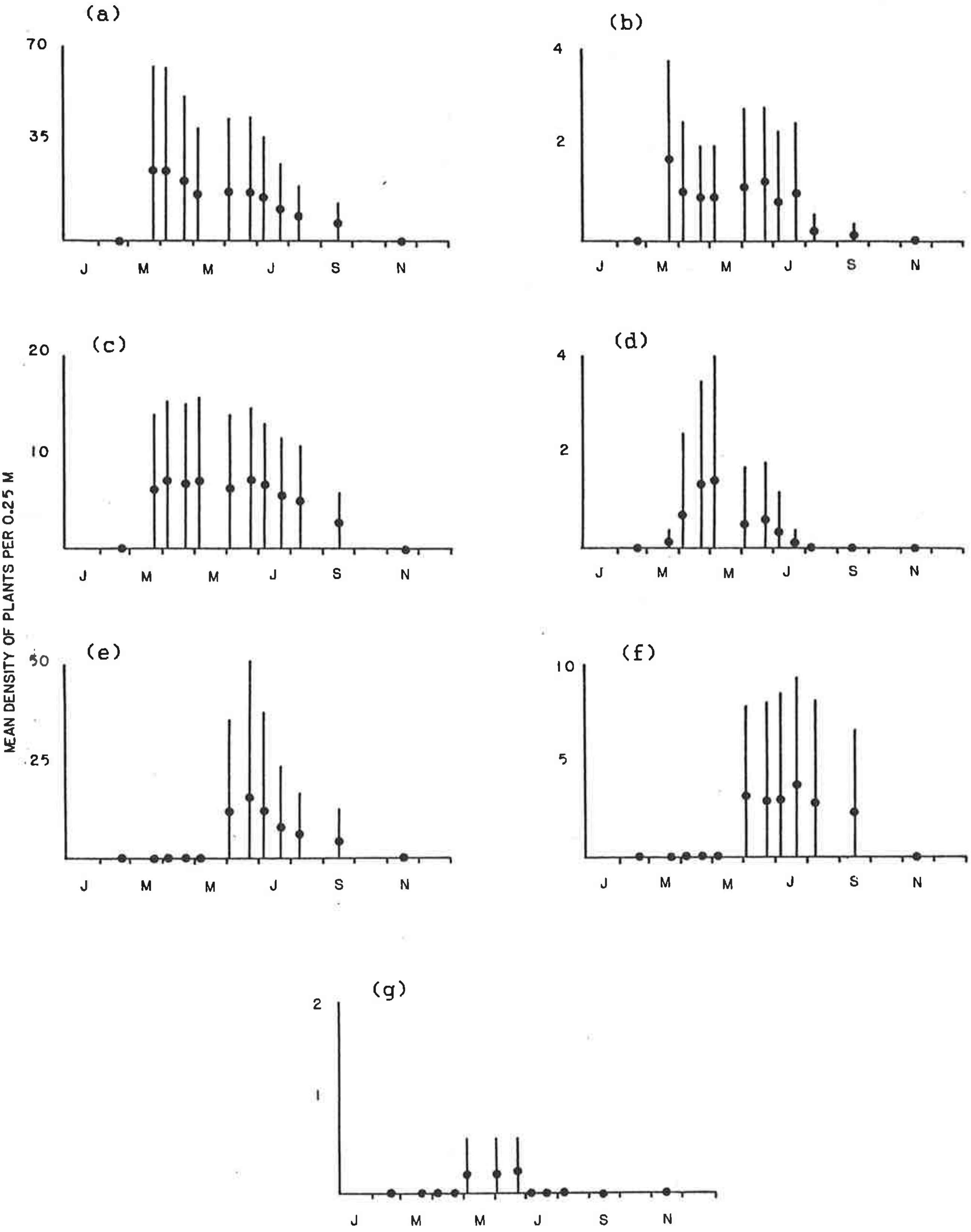


Figure 4.4 Mean density of annual plants at the *Atriplex vesicaria* site;February 1979 - November 1979, Quadrat size 0.5m X 0.5m, (a) *Erodium cygnorum* (b) *Plantago drummondii* (c) *Danthonia caespitosa* (d) *Euphorbia drummondii* (e) *Medicago minima* (f) *Sclerolaena obliquicuspis* (g) *Tetragonia eremaea* (h) *Hypochoeris glabra*.



<u>Figure 4.5</u> Mean density of annual plants at the <u>Atriplex vesicaria</u> site;February 1979 - November 1979, Quadrat size 0.5 m X 0.5 m. (a) <u>Helipterum floribundum</u> (b) <u>Erodium cicutarium</u> (c) <u>Sonchus oleraceus</u> (d) <u>Calotis hispidula</u> (e) <u>Daucus glochidiatus</u> (f) <u>Brachycome lineariloba</u> (g) <u>Emex australis</u>.

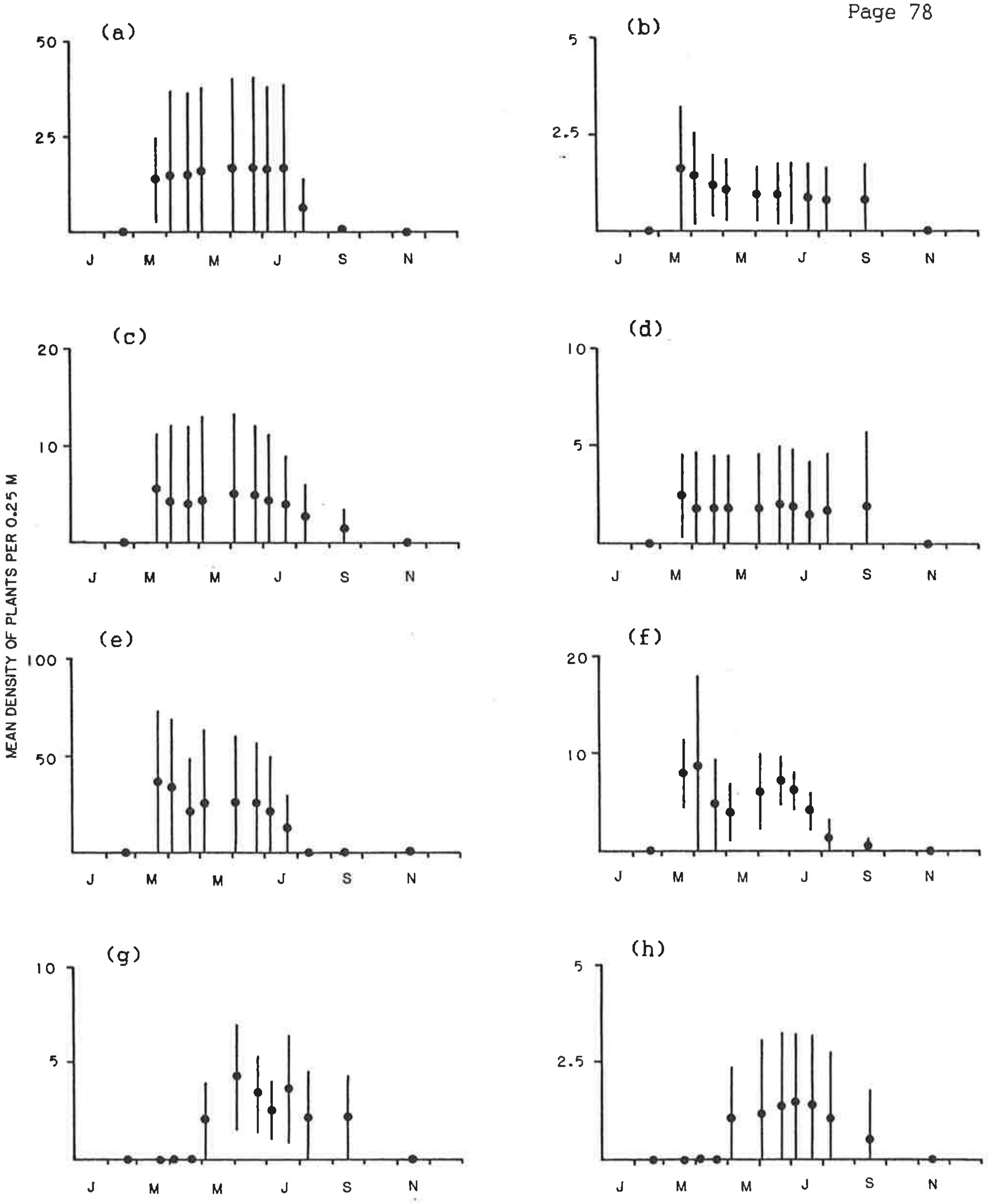


Figure 4.6 Mean density of annual plants at the *Maireana pyramidata* site; February 1979 - November 1979, Quadrat size 0.5 m X 0.5 m. (a) *Calotis hispidula* (b) *Euphorbia drummondii* (c) *Sclerolaena obliquicuspis* (d) *Tripogon loliiformis* (e) *Gnephosis burkittii* (f) *Actinobole uliginosum* (g) *Tetragonia eremaea* (h) *Helipterum pygmaeum*.

PLATE 1

Annual growth in one quadrat at the *Maireana pyramidata* site in 1979.

(1) February 1979	(2) April 1979
(3) June 1979	(4) September 1979

5. STABILITY OF ANNUAL PATTERN

5.1 Introduction

The results of the preliminary study (Chapter 3) indicated that the spatial distribution of annuals was largely independent of the perennial vegetation communities in the Middleback region. This was the consequence of a high degree of variability in both the incidence and the density of annuals.

It is evident that a conceptual approach to the description and summary of the environmental relationships of patterns in annuals will need to be different to that used for perennials. In the case of perennials, observed spatial patterns are conventionally accounted for in terms of plant "habitat", meaning a corresponding patterned layout of sedentary features of the physical environment. Under this approach boundaries to plant distributions are correlated with those of soil types. Because soil-type distributions, as sedentary habitat factors, are stable, there is a like stability in distributional patterns of the perennials that react to them. In the case of annuals, it seems intuitively much more likely that the correlated determining factors are themselves of unstable pattern from year to year.

Populations of annuals are discrete, separated temporally by periods of unfavourable conditions. It can hardly be disputed,therefore, that variation in climatic pattern from year to year stands as the most likely unstable habitat factor that might correlate with pattern in annuals. In this chapter changes in the floristic composition and the spatial patterns of annual plants from 1979 to 1983 are described. The aim of the study was to determine whether changes in composition and pattern could be attributed to yearly climatic variation.

5.2 Methods

5.2.1 Site

The site selected for this study was located in the south-eastern corner of Overland Paddock (Fig. 2.1) and was positioned to avoid drainage lines, both natural and man-made, as these are often dominated by dense stands of introduced weeds, namely *Carthamus lanatus*, *Emex australis* and *Marrubium vulgare*. An exclosure 100 m x 50 m designed to exclude sheep was erected. Both rabbits and kangaroos were allowed access, the former through the sheep-proof netting of the fence and the latter by keeping the fence low enough for them to jump easily.

5.2.2 Topography

The surface relief of the site was measured using a Dumpy level and staff. The differences in elevation across the exclosure were measured between the bushes, avoiding the mounds that are common beneath the bushes. The resultant contour map (Fig. 5.1) shows the relief of the site. It sloped gently downwards from the northern to the southern end of the exclosure. Throughout the period of the study, there was no evidence of stream flow through the site and after heavy rainfall events sheet flow would occur across most of the site and drain off through man-made drainage lines south of it. There were no areas where water could pond for any period of time.

In the south-west corner of the site there was an unusual topographic feature. A small mound of earth of different soil appearance rose slightly above the surrounding area (Fig. 5.1). These mounds can be found scattered throughout the region and although their exact origin is not known, it has been suggested by long term residents of the area that they may be the remains of old warrens of rabbits or wombats.

5.2.3 Vegetation

The vegetation of the study site was typical of much of the surrounding region (Section 2.4). The predominant bushes were *Maireana sedifolia* and *Atriplex vesicaria* with less common individuals of *Maireana pyramidata*, *Rhagodia ulicina* and *Lycium australe*. The site was selected to avoid any of the larger shrubs such as *Acacia papyrocarpa*, *Myoporum platycarpum* and *Heterodendrum oleaefolium*.

5.2.4 Sampling

The quadrat size used in this study was 0.5 m X 0.5 m. This quadrat size has been used in other studies of annuals (Loria & Noy-meir, 1980; Inouye, 1980) and has a number of advantages. The quadrat is small enough to fit in the spaces between the bushes, which carries a growth of annuals that are not "bush-protected", without ever overlapping the "bush-protected" part of the system. Thus the two situations of annuals in the exclosure were not confounded. This quadrat size also allows for high densities of plants to be counted when conditions are favourable for germination. Vertical photographs can also be taken as a permanent record.

Five transects each 100 m long and 10 m apart were marked out and quadrats were positioned at 5 m intervals along the transects (Fig. 5.2). Where the quadrat position coincided with a perennial bush the quadrat was offset to the left or right of the transect the minimum distance required to avoid the bush. Quadrat positions were marked with metal pins in the north-west and south-west corners; the quadrat was then defined by a metal frame placed over the pins.

The density of all plants in all quadrats was recorded on 11 occasions. The times at which the density was recorded was dictated by the times at which annuals were present. Species densities were recorded in October 1979, January 1980, July 1980, October 1980, January 1981, October 1981, January 1982, June 1982, August 1982, Februrary 1983 and April 1983. The quadrats were checked on numerous other occasions to monitor the progress of the annual plants.

The soil moisture levels were not measured during the study, however, a model of the soil moisture for the region, described by Noble (1975) and Noble and Crisp (1980), was applied to this study. The model considers the soil moisture to be the result of the balance between rainfall (RF), run-off or run-on (RO), actual evapotranspiration (AE) and deep drainage (DD). The relationship can be described by the equation:

$$SM_{t+1} = SM_t + RF + \underline{R}O - AE - DD$$

where SM_{t+1} and SM_t are the soil moisture at time t+1 and t. The run-off was calculated from the equation of Branson el al. (1972):

$$RO = (RF - 0.2 * d)^2 / (RF + 0.8 * d)$$

where d is the moisture deficiency.

Noble(1975) used an empirical equation to describe the evapotranspiration:

$$EV = -6.62 + 0.125 * TE + 0.654 * DL \quad \text{mm day}^{-1}$$

where EV was the daily evaporation rate, TE the maximum daily temperature (°C), and DL was mean day length in hours. The actual evopotranspiration was then calculated from EV using two empirical functions, Z a function describing the relationship between AE and PE (potential evapotranspiration) and a function K to account for root density. The model was used by Noble (1975) to estimate soil moisture in the zones of different depth. In this study the model was used only to model the top 10 cm of the soil surface.

The model of Noble (1975) is an empirical model designed for the Middleback situation and it was verified by him against known soil moisture sequences at Middleback Station. The model however may not hold in other areas.

5.3 Grazing

Throughout the period of the study no sheep entered the exclosure although they grazed up to the fence. It was mentioned in Section 5.2.1 that both rabbits and kangaroos had access to the exclosure. The effects of these herbivores were not measured although they did not appear to have a major influence upon the annual vegetation. There was evidence of minor rabbit activity in the exclosure throughout the whole period of the study although there were no warrens in the exclosure. The main evidence of rabbit activity was the presence of buck heaps and occasional distinctive digging. The activity of kangaroos was episodic and kangaroo egesta was found in large quantities in the exclosure only during the drought of 1983, when there were no live annuals present.

The herbivores which did appear to effect the annual plants were the large variety of insects, especially grasshoppers. At times when the insects were abundant they appeared to have a marked effect upon the population by the selective grazing of certain species, especially _Erodium cygnorum_. The possible effect of this herbivory is discussed later in this thesis.

5.4 Quadrat data

5.4.1 Introduction

The results are divided into three main sections. The first considers the floristics of the site, the second details the changes in the frequency and density of selected species and the third considers changes in species distributions over the period of the study.

It is not possible to discuss the behaviour of all species recorded in the quadrats. To condense the large amount of information obtained for the purpose of presentation, it has been necessary to present much of the information in summary tables and figures. The discussion concentrates primarily upon selected species which demonstrate different behavioural patterns.

5.4.2 Results

Floristics

Thirty-four herbaceous species were recorded in the quadrats from October 1979 to August 1983. The species represented a wide range of families (Table 5.1). The most common family was the Asteraceae with 11 species represented and the second most common family was the Poaceae with 5 species. There were also a number of species present in the exclosure which, due to their low density or restricted distribution, were not recorded in the quadrats. These were *Alyssum linifolium*, *Hordeum leporinum*, *Helipterum floribundum*, *Thysanotus* sp., *Sisymbrium irio*,*Calandrinia eremaea* and *Convolvulus erubescens*. This list applies only to the site and is not a full regional list.

The number of species recorded in the quadrats at the different readings (Table 5.2) showed marked fluctuations over the period of the study. At the time the study was commenced in October 1979, 23 species were recorded. During the summer months the number fell to 4, but by July 1980 the number had increased to 34. The number then decreased to 17 by October and then to 8 by January 1981. There was an increase in the latter part of 1981 when 23 species were recorded in October. In the drought year of 1982 the conditions were reflected in the number of species recorded; only 2 in January and 10 in June. No annuals were then recorded until April 1983 when 20 species were present.

Frequency and density

The number of quadrats in which the species were recorded at the various sampling times is presented in Figure 5.3 and Table 5.3. Not all the species recorded in the quadrats can be regarded as true annual plants. *Danthonia caespitosa*, *Stipa nitida*, *Maireana sclerolaenoides* and *Sclerolaena obliquicuspis* are all species that can behave as short lived perennials when conditions are suitable. These species all showed high frequency of occurrence especially in the early part of the study.

Danthonia caespitosa and *Stipa nitida* were the dominant species of this group. Both showed an increase in frequency between October 1979 and October 1980 (Plate 2) but then decreased in frequency until neither species was recorded in October 1982. There was a marked increase in frequency of [illegible][1] [illegible]

INSERT

1. In April 1983 both Danthonia caespitosa and Stipa nitida were present as newly germinated seedlings. At that time it was not possible to individually identify all the seedlings on all the quadrats and so the frequency and density of these two species is not shown in Figures 5.3 and 5.4.

[illegible] between these periods of high frequency [illegible] species was present only at low frequency or was absent. The other species, *Euphorbia drummondii*, *Daucus glochidiatus* and *Sonchus oleraceus* showed a different pattern in their frequency. These species showed intermediate frequencies in October 1979 and June 1980. There was a marked reduction in frequency following these readings. Euphorbia drummondii and D.glochidiatus showed an increase in frequency in April 1983.

The frequencies of the remaining species recorded in the study are presented in Table 5.3. Most of these species showed marked fluctuations in frequency during the period of the study. Species such as Senecio quadridentatus, Emex australis, Bulbine semibarbata, Carthamus lanatus, Podocoma nana and Vella annua were recorded on few occasions and at very low frequency.

There were a number of species which showed unusual frequency patterns. Schismus barbatus was recorded on only three occasions. It was present in 50 of the quadrats at the initial reading but then declined in frequency and was not recorded in the quadrats subsequent to October 1980. Lophochloa pumila showed a similar behaviour but was recorded initially at a lower frequency than S.barbatus. Zygophyllum crenatum was recorded at low frequency for the first 2 readings (Table 5.3). There was a large increase in the frequency of this species in April 1983 when it was a dominant annual. Tetragonia eremaea was present at high frequency on two occasions, July 1980 and April 1983. The only other occasion this species was recorded was at low frequency in October 1981.

The remaining species were generally present in the early stages of the study but then declined through 1981 and 1982. Many were again present in April 1983.

Changes in annual density

The information provided by this study is considered here in two ways. The first concerns the changes in the mean density of the species from one reading to the next. The second type of information provided concerns the changes in the spatial arrangement of the density patterns with time.

The mean density and the associated standard deviations for each selected species are shown in Figures 5.4 & 5.5. The mean densities of the less common species are shown in Table 5.4. The dominant species which showed the highest mean densities were Danthonia caespitosa, Stipa nitida, Erodium cygnorum, Calotis hispidula and Tetragonia eremaea. The changes in the mean density of these species showed a similar trend to the species frequencies. Increases or decreases in the species frequencies were usually accompanied by a similar change in their mean density.

An interesting aspect of the density results is the magnitude of the standard deviations. For most species at most readings the standard deviation exceeded the mean and in some instances was much greater than the mean. This indicates that the annual vegetation was highly variable in density across the quadrats.

The best example of this was Plantago drummondii (Fig. 5.5) which was present at a mean density of 7.9 per quadrat (31.6 m^{-2}) in June 1980 but at this reading the maximum density in a quadrat was 287 (1148 m^{-2}). Other species which were recorded at high maximum densities were Erodium cygnorum (516 m^{-2} ; April 1983), Danthonia caespitosa (304 m^{-2} ; October 1979), and Tetragonia eremaea (352 m^{-2} ; April 1983). These density values appear low when compared to 3000 m^{-2} observed by Went (1949).

The density patterns of selected annual species are shown in Figures 5.6 - 5.28 . The quadrats with a high density of Danthonia caespitosa (Figs. 5.6 & 5.7) were located in the southern half of the exclosure. The northern half of the exclosure had a lower density and in a number of the quadrats the species was never recorded. There was little change in the density pattern to October 1980 although there was a slight increase in the frequency, indicating an expansion of the population into quadrats it had not previously occupied. There was a marked reduction in the density of D.caespitosa in many of the quadrats following January 1981 although the overall distribution of this species was similar to that in October 1979. The major change over the total period was a decrease in the density on quadrats that had high density at the initial reading in October 1979. There were only small changes in the distribution of this species within the exclosure throughout the study.

The behaviour of Stipa nitida (Fig. 5.8 & 5.9) was similar to that of D.caespitosa although some of the changes were more pronounced. There was a marked reduction in the density in 3 quadrats on the eastern side of the exclosure between October 1979 and July 1980. A decrease in density and the reduction of the range of this species within the exclosure was very pronounced by January 1981. The population appeared to be declining with time.

The changes in density distribution of Maireana sclerolaenoides (Fig. 5.10 & 5.11) were similar. There were few changes in the density distribution between October 1979 and October 1980, but following that reading there was a steady decline in the number of quadrats in which the species was recorded and also in the density on those quadrats. There was a marked increase in the population of this species in April 1983.

Erodium cygnorum differs from the previous species in that it is a true annual and each reading represents a new population. This species showed little change in the distribution when October 1979 is compared to April 1983. There were few individuals present at October 1980 and January 1981 and these were scattered across the site (Fig. 5.12 - 5.14).

Tetragonia eremaea showed a band of occurrance across the centre of the exclosure in October 1979 (Fig. 5.15). There was a marked decrease in the population the following year. This species was not recorded again in significant numbers until April 1983. The pattern of distribution in April 1983 was similar to October 1979 but there had been an increase in frequence and density.

The population of Sonchus oleraceus showed considerable fluctuations over the period of the study (Fig. 5.16). There were increases in density in some quadrats and changes in the distribution between readings. There appeared to be an increase in the population between October 1979 and July 1980. The population had declined by October 1980 and was further reduced by October 1981.

Plantago drummondii (Fig. 5.17) was present at low density in October 1979. The pattern for July 1980 showed a similar distribution but there was a marked increase in the density in some quadrats. The second population (July 1980) appears to be a direct result of seed fall from the previous (1979) population. The similarity in distribution suggests that the seed was dispersed close to the parent plant and then, in 1980, the correct conditions for germination were present which caused germination of the seed released in 1979.

A similar behaviour was shown by Daucus glochidiatus (Fig. 5.18). The density distribution for July 1980 was similar to that of October 1979 but the density had increased in many quadrats. The next recorded population, in April 1983, was of lower frequency and density but the quadrats which possessed this species at this reading were predominantly those in which the species was recorded in July 1980. The density distribution of other species are presented in Figures 5.19 - 5.28.

The soil moisture prediction for 1979 (Fig. 5.29) showed there were five occasions when the surface 10 cm would have reached field capacity (approx. 22%). The first heavy rainfall event in February was followed by considerable germination of annual plants. There was a rapid decline in soil moisture following this rainfall event due to high, late summer temperatures. Subsequent falls in April and May maintained the soil moisture at a high level. The next occasion that soil moisture reached field capacity was late August to October. For the October 1979 quadrat reading it is not possible to identify which rainfall events initiated germination for the different annual species.

In 1980 no rainfall was recorded in the first three months of the year, however, there were significant rainfall events in the cooler months and a relatively high soil moisture was maintained through this period. The rainfall in 1981 and 1982 was considerably less than in the two previous years and this was reflected in the soil moisture levels (Fig. 5.29) and ultimately in the annual vegetation for that year. The model predicted that field capacity would have been reached once in 1981 during July and would never have been reached in 1982.

5.4.3 Discussion

Many of the ephemeral species recorded in this study have been reported for other semi-arid regions of Australia, (Williams,1955, 1956,1961,1968,1969,1970; Williams & Rowe,1975; Biddiscombe et al.,1954;Wilson & Leigh,1964; Osborn et al.,1935; Crisp,1975; Noble & Crisp,1980). Those studies document a range of species responses to environmental conditions, some of which are at variance to the results obtained in this study. A major difference occurs in the reported behaviour of the ephemeral species, *Danthonia caespitosa*, *Maireana sclerolaenoides* and *Stipa nitida*.

Williams (1970) monitored the age distribution of *Danthonia caespitosa* in one particular locality in New South Wales and found it had a half life of 15 - 30 months. Williams & Roe (1975) found that *Danthonia caespitosa* recruited annually and could survive for up to 18 years. These results contrast with my study where it was found that the maximum survivorship of *Danthonia caespitosa* was about 3 years (Fig. 5.3). During this period the density steadily decreased from the population that germinated in early 1979 and all individuals of D.caespitosa had died by October 1980. The density recorded was generally much lower than that found in the Riverine Plain of N.S.W, (Williams,1955,1970). Substantial mortality of D.caespitosa can be attributed to dry summers and the failure of early autumn rains, however in the Riverine region recruitment is sufficient to offset the losses (Williams,1968). This observation may explain the difference in the behaviour of this species in the Riverine region as opposed to the Middleback region, where summer and early autumn rains are infrequent (Table 4.1) and recruitment is not on an annual basis.

Another species for which there appear to be conflicting reports is Stipa nitida. Osborn et al. (1935) reported that this species germinated in late summer, grew through autumn and winter, flowered in spring and set seed the following summer. Wood (1936), however, suggested that this species germinated best after early winter rains and Crisp (1975) reported germination from January to April. Detailed analysis of the Koonamore photo point records (Noble & Crisp,1980) indicated germination for this species from autumn to winter with individuals dying from spring to summer. They found that the life span of this species rarely exceeded 9 months, only 9 % survived to a second year. Williams & Roe (1975) found in one area that the life span rarely exceeded 5 years and only 1 year in another.

Observations made in my study indicate that Stipa nitida can germinate throughout much of the year. Initial germination followed the late February rain in 1979 (Fig. 5.29), subsequent germination occurred in early October 1979 and April 1980. The resultant population was of mixed age structure and as fates of individuals was not recorded it was not feasible to determine the life span of this species in this study.

Variation in floristic composition and density of the annual vegetation from one reading to the next can be attributed to differences in prevailing environmental conditions. There were significant differences in the amount of rain and its distribution from one year to the next.

The behaviour of the annual plants can be related to the rainfall (Went & Westergaard,1949; Went,1949; Tevis,1958a; Williams,1969). However, the amount of rainfall in a year or even the magnitude of individual falls may not give a good indication of their effectiveness for annual germination and growth (Noble & Crisp,1980). A heavy rainfall event may have the same effect upon soil moisture as a rainfall event of considerably smaller magnitude. Once sufficient moisture has been absorbed by the soil to reach field capacity then any subsequent rainfall causes run off and does not increase soil moisture levels (Branson et al., 1972). A number of light falls within a period of a few days may appear to be ineffective, but in fact may be additive to the soil moisture and maintain or even raise the soil moisture level. The soil moisture model (Noble,1975) takes into account the evaporation rates at different times of the year, so that light falls in winter may have a significant effect upon the level of soil moisture. Falls of the same magnitude in the hotter months may be less effective.

The behaviour of the annual plants can be related to soil moisture levels predicted by the model for the period of the study. The annual vegetation appears related to the time of year that the rainfall events occurred. The 1979 annual vegetation was the result of germination following a number of significant falls throughout the year. In 1980 a quite different distribution of rainfall was recorded and it was found that in July of that year there was an extensive annual vegetation of greater diversity than the previous October. The annual vegetation in October 1980 however was less diverse than that found in July of that year. It would appear from these results that the most extensive flora of annuals is obtained following winter rainfalls. A similar situation has been found in numerous other arid areas (Went & Westergaard,1949; Went,1949; Tevis,1958a; Beatley,1974; Williams,1956).

A rainfall event in summer does not necessarily imply that it will be accompanied by high temperatures. Potentially there could be up to a 20° C difference in daily temperatures following a rainfall event. Temperature differences are not restricted to seasonal trends. Annual plants will be influenced by daily temperatures at germination (Went & Westergaard,1949; Tevis,1958a,b; Mott,1972a). A similar rainfall event in subsequent years at the same time of year may produce a quite different annual vegetation depending upon the temperature conditions immediately following the rainfall event.

During 1981, 1982 and 1983 there was considerably less effective rainfall and this was reflected in the annual vegetation. There were fewer species recorded and those that were present were usually at a lower density than during 1979 and 1980. There were two species which showed the opposite trend, namely _Tetragonia eremaea_ and _Zygophyllum crenatum_, which showed highest frequency and density in April 1983. A possible explanation is that the temperature conditions at the time of the rainfall events in the previous years were unfavourable for germination of these species.

The soil moisture model was used to predict the moisture in the top 10 cm of the soil profile, as it was thought that this zone would exert the greatest influence upon the behaviour of annual plants. In terms of the growth of annual plants this is probably an acceptable assumption, however in relation to the germination of annual plants a much shallower surface zone is probably important. Germination usually occurs on the soil surface or within a few centimetres of it. The germination zone may include only the top 2-3 cms of the soil surface (Harper, 1977). The rate of moisture loss from this zone would be expected to be more rapid than from the top 10 cm. In the field it has been observed that following summer rains the soil surface can appear dry within 24 hours of the event.

The seed of some species can escape from desiccation at the soil surface. The three dominant species at the study site ,*Danthonia caespitosa*, *Stipa nitida* and *Erodium cygnorum* , all possess a common feature in their seed morphology. Their seeds are enclosed by a sharp pointed dispersal unit with a long hygroscopic awn. A function of the hygroscopic awn is to facilitate the burying of the seed (Peart, 1979). Changes in humidity or alternate periods of wetting and drying cause the awn to rotate. If the awn catches on an obstruction the seed rotates and this forces it into the ground. Following rainfall, when these species have seed on the ground, the awns can be seen protruding from cracks in the soil surface. When these species germinate the small seedlings appear from the cracks in the ground.

The ability of species to escape desiccation at the surface could be one explanation for the dominance of these species. Species which do not possess a mechanism for burying their seed would have to rely on the seed falling down cracks (Williams,1955), locating micro-habitats where moisture loss is less rapid or germinating during the times when the rate of moisture loss from the surface is reduced.

5.5 Vegetation analysis

5.5.1 Introduction

Vegetation studies are often designed to classify vegetation samples into different groups or communities. It was demonstrated that this could not be satisfactorily done for annuals at a broad scale in the study region (Chapter 3), in the sense that no sample groupings could be logically demonstrated to correlate with the physical habitat factors that correlated with the distributions of the perennial plants. The analysis presented in this section uses association analysis to determine whether there are spatial interactions between species, even if these are unaccountable by generalized "habitat features. This type of analysis has been used by Goodall (1953) and Williams and Lambert (1959) to classify vegetation types. The main aim of this section is not to classify the vegetation but to determine if interspecific associations exist and if these associations reoccur in subsequent annual populations.

5.5.2 Methods

Species association was determined by calculating X^2 from 2 x 2 tables for the species present at each reading. Each reading of the quadrats resulted in a species x quadrats matrix for that date. From this a species x species matrix was compiled, in which entries were X^2 , signed positive or negative, for each species pair in turn, calculated from 2 x 2 contigency tables based on all quadrats.

5.5.3 Results

The results are presented for each reading in Tables 5.5 to 5.8. There were no significant associations between species for the readings in the period January 1981 to August 1982. The nodes of associated species are presented in Figures 5.30 to 5.33. A "node" of associated species deals soley with the information about a group of species which are mutually linked through significant associations, leaving aside from immediate consideration those other species which are not demonstrably linked to them by association. Each node is considered (Lange,1968) to depict a separate outcome of many different environmental factors and sets of factors that influence the growth of plants. A summary table of species pairs which were associated or dissociated is presented in Table 5.9.

The main feature of this table is the very large number of associations which were found over the whole period, however, very few of these associations were recorded at more than one reading. Only nine interactions were found on two occasions. The associations must be considered in relation to the occurrence of the species. Three different possibilities are represented in Table 5.9. Both species were present and associated or both species were present but were not associated or one or both species did not occur at that reading. The Table indicates that there were a large number of instances where one or both species was absent. There were fewer occasions where both species were present but not associated. It is important to note that the Table (5.9) does not include all possible combinations of species pairs. The total number of possible combinations is 561, the table only represents associations found where the significance was $p<0.01$.

To demonstrate the spatial pattern of association, influence analysis (Lange,1968) was used on the Danthonia caespitosa - Euphorbia drummondii association. The resulting patterns of influence ratings are shown in Figure 5.34.

5.5.4 Discussion

The results show that the association between a pair of species was not necessarily consistent from one reading to the next. The lack of association between a pair of species from one occasion to the next may be due to one of two reasons, only one of which is capable of ecological interpretation. This is where both species occur in quadrats at frequencies sufficient to avoid the constraints on the interpretation of 2 x 2 tables (such as expected frequencies in any cell of the 2 x 2 table less than 5), then the association demonstrated can be taken to imply ecological "cause" of some sort. But where frequencies are too low or one or both species are absent, then the inconsistancy of association from one growth flush to the next involves an element that includes the inapplicability of the statistical test.

Associations can also be lost if the spatial arrangement as opposed to the frequencies of species, changes. If the species distributions change markedly from one reading to the next, such that the species do not occur together in quadrats, then the association is lost. The question that these results raises is the meaning of the associations between species in the context of this study.

Interspecific association measures whether two species are found to occur together more often than would be expected due to chance alone. Within the field of vegetation ecology the presence of association is considered to have real meaning as a description of interactions between species. When an association is found it is considered that there is a cause and the cause is usually found in the characteristics of the habitat. The distribution of the species is often explained in terms of soil type (Lange,1971) or external influences such as grazing (Barker,1972; Reid,1979). In the situation described in this study the cause is more obscure.

Annuals by nature are opportunistic plants, their main function is to germinate, grow, flower and produce seed. An annual is successful if it produces seeds as this is the stage of the life cycle which ensures there will be subsequent populations. This absolute dependance upon the seed as the only link between successive populations means that the spatial arrangement of the species may be largely determined by the distribution of seed in the soil as a result of seed dispersal from a population.

The variation in climatic conditions , specifically rainfall and temperature, may elicit different responses from different species. Two species associated on one occasion may demonstrate different responses to a different set of climatic conditions, so that the two species may no longer be associated. An hypothetical example could be two species with similar growth requirements and the same optimal germination temperature. The two species however, have quite different ranges of temperature within which they can germinate, one a broad range, the other narrow. If a rainfall event occurs at a temperature close to the optimum both species will germinate. If, however, the temperature at the time of the rainfall event is further from the optimum then the germination of one species only may occur.

The same can be hypothesised concerning the microhabitat where germination takes place. As soil moisture increases there is likely to be a reduction in the number of unsuitable microsites for germination. For example species which can bury their seeds may be advantaged under moderate conditions over those species which must germinate on the surface. If a very heavy rainfall event occurs the difference in soil moisture between the soil surface and the microhabitat of a crack in the soil may be reduced.

The variable climatic conditions may cause major changes in the available habitats. Williams (1955) observed patterns in the annual flora associated with gilgai micro-relief. Species could be identified as being restricted to certain micro-features associated with the gilgai. However, when unusually wet conditions occurred the pattern in species distribution was less obvious. The conditions had changed the habitats and the species could grow in areas previously unsuitable.

In some instances species can be influenced by minute relief differences. Wilson & Leigh (1964) found that microtopographical changes as small as 2 cm could affect the distribution of annual species. By the creation of artificial mounds and depressions, it was found that the species responses were due to run-off run-on effects and not due to differences in soil type between microtopographical features.

5.6 Conclusions

The main conclusion that can be drawn from the results presented in this chapter is that the patterns of annual plants change to a very large degree from one year to the next. The occurrence of a species, its abundance and spatial pattern may change from one growth event to the next.

The most important influence upon the abundance and pattern of annuals are the environmental conditions at the time of germination. Changes in rainfall and the temperature at the time of that rainfall event cause germination of different species and in different quantities. The composition of the annual vegetation appears to be determined at germination, as was suggested by Went (1948).

From this study the initial reaction is to state that annual patterns are unstable. In the short term this appears to be the case. Over much longer periods it may be found that there is stability in annual pattern. This could be determined by comparing the vegetation that germinated under similar conditions at different times. It may be that many years pass before similar conditions are encountered.

Rainfall events similar to that which occurred in February 1979 have occurred six times in that month since 1925.

The changes in species associations from one year to the next do not imply that populations of plants are "moving" spatially relative to each other. Rather it is probably the consequence of an individual species response to rainfall and temperature causing differential germination. If distribution of seed in the soil was similar from one year to the next then potentially the same associations would re-occur given the correct conditions.

ASTERACEAE
Actinobole uliginosum
Brachycome lineariloba
Calotis hispiula
Carthamus lanatus
Gnephosis burkittii
Helipterum floribundum
Helipterum pygmaeum
Hypochoeris glabra
Isoetopsis graminifolia
Ixiochlamys nana
Senecio quadridentatus
Sonchus oleraceus
Vittadinia cuneata

BORAGINACEAE
Omphalolappula concava

BRASSICACEAE
Allyssum linifolium
Carrictera annua
Sisymbrium erysimoides
Sisymbrium irio

CAMPANULACEAE
Whalenbergia gracilis

CARYOPHYLLACEAE
Hernaria hirsuta
Spergularia rubra
Stellaria multiflora

CHENOPODIACEAE
Maireana sclerolaenoides
Sclerolaena obliquicuspis
Sclerolaena patenticuspis

CRASSULACEAE
Crassula colorata
Crassula sieberana

EUPHORBIACEAE
Euphorbia drummondii

GERANIACEAE
Erodium cicutarium
Erodium cygnorum

GOODENIACEAE
Goodenia pusilliflora

GRAMINEAE
Danthonia caespitosa
Hordeum leporinum
Lophochloa pumila
Schismus barbatus
Stipa nitida

LEGUMINOSEAE
Medicago minima
Swainsona oliverii

LILIACEAE
Bulbine semibarbata
Thysanotus baueri
Oxalis corniculata

PLANTAGINACEAE
Plantago drummondii

UMBELLIFEREAE
Daucus glochidiatus

ZYGOPHYLLACEAE
Zygophyllum crenatum
Zygophyllum ovatum

Table 5.1 List of all the ephemeral species observed within the exclosure at the Overland Paddock study site from October 1979 to April 1983. Not all the species in the above list were recorded in the 100 quadrats.

DATE		NO OF SPECIES
OCTOBER	1979	23
JANUARY	1980	4
JULY	1980	34
OCTOBER	1980	17
JANUARY	1981	8
OCTOBER	1981	23
JANUARY	1982	4
JUNE	1982	10
AUGUST	1982	0
FEBRUARY	1983	0
APRIL	1983	20

Table 5.2 The number of species present in the 100 quadrats at the Overland paddock study site on 11 sampling occasions.

	OCT 79	JUL 80	OCT 80	JAN 81	OCT 81	JUN 82	APR 83
Actinobole uliginosum	6	11	-	-	1	-	-
Atriplex spongiosa	-	5	-	-	-	2	-
Brachycome lineariloba	21	45	-	-	3	-	2
Bulbine semibarbata	5	1	-	-	-	-	-
Calotis hispidula	56	70	2	-	-	-	22
Carthamus lanatus	-	3	3	-	-	-	2
Crassula colorata	-	39	-	-	-	-	40
Emex australis	-	1	-	-	-	-	-
Goodenia pusilliflora	16	24	1	-	14	1	12
Heliperum pygmaeum	18	28	-	-	3	-	3
Hernaria hirsuta	-	38	9	-	1	-	1
Hypochoeris glabra	-	9	3	-	2	-	-
Isoetopsis graminifolia	21	29	-	-	1	-	13
Lophochloa pumila	36	2	-	-	-	-	-
Medicago minima	4	9	1	-	1	-	4
Plantago drummondii	20	29	6	-	1	-	3
Podocoma nana	-	6	-	-	1	-	1
Schismus barbatus	50	1	14	-	-	-	-
Senecio quadridentatus	-	11	-	-	-	-	-
Swainsona oliveri	-	12	1	2	2	-	7
Tetragonia eremaea	-	49	-	-	12	-	70
Vittadinia cuneata	26	65	49	-	1	3	8
Vella annua	-	2	-	-	2	-	-
Zygophyllum crenatum	16	1	-	-	1	-	64

Table 5.3. The frequency of annual species not shown in figure 5.3. The numbers represent the number of quadrats of a possible 100 quadrats in which the species occurred.

	OCT	JUL	OCT	JAN	OCT	JUN	APR
	79	80	80	81	81	82	83
Actinobole uliginosum	0.31	1.30	-	-	0.09	-	-
Atriplex spongiosa	-	0.01	-	-	0.01	0.02	-
Bulbine semibarbata	-	0.01	-	-	-	-	-
Carthamus lanatus	-	0.05	0.04	-	-	-	0.02
Emex australis	-	0.01	-	-	-	-	-
Hypochoeris glabra	-	0.27	0.16	-	0.02	-	-
Lophochloa pumila	2.60	0.02	-	-	-	-	-
Medicago minima	0.04	0.10	0.01	-	0.03	-	0.04
Podocoma nana	-	0.13	-	-	0.01	-	0.01
Schismus barbatus	1.56	0.04	0.38	-	-	-	-
Senecio quadridentatus	-	0.14	-	-	-	-	-
Swainsona oliveri	-	0.16	0.01	0.04	0.03	-	0.09
Vella annua	-	0.03	-	-	0.02	-	-
Vittadinia cuneata	0.42	3.13	1.96	-	0.01	0.05	0.14

Table 5.4 Mean density per quadrat (0.5 m X 0.5 m)for the less common species not presented in Fig. 5.4 & 5.5. None of the above species were present in January 1982 or August 1982.

Species number

	2	3	4	5	6	7	8	9	10	11	12
1	0.3	1.0	6.9 **	0.3	1.0	3.3	6.9 -**	0	0.6	0	0.6
2		6.9 **	0.1	9.2 **	10.8 **	13.0 ***	5.2 *	0	15.7 ***	0	9.5 **
3			1.2	0	0	18.0 ***	0.5	0	1.7	0	0.1
4				0	0	0.1	1.5	2.3	0.6	1.7	0
5					9.0 **	1.3	0	0.4	8.0 **	0	5.4 *
6						2.0	0	0	7.0 **	0.2	0.9
7							2.0	3.1	4.9 *	0.7	3.6
8								11.2 **	4.5 *	15.1 ***	3.8 *
9									0.1	18.0 ***	1.5
10										2.8	8.6 **
11											3.4

Table 5.5 Association Analysis :October 1979. The values in the table are X^2 ; *, 0.05 > p > 0.01; **, 0.01 > p > 0.001; ***, p<0.001. Species are 1. Danthonia caespitosa 2. Daucus glochidiatus 3. Sonchus oleraceus 4. Euphorbia drummondii 5. Helipterum pygmaeum 6. Isoetopsis graminifolia 7. Goodenia pusilliflora 8. Brachycome lineariloba 9. Actinobole uliginosum 10. Lophochloa pumila 11. Bulbine semibarbata 12. Schismus barbatus

Species number

	3	4	5	6	7	8	9	10	11	12	13	14	15
1	1.2	1.2	11.9 ***	18.2 ***	1.7	3.8	0.4	1.3	3.3	1.1	0	0.5	6.4 -*
2	7.3 **	4.0 *	3.5	3.6	1.5	1.9	1.0	3.3	4.8 *	1.7	4.5 *	5.5 *	1.4
3		4.3 *	3.9 *	3.4	4.0 *	2.9	13.4 ***	11.5 ***	11.5 ***	14.7 ***	0.4	5.3 *	0.2
4			8.0 **	1.6	0.1	3.3	5.8 *	4.8 *	7.9 **	22.2 ***	7.7 **	6.8 **	0
5				4.6 *	3.4	6.1 *	0	9.1 **	9.7 **	13.7 ***	0.2	4.3 *	0.4
6					0.3	6.8 **	0	1.6	3.7	1.5	0	2.4	12.0 -***
7						12.5 ***	0.2	7.3 **	1.3	1.8	0.2	1.1	0
8							0	8.6 **	2.6	0.9	2.2	11.6 ***	2.3
9								9.6 **	9.0 **	12.5 ***	5.3 *	3.5	0
10									19.4 ***	17.5 ***	4.9 *	3.2	0
11										13.1 ***	7.4 **	5.5 *	0
12											5.8 *	11.4 ***	0

Table 5.6 Association Analysis :July 1980. The values in the table are X^2. *, $0.05 > p > 0.01$; **, $0.01 > p > 0.001$; ***, $p<0.001$. Species are 1. *Danthonia caespitosa* 2. *Plantago drummondii* 3. *Daucus glochidiatus* 4. *Sonchus oleraceus* 5. *Euphorbia drummondii* 6. *Calotis hispidula* 7. *Crassula colorata* 8. *Hernaria hirsuta* 9. *Helipterum pygmaeum* 10. *Goodenia pusilliflora* 11. *Isoetopsis graminifolia* 12. *Brachycome lineariloba* 13. *Medicago minima* 14. *Atriplex spongiosa* 15. *Podocoma nana*

Species number

	2	3	4	5	6	7	8	9	10
1	0.5	10.4 **	0.6	10.8 **	4.3 *	0	0.8	0.8	0
2		0.7	0	6.0 -**	0	0	0.3	3.1	0
3			4.8 *	7.6 *	0.7	0	9.6 **	2.3	0
4				3.5	0	0.1	3.5	0.4	0.1
5					2.0	0	6.3 *	0.2	0
6						0	0	7.6 *	0
7							0	0	24.4 ***
8								0	0
9									0

Table 5.7 Association Analysis : October 1980. The values in the table are X^2. *, $0.05 > p > 0.01$; **, $0.01 > p > 0.001$; ***, $p < 0.001$.
Species are 1. *Plantago drummondii* 2. *Maireana sclerolaenoides* 3. *Sonchus oleraceus* 4. *Euphorbia drummondii* 5. *Hernaria hirsuta* 6. *Swainsona oliveri* 7. *Goodenia pusilliflora* 8. *Carthamus lanatus* 9. *Hypochoeris glabra* 10. *Podocoma nana*.

Species number

	2	3	4	5	6	7	8	9	10	11	12
1	0.1	0.3	0	4.5 *	0.1	0.1	0.1	0.3	2.3	0.1	0.4
2		0.1	0.8	1.4	0.1	2.0	3.3	0.3	4.2 *	1.3	0.1
3			1.2	0	0.1	0.1	0.8	3.6	1.3	0	1.6
4				9.1 **	1.6	0.8	9.4 **	0.1	5.1 *	2.6	5.1 *
5					2.4	1.4	9.5 **	0.4	18.9 ***	9.0 **	7.2 **
6						0.1	0.8	0.1	0.5	0.3	3.9 *
7							10.7 ***	22.2 ***	4.2 *	1.3	0.1
8								6.4 *	36.5 ***	17.4 ***	3.5
9									3.1	4.9 *	0
10										21.3 ***	2.6
11											0

Table 5.8: Association Analysis : April 1983 The values in the table are X^2. *, $0.05 > p > 0.01$; **, $0.01 > p > 0.001$; ***, $p < 0.001$. Species are 1. Erodium cygnorum 2. Plantago drummondii 3. Daucus glochidiatus 4. Euphorbia drummondii 5. Calotis hispidula 6. Sclerolaena obliquicuspis 7. Helipterum pygmaeum 8. Isoetopsis graminifolia 9. Swainsona oliveri 10. Goodenia pusilliflora 11. Medicago minima 12. Tetragonia eremaea

	Sampling times								
	1	2	3	4	5	6	7	8	9
Danthonia-*Euphorbia*	*	*	+	+	+	-	+	-	+
Danthonia-*Brachycome*	*	+	-	-	+	-	-	-	+
Daucus-*Sonchus*	*	+	-	-	-	-	-	-	-
Daucus-*Helipterum*	*	*	-	-	-	-	-	-	+
Daucus-*Isoetopsis*	*	*	-	-	-	-	-	-	+
Daucus-*Goodenia*	*	*	-	-	-	-	-	-	+
Daucus-*Lophochloa*	*	+	-	-	-	-	-	-	-
Daucus-*Schismus*	*	+	-	-	-	-	-	-	-
Sonchus-*Goodenia*	*	*	-	-	+	-	-	-	-
Isoetopsis-*Helipterum*	*	*	-	-	+	-	-	-	+
Helipterum-*Lophochloa*	*	+	-	-	-	-	-	-	-
Lophochloa-*Isoetopsis*	*	+	-	-	-	-	-	-	-
Brachycome-*Actinobole*	*	+	-	-	+	-	-	-	-
Brachycome-*Bulbine*	*	+	-	-	+	-	-	-	-
Actinobole-*Bulbine*	*	+	-	-	-	-	-	-	-
Schismus-*Lophochloa*	*	+	-	-	-	-	-	-	-
Danthonia-*Calotis*	+	*	-	-	-	-	-	-	+
Plantago-*Daucus*	+	*	-	-	-	-	-	-	+
Daucus-*Brachycome*	+	*	-	-	-	-	-	-	+
Sonchus-*Euphorbia*	+	*	+	-	+	-	-	-	-
Sonchus-*Brachycome*	+	*	-	-	+	-	-	-	-
Sonchus-*Medicago*	+	*	+	-	+	-	-	-	-
Sonchus-*Atriplex*	-	*	-	-	+	-	-	-	-
Euphorbia-*Isoetopsis*	+	*	-	-	+	-	-	-	*
Euphorbia-*Goodenia*	+	*	+	-	+	-	+	-	+
Euphorbia-*Brachycome*	+	*	-	-	+	-	-	-	+
Hernaria-*Calotis*	-	*	+	-	-	-	-	-	+
Hernaria-*Podocoma*	-	*	-	-	+	-	-	-	+
Crassula-*Hernaria*	+	*	-	-	-	-	-	-	+
Crassula-*Calotis*	+	*	+	-	-	-	-	-	+
Hernaria-*Atriplex*	+	*	-	-	+	-	-	-	+
Helipterum-*Goodenia*	+	*	-	-	+	-	-	-	+
Helipterum-*Brachycome*	+	*	-	-	+	-	-	-	*
Goodenia-*Isoetopsis*	+	*	-	-	+	-	-	-	+
Goodenia-*Brachycome*	+	*	-	-	+	-	-	-	+
Goodenia-*Medicago*	+	*	+	-	+	-	-	-	*
Goodenia-*Swainsona*	-	*	+	-	+	-	-	-	+
Brachycome-*Atriplex*	-	*	-	-	+	-	-	-	-
Medicago-*Swainsona*	-	+	+	-	+	-	-	-	+
Plantago-*Sonchus*	+	+	*	-	+	-	-	-	-
Plantago-*Hernaria*	+	+	*	-	+	-	-	-	+
Hernaria-*M.sclerolaenoides*	+	+	*	-	+	-	-	-	+
Sonchus-*Carthamus*	-	+	*	-	-	-	-	-	-
Goodenia-*Podocoma*	-	+	*	-	+	-	-	-	+
Euphorbia-*Calotis*	+	+	+	-	-	-	-	-	*
Calotis-*Isoetopsis*	+	+	-	-	-	-	-	-	*
Calotis-*Goodenia*	+	+	+	-	-	-	-	-	*
Calotis-*Medicago*	+	+	+	-	-	-	-	-	*
Calotis-*Tetragonia*	-	+	-	-	-	-	-	-	*
Helipterum-*Swainsona*	-	+	-	-	+	-	-	-	*
Medicago-*Isoetopsis*	+	+	-	-	+	-	-	-	*

Table 5.9 Species pairs which showed significant associations ($p < 0.01$) at the Overland paddock site 1979 - 1983. * indicates a significant association. + indicates both species present but no significant association. - indicates either one or both species absent. Sampling times : 1. October 1979 2. July 1980 3. October 1980 4. January 1981 5. October 1981 6. January 1982 7. June 1982 8. August 1982 9. April 1983.

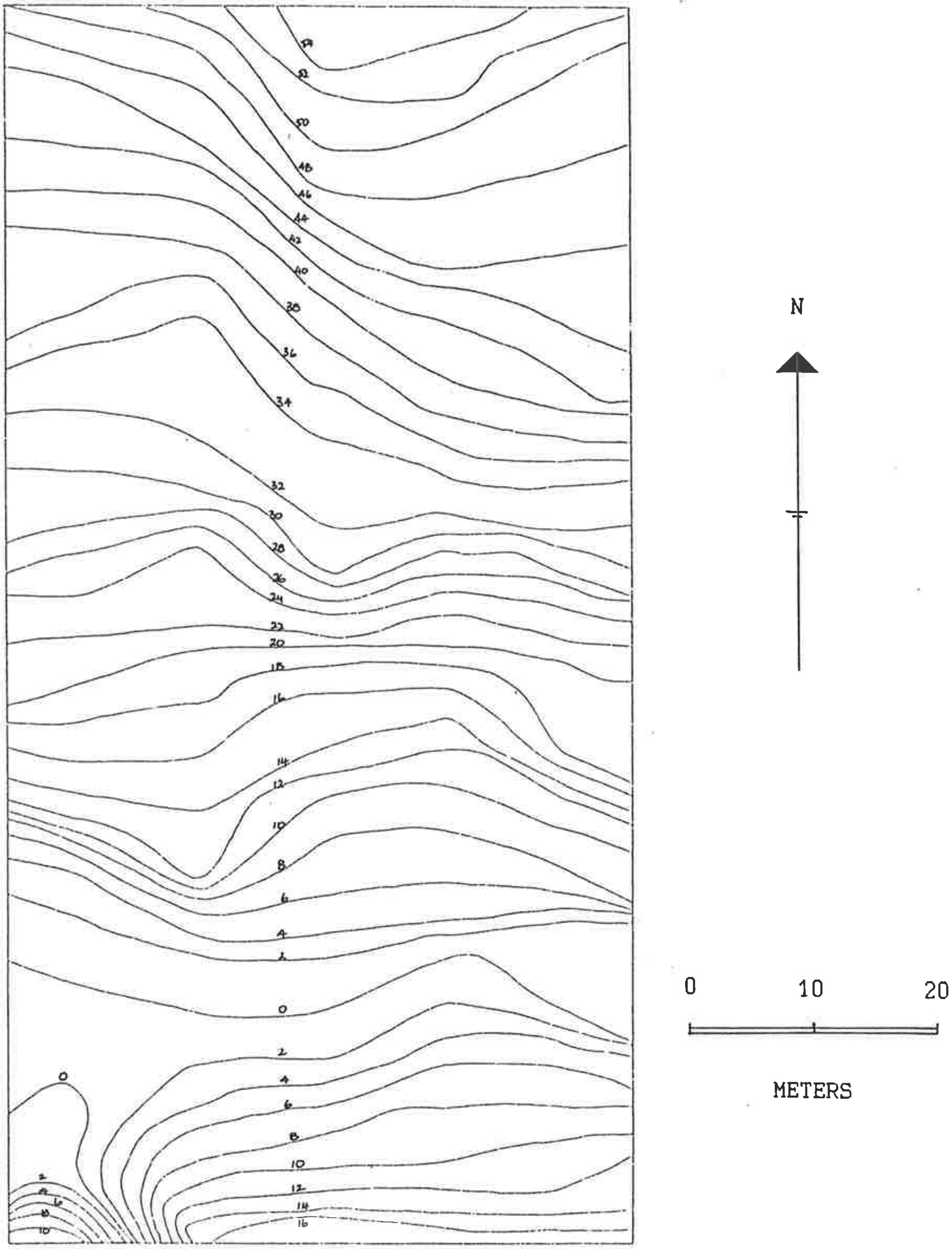


Figure 5.1 Contour map of Overland Paddock study site.
Contours in cm.

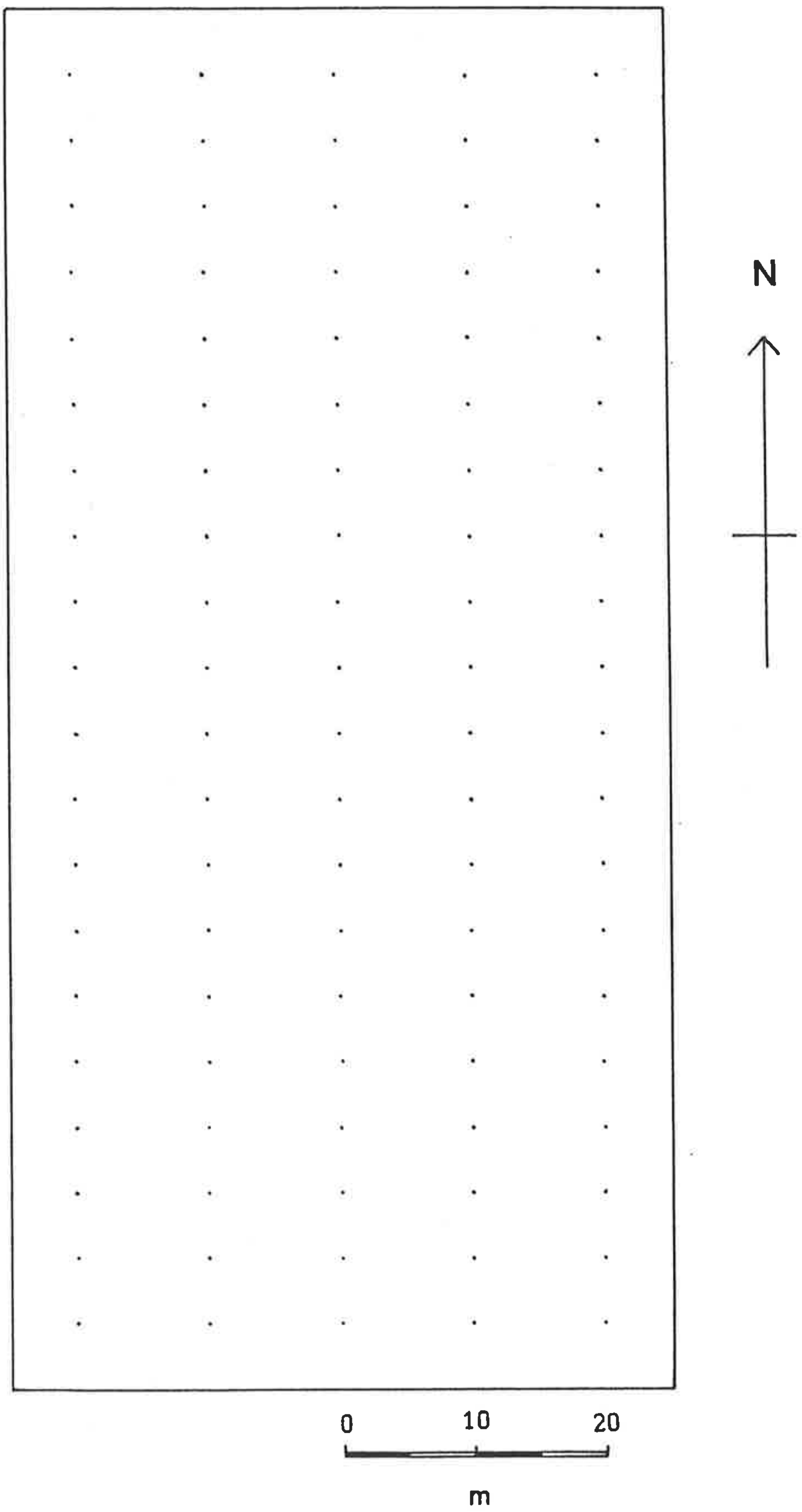
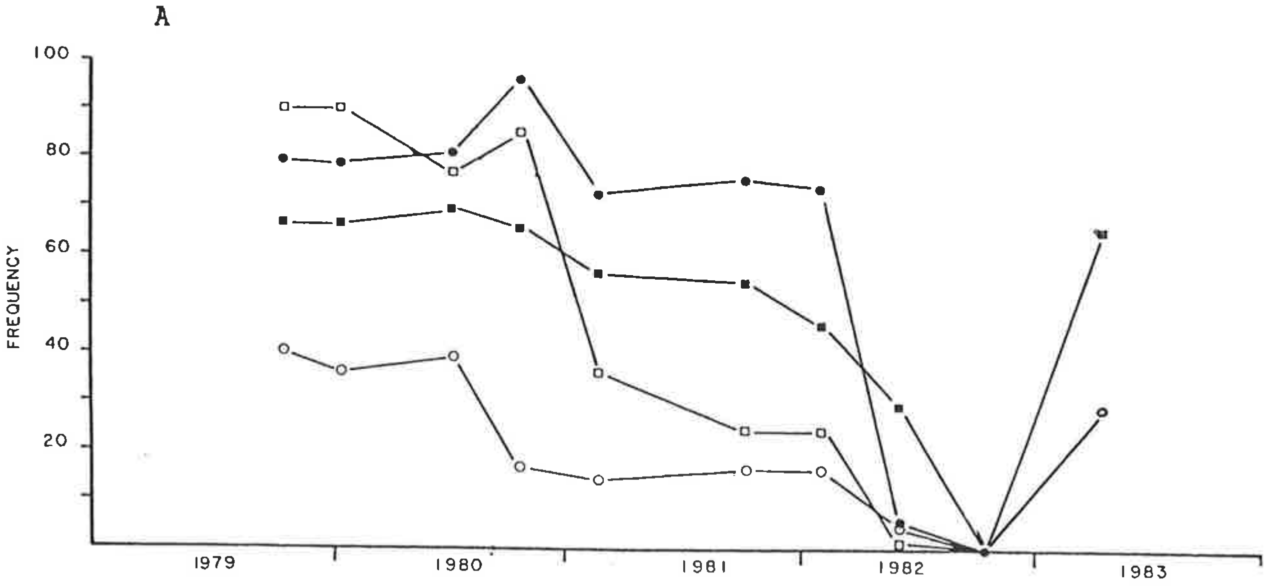


Figure 5.2 Layout of the overland paddock site with quadrat positions shown.



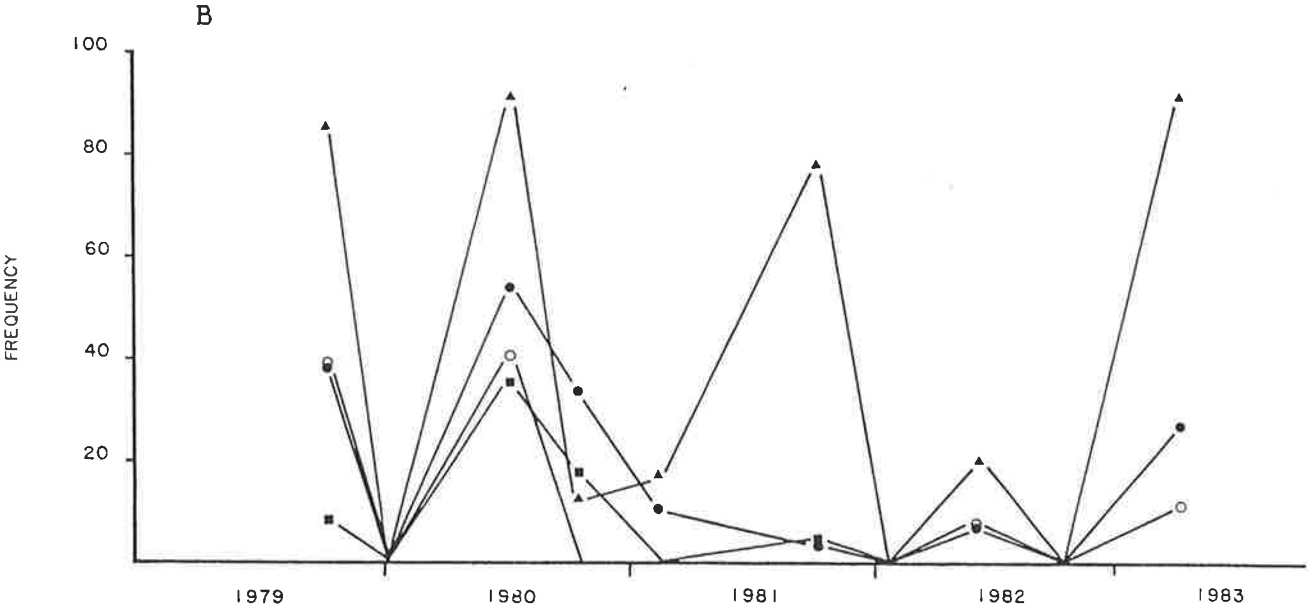
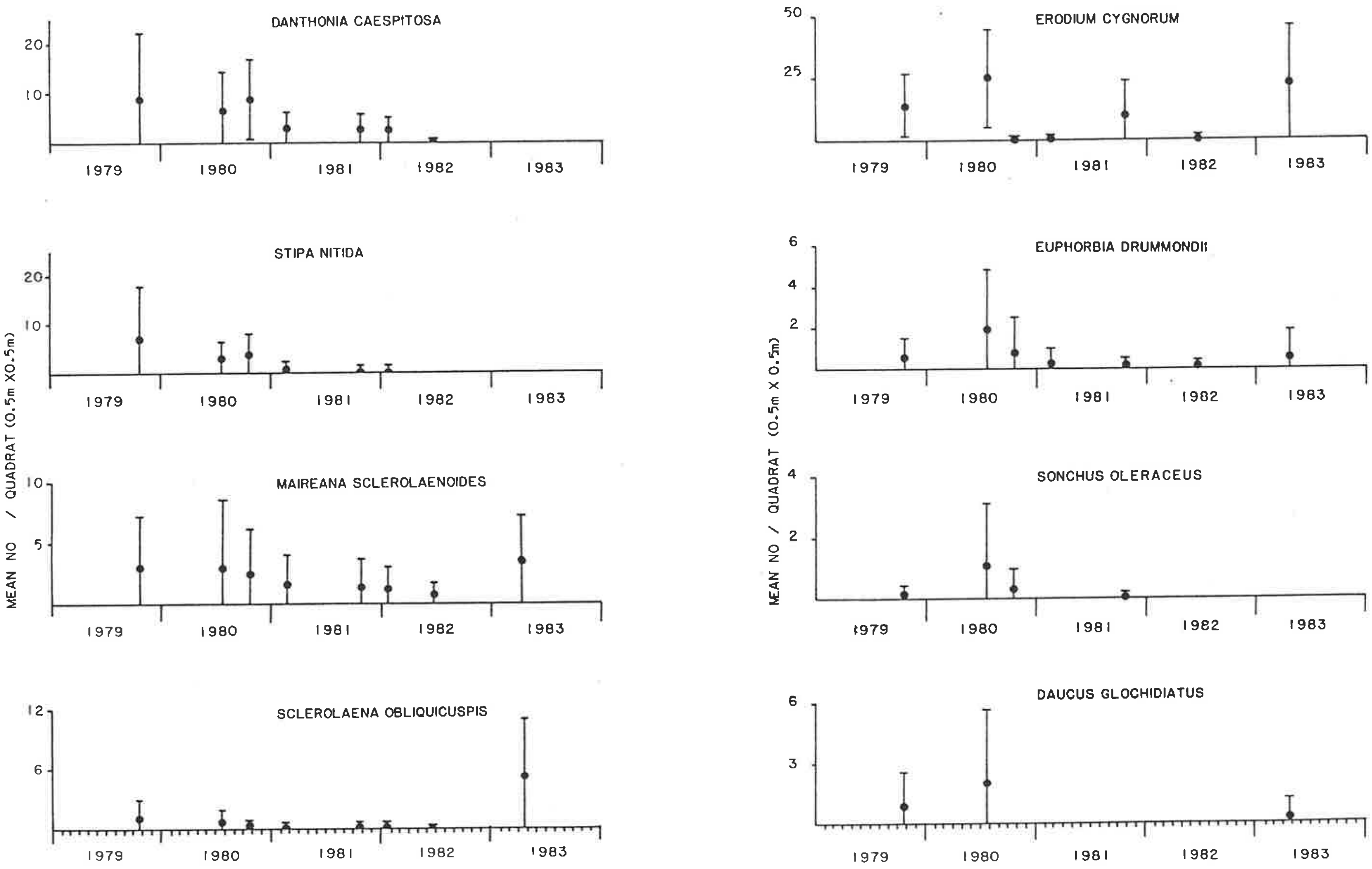


Figure 5.3 Frequency of selected species recorded from 1979 to 1983
A (□) *Stipa nitida* (■) *Maireana sclerolaenoides* (●) *Danthonia caespitosa* (○) *Sclerolaena obliquicuspis*

B (■) *Daucus glochidiatus* (○) *Sonchus oleraceus* (●) *Euphorbia drummondii* (▲) *Erodium cygnorum*



<u>Figure 5.4</u> Mean density (●) and standard deviations bars of selected annual plants at the Overland paddock study site, 1979 - 1983.

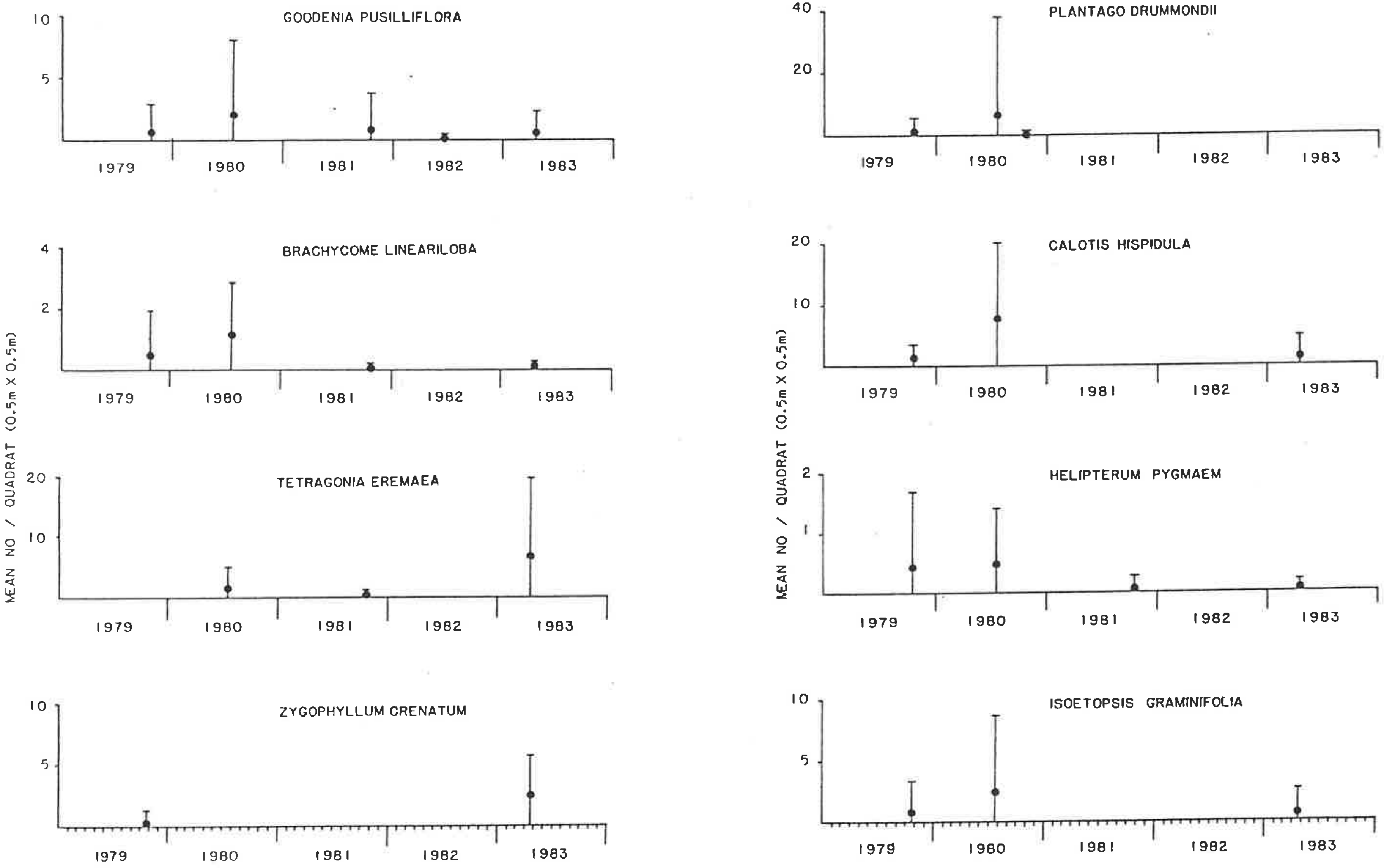


Figure 5.5 Mean density (●) and standard deviations bars of selected annual plants at the Overland paddock study site, 1979 - 1983.

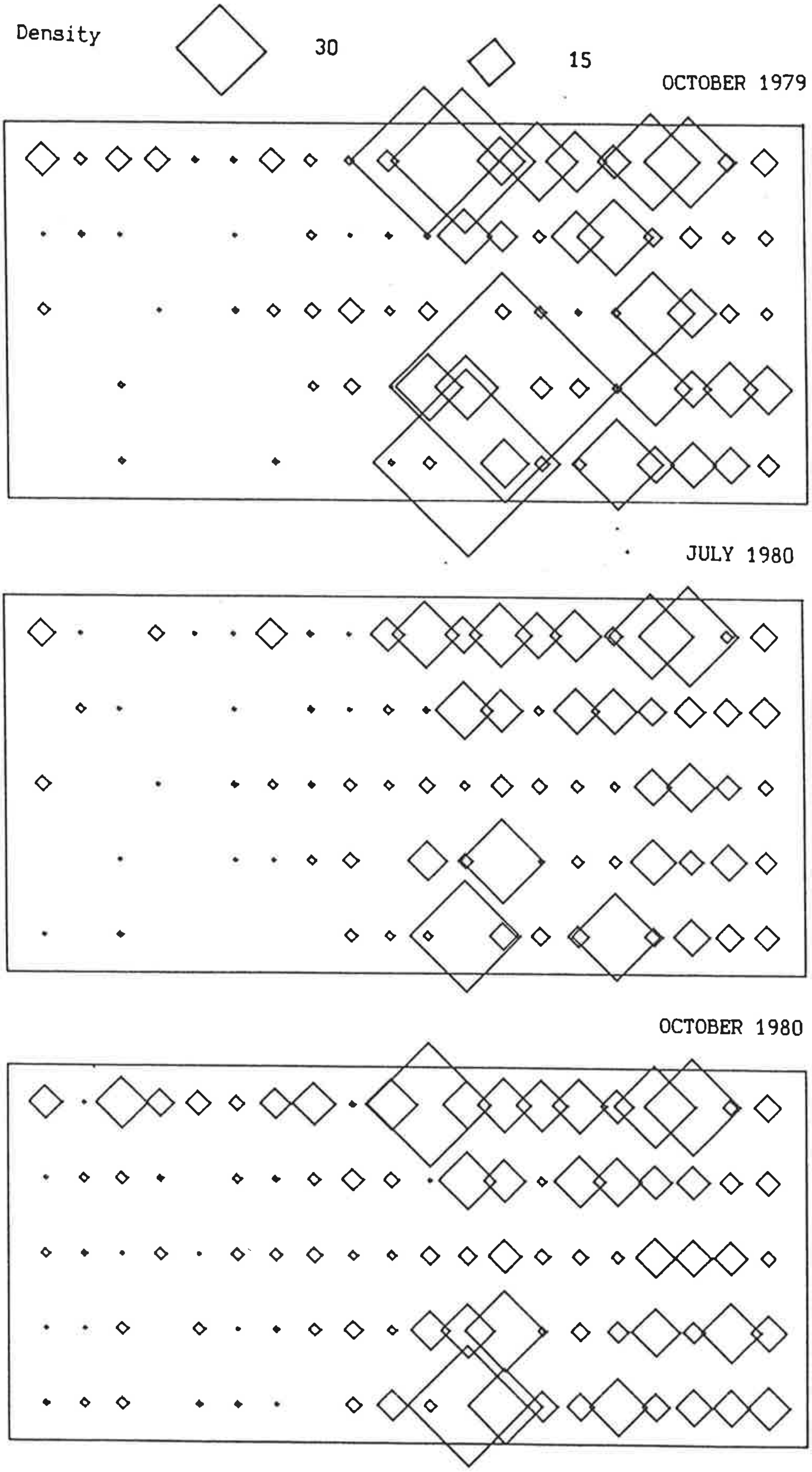


Figure 5.6 Density distribution of *Danthonia caespitosa* at the Overland paddock study site.

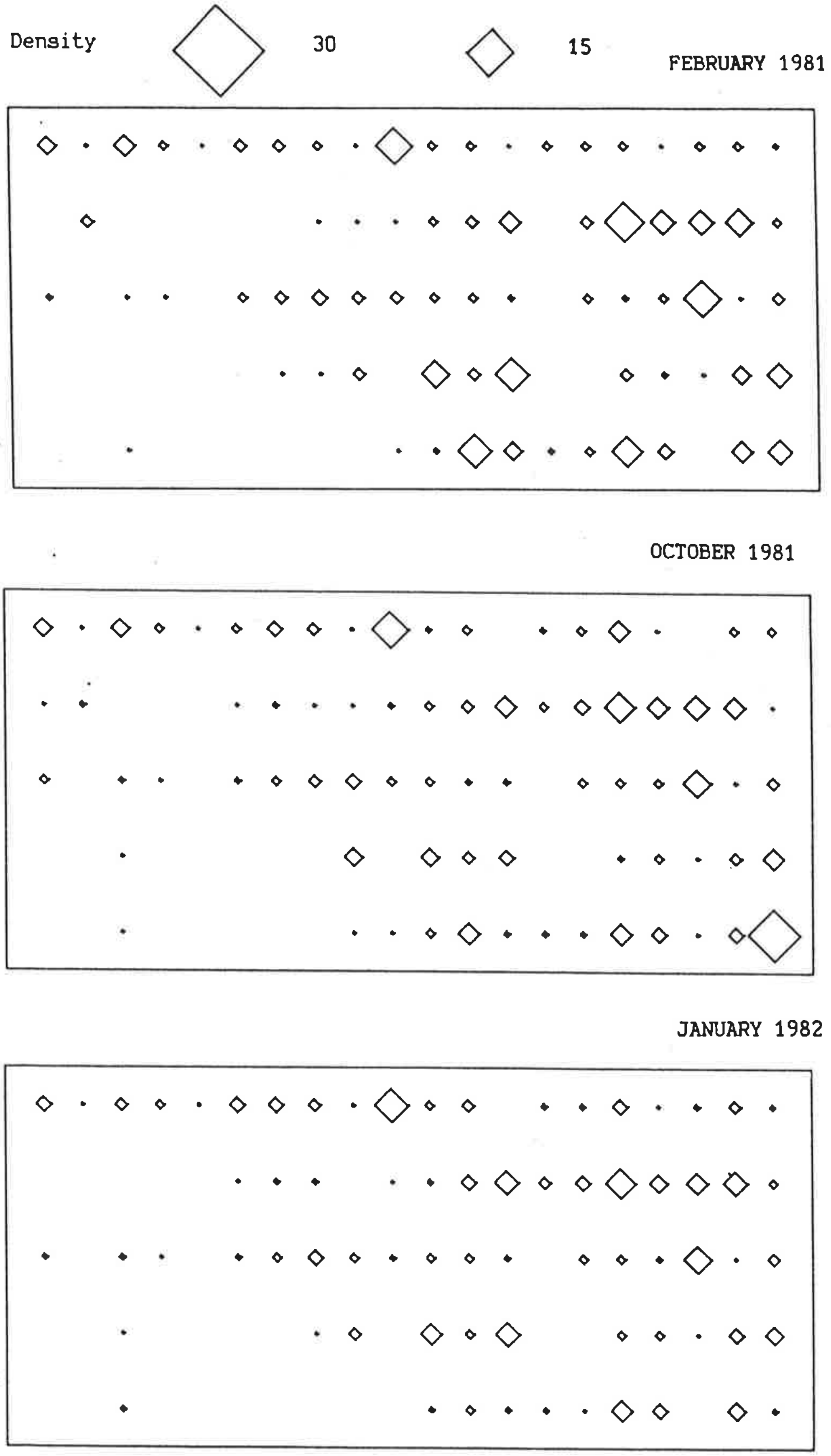


Figure 5.7 Density distribution of *Danthonia caespitosa* at the Overland paddock study site.

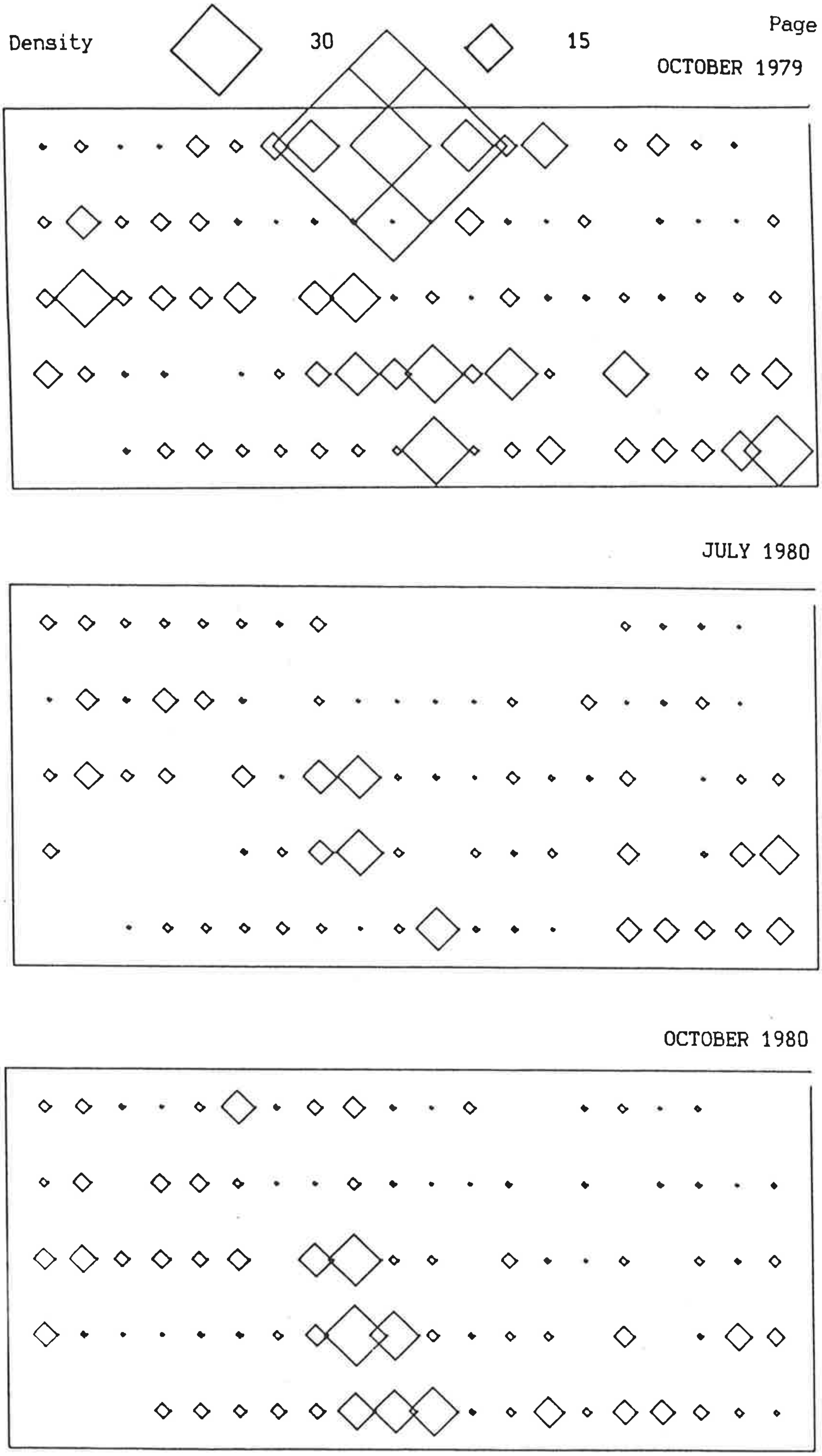


Figure 5.8 Density distribution of *Stipa nitida* at the Overland paddock study site.

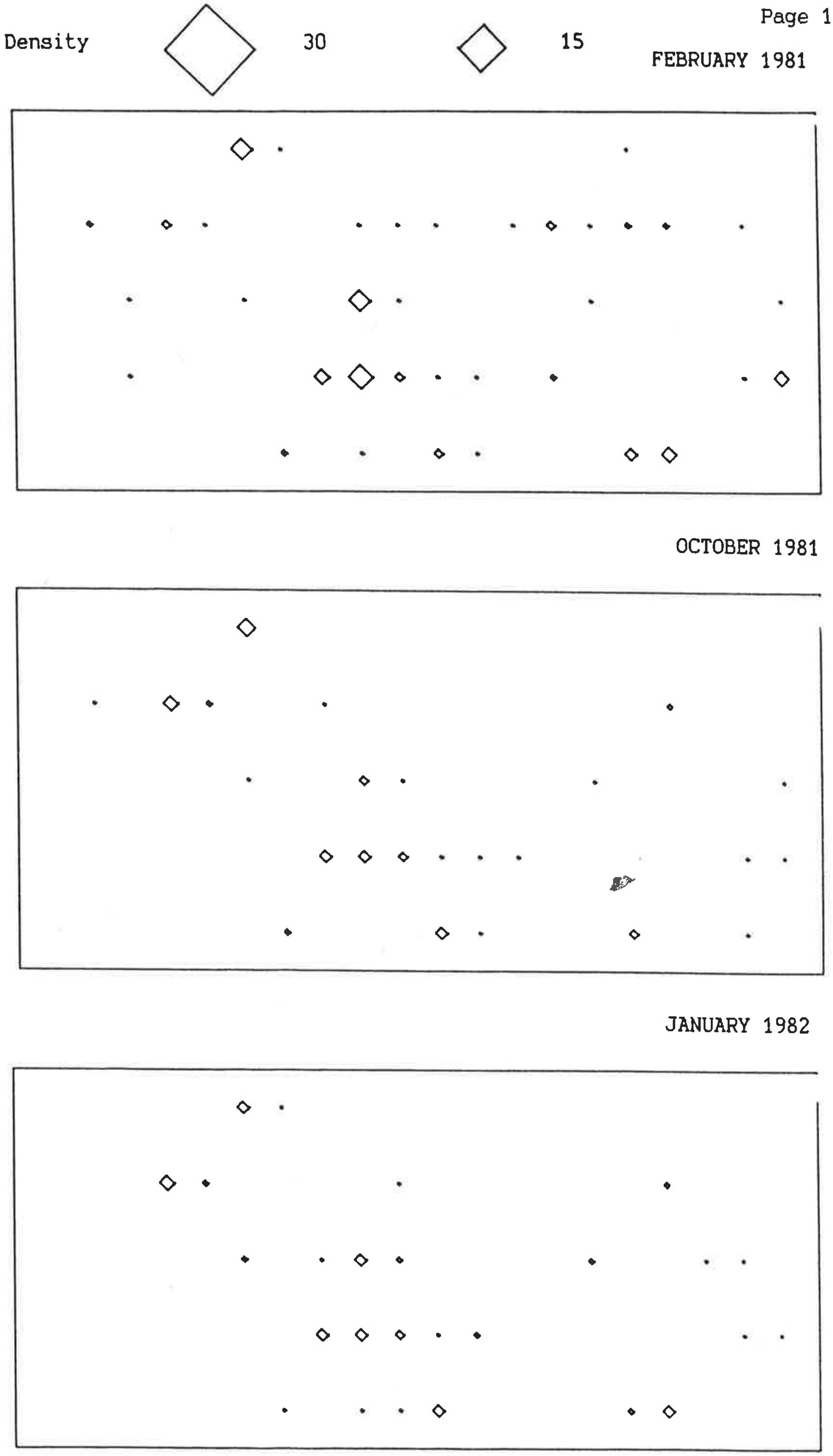


Figure 5.9 Density distribution of *Stipa nitida* at the Overland paddock study site.

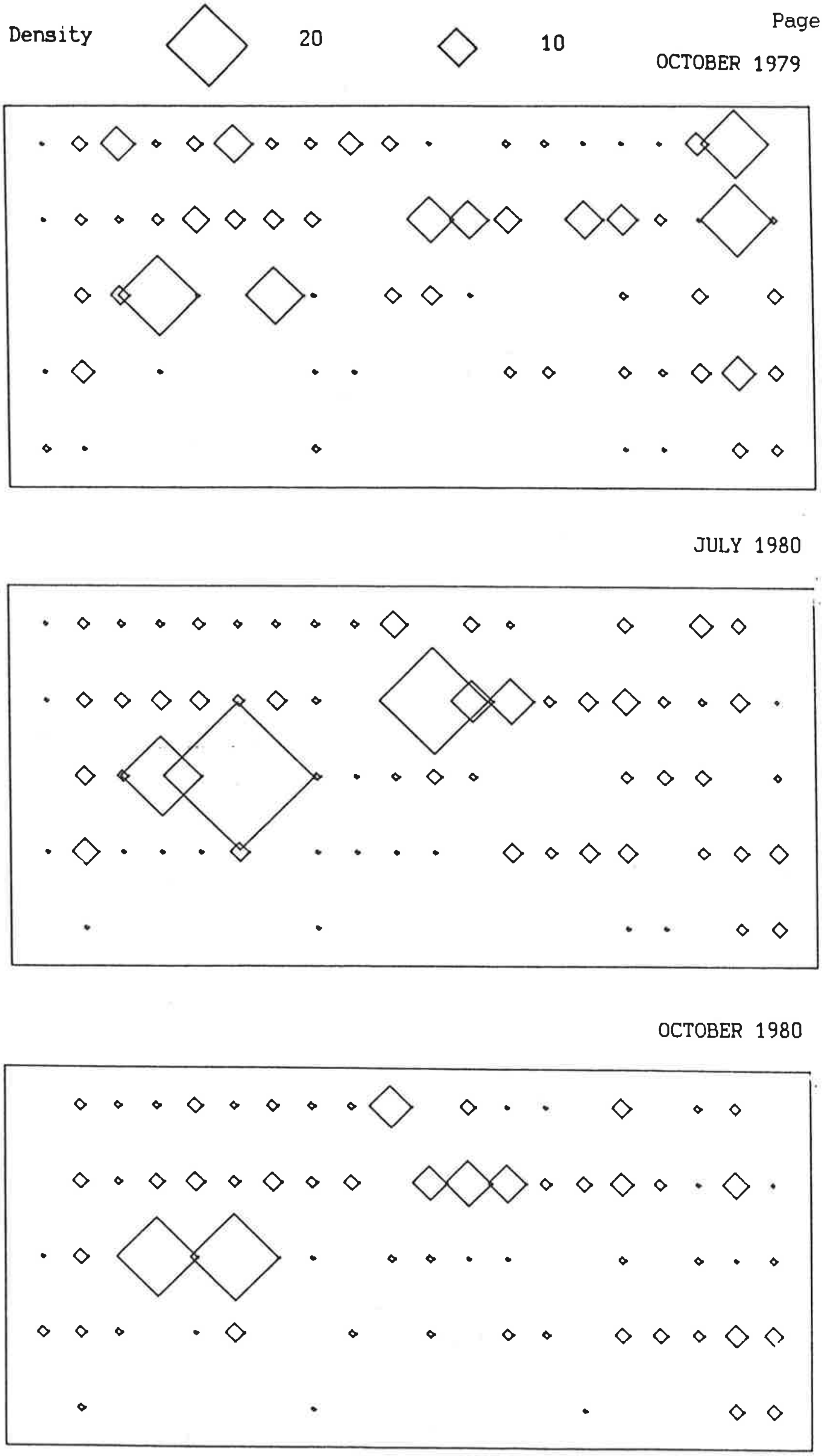


Figure 5.10 Density distribution of *Maireana sclerolaenoides* at the Overland paddock study site.

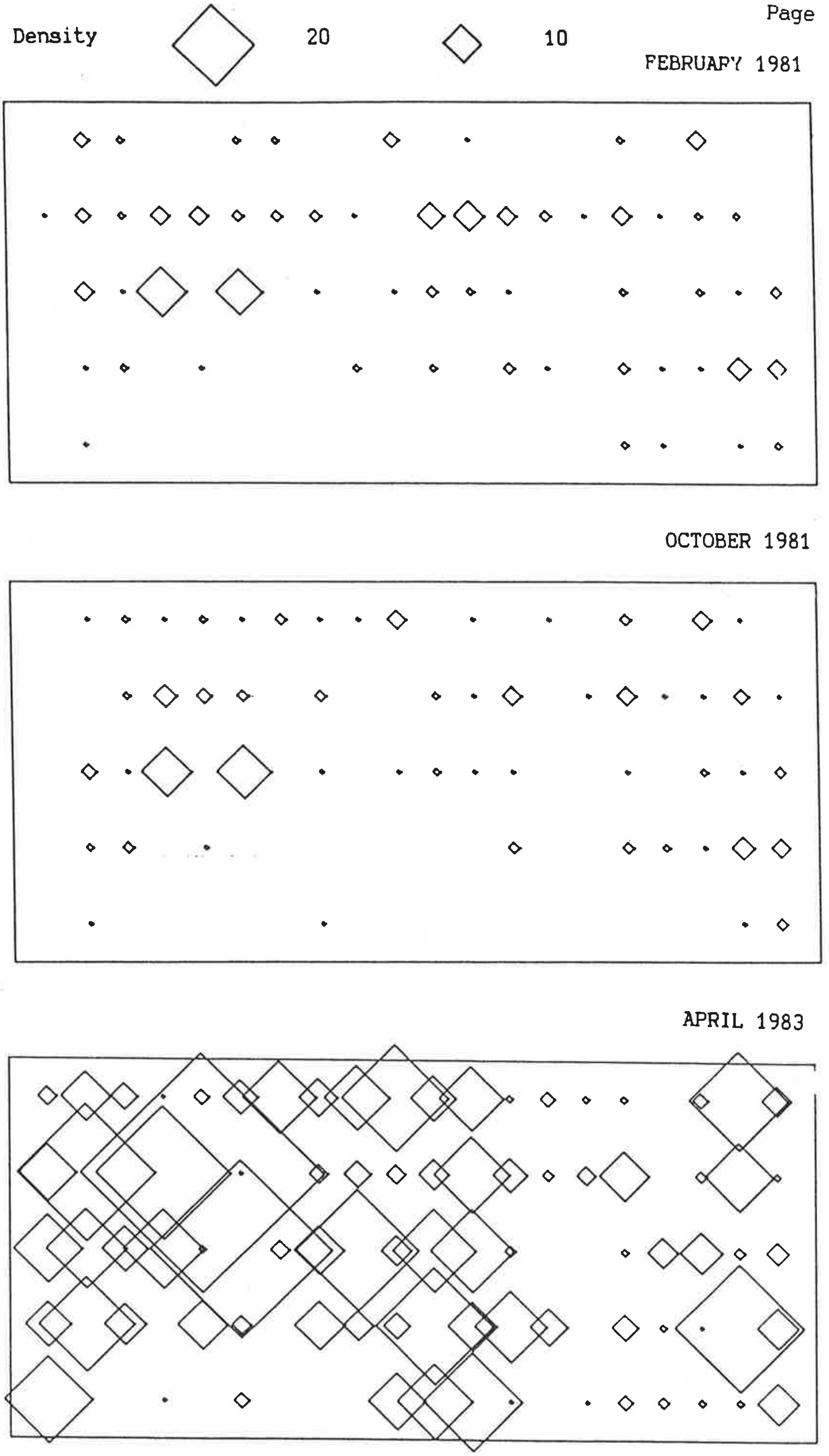


Figure 5.11 Density distribution of *Maireana sclerolaenoides* at the Overland paddock study site.

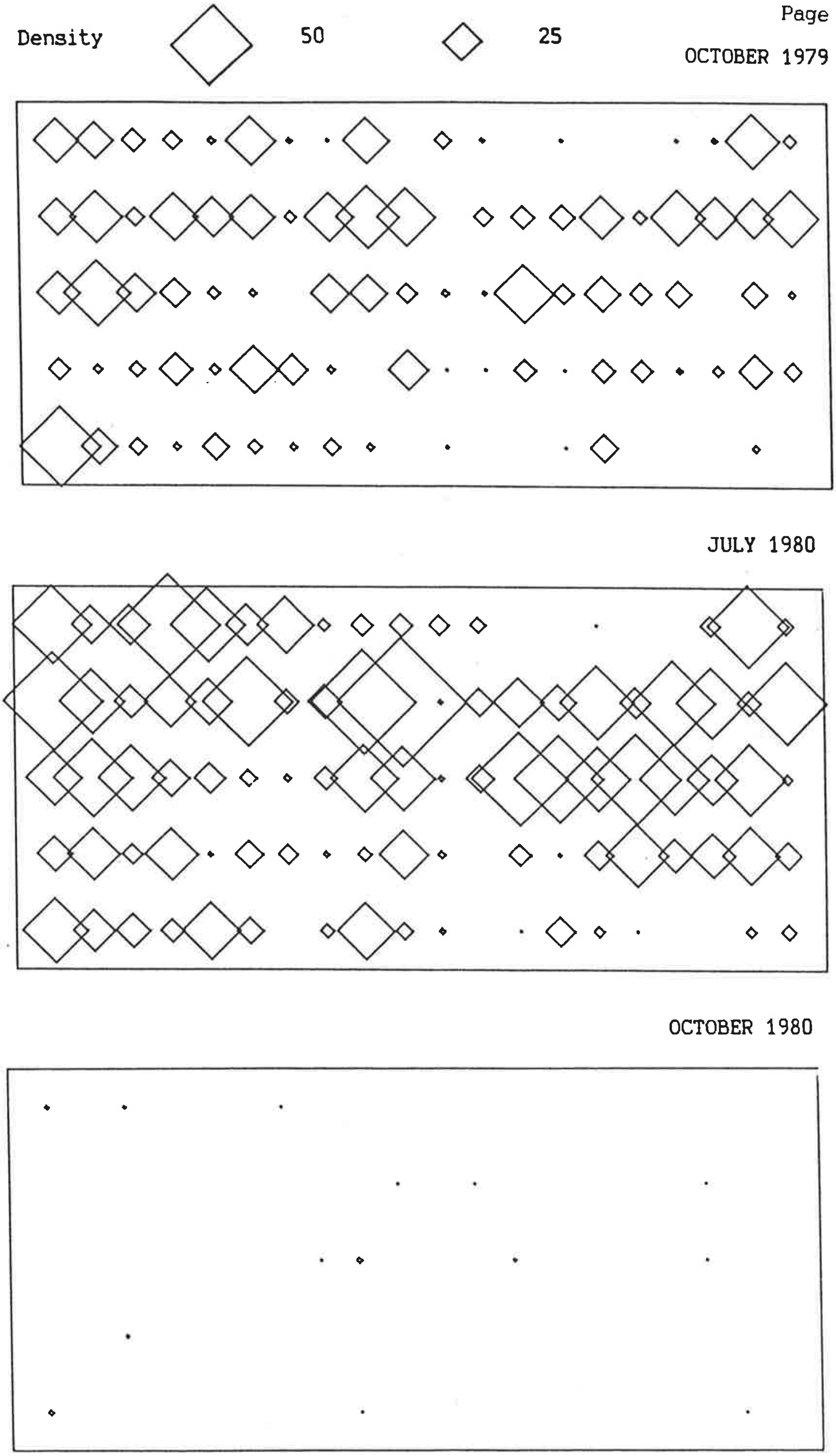


Figure 5.12 Density distribution of *Erodium cygnorum* at the Overland paddock study site.

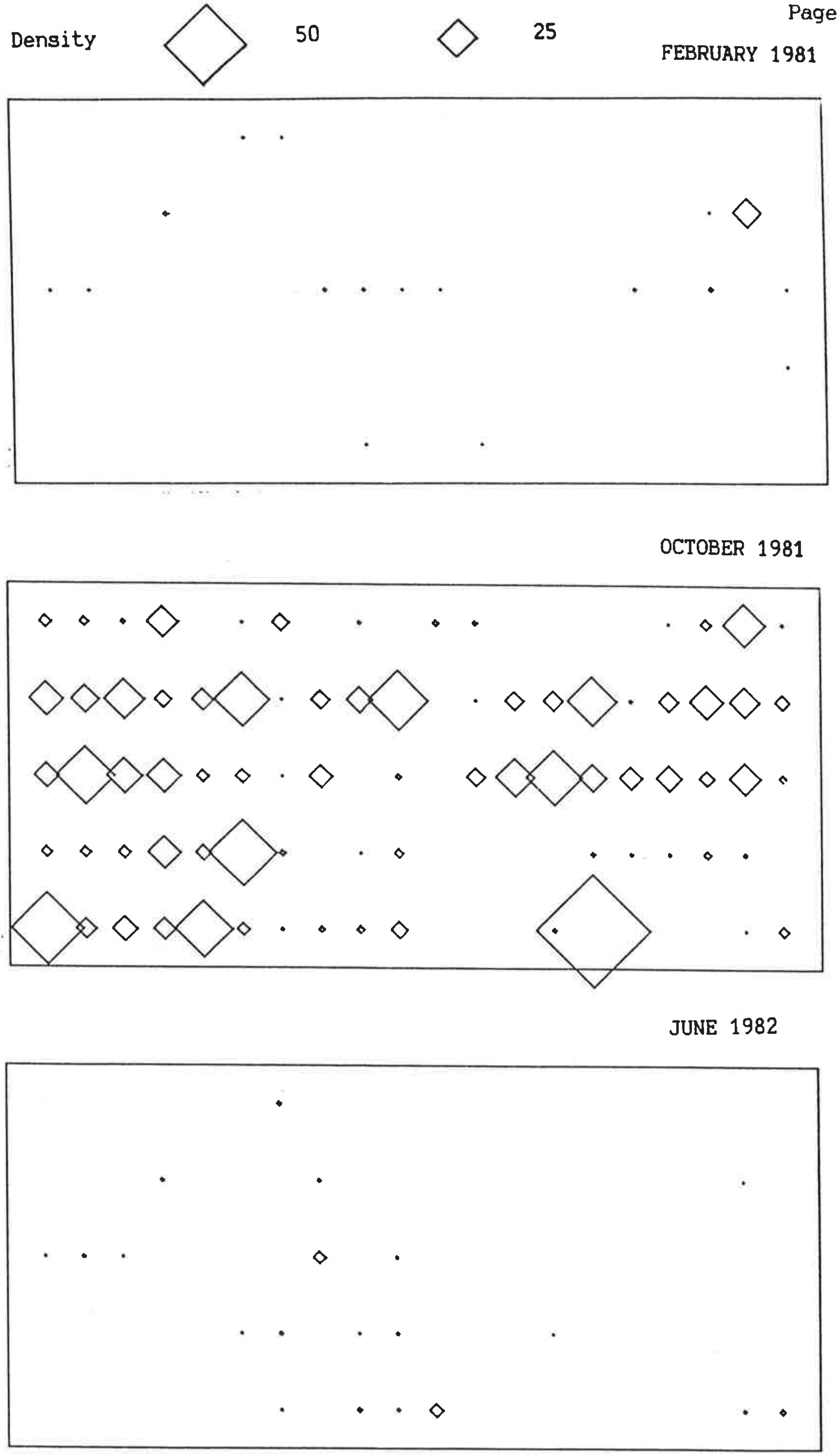


Figure 5.13 Density distribution of *Erodium cygnorum* at the Overland paddock study site.

APRIL 1983

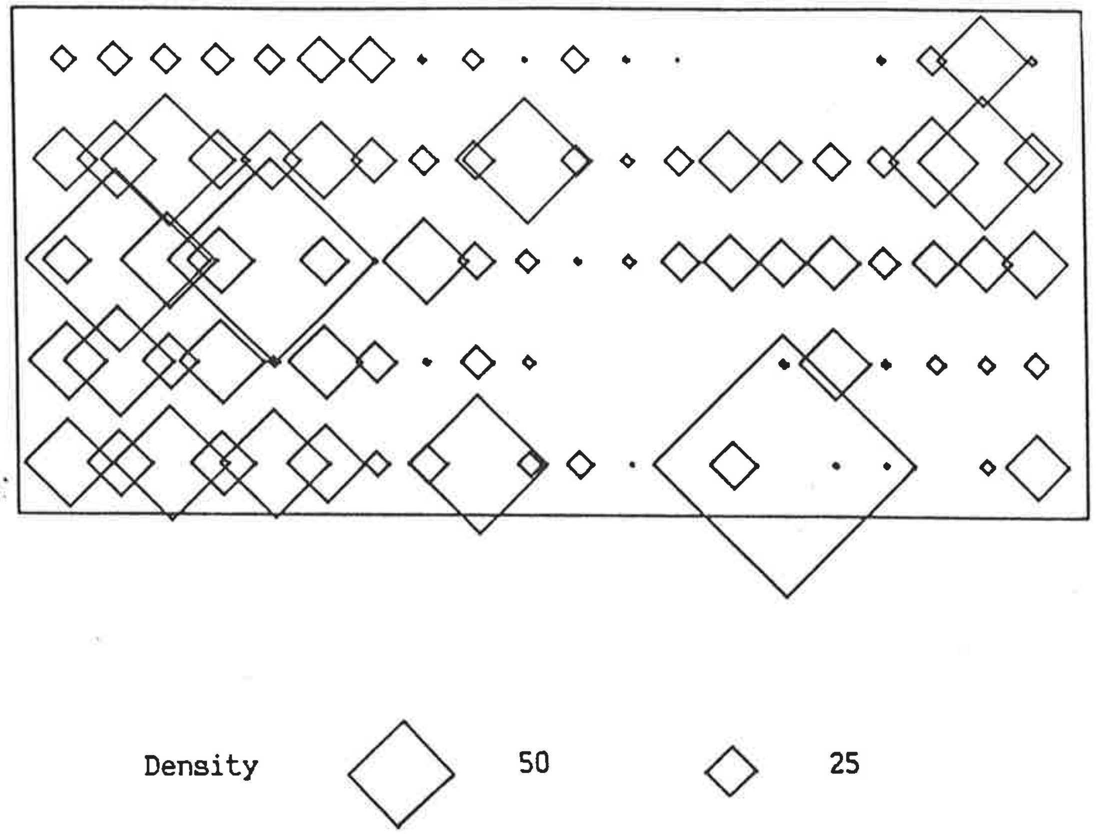


Figure 5.14 Density distribution of Erodium cygnorum at the Overland paddock study site.

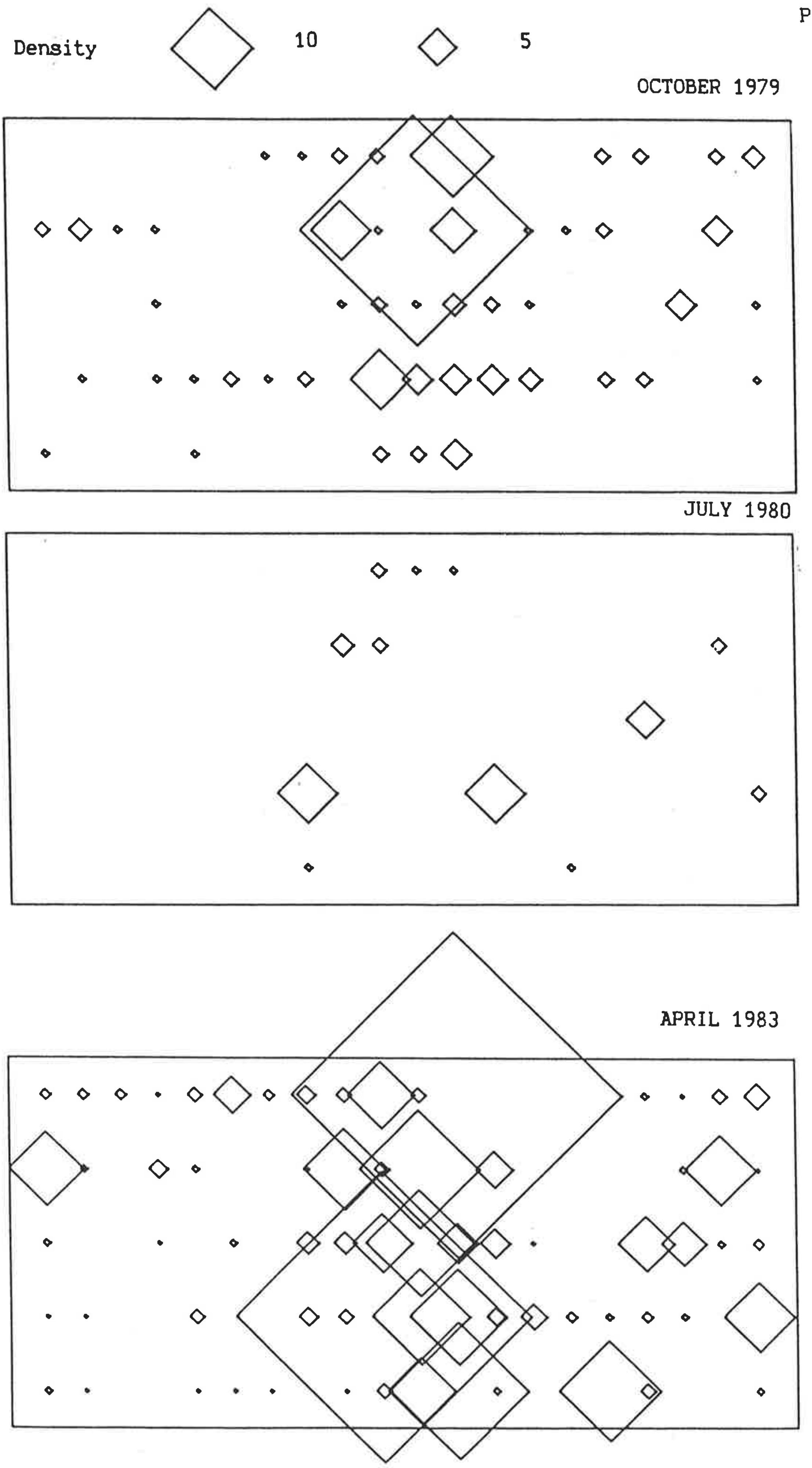


Figure 5.15 Density distribution of *Tetragonia eremaea* at the Overland paddock study site

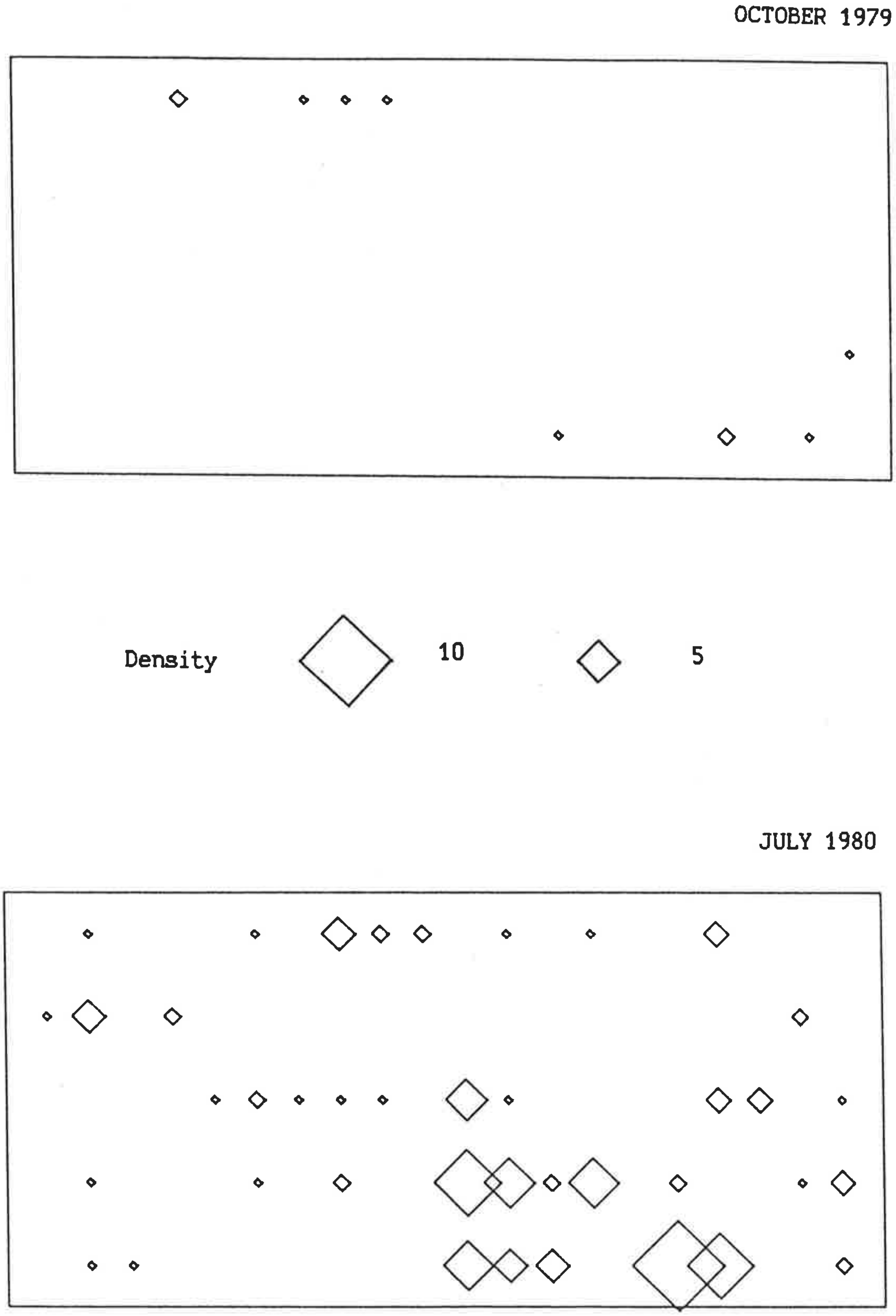


Figure 5.16 Density distribution of *Sonchus oleraceus* at the Overland paddock study site.

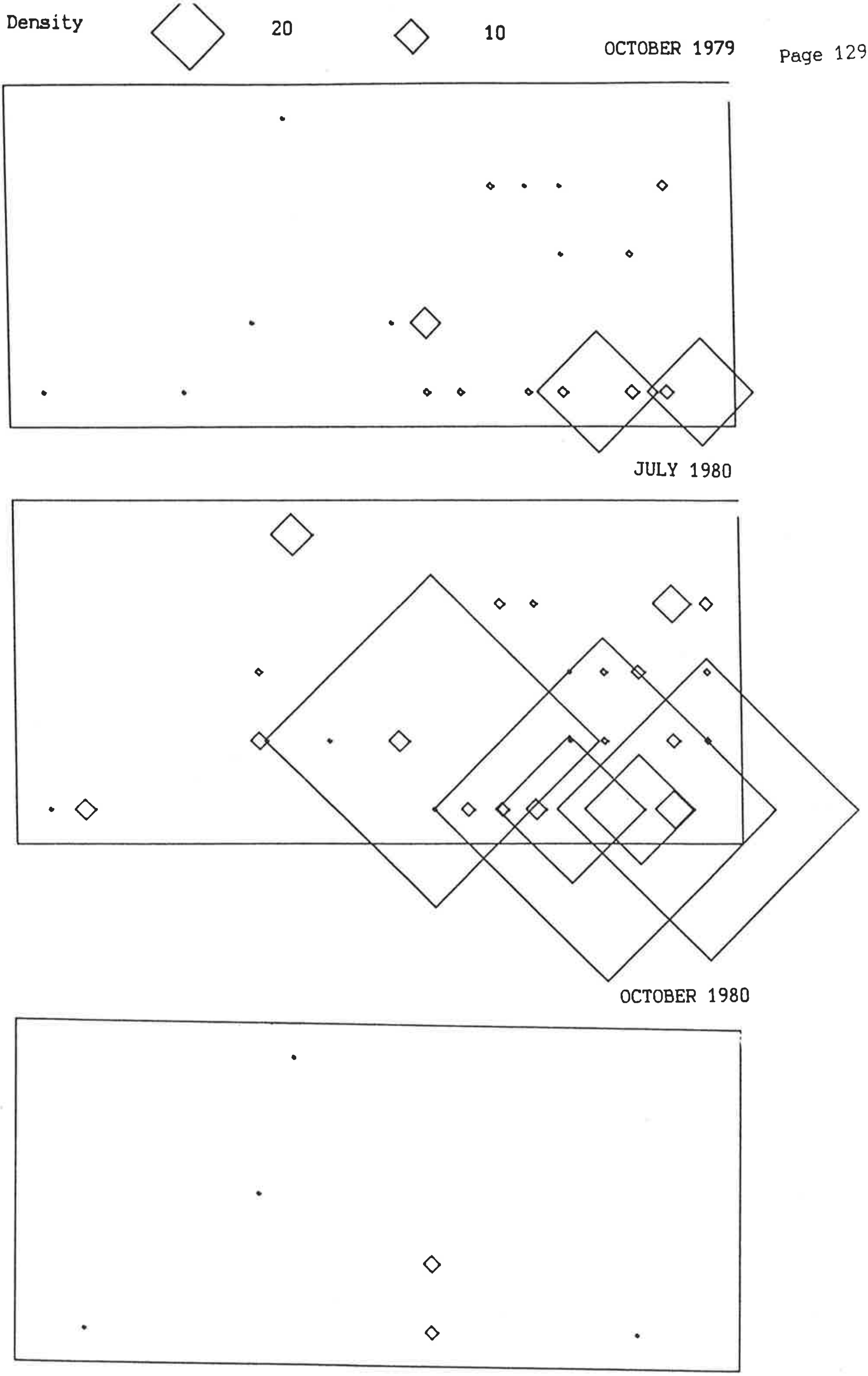


Figure 5.17 Density distribution of *Plantago drummondii* at the Overland paddock study site.

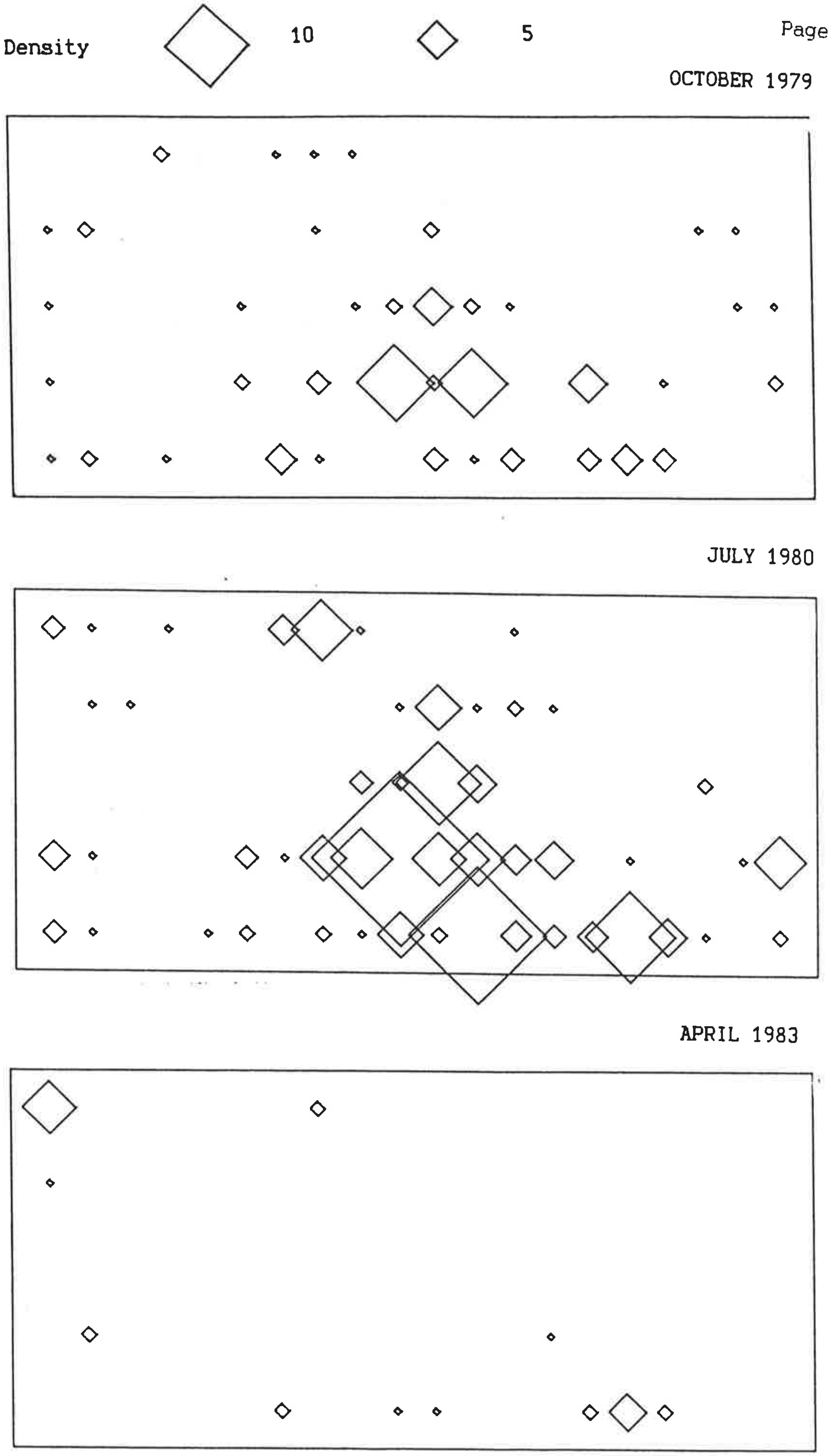


Figure 5.18 Density distribution of Daucus glochidiatus at the Overland paddock study site.

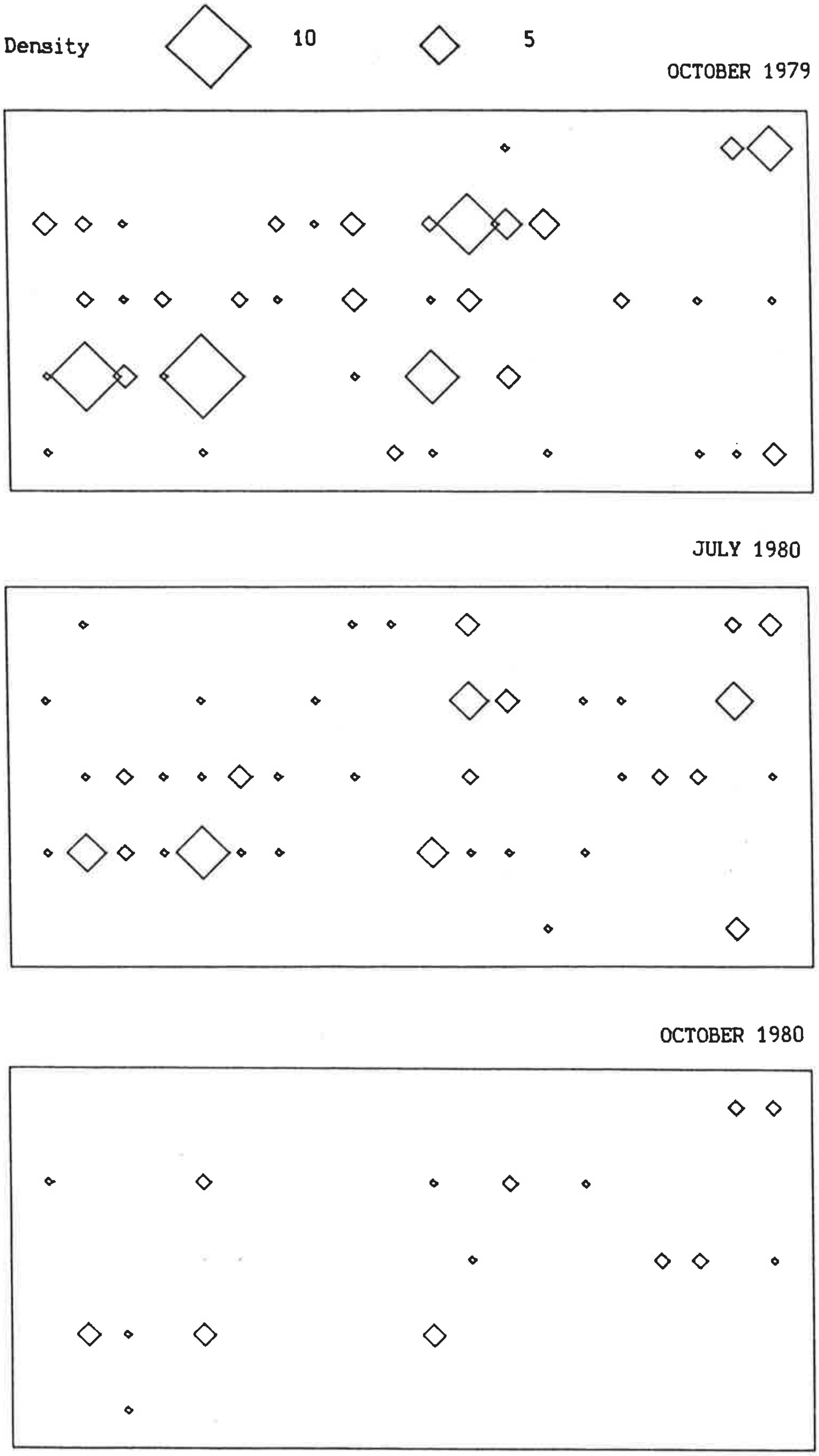


Figure 5.19 Density distribution of *Sclerolaena obliquicuspis* at the Overland paddock study site.

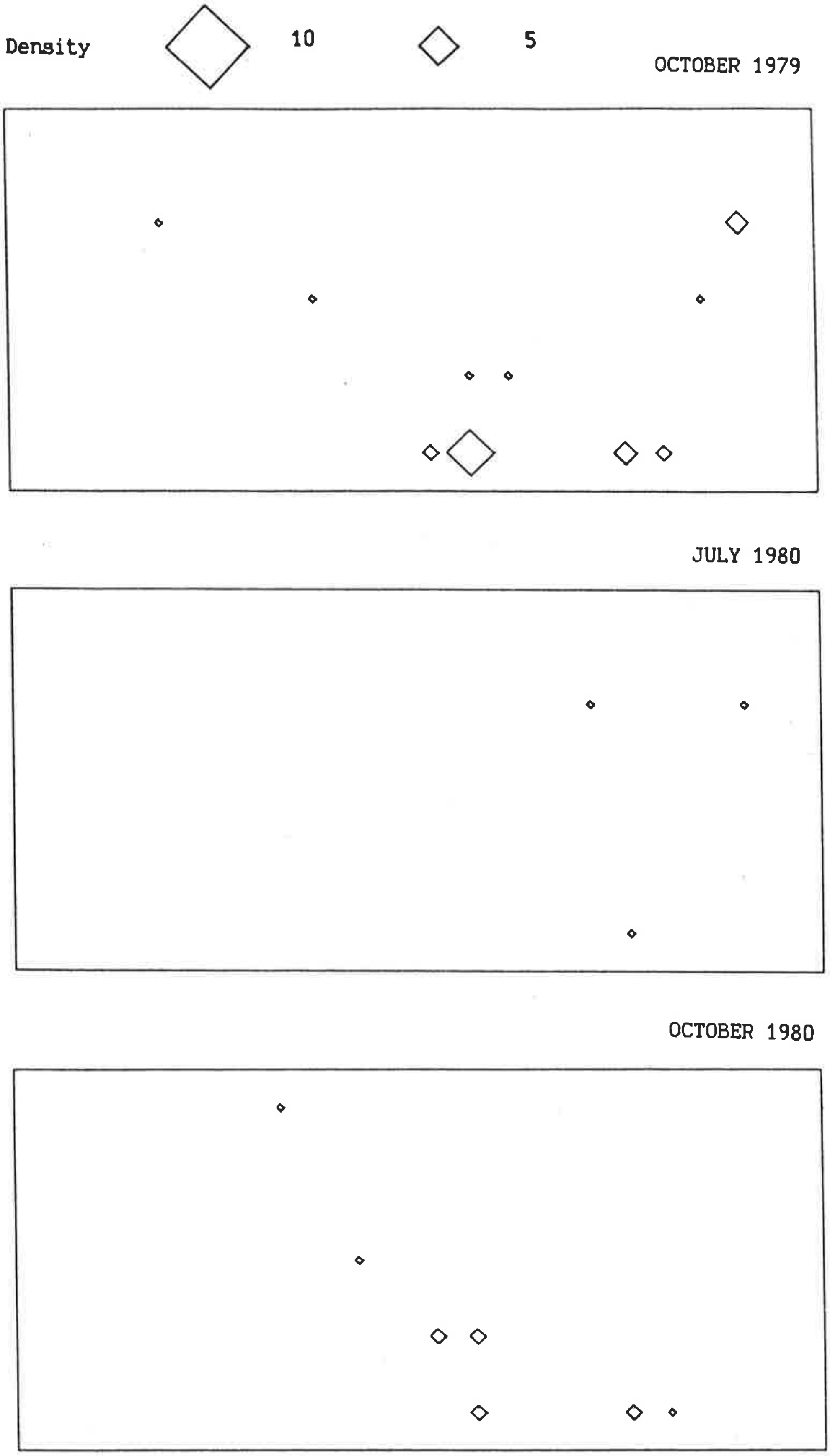


Figure 5.20 Density distribution of *Euphorbia drummondii* at the Overland paddock study site.

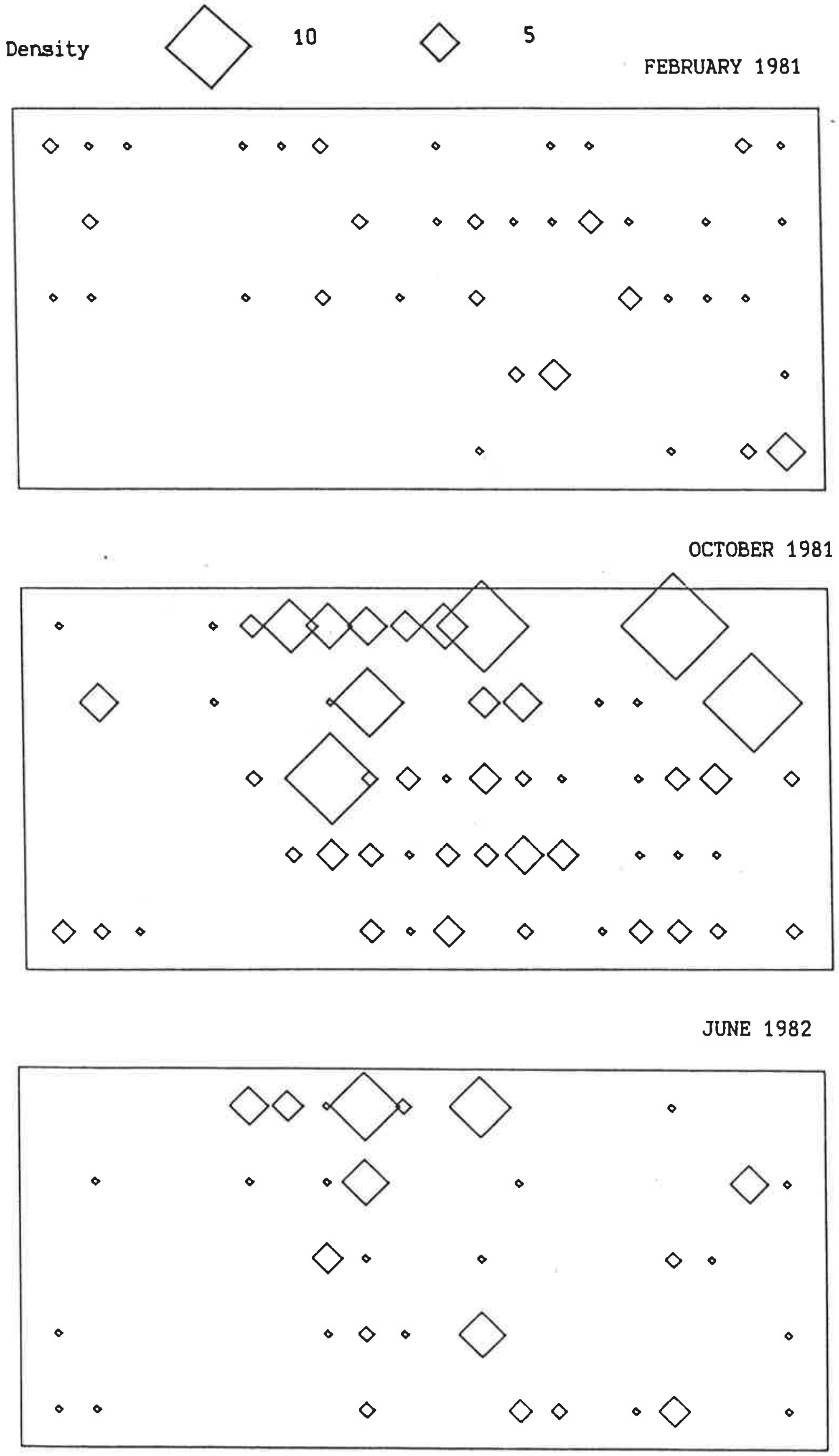


Figure 5.21 Density distribution of *Euphorbia drummondii* at the Overland paddock study site.

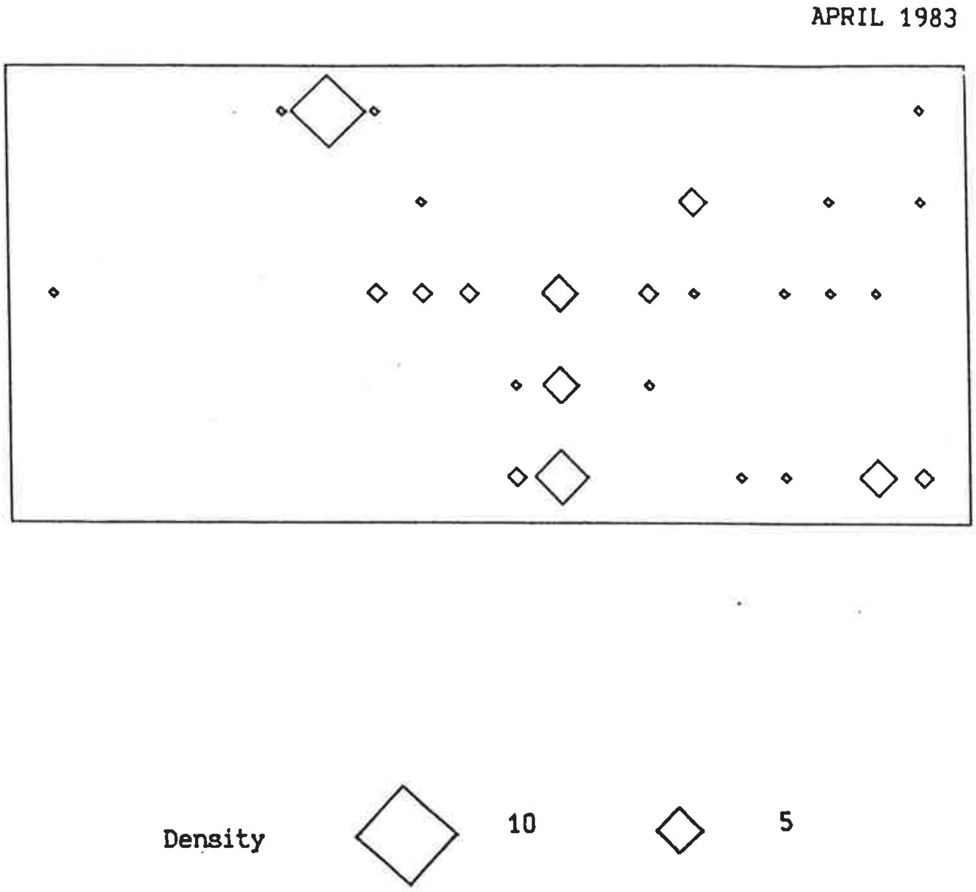


Figure 5.22 Density distribution of *Euphorbia drummondii* at the Overland paddock study site.

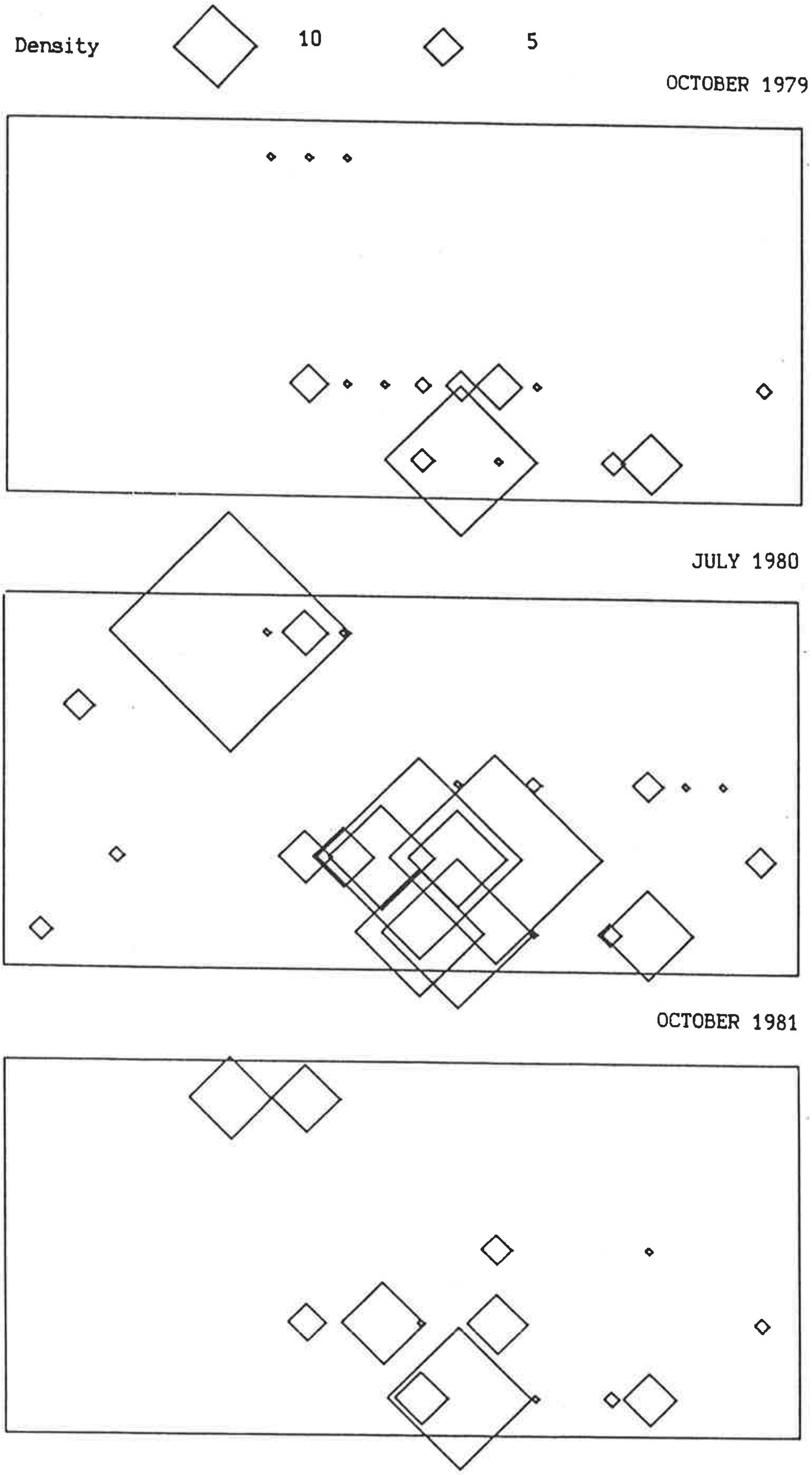


Figure 5.23 Density distribution of *Goodenia pusilliflora* at the Overland paddock study site.

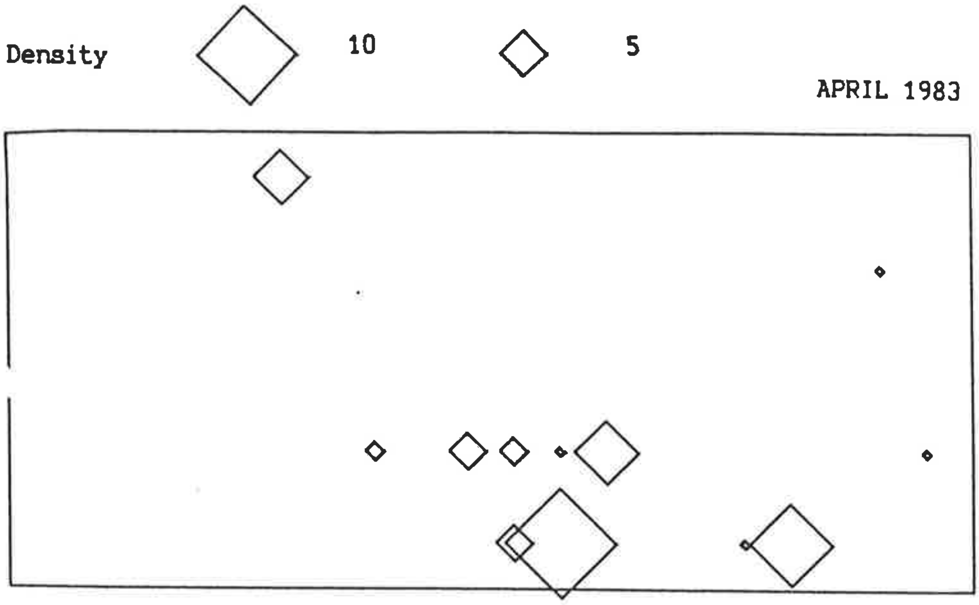


Figure 5.24 Density distribution of Goodenia pusilliflora at the Overland paddock study site.

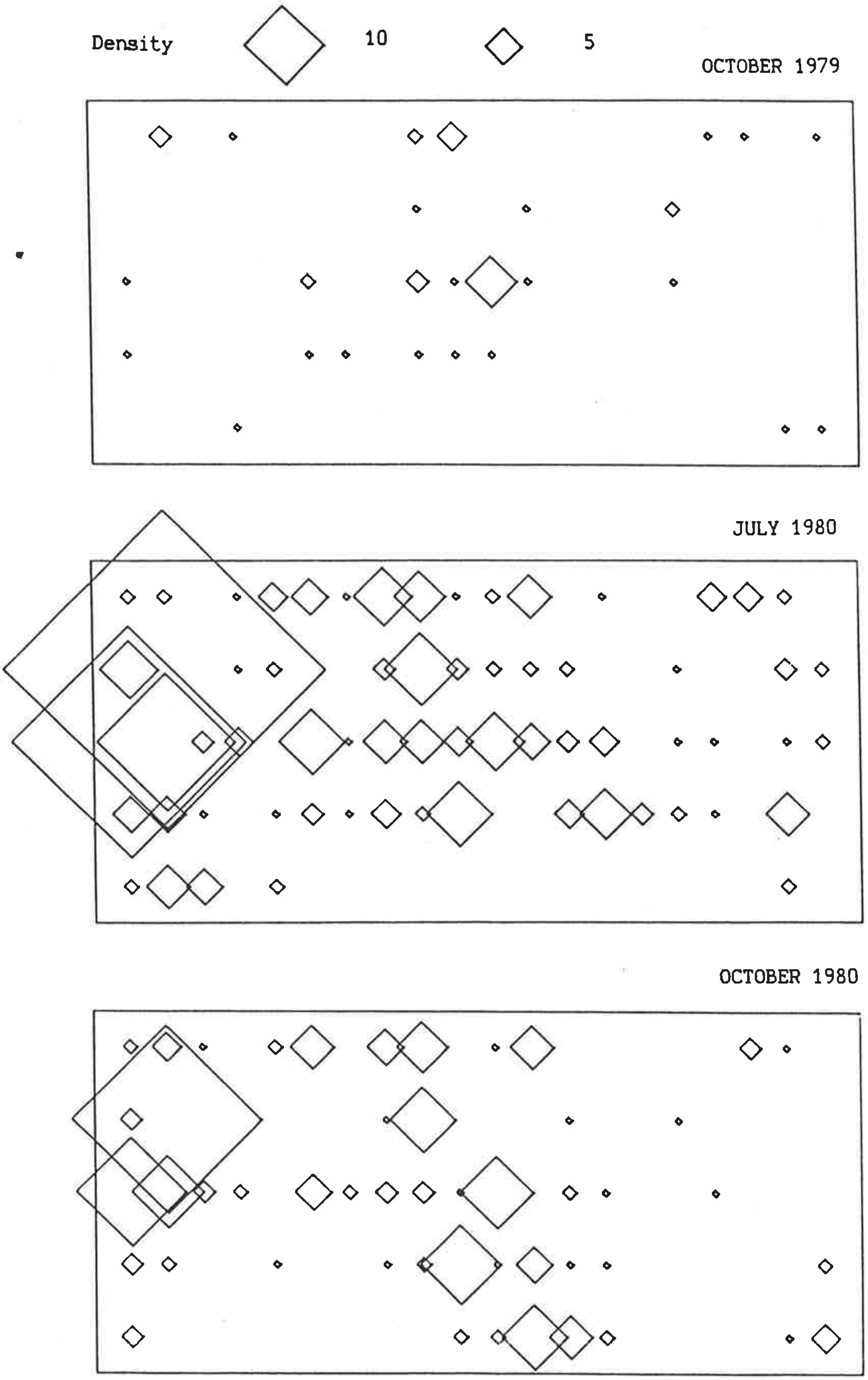


Figure 5.25 Density distribution of Vittadinia cuneata at the Overland paddock study site.

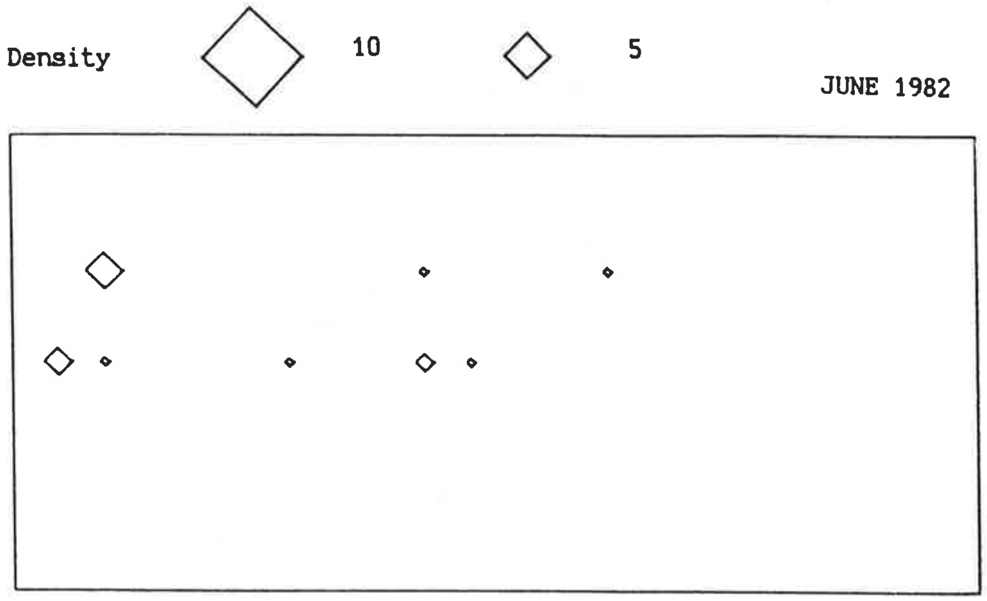


Figure 5.26 Density distribution of *Vittadinia cuneata* at the Overland paddock study site.

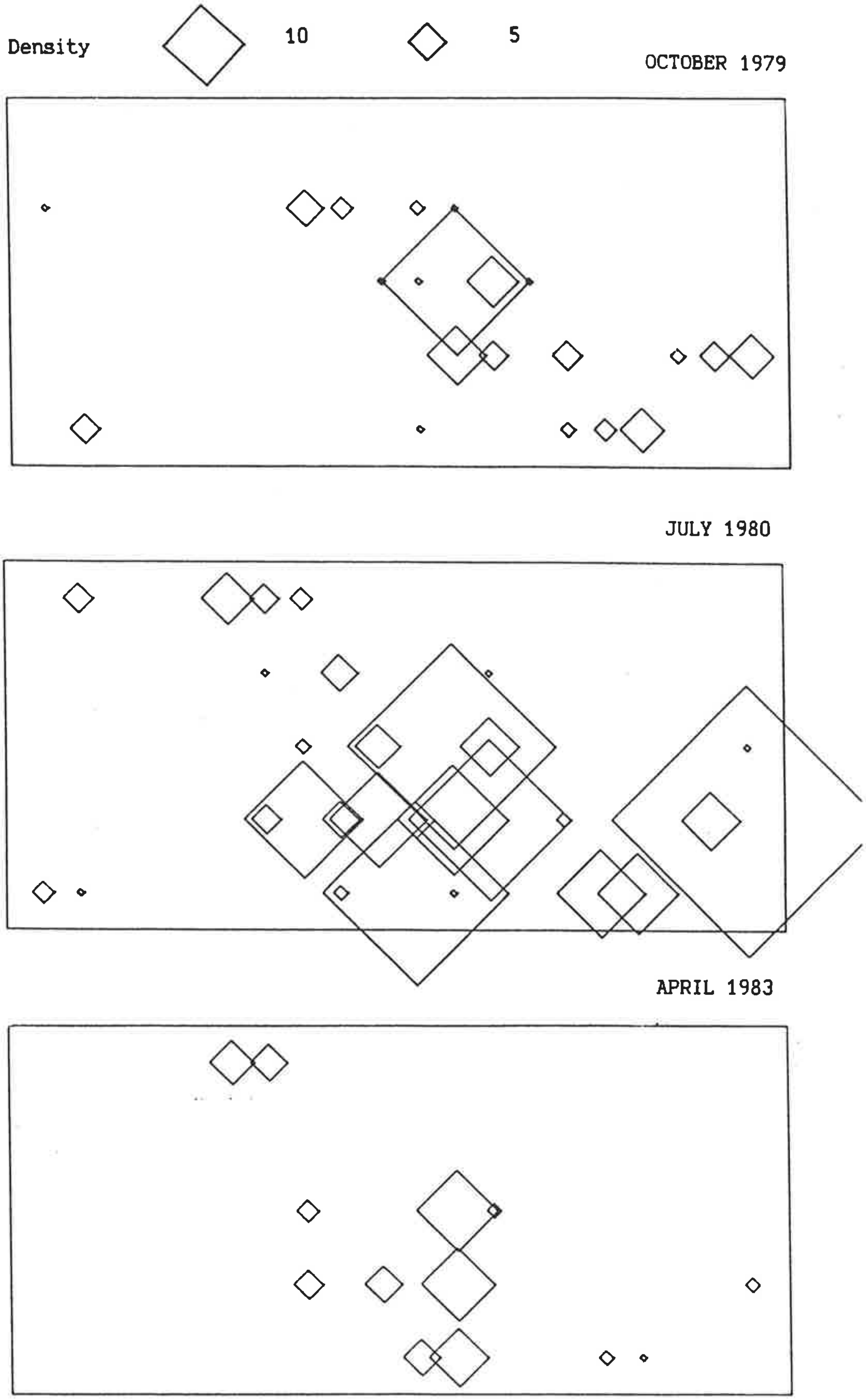


Figure 5.27 Density distribution of *Isoetopsis graminifolia* at the Overland paddock study site.

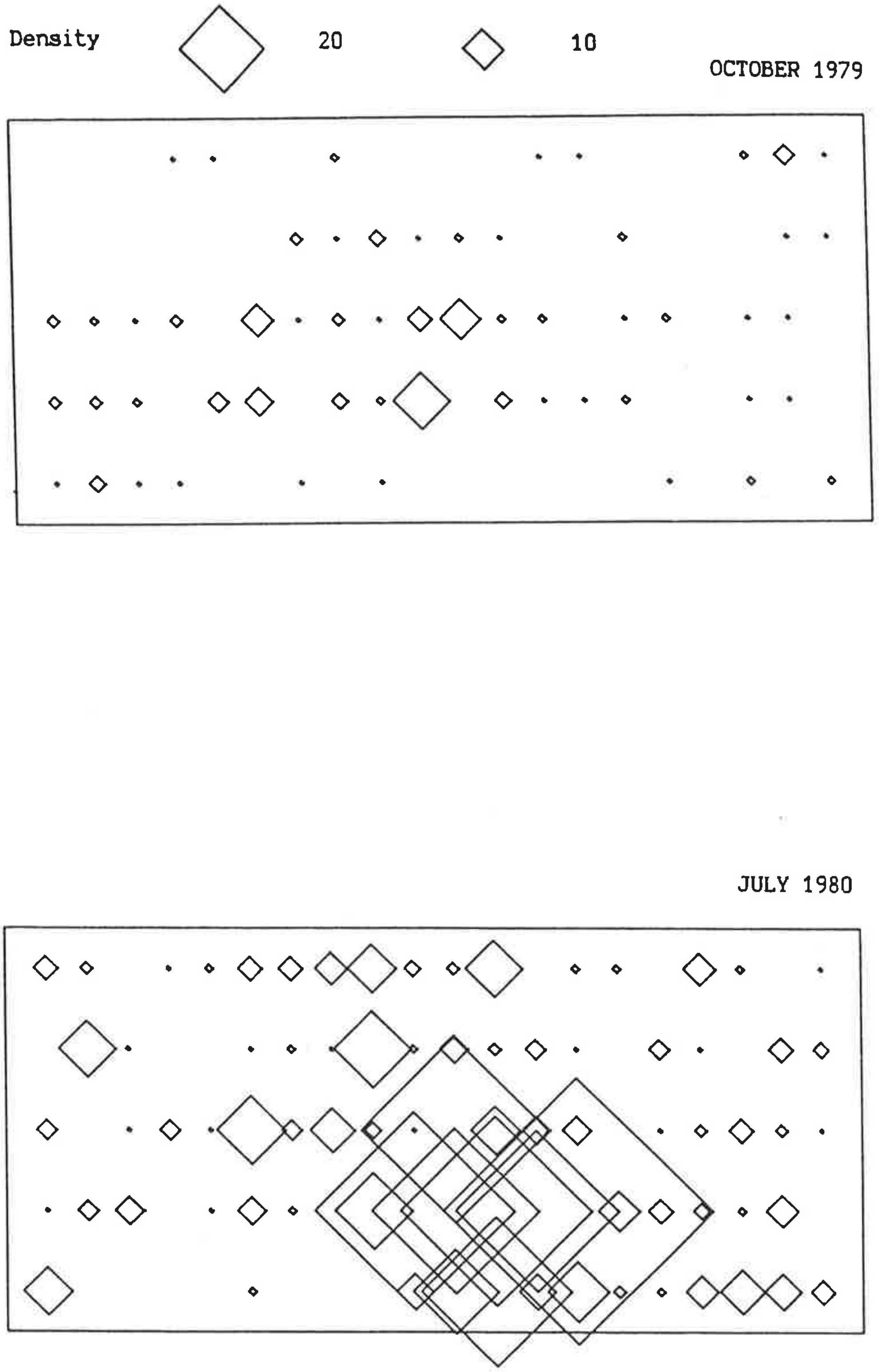


Figure 5.28 Density distribution of *Calotis hispida* at the Overland paddock study site.

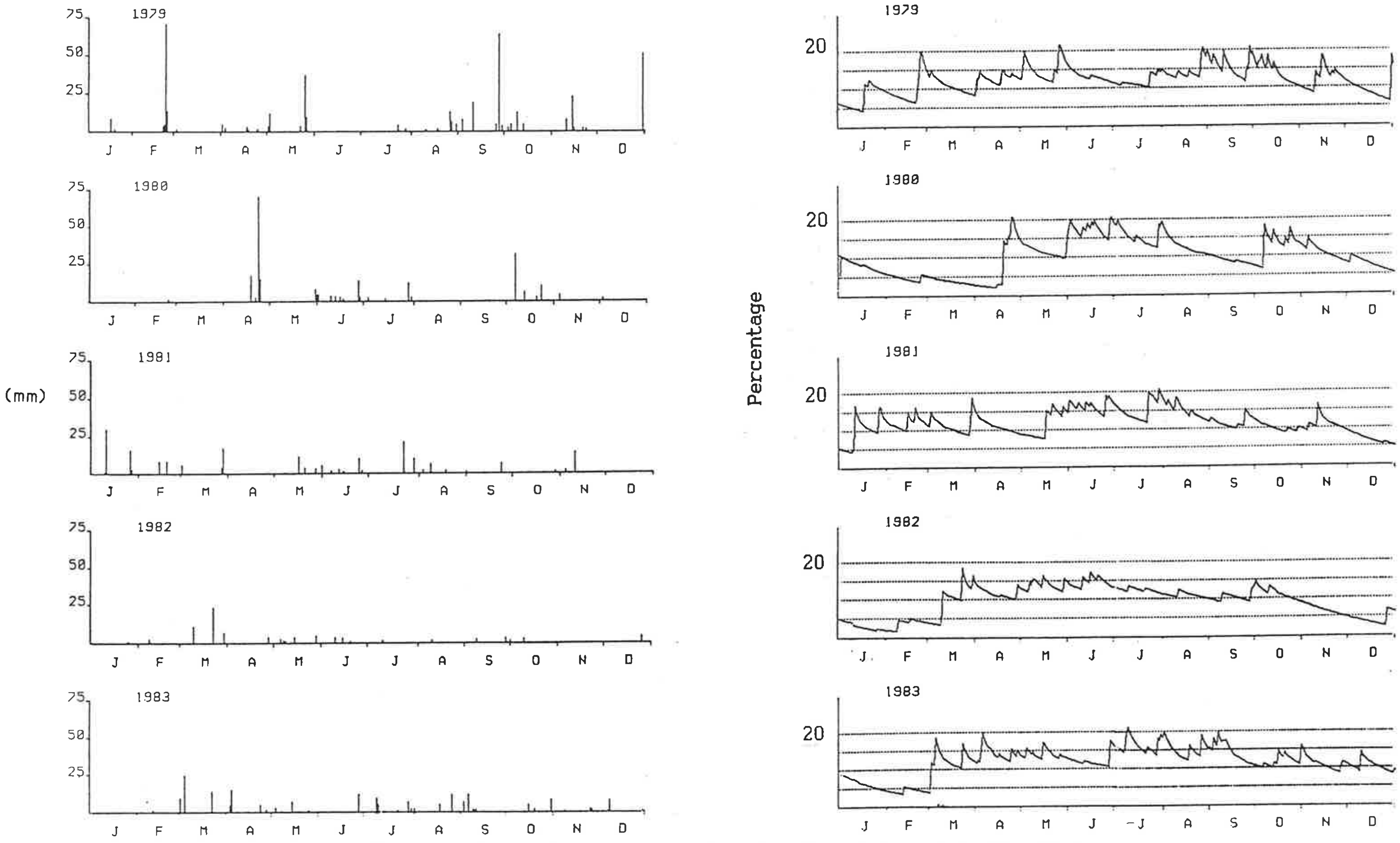
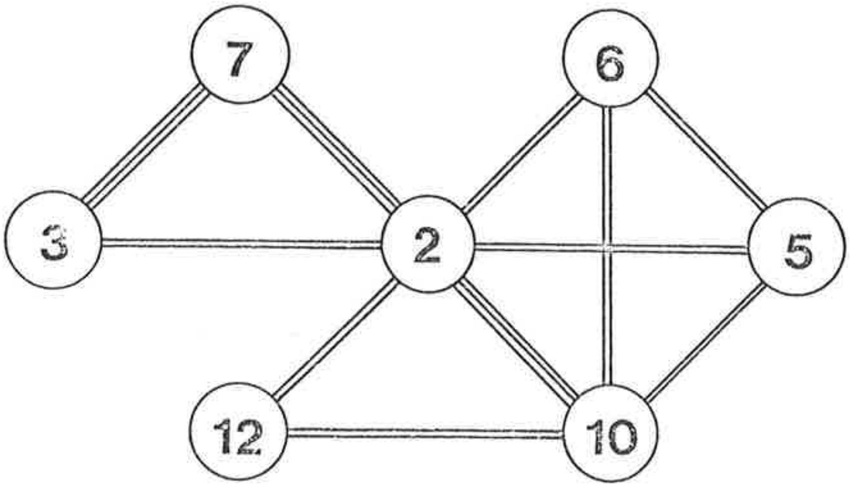


Figure 5.29 Rainfall (lefthand) and soil moisture (righthand) for Middleback station 1979 - 1983. The soil moisture sequence was calculated from the model of Noble (1975).

NODE A



NODE B

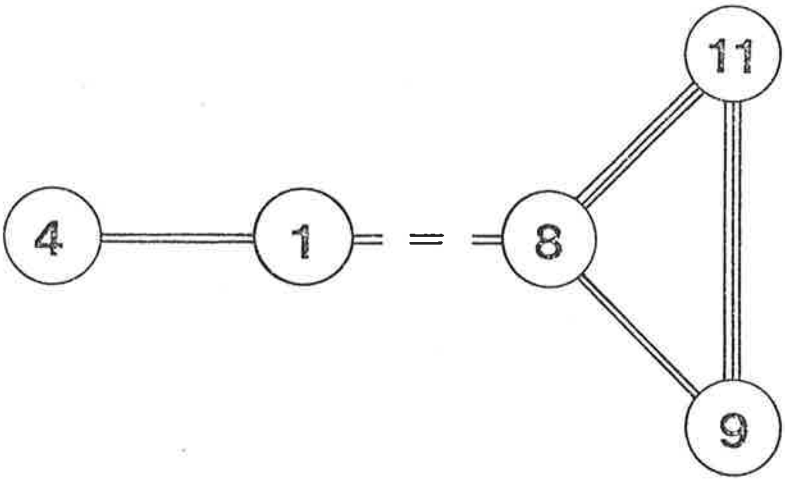


Figure 5.30 Nodes of associated species, October 1979 $0.001 < p < 0.01$ (double lines); $p < 0.001$ (Triple lines), dashed lines indicate dissociation. (1) *Danthonia caespitosa* (2) *Daucus glochidiatus* (3) *Sonchus oleraceus* (4) *Euphorbia drummondii* (5) *Helipterum pygmaeum* (6) *Isoetopsis graminifolia* (7) *Goodenia pusilliflora* (8) *Brachycome lineariloba* (9) *Actinoble uliginosum* (10) *Lophochloa pumila* (11) *Bulbine semibarbata* (12) *Schismus barbatus*

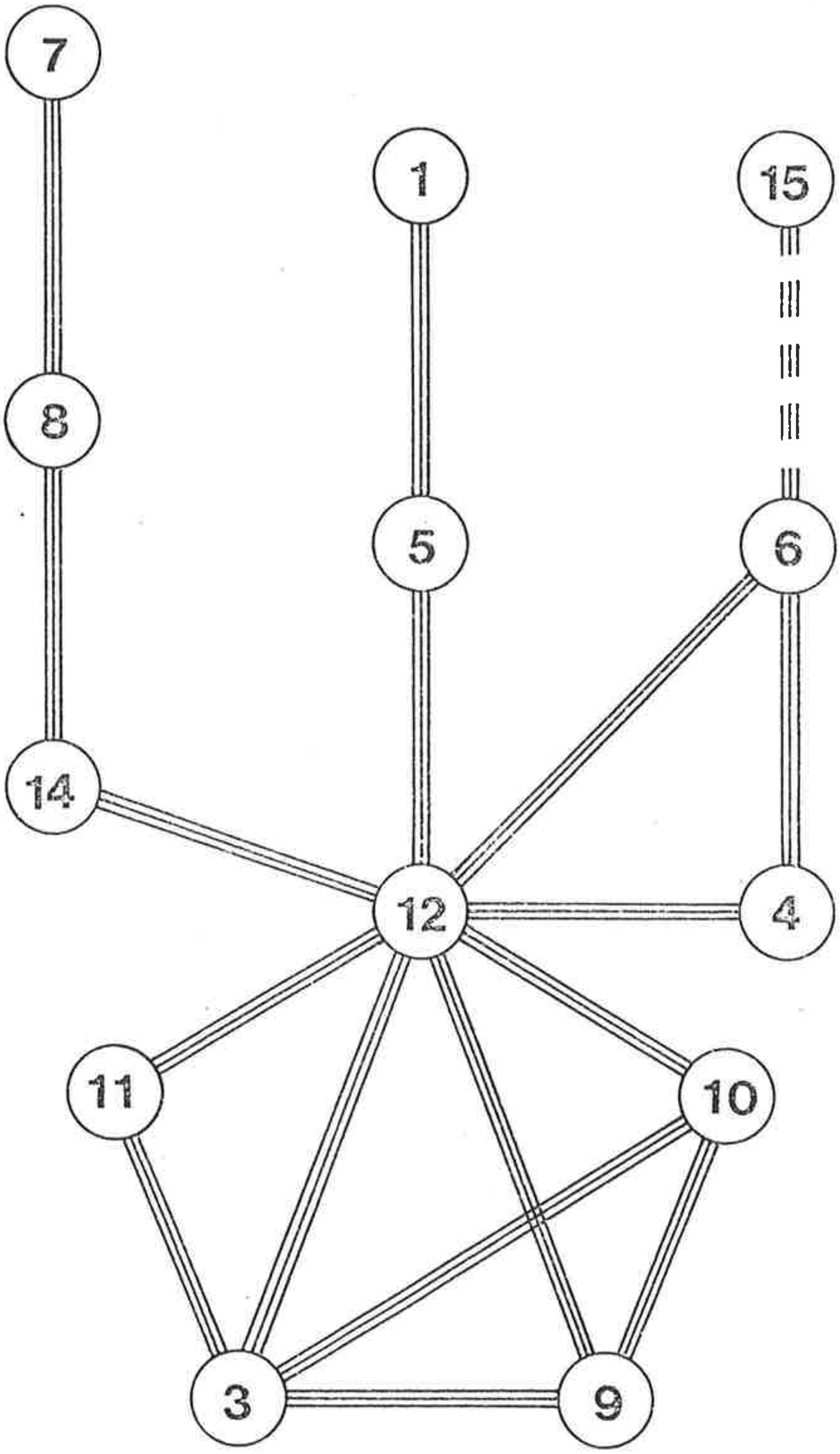
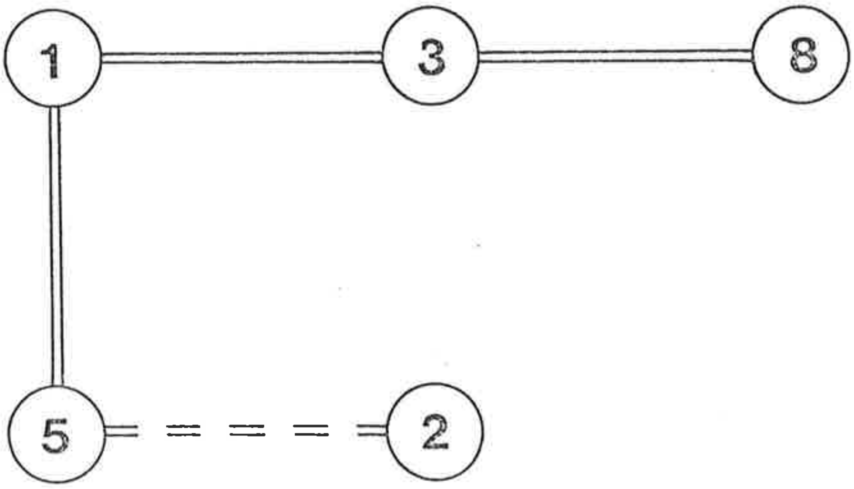


Figure 5.31 Node of associated species, July 1980 $p < 0.001$, dashed lines indicate dissociation. (1) *Danthonia caespitosa* (3) *Daucus glochidiatus* (4) *Sonchus oleraceus* (5) *Euphorbia drumondii* (6) *Calotis hispidula* (7) *Crassula colorata* (8) *Hernaria hirsuta* (9) *Helipterum pygmaeum* (10) *Goodenia pusilliflora* (11) *Isoetopsis graminifolia* (12) *Brachycome lineariloba* (14) *Atriplex vesicaria* (15) *Podocoma nana*

Node A



Node B

Figure 5.32 Nodes of associated species October 1980 $0.01 > p > 0.001$ (double lines); $p < 0.001$ (Triple lines), dashed lines indicate dissociation. (1) *Plantago drummondii* (2) *Maireana sclerolaenoides* (3) *Sonchus oleraceus* (5) *Hernaria hirsuta* (7) *Goodenia pusilliflora* (8) *Carthamus lanatus* (10) *Podocoma nana*

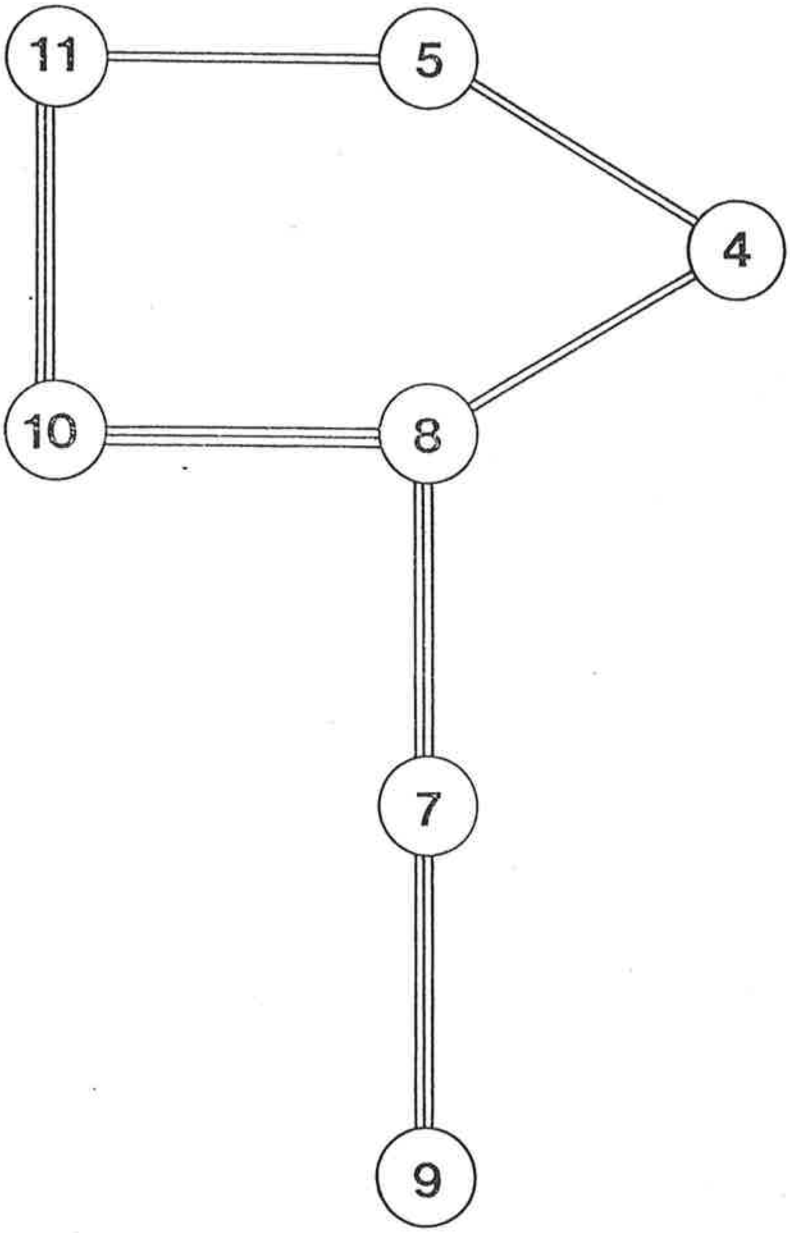


Figure 5.33 Node of associated species, April 1983 $0.01 > p > 0.001$ (double lines); $p < 0.001$ (Triple lines). (4) *Euphorbia drummondii* (5) *Calotis hispidula* (7) *Helipterum pygmaeum* (8) *Isoetopsis graminifolia* (9) *Swainsona oliveri* (10) *Goodenia pusilliflora* (11) *Medicago minima*

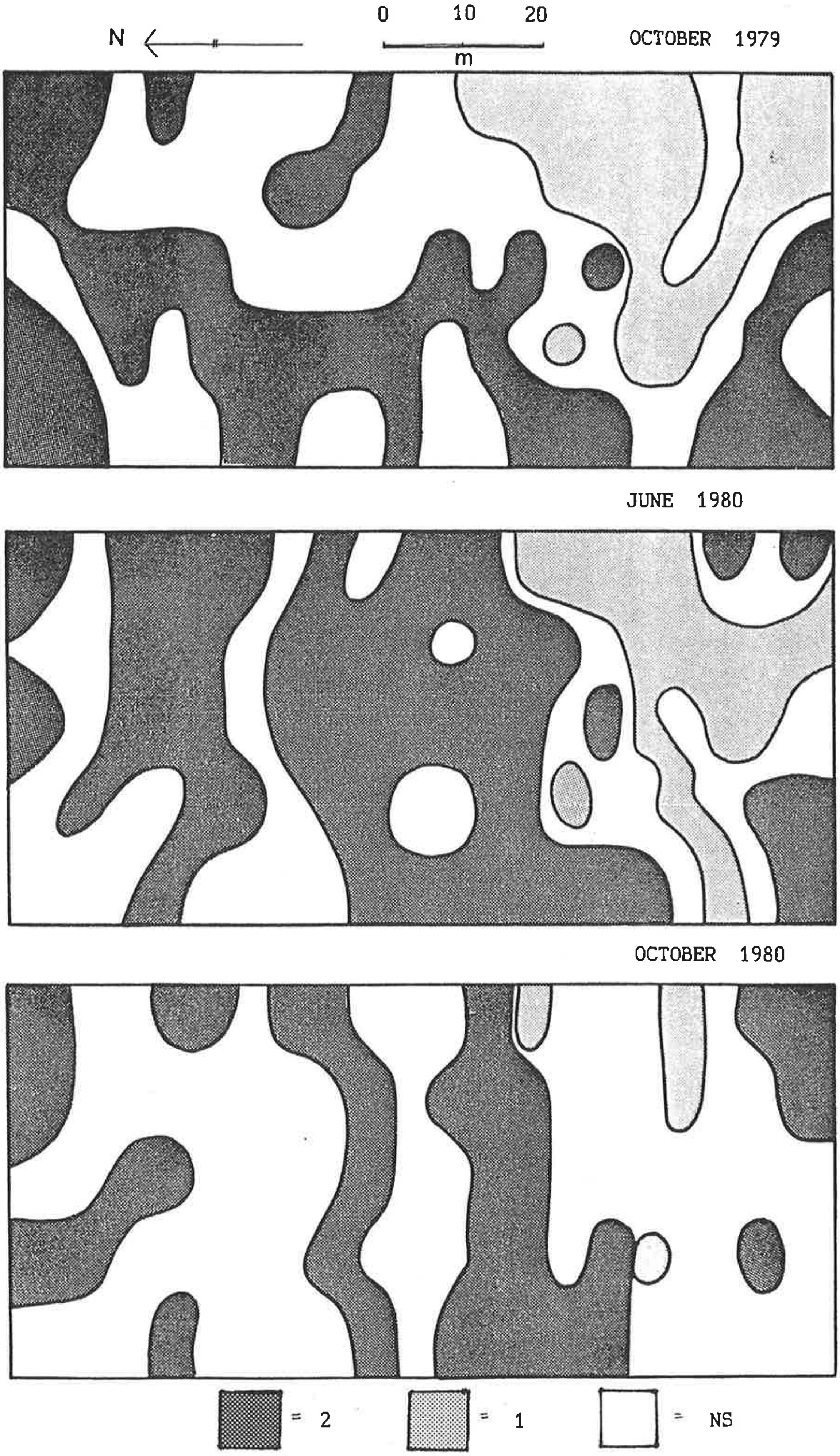


Figure 5.34 Influence analysis for the association between *Danthonia caespitosa* and *Euphorbia drummondii*

PLATE 2

Changes in the annual flora with time:

(1) Annual growth in October 1980 at the Overland Paddock study site, dominated by the two grass species *Stipa nitida* and *Danthonia caespitosa*.

(2) Annual growth in April 1983, dominated by *Erodium cygnorum*.

6. THE INFLUENCE OF BUSHES UPON PATTERN IN ANNUAL VEGETATION

6.1 Introduction

In this chapter the influence of perennial bushes upon the occurrence and distribution of annual species in the area immediately around them is considered. Observations of the distribution of annuals in the field indicate that there is a high density of plants growing beneath the canopies of perennial bushes.

The studies were designed to test: (1) whether certain annuals occurred beneath perennial shrubs more often than would be expected due to chance and (2) if annual plants were distributed evenly around the bushes.

6.2 Species incidence

6.2.1 Introduction

Three sites, two dominated by *Atriplex vesicaria* - *Maireana sedifolia* and the other by *Maireana pyramidata*, were selected to determine whether the pattern of annual plants differed beneath perennial bushes as opposed to the interbush region. The study was also repeated at one of the *A.vesicaria* - *M.sedifolia* sites over three readings to determine whether the pattern changed from one year to the next. The *M.pyramidata* site was located at Cocoa dam in Depot paddock.

One A.vesicaria-M.sedifolia site was in the north-east of Railway paddock and the other at the site described in Chapter 5 in the south-east of Overland paddock (Fig 2.1).

6.2.2 Methods

A circular quadrat with a radius of 0.6 m centered on the middle of the bush was used to sample beneath the bushes. In the A.vesicaria - M.sedifolia vegetation type the two species are usually found growing in very close association. In this case it was not possible to record the annuals separately for the two perennial species, cosequently they were considered as the equivalent of one bush unit.

A bush was arbitrarily chosen and the annual species growing beneath it were recorded. A second bush at least 3 m away was selected and the annual species were recorded in a quadrat placed at the mid point between the two bushes. This procedure was repeated until 25 bush and 25 interbush regions had been sampled. If a different perennial species occupied the interbush region then an alternative interspace was selected.

Initially all three sites were sampled in June 1980. The site in Overland paddock was sampled again in October 1980 and October 1981. On these occassions the same area was sampled but not necessarily all the same individual perennial plants.

The patterns of occurrence were tested to determine if the species were occurring in either of the quadrats more often than would be expected due to chance alone. This was done by comparing the recorded values with the expected values using the X^2 test. The 2 x 2 table in this case differs to that used for the usual X^2 calculation because equal numbers of bush and interbush quadrats were sampled and this resulted in two of the marginal totals being fixed and equal. A table of this form is often called an homogeneity table.

6.2.3 Results

Site 1. *A.vesicaria* - *M.sedifolia*

Twenty seven annual species were recorded at the *A.vesicaria* - *M.sedifolia* site in Railway Paddock. Ten of these species were found to be significantly associated with the perennial bushes. These were *Zygophyllum* sp., *Sonchus oleraceus*, *Daucus glochidiatus*, *Omphalolappula concava*, *Tetragonia eremaea*, *Maireana turbinata*, *Atriplex vesicaria* (seedling), *Brachycome lineariloba*, *Dissocarpus biflorus* and *Sclerolaena obliquicuspis* (Table 6.1). *Erodium cygnorum* was the only species significantly dissociated from the bushes indicating that it mainly occurred between the bushes.

A number of the species found in the study were present at very low frequencies, some represented by only a single occurrence. The low frequency does not provide information upon the distribution of the species other than the fact that it is uncommon in the area sampled. It is more useful to define a separate group in which such species of "unknown" behaviour can be placed and to discuss the groups separately.

Site 2. *A.vesicaria* - *M.sedifolia*

At the *A.vesicaria* - *M.sedifolia* site in Overland Paddock, 22 annual species were recorded of which 5 were associated with the perennial bushes. These were *Sonchus oleraceus*, *Daucus glochidiatus*, *Tetragonia eremaea*, *Omphalolappula concava* and *Maireana excavata* (Table 6.1). As for site 1 there were several species of annuals that occurred both beneath the bushes and in the interbush region. There were also a number of species of low frequency.

When a similar study was conducted at a later date (Oct 1980) at the same site, a slightly different result was obtained (Table 6.1). A total of 26 annual species were recorded of which 13 showed significant associations. Positive associations were shown by 10 species: *Sonchus oleraceus*, *Brachycome lineariloba*, *Daucus glochidiatus*, *Isoetopsis graminifolia*, *Omphalolappula concava*, *Maireana excavata*, *Goodenia pusilliflora*, *Helipterum pygmaeum*, *Podocoma nana* and *Maireana turbinata*. Negative associations were recorded with *Zygophyllum* sp. and *Euphorbia drummondii*. *Erodium cygorum*, *Danthonia caespitosa* and *Sclerolanea obliquicuspis* were all present at high frequency but occupied both between bush and beneath bush habitats.

In June 1981 the annual flora was not as extensive and only 12 species were recorded. The only annual species associated with the bushes was *Tetragonia eremaea*. The species *Danthonia caespitosa*, *Erodium cygnorum* and *Maireana sclerolaenoides* again showed no preference. A number of the species such as *Brachycome lineariloba*, *Daucus glochidiatus* and *Isoetopsis graminifolia* were only found beneath the bushes but their frequency of occurrence was too low to demonstrate this conclusively.

Site 3. *Maireana pyramidata*

At the *M.pyramidata* site a total of 29 annual species were recorded (Table 6.1) of which 6 showed significant interactions with the perennial bushes. *Tetragonia eremaea* and *Wahlenbergia gracilis* were associated with the bushes. *Tripogon loliiformis*, *Actinobole uliginosum*, *Goodenia pusilliflora* and *Calotis hispidula* were dissociated from the shrubs. The majority of annual species at this site appeared to show no preference for either the bush or the interbush region but occured in either habitat.

6.2.4 Discussion

In some respects the results show a pattern of annual plant occurrence similar to that observed by Went (1942). Three main groups of plants can be recognised on the basis of their interactions with the bushes. The first group consists of those species which are found associated with the perennial shrubs. The second group of species predominantly occurs in the region between the shrubs. The third group consists of those species which could be found both beneath the bushes and in the interbush region, showing no preference for either habitat . A fourth group contains those species which were found at such low frequency that they could not be classified into any of the first three groups. Table 6.2 presents a summary of the species found for the three main groups.

The study described here was different to that of Went (1942) in that the patterns of the annual plants were considered at a number of sites and at one of these sites the changes with time were also studied. The upper half of Table 6.2 records species that were consistent in their association with the bushes; that is they were found only to exhibit one association pattern on all occassions and in all studied places. The lower half of the table records species that exhibited more than one type of pattern. On some occasions the species were either associated with or dissociated from the bushes while at other sites or at other times the same species could be found to show no preference for either the bush or the interbush region. The small annual Goodenia pusilliflora showed all three pattern types. This raises interesting questions concerning the stability of these annual patterns and the possible causes of the species patterns.

In a study on mosses in the Middleback region (Howarth, 1983) a similar pattern to that observed for the annual plants was found. Howarth (1983) argued that the bushes offered a shaded habitat where moisture loss was reduced. A similar explanation may apply to the annual species. The work described in previous chapters indicated that annual plants are sensitive to environmental conditions and that there may be differences in annual vegetation from one year to the next due to variation in the prevailing conditions of moisture and temperature. The region beneath a bush may provide a habitat in which there is a slightly higher soil moisture due to reduced evaporation from the soil as a consequence of the shading effect and this may facilitate the germination and survival of annuals.

The two bush species often develop a mound of soil and litter around their base, possibly the result of the accumulation of wind blown material (Anderson, 1969). These mounds have been shown to have a higher nutrient status than the interbush regions (Correll, 1966) and this may also influence the behaviour of the annual plants.

The study by Went (1942) was expanded by Muller (1953) and Muller & Muller (1956) who found that an inhibitor released from certain species of perennials influenced the behaviour of annual plants. A major difference between that study and the one described here was that different perennial species often demonstrated different influences upon the annual plants. From this study it is not possible to draw conclusions on the differences in the annual plants found beneath Atriplex vesicaria - Maireans sedifolia clumps and beneath Maireana pyramidata. For comparisons of this type the perennial species would have to be investigated at the same site. Unfortunately no areas could be found where all these three perennial species occurred together.

The differences in annual pattern from one year to the next may be the consequence of different environmental conditions. When soil moisture conditions in the interbush region are marginal for the survival of annuals, the bushes may provide a more mesic habitat. In years of above average rainfall many of these annuals could survive in the region between the bushes due to the higher soil moisture. This hypothesis is supported by the results presented in Chapter 5. In October 1979 and July 1980 the frequency and density of a number of species (which were recorded as bush-associated in this chapter) were high although the quadrats in that study were placed away from the bushes. This provides more evidence on the instability in annual distribution and occurrence over time.

6.3 Pattern beneath individual bushes

6.3.1 Introduction

The distribution of annual plants does not appear to be uniform beneath perennial bushes. Bushes of A.vesicaria and M.sedifolia were sampled to test whether there were differences in the distribution of annual plants around the base of these species.

6.3.2 Methods

The study was conducted in the exclosure in the south-east corner of Overland Paddock (described in Chapter 5). Ten individuals each of Atriplex vesicaria and Maireana sedifolia were arbitrarily selected. Individuals with a dense foliage were chosen, clumps of bushes or partially defoliated individuals were not sampled.

Individuals of M.sedifolia are often larger than those of A.vesicaria and so different sized quadrats were used depending upon the species which was being sampled. For A.vesicaria the quadrat was a circle of 0.4 m radius centered on the individual. For M.sedifolia a circle of 0.6 m radius was used. The circular quadrat was divided into eight sub-quadrats representing 45° arcs clockwise from north (Fig.6.1).

The number of plants within each sub-quadrat was counted. The dominant herbaceous species Danthonia caespitosa, Maireana sclerolaenoides and Sclerolaena obliquicuspis were harvested and their dry weight determined.

6.3.3 Results

Density

Twenty-six annual species were found beneath bushes of A.vesicaria and 29 beneath M.sedifolia. The mean number of plants in each sub-quadrat for the more abundant species are presented in Figures 6.2 & 6.3. The means and standard deviations of all species are presented in Appendix 3.

The total number of individuals recorded around the two species of bush is shown in Figure 6.5. For both bush species there was a trend for more annual species to be present around the southern side of the bushes, although this was more pronounced for M.sedifolia than for A.vesicaria. The same applies to the number of individuals present around the plants. For M.sedifolia there were approximately 3 times as many individuals beneath the southern parts of the bushes as beneath the northern parts. Again the trend was not as clear for annual plants under A.vesicaria. For this species the lowest numbers of individuals were found in the range north-east to west and the highest number were found in the range south to north-east.

The distribution of annual species which are not presented in the figures was patchy with no clear trends, although some showed a slight tendency to occur around the southern sides of the bushes. Examples of this were from data for Calotis hispidula, Goodenia pusilliflora and

Senecio quadridentatus beneath *Maireana sedifolia* and *Medicago minima*, *Senecio quadridentatus* and *Zygophyllum* sp. beneath *Atriplex vesicaria*.

Biomass

The biomass results for the three dominant herbaceous species, *Danthonia caespitosa*, *Sclerolaena obliquicuspis* and *Maireana sclerolaenoides*, are presented in Figure 6.4. The results are presented in two different ways. Firstly the total biomass of the harvested species in the sub-quadrats is plotted and secondly the mean individual plant biomass (the total biomass per species per subquadrat / the total number of individuals per subquadrat of that species) is shown.

The biomass of *Danthonia caespitosa* beneath *Maireana sedifolia* was greater, on average, in the southern than in the northern subquadrats. For *A.vesicaria* there was a high biomass in the range west to south with a secondary peak between east and north-east. The mean plant biomass shows a quite different pattern. Beneath *A.vesicaria* the individuals of *Danthonia caespitosa* were larger on the northern side whereas beneath *M.sedifolia* the largest mean individual biomass was obtained in the region north-west to south-west.

The greatest biomass of *Maireana sclerolaenoides* occurred on the northern side of *M.sedifolia* individuals with the lowest biomass occurring on the southern side. The biomass of *M.sclerolaenoides* was low beneath *A.vesicaria* with only a slight increase on the northern side. The mean plant weights showed a similar trend with the greatest plant size on the northern side for *M.sedifolia* and a very pronounced peak obtained between east to north-east for *A.vesicaria*.

Sclerolaena obliquicuspis, showed a similar result to M.sclerolaenoides with a high biomass on the northern side of the M.sedifolia individuals. The mean individual weight was also greatest in this region. The trend beneath A.vesicaria was not as clear due to the very low biomass beneath this species.

6.3.4 Discussion

The results presented for the total flora indicate that there was pattern in the number of individuals that occurred around the bushes. The differences around the bushes were far more pronounced for Maireana sedifolia than for Atriplex vesicaria. The results are more difficult to interpret at the level of individual annual species. Species such as Daucus glochidiatus and Wahlenbergia gracilis show clear trends, occurring in greater numbers on the southern sides of the bushes. In contrast other species showed no clear pattern of occurrence around the bushes.

A similar phenomenon to that described for annuals has also been observed for moss species in the same area (Howarth, 1983). Her explanation in the case of the mosses was that the southern side of the bush was shaded for much of the day. The temperature was lower in this area as a consequence and there was a reduction in the loss of moisture by the moss. This may also apply to annual plants. Lower temperatures at the soil surface would reduce the rate of moisture loss and this may enhance the germination of annual species whose seeds germinate on or near the surface. In contrast, the northern side of the bush which has direct radiation for most of the day would have a much higher rate of moisture loss from the soil. The northern side of the bush may not differ significantly from the interbush region in terms of microclimatic characteristics.

The leaf cover of the two species varies. Maireana sedifolia often has a very dense canopy whereas A.vesicaria is open. Maireana sedifolia may more effectively shade the region beneath the bush than A.vesicaria and this may lead to the more pronounced zonation of annuals around this species as observed in this study.

Once pattern in the distribution of annuals beneath the bushes has developed it may be self maintaining. The bushes act as a wind break and the wind velocity in the lee of the bushes may be reduced considerably. The seed of species growing between the bushes may be dispersed beneath the bushes but the seed of plants beneath the bushes may not move away from the parent plant. (Chapter 7)

6.4 Conclusions

The distribution of annual plants is patterned with respect to individual perennial bushes at Middleback Station. A group of species was identified which occurs predominantly beneath the bushes. Another group avoids the bushes. A third group consists of those species with no preference for either area. This corresponds closely with the findings of Went (1942), except that at Middleback Station a group of plants was found which could occur in different habitats depending upon the prevailing seasonal conditions. Under good growing conditions plants in this group were able to expand their distribution from the mounds beneath the bushes to include the interbush region.

As well as the patterns between the bush and the interbush region, patterns were found in the distribution of annuals around the base of the bushes. There was a greater species diversity on the southern side of both <u>A.vesicaria</u> and <u>M.sedifolia</u> and a greater number of individuals in this region. The information at the species level was more difficult to interpret. Some species showed distinctive patterns around the base of the plants whereas others showed little pattern.

The pattern of annual plants around the bushes is probably a consequence of the variation in microhabitats around the base of the bushes. The shading effect of the bush causes lower temperatures and reduced moisture loss on the southern side which may provide a suitable habitat for a number of annual species. The species which were restricted to the region under the bushes were often found in greater numbers on the southern side of the bushes.

	A Jun 1980	B Jun 1980	B Oct 1980	B Oct 1981	C Jun 1980
Actinobole uliginosum	-	-	-	-	-***
Atriplex spongiosa	-	-	-	-	ns
Brachycome lineariloba	***	ns	***	ns	ns
Bulbine semibarbata	-	-	-	-	ns
Calotis hispidula	ns	ns	ns	-	-*
Carrichtera annua	-	ns	ns	-	-
Chenopodium cristatum	-	-	-	-	ns
Crassula sp	-	-	-	-	ns
Danthonia caespitosa	ns	ns	ns	ns	ns
Daucus glochidiatus	***	***	***	ns	-
Dissocarpos biflorus	**	-	-	-	-
Erodium cicutarium	-	-	-	-	ns
Erodium cygnorum	-***	ns	ns	ns	ns
Euphorbia drummondii	ns	ns	-***	ns	ns
Emex australis	-	-	ns	-	ns
Gnephosis burkittii	-	-	-	-	ns
Goodenia pusilliflora	ns	-	*	-	-***
Helipterum floribundum	ns	-	-	-	-
Helipterum pygmaeum	ns	ns	*	-	ns
Hernaria hirsuta	-	-	-	-	ns
Hordeum leporinum	ns	-	-	-	ns
Isoetopsis graminifolia	-	-	***	ns	-
Maireana sclerolaenoides	ns	ns	ns	ns	ns
Marrubium vulgare	-	-	-	-	ns
Medicago minima	ns	-	ns	ns	ns
Omphalolappula concava	***	***	***	-	-
Oxalis corniculata	ns	-	-	-	-
Plantago drummondii	ns	ns	ns	-	-
Podocoma nana	ns	-	*	-	-
Schismus barbatus	-	-	-	-	ns
Sclerolaena obliquicuspis	**	ns	ns	ns	ns
Sclerolaena dicantha	-	ns	-	-	-
Sonchus oleraceus	***	***	***	-	ns
Stipa elegantissima	-	ns	-	-	-
Stipa nitida	-	-	ns	ns	ns
Swainsona oliveri	-	ns	ns	-	-
Tetragonia eremaea	***	***	ns	**	***
Tripogon loliiformis	-	-	-	-	-***
Lophochloa pumila	ns	-	-	-	ns
Vittadinia cuneata	-	-	ns	ns	-
Whalenbergia gracilis	-	-	-	-	*
Zygophyllum sp.	***	ns	ns	-	-
Zygophyllum sp.	ns	ns	-***	-	-

Table 6.1 Associations between annual plants and perennial bushes. *, 0.05>p>0.01 : **, 0.01>p>0.001 :***, p<0.001. Negative sign to the association indicates significant dissociation.
ns = non significant. - indicates species absent
A = Overland site (*A.vesicaria* / *M.sedifolia*). B = Railway paddock site (*A.vesicaria* / *M.sedifolia*). C = *M.pyramidata* site

ASSOCIATIONS Group A	NO PREFERENCE Group B	DISSOCIATIONS Group C
Daucus glochidiatus	Gnephosis burkitii	Actinobole uliginosum
Dissocarpos biflorus	Crassula colorata	Tripogon loliiformis
Helipterum pygmaeum	Danthonia caespitosa	
Isoetopsis graminifolia	Emex australis	
Omphalolappula concava	Hernaria hirsuta	
Tetragonia eremaea	Hordeum leporinum	
Wahlenbergia gracilis	M. sclerolaenoides	
Zygopyyllum sp	Medicago minima	
	Plantago drummondii	
	Schismus barbatus	
	Stipa nitida	
	Lophochloa pumila	
	Vittadinia cuneata	
A:B	Brachycome lineariloba	
	Podocoma nana	
	Sclerolaena obliquicuspis	
	Sonchus oleraceus	
	B:C	Calotis hispidula
		Erodium cygnorum
		Euphorbia drummondii
		Zygophyllum sp
A:B:C	Goodenia pusilliflora	

Table 6.2. Summary of the behaviour of the annual species recorded in the study. Group A plants were associated with the perennial bushes. Group B plants showed no preference for either habitat and Group C were dissociated. (A:B) were plants found in groups A and B. (B:C) were found in groups B and C, and (A:B:C) were in all three groups. The combination A and C did not occur.

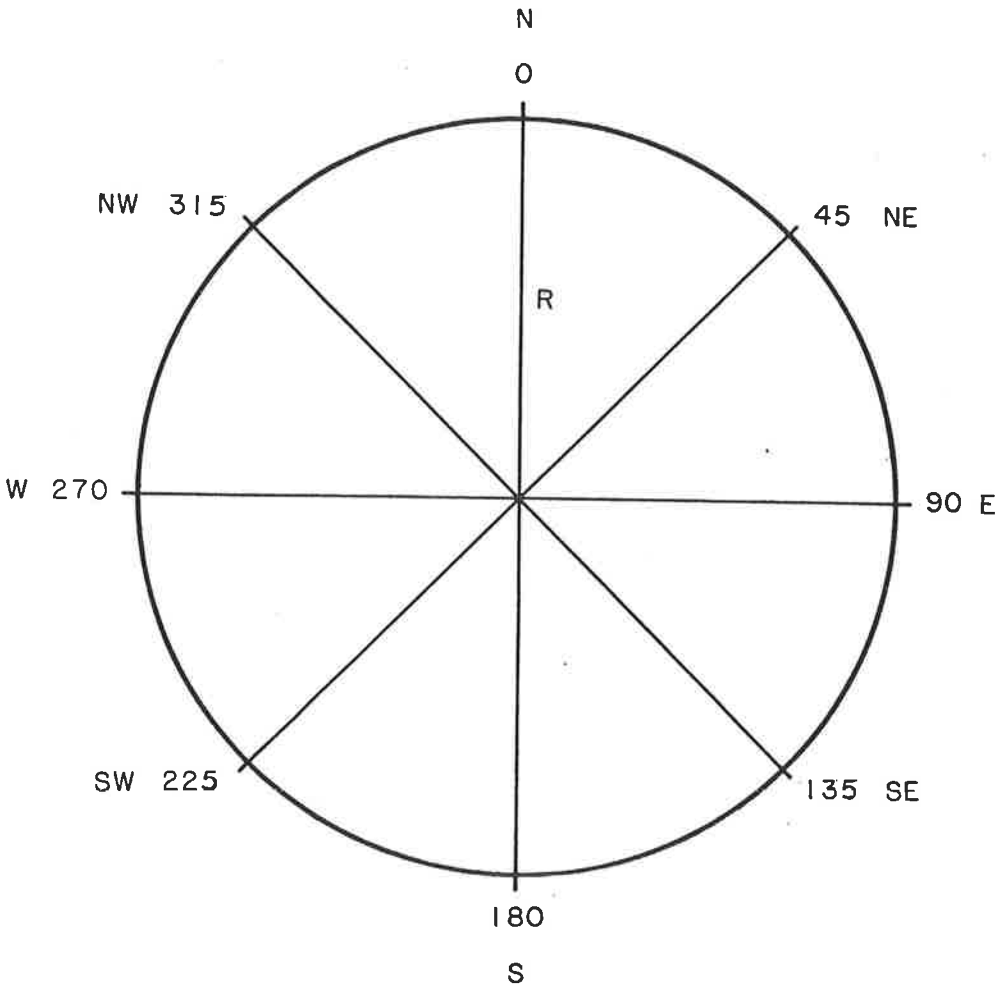


Figure 6.1 Circular quadrat divided into eight sub-quadrats used for sampling the density and biomass of annual plants beneath the perennial bushes. When sampling *Atriplex vesicaria* a radius of 0.4 m was used and for *Maireana sedifiolia* a radius of 0.6 m.

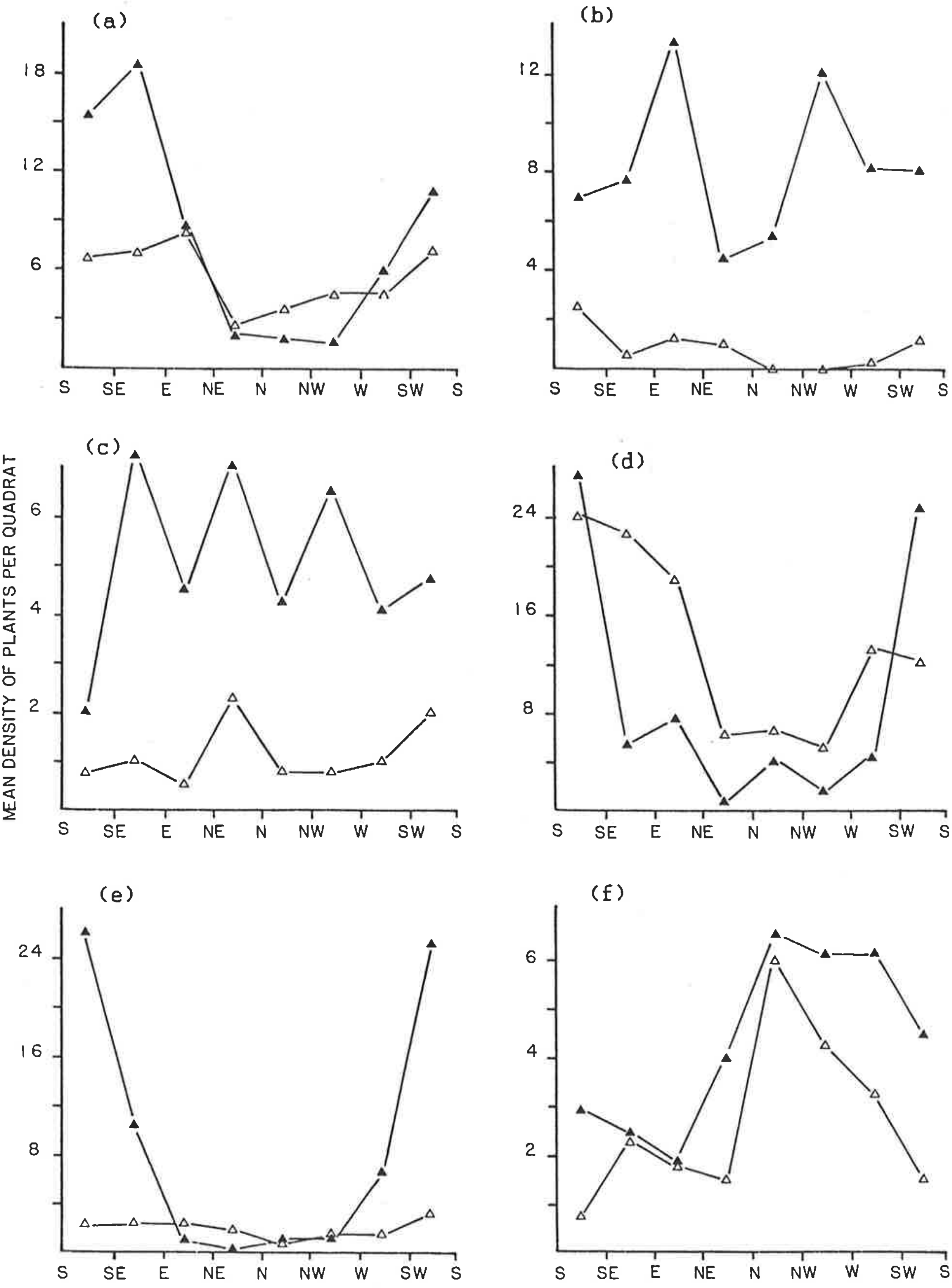


Figure 6.2 Mean number of plants per sub-quadrat beneath *Atriplex vesicaria* (△) and *Maireana sedifolia* (▲). (a) *Danthonia caespitosa* (b) *Sclerolaena obliquicuspis* (c) *Maireana sclerolaenoides* (d) *Daucus glochidiatus* (e) *Brachycome lineariloba* (f) *Erodium cygnorum*.

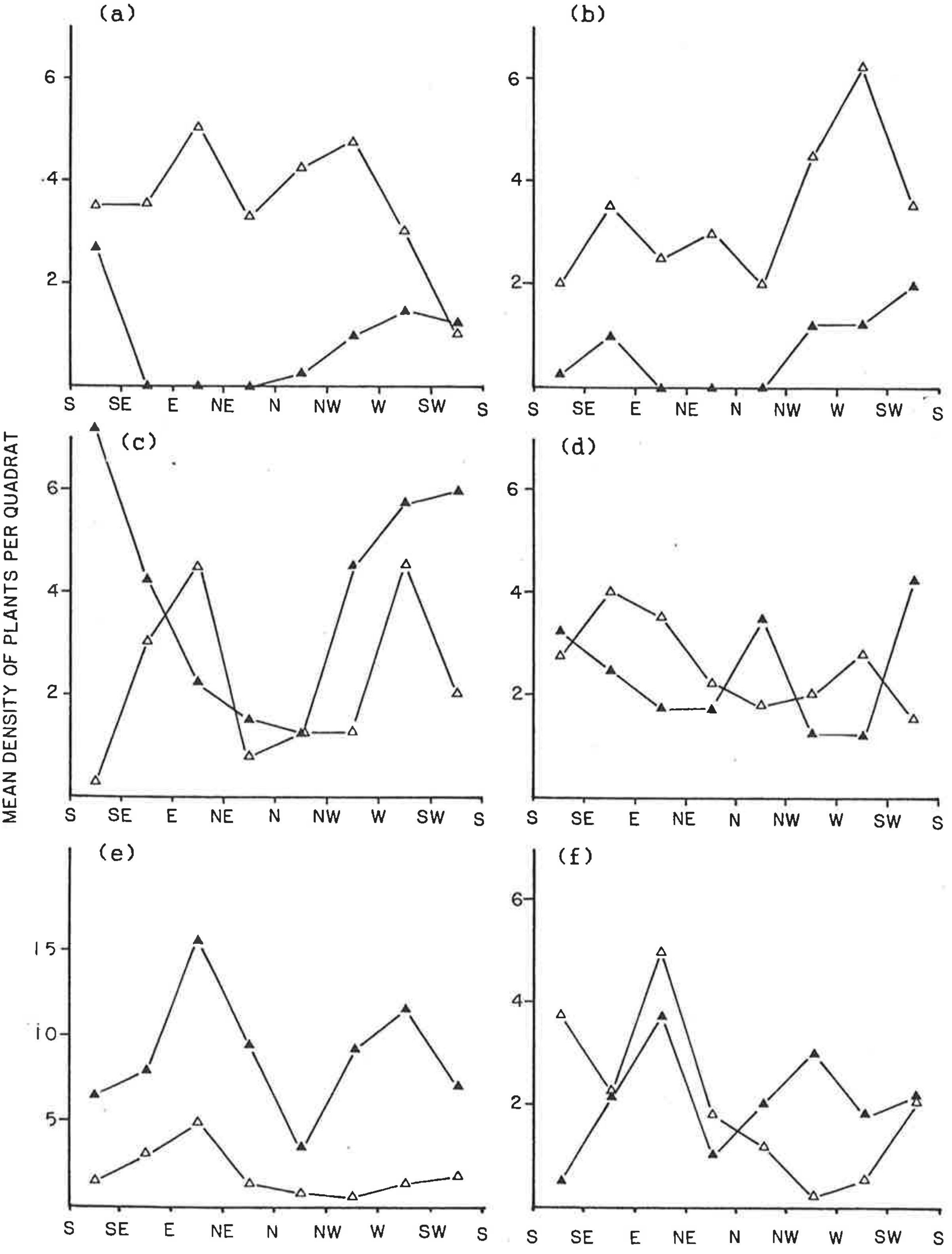


Figure 6.3 Mean number of plants per sub-quadrat beneath *Atriplex vesicaria* (△) and *Maireana sedifolia* (▲) (a) *Isoetopsis graminifolia* (b) *Plantago drummondii* (c) *Whalenbergia gracilis* (d) *Sonchus oleraceus* (e) *Tetragonia eremaea* (f) *Omphalolappula concava*

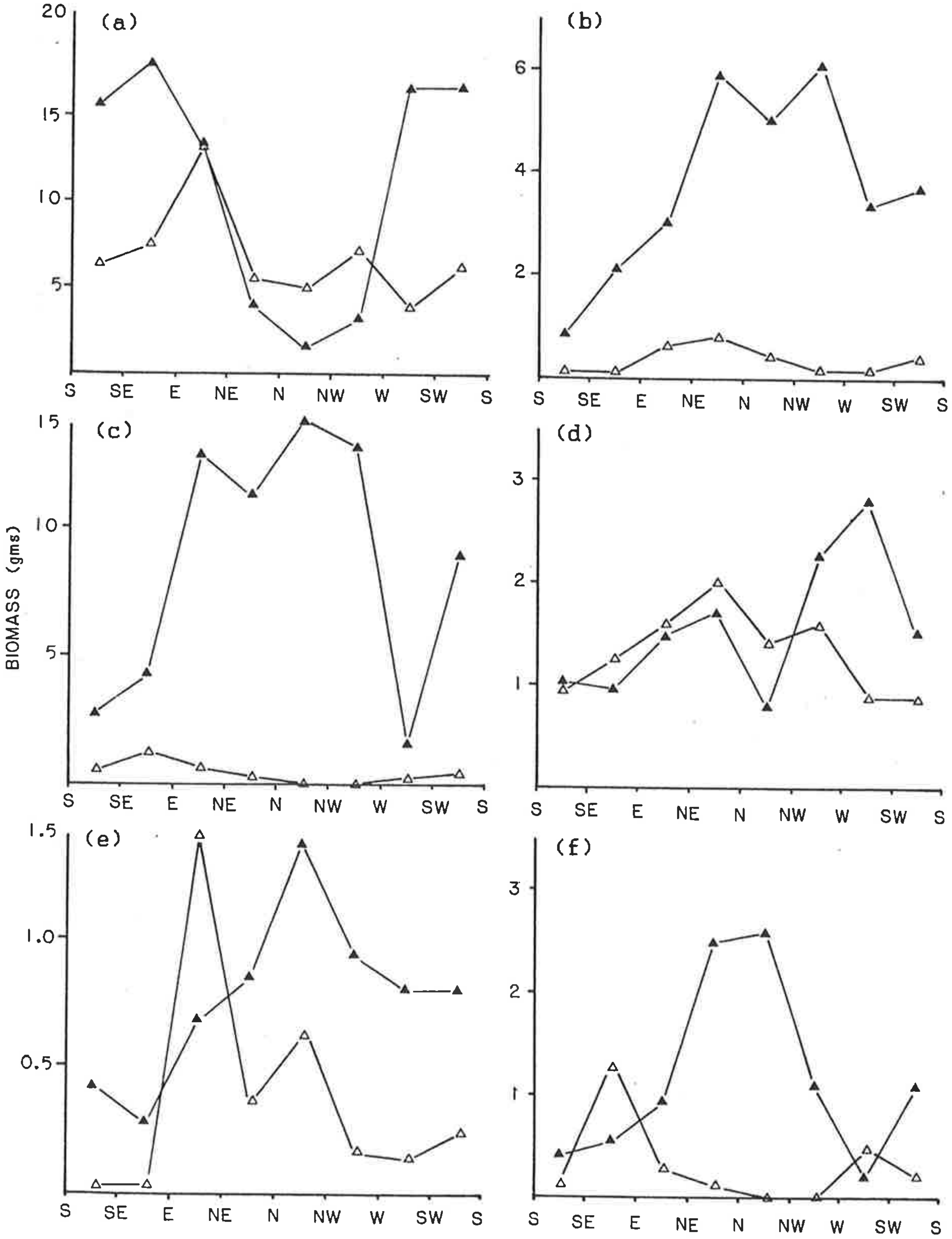


Figure 6.4 Mean biomass (gm) per sub-quadrat beneath Atriplex vesicaria (△) and Maireana sedifolia (▲). Species (a) Danthonia caespitosa (b) Maireana sclerolaenoides (c) Sclerolaena obliquicuspis. Mean plant weight (gm) beneath Atriplex vesicaria (△) and Maireana sedifolia (▲). Species (d) Danthonia caespitosa (e) Maireana sclerolaenoides (f) Sclerolaena obliquicuspis

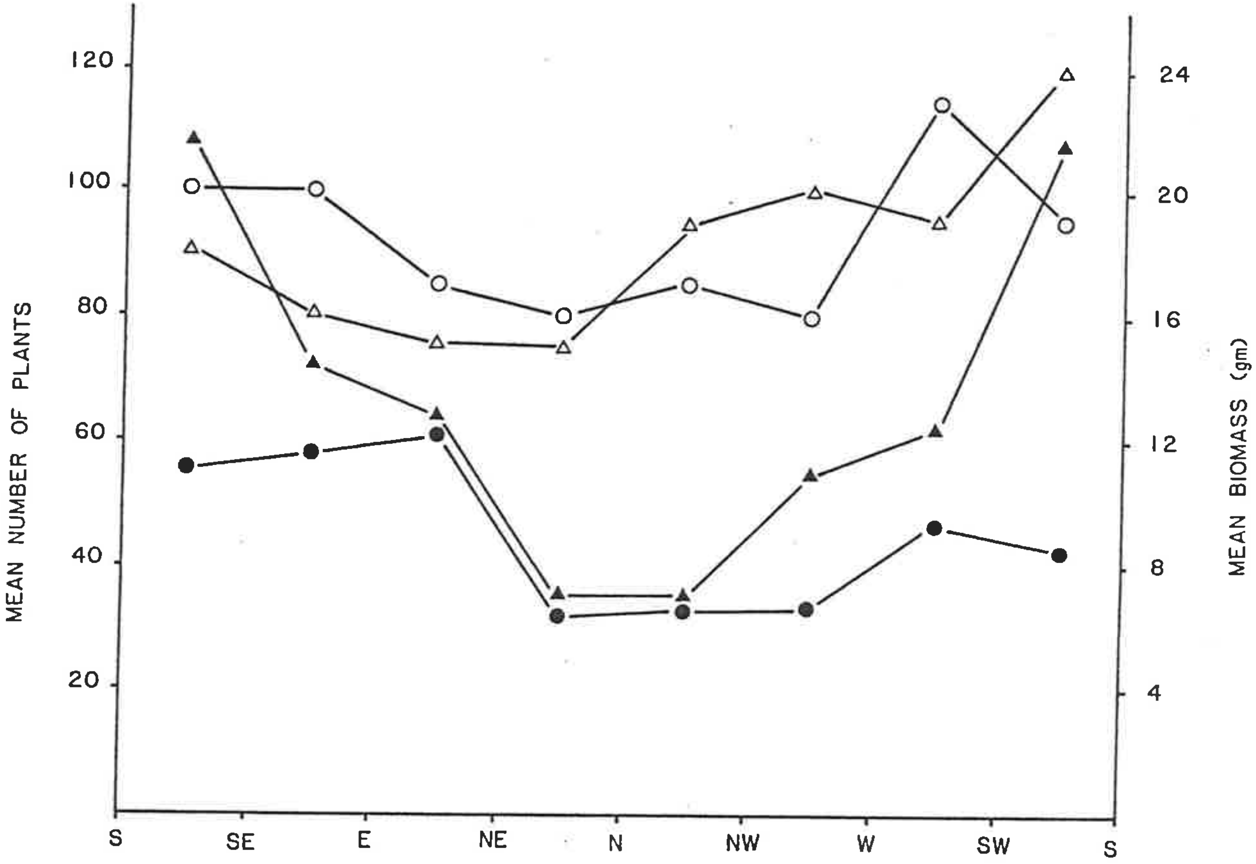


Figure 6.5 Mean number of plants per sub-quadrat and mean biomass per sub-quadrat.

Atriplex vesicaria number (●) , biomass (○)
Maireana sedifolia number (▲) , biomass (△)

7. Seed Dispersal Of Annuals

7.1 Introduction

Seed dispersal has been the subject of numerous investigations (e.g. Small,1918; Praeger,1923; Fielding,1964; Gutterman et al.,1967; Bullock,1977; Friedman & Stein,1980; Bansal & Sen,1981; Howe & Smallwood,1982). The main function of seed dispersal is often considered to be the movement of seeds long distances from the parent plant (Ridley,1930; Pijl,1969). In terms of the biology of a population of plants, two main functions of dispersal can be identified. The first is expanding the range or population size of a species and the second is the maintenance of an already existing population of plants (Harper,1977).

The dispersal of seeds from parent plants is achieved through three main agents, wind, water and animal. There are a number of species in the study area that are animal dispersed but these are predominantly perennial species. The main agent which disperses the seeds of annual plants in the study region appears to be wind and for this reason only this method of dispersal has been considered in detail in this study. The influence of ants on the dispersal of annuals is briefly mentioned in later sections.

7.2 Theoretical considerations

The dispersal of seeds by wind can be divided into a number of distinct phases. These were termed trajectories by Burrows (1973). The primary trajectory is the movement of seed through the air from the parent plant to the ground. If the seeds are subsequently blown from the ground into flight again these were termed secondary, tertiary,.... trajectories depending upon the number of times this occurrs. If the seed rolls across the surface then this is termed the degenerate trajectory. The division of seed movements into trajectories provides a framework for the detailed description of seed behaviour. However in the field it is difficult to obtain the necessary accuracy to describe seed movement in these terms.

Watkinson (1978) used a simplified terminology dividing the movement of seeds into two phases. Phase I dispersal described the flight of the seed through the air and Phase II dispersal referred to all subsequent movements after the seed landed on the ground. This terminology is more suitable for describing seed movement in the field and is adopted in this study.

7.2.1 Phase I Dispersal

The number of seeds that fall upon a unit area of ground is a function of the following variables: (1) The height and distance from the seed source, (2) The concentration of the seeds at the source, (3) The dispersability of the seed and (4) The activity of the dispersing agent (Harper,1977).

In the case of the flight of seeds a simple relationship may be expected between the density of dispersed seed and the distance from the seed source. Burrows (1973,1975a,1975b) refined these assumptions and produced predictive equations to describe the Phase I dispersal of plumed seeds through the air. The flight of the seeds was described by three variables: (1) The height of seed release, (2) the terminal velocity of the seed, and (3) the wind velocity. The terminal velocity reflects the size and shape of the seed. The pappus on plumed seeds acts as a drag parachute which slows the rate of fall of the seed. The more effective the pappus, the lower the terminal velocity. The slower the seed falls through the air the greater the influence of the wind in causing lateral movement.

The equations used by Burrows (1973) to describe the flight of seeds were:

for horizontal movement

$$Uw = dx/dt$$

where Uw is the velocity of the wind, x is distance and t is time;

and for the vertical direction

$$V = C-Vc$$

where V is the vertical velocity, C the terminal velocity and Vc the convection velocity.

The distance (D) moved by a seed released at a height (H) can be described by the equation

$$D = Uw*H/V$$

These equations were also expanded by Burrows (1973) into non-dimensional forms and also included boundary layer effects. This added complexity increased the difficulty of applying the equations to field studies of seed dispersal. To simplify the equation even further in this study, the convection velocity (Vc) was always assumed to be zero.

The above equation indicates that if the wind velocity and the height of seed release are kept constant for different species then any differences in dispersal distance can be explained in terms of the terminal velocities. The terminal velocity can be used as an index of the dispersability of different species.

The same factors will to some extent influence species which do not have plumed seeds. The exceptions are dust seeds which are so light that convection velocities play a major role in their dispersal and also winged seeds which can glide laterally through still air.

In this study it was proposed to measure the relative dispersability of selected annual species. Using measurements of terminal velocity and height of seed release it was proposed to predict Phase I dispersal for these species for a range of wind speeds. The hypothesis proposed was that Phase I dispersal is only a minor component of the overall dispersal distance for these annual species.

7.2.2 Methods

The method used by Sheldon and Burrows (1973) to determine the terminal velocities of seeds involved sophisticated equipment which accurately measured the time taken for seeds to fall known distances in still air (Sheldon & Lawrence,1973). In this study the terminal velocity of seeds of selected species was determined by releasing seeds from a known height and timing their fall with a stopwatch. It was not possible to measure the terminal velocities of species with large velocites by this method. A rank ordering of the species terminal velocities was obtained by simultaneously releasing seeds of two species and recording which fell faster. All dispersal units were checked to ensure that they possessed a mature seed.

The height of seed release was obtained by measuring the heights of inflorescences on plants in the field. In many species seeds are released from a range of heights on a single plant. In this study the maximum height was measured, since the main objective was to determine the maximum horizontal distance a seed could move through the air. The numbers of seeds produced by Erodium cygnorum, Helipterum pygmaeum and Goodenia pusilliflora were counted on individuals in the field. The numbers of seeds produced by the remaining species were estimated, determining the averge number of seeds per inflorescence and the average number of inflorescences per plant.

7.2.3 Results

The terminal velocities of the species are shown in Table 7.1 and the average height and numbers of seeds are shown in Table 7.2. The values give an indication of the relative disersability of the species. The terminal velocity was combined with the height data using the equations of Burrows (1973 ; see section 7.2.1) to predict the flight distance of the different species under different wind conditions (Table 7.3).

7.2.4 Discussion

The predicted distances that seeds may move under different wind velocities demonstrates the limited influence of Phase I dispersal on the movement of seeds of annual plants in this study. The two composites Vittadinia cuneata and Helipterum pygmaeum have low terminal velocities which suggests that the seed is adapted for flight through the air. Both species have a pappus which would be expected to act as a drag parachute (Sheldon & Burrows, 1973). The low height at which the seeds are released from these species reduces the potential advantage of their low terminal velocities. Species which have greater terminal velocities but which are released from a greater height may be dispersed further. Horizontal distance moved is proportional to the height of seed release but inversely proportional to the terminal velocity. Therefore a species with double the terminal velocity but with seeds released from twice the height would be dispersed the same distance.

The predicted distances that seeds move may vary from one year to the next depending upon the quality of the growing season. In good years the plants may grow taller and so release their seed from a greater height and therefore have greater Phase I dispersal. The release height may also vary considerably on one plant. The height used in this study was the mean maximum height of release. This would tend to overestimate the overall influence of Phase I dispersal for a species.

One of the assumptions made by Burrows (1973) was that the seeds were falling at their terminal velocities. For seeds released at very low heights it is unlikely that they would have reached their terminal velocities.They would be falling at a slower rate and so may be dispersed further.

The distance that seeds are predicted to move under influence of the wind increases linearly with wind velocity. The predicted values for seed movement are based upon a constant wind velocity. In the field constant wind conditions are highly improbable. The usual situation is for the wind velocity to fluctuate markedly. The magnitude of the gusts of wind may be more important for Phase I dispersal than the mean wind velocity.

Phase I dispersal is limited in the annual plants found in the study region. There are however numerous difficulties in direct extrapolation to a field situation of the predicted distances seeds move. It was proposed therefore to measure the field dispersal patterns (Phase I Phase II) of selected species and to compare these results to the predicted distances for Phase I (Table 7.3).

7.3 Field dispersal patterns

7.3.1 Introduction

The previous section gave some indication of the potential dispersability of selected species. The situation in the field may produce different results regarding the distances seeds move. In the movement of seed through air the shape and size characteristics of the seed were accounted for in the terminal velocity (Burrows,1973), however in field dispersal studies it is not possible to differentiate between Phase I and Phase II dispersal. The factors that influence the movement of seeds on the ground would be quite different to those through air. The shape and size of seeds would be important factors influencing the distance seeds move along the ground. This section describes the patterns of seed dispersal observed around annual plants in the field.

Maireana pyramidata is one of the dominant perennial bushes of the region. An individual was seeding while the other dispersal studies were being conducted and so it was decided to compare its behaviour with the annual species.

7.3.2 Methods

A number of different techniques have been used to monitor the dispersal of seeds and spores. Possibly the most common method is the use of seed traps. Traps are placed at varying distances from the target plants and the number of seeds in each trap are scored (Werner,1975). This technique has been most useful when studying the dispersal of seeds or spores from the margin of a stand of trees or weeds but has disadvantages. The seeds or spores found in the traps cannot be identified as having being released from any individual plants unless isolated individuals are being studied. Seed traps only measure the extent of Phase I dispersal and do not allow the measurement of Phase II dispersal.

Other techniques that have been used are radioactive tracers (Colwell,1951) or paints and dyes (Watkinson,1975). Using these techniques it is possible to positively identify which individual plant the seeds were released from. These techniques can also be used in conjunction with seed traps.

The method used in this study to determine the movements of seeds was a modification upon the paints or dye technique. Fluorescent dyes were applied to seeds or dispersal units while still attached to the parent plant (Plate 3). The technique used to apply the dye depended upon the morphology of the species. A commonly used method was to place a single drop of dilute dye on the seed or dispersal unit using a small capillary tube. The dye is dissolved in organic solvent which rapidly dries and leaves a fine film of fluorescent material adhering to any irregularities or hairs on the surface of the dispersal unit. Alternatively, a fine paint brush was used to apply the dye. Care was used to apply only a minimum amount of dye. A large quantity of dye would increase the weight of the dispersal unit and change its dispersal characteristics.

The results are calculated as percentages of the recovered seed. In tagging the seeds on the plants the aim was to tag as many seeds as possible per plant. It was not feasible to count the number of tagged dispersal units. It was found from studies where known numbers of seeds were released on the ground, that the recapture rate for seed exceeded 95% (Sect.7.5). The exception to this was Vittadinia cuneata which was highly mobile under strong wind conditions. To ensure the highest possible recapture rate was achieved the area beyond the farthest located seed was systematically searched.

The dye was applied only to plants with mature seeds. After the seeds were released from the plants they were relocated at night using a UV lamp run from a portable 12 V battery pack. The plants were inspected every second night and any seed on the ground was recorded. The seeds with dye showed brightly against the dark soil. The distance and direction of the seeds were measured from the parent plant.

Dyes of different colours were used which allowed the dispersal of a number of individuals of the same species in close proximity to be studied at the same time. The species studied by this method were, *Danthonia caespitosa*, *Stipa nitida*, *Erodium cygnorum*, *Helipterum pygmaem*, *Vittadinia cuneata*, *Sclerolaena obliquicuspis*, *Maireana sclerolaenoides* and *M.pyramidata*.

The study of the field seed dispersal patterns for *Danthonia caespitosa* consisted of two separate groups of tagged plants. The first group (A) consisted of 10 individuals in a dense stand of *Danthonia caespitosa* in Overland Paddock. These individuals were outside the eastern fence of the study site described in Chapter 4. This group was considered to represent a usual field situation. The second group of plants (B) consisted of 5 individuals alongside the Middleback homestead. This second group of plants were at a lower density and were much larger than the individuals of the first group. Both groups of plants were monitored concurrently.

Sclerolaena obliquicuspis is not a true annual but an ephemeral, in that it may live for more than one year when conditions are suitable. It does behave as an annual when the seasons are distinctly separated. The structure of this plant is such that it has a woody skeleton and when the plant dies the skeleton remains standing with the fruiting perianth still attached. Over a period of time the fruiting perianths are released from the skeleton. Because of the slow release of the fruits, two separate readings three months apart were taken from 10 replicate plants.

7.3.3 Results

Danthonia caespitosa

The dispersal pattern (Fig. 7.1) was similar for both groups. Peak seed fall was in the range 0.2 m to 0.4 m from the parent plant. The percentage of seed found in this range was 27% for group A plants and 20% for group B plants. There was a steady decrease in the percentage of seed found in successive distance intervals. The cumulative percentages (Table 7.4) possibly give a better indication of the dispersal distance for this species. For the group A individuals, 52% of the seed was found within 0.4 m of the parent plant and for group B individuals only 34% was found within the same distance. Within 1.0 m of the plant these percentages had risen to 92% and 80% for groups A and B respectively. Virtually all the seed was found within 2.0 m of the parent plant, for group A, 99% and group B, 98%.

The seed from group A plants was dispersed slightly closer to the parent plant than for group B plants. The seed from group B was distributed slightly more evenly throughout the range of dispersal although the maximum distance moved by the seed was similar for each of the groups.

Sclerolaena obliquicuspis

The dispersal pattern is shown in Figure 7.1. The peak seed fall was found in the range 0.1 m to 0.2 m from the parent plant. From this peak there was a very rapid decrease in the distance dispersed and few fruits were found greater than 1.0 m from the plant. For the cumulative percentages (Table 7.4) 61% of the seeds fell within 0.2 m of the plants for the first reading and 40% for the second reading. However, 99% of the seed was relocated within 1.0 m of the plants for the first reading and 94% for the second reading.

The seeds did not move far from the parent plant. The seed from the second reading was dispersed slightly further than seed from the first reading. In comparison with the results for *Danthonia caespitosa* the distribution of dispersal distances was less for *S.obliquicuspis* and the peak was more marked.

Maireana sclerolaenoides

The dispersal pattern for this species (Fig 7.2) indicates that peak seed fall occurred in the range 0.1 m to 0.2 m from the parent plant. There was a rapid decline in the numbers of seeds found in subsequent intervals. The cumulative pecentages (Table 7.4) show that 70% of the seed was found within 0.4 m of the plant and 98% within 2.0 m. The maximum distance a seed was recorded from the parent plants was 2.07 m.

Erodium cygnorum

The peak seed fall was in the range 0 - 1 m (Fig 7.2) and then there was a steady decrease in the amount of seed that was found. The cumulative percentages (Table 7.4) show that 53% of the seed was found within 1 m and 80% within 2 m of the plants. The maximum distance a seed moved was 4.2 m.

Helipterum pygmaeum

This species is a small composite with relatively large achenes. The pattern of dispersal of Helipterum pygmaeum was different to the previous species. The peak seed fall was found within 0.05 m of the plants and this rapidly decreased such that few seed were found greater than 0.2 m from the plants (Fig 7.3). This is reflected in the cumulative percentages (Table 7.4) where 90% of the seed was found within 0.2 m and 100% within 1m of the parent plant. The maximum distance moved by a seed of this species was 0.9 m.

The restricted dispersal of this species was influenced by a rainfall event at the time of seed release. The pappus and achene release a sticky substance when wet and this causes the achene to adhere to the ground surface.

Maireana pyramidata

The peak seed fall was in the range 0.2 m to 0.4 m from the plant (Fig 7.3). The cumulative percentages (Table 7.4) show that 50% of the seed was found within 0.4 m and 79% within 1.0 m and 90% within 2.0 m. The maximum distance a fruit was recorded from the parent plant was 5.4 m.

7.3.4 Discussion

The dispersal patterns observed for the species in this study are similar to those obtained for *Eucalyptus regnans* (Cremer, 1965), *Verbascum thapsus* (Salisbury, 1961), *Senecio jacobaea* (Poole & Cairns, 1940), *Tussilago farfara* (Bakker, 1960), *Picea engelmannii* (Roe, 1967) and *Pinus echinata* (Yocom, 1968). They are also similar in form to the pattern of dispersal pollen from *Pinus coulteri* (Colwell,1951). The greatest numbers of dispersed seeds are generally found near the plants and there is a rapid decrease in the number found with distance from the source. The distance which seeds are dispersed depends upon the species and can vary considerably. For some species it may be only metres (Poole & Cairns,1940) and for others it may be as far as kilometres (Bakker, 1960).

The species studied at Middleback all demonstrated restricted dispersal patterns with the seed not moving more than a few metres from the parent plants. There were, however, differences in the dispersal patterns of the species even within this restricted dispersal. In general, the results were similar to that obtained by Poole & Cairns (1940) for *Senecio jacobaea* where it was found that 60% of the seed fell around the base of the plants and only 0.39% of the seed was found greater than 4.6 m from the plants.

The studies of Poole & Cairns (1940), Roe (1967) and Yocom (1968) were all from the edge of dense stands. Cremer (1965) demonstrated a difference in the behaviour of seed from the margin of dense stands of Eucalyptus regnans and individuals of the same species. The densest seed fall was at the margins of dense stands but up to 30 m from isolated individuals. All species described in this study were isolated individuals and showed dense seed fall near the parent plant.

The slight peak in the numbers of seeds found just away from the parent plant probably indicates that this was the range where the majority of the seeds fell (Phase I) and then subsequent movement of Phase II dispersal occurred, which would account for the larger distances moved by a few seeds. The three most dominant species over the study region are Danthonia caespitosa, Stipa nitida and Erodium cygnorum, obviously these species are not disadvantaged in terms of their continued survival by their apparent restricted dispersal.

As well as the distance moved there is also the aspect of the direction that the dispersal units are dispersed. The percentage of dispersal units found in eight, 45 ° arcs around the plants (Fig. 7.5) indicates that the dispersal units of different species may move different directions. The species all release their seeds at different times and the patterns are the result of different wind conditions at the time of seed release.

7.4 Density of seed fall

7.4.1 Introduction

The results presented in the previous section have been concerned with measuring the distances that seeds move from the parent plant. The results describe the movement of the seeds but do not provide information upon the consequence of dispersal in terms of the numbers of seeds that land per unit area of ground surface. The density of seeds on the ground surface is important in determining the consequence of seed dispersal upon the seed store and the density of germinated individuals.

7.4.2 Methods

In the previous sections, distance intervals were used to describe the movement of seeds from the parent plant. This information can be converted to a density measure by calculating the area of successive distance intervals around the plant and by knowing how many seeds fell in each interval. The expected result is that the density of seeds on the ground would decrease with distance from the plant.

7.4.3 Results

The density of seeds per unit area was found to decrease rapidly with distance from the plant in an exponential manner. The data was converted to logarithmic form and it was found that a linear relationship existed between the logarithm of seed density and the distance from the plant (Fig.7.4).

The relationship was of the form:

$$\text{Log seed density} = - A * \text{distance} + C$$

The variable A is the slope of the linear relationship with the negative sign indicating that there was a decrease of seed density with distance.

Equations of this form were calculated for all species studied in the previous section. The values for the variables A and C and the significance of the regressions are presented in Table 7.5.

7.4.4 Discussion

The seed falling on a unit area of ground has been suggested to be a function of three variables (Harper,1977) and that some simple relationship probably exists between the density of dispersed seed and the distance from the source. The study of Roe (1967) on *Picea engelmannii* showed a regular relationship between the logarithm of the density of seed deposited and the distance from the margin of the forest. The same relationship was found for the species studied here. The highest density of seed was found directly beneath the plant and then there was a decrease in density away from it.

The relationship between seed density and distance from the source was considered by Harper (1977). The model used was that of Van der Plank (1963) who related the logarithm of distance to the logarithm of infection density for crop disease epidemics. The slope of the line relating disease intensity and distance gives information on the ways in which an invasion could spread. Generally, if the slope is that of the inverse square law or steeper a population will spread into colonisable territory as an advancing front. The steeper the slope the more sharply defined the front. Dispersal curves with slopes less than that of the inverse square law will lead to a spread-out pattern of isolated colonists which may act as foci for new infections.

When this was applied to seed dispersal it was found that there was a wide range of slopes. The species which showed the steepest slopes were those with no special adaptations for wind dispersal. The species with specialised mechanisms for wind dispersal generally would tend to colonise not as an advancing front or a horizon of colonisation but as isolated individuals over a great distance. In this study Erodium cygnorum, Danthonia caespitosa and Maireana pyramidata all had slopes less than the inverse square law, and the remaining species had steeper slopes.

The analogy of advancing fronts is probably more applicable in studies on succession. In the case of self-perpetuating vegetation it means that seeds for those species with steep slopes are dropped near the parent plant while those with slopes less than the inverse square law have a tendency to disperse and attempt to find new suitable habitats for colonisation.

7.5 The movement of seeds along the ground

7.5.1 Introduction

Once the seed has reached the ground it does not necessarily mean that the dispersal of that seed is completed. There are three possible fates for seeds following Phase I dispersal: 1. The seed may remain in the position in which it lands and be incorporated into the soil seed store. 2. The seed may be removed by predators such as birds, ants or small mammals. 3. The seed may move across the ground in response to the dispersal agents and then be incorporated into the seed store or removed by predators.

In the first instance dispersal is completed after Phase I dispersal. The effect of seed removal by a predator is considered in a later section (7.6). The final possibility, that of the seed moving across the ground surface, is probably the most common fate for seeds following Phase I dispersal.

The movement of seeds across the soil surface will be influenced by three main factors, wind velocity, characteristics of the seeds i.e. shape and size, and characteristics of the soil surface. When viewed from a distance the soil surface may appear uniform with little relief but if it is considered at a scale important to the seed, then the surface is highly heterogeneous. The surface can be regarded as a mosaic of different features. For the purpose of this study three broad categories were recognised: Surface texture, surface topography and obstructions on the surface.

In the context of this study, surface texture is considered to be the size of the soil particles on the surface. Throughout much of the study region the soil has an extensive cover of cryptogams (Rogers, 1970). In areas where there has been heavy grazing the lichen crust has been broken up by the trampling of sheep and is replaced by a fine layer of gravel or sand. The size of the gravel or sand particles will influence the movement of seeds across the surface. The larger the grains the greater the chance of seeds becoming caught between the grains. The ability of the surface to trap seed will also depend upon the morphology and size of the dispersal unit. Very small seeds may be trapped by fine surfaces whereas larger seeds may move across the same surface unimpeded.

Surface topography refers to the irregularities or microrelief of the ground surface and this would be expected to be one of the major factors influencing the movement of seeds across the ground surface. The effect on seed movement would be much the same as the effect of surface textures. The surface of the ground is not even or regular but is a mosaic of small depressions and rises. The frequency and size of the irregularities may determine how far a seed will move on the surface.

In a study by Harper et al. (1965) a device was used to measure the irregularity of soil surfaces. The device consisted of a number of pins which were lowered to touch the soil surface. The heights of the pins were measured and the irregularity of the surface was measured as the variance of the heights of the pins and was refered to as the soil microtopographical variance (SMTV). In the study by Mortimer (1974) the device was used to measure the SMTV of prepared surfaces of greatly differing SMTV. Seeds were then released upon these surfaces and their movement followed. In the study described in the following section an attempt was made to measure the SMTV of the ground surface under natural conditions and then to determine if a relationship existed between the soil microtopography and the Phase II dispersal of selected species.

Another aspect that may influence the movement of seeds across the soil surface is the presence of objects which may trap seeds and prevent their movement. Surface obstructions in this instance refer primarily to litter on the ground and other plants that may stop seed movement.

In this study the movement of seeds across the ground surface was investigated to determine the importance of this dispersal phase relative to the dispersal process overall.

7.5.2 Methods

To determine the influence of surface texture upon seed movement a range of different textured surfaces was prepared and the movement of seed across these surfaces was monitored. The surfaces were obtained by passing sand through a nest of sieves to obtain three fractions of different particle size. The range of each fraction was:

1. Fine (< 0.5 mm)
2. Medium (0.5 mm - 1.5 mm)
3. Coarse (> 1.5 mm)

These fractions were then spread carefully on the ground to form three flat surfaces each 1 m X 1 m. The surfaces were smoothed to remove all irregularities other than particle size that may have influenced the movement of seeds. Care was taken not to compact the surfaces.

The seeds of the species to be studied were tagged with fluorescent dye as described in Section 7.3.2. For species where the seed was enclosed in a dispersal unit care was taken to ensure that each dispersal unit contained a mature seed. The seeds were then placed on the surfaces in a line perpendicular to the direction of the wind on the day of the study. A number of different species were used for each observation. The seeds of the different species were placed alternately along the line. Fifty seeds of each species were used. The distance the seeds had moved after 6 hours was measured perpendicular to the line at which they were released.

The surface topography of an area was determined using a device similar to that used by Harper et al. (1965). Seeds of selected species were released on the area where the where the SMTV had been determined. With this type of study it must be ensured that the seeds are released under similar conditions. The seeds were released onto a circular perspex plate of 40 cm diameter which was placed flat on to the surface. The perspex provided a very smooth minimum friction surface which did not significantly restrict seed movement. The seeds were free to move across the surface of the disc until they reached the edge, at which stage movement was influenced by the soil surface. The distance moved was measured from the edge of the disc.

The seeds were fluorescently tagged as described in Section 7.3.2. The distance the seeds moved was measured and expressed as a mean distance moved for each species. The SMTV was also determined around the disc as described above. The study was repeated on two different occasions under different wind conditions.

The influence of surface obstructions was determined by selecting two adjacent areas, 3 m X 1.5 m, and removing all surface obstructions from one area. All twigs and litter were carefully removed and any annual plants were harvested with as little disturbance as possible to the soil surface. Batches of 50 fluorescent painted seeds for selected species were placed on perspex plates as described above. After 24 hours the seeds were relocated using the UV lamp and the microhabitat where the seeds were found was recorded and the mean distance from the margin of the plate measured.

Not all the species were studied on the same day and so differences in direction and speed may be responsible for some inter species differences. For any species the movement of seed across the two areas was studied on the same day under similar wind conditions. For this reason the discussion is primarily concerned with the difference in the behaviour across the two areas. Only minor consideration is given to inter species comparisons and only for gross differences in behaviour.

The morphology of the species discussed in detail in the following sections is shown in figure 7.6. The weights of the dispersal units (Table 7.6) also give an indication as to the size differences between the species.

Wind speed was recorded from a fixed anemometers above bush height. The wind information has not been presented in this thesis. A problem encountered in the study was an accurate determination of the influence of wind speed upon the seed movements. The recorded wind speeds were the average over the period of each study. This does not necessarily give an indication of the conditions which are influencing the seed. The wind velocity at the ground surface will be lower than that measured above bush height. Also, the average wind velocity may not give a true indication of the conditions. The wind does not have a constant velocity but fluctuates. It was felt that it would be misleading to present the actual wind data and so trends in seed movement are discussed relative to trends in wind conditions.

7.5.3 Results

In this section figures are presented to show the behaviour of selected species. Where species showed very similar patterns of movement, the results for only one species are presented in the figures.

The species can be divided into three groups depending upon their response to wind speed and surface texture. The first group consisted of two species, Plantago drummondii (Fig. 7.7) and Calotis hispidula which showed very little movement on any surface and at most wind speeds. Both these species have small seeds. The only wind conditions which caused movement were winds which were strong enough to cause considerable movement of the surface particles.

The second group consisted of four species which were highly mobile on all surfaces. On all surfaces and at all wind speeds most of the seeds moved off the prepared surfaces. Three of these species, Danthonia caespitosa (Fig. 7.8), Erodium cygnorum (Fig. 7.9) and Stipa nitida all possess a large hygroscopic awn which holds the seed at an angle to the ground (Peart,1979) or off the ground. This position allows the dispersal unit to move across the surface in response to low wind velocities. Vittadinia cuneata has a small dispersal unit with a fine pappus which moved across the surface in response to light winds, producing a similar pattern to that presented in Figure 7.8.

The remaining three species were intermediate between these two groups, showing varying degrees of movement in response to both surface texture and wind conditions. The response of *Sclerolaena obliquicuspis* to these two variables is shown in Figure 7.10. The stronger wind speeds moved more seeds across the surface and the movement of seeds was greater on the finely textured surface than the coarse surface. The second species in this group, *Goodenia pusilliflora*, has a small saucer shaped dispersal unit (Fig.7.6) and the response of this species was much the same as that of *Sclerolaena obliquicuspis* with stronger wind speeds moving more seeds across the surface. The movement was more pronounced on surfaces of smaller grain size.

Carthamus lanatus (saffron thistle) differs from the other species considered in this study in that each flower head produces two seeds of different morphology. The inner florets produce an achene with a sturdy pappus whereas the outer florets produce a naked achene. The two morphologies were studied and this allowed an estimation of the effectiveness of the pappus for this species. The achenes which possessed a pappus were more mobile than the naked achenes (Fig. 7.11 & 7.12). The naked achenes did not move far except under strong wind conditions and even under these conditions none of the achenes moved all the way across the surfaces. In contrast, the plumed achenes moved much greater distances and this movement was greater on the fine and medium textured surfaces than on the rough surfaces. The pappus appeared to become trapped between the surface particles on the rough surfaces whereas this did not occur on the fine surfaces and occurred to a lesser extent on the medium surfaces.

The study of the movement of seeds across an area of soil where the SMTV had been measured did not produce the expected result. Of the species studied only three species of seed appeared to be influenced by the surface irregularities. These species were *Plantago drummondii*, *Calotis hispidula* and the non plumed seeds of *Carthamus lanatus*. The seeds of the other species studied moved freely across the surface and beyond the measured area.

The seeds of *Plantago drummondii* were never found further than 2 cm from the edge of the perspex plate. These seeds are very small with no appendages and are therefore effectively trapped by irregularities in the soil surface, as these irregularities are of a scale greater than the size of the seeds themselves. The behaviour of *Calotis hispidula* was similar to that of *P.drummondii* with the seeds not moving further than 6 cm from the edge of the perspex plate and 90 % of the seed found within 2 cm of the plate. Again the small size of the seeds of this species is the reason for the lack of movement. This species also has small spines on the dispersal unit which would restrict movement on the ground surface.

The third species which showed little movement was the non plumed form of seed from *Carthamus lanatus*. Seeds of this species were not found further than 14 cm from the edge of the plate and 92 % were within 8 cm of the plate. The reason for the lack of movement by this species is probably quite different to those for the previous two species. The seed in this case is much larger and of a near spherical shape. The large size tends to restrict its movement as greater wind velocities are required to move the seed. The plumed form of the same species was more mobile under similar wind velocities. Of the remaining species of seed used in this study, only occasional seeds were found on the measured area and this was usually the result of the seed becoming trapped by a crack in the soil surface.

The results on the influence of obstructions upon the movement of seeds (Table 7.7) show a marked difference between the species. Three species, Plantago drummondii, Helipterum pygmaeum and Goodenia pusilliflora, showed very little movement of their seeds. In general the seeds of these species were trapped by irregularities in the soil surface soon after they had blown off the perspex plate. They did not move far enough from the plate to be influenced by the presence of annual plants or litter.

The movement of more mobile species such as Danthonia caespitosa, Vittadinia cuneata, Erodium cygnorum, Maireana sclerolaenoides and Stipa nitida appeared to be influenced by the presence of annual plants or litter on the ground. A large number of the seeds of these species lodged against obstructions. The mean distance moved by the seeds also shows the effect of obstructions. In the area where obstructions were present the mean dispersal distance was less than for the bare area.

7.5.4 Discussion

The results indicate that for some of the species studied, seed movement was restricted due to the texture of the surface. Other species were not greatly influenced by the surface texture. The degree to which a species moved across the surfaces also depended upon the wind strength. The species could be divided into three groups based upon their dispersability. There were two extreme groups of non-mobile and highly mobile species. The third group was intermediate between these two groups. A similar study on the movement of seed along the ground was conducted by Mortimer (1974) who also found that the movement of seeds was influenced by the soil texture and the seed morphology. In that study the differences in the textures were much greater than those used here. The textures used here were similar to the field conditions that may be experienced by a seed in the study region.

The study emphasises the importance of the seed morphology in influencing the movement of seeds across the ground. Naked seeds do not move greatly across the ground surface, as was shown by Plantago drummondii and Carthamus lanatus even though there was a considerable difference in the seed size between these two species (Table 7.6). It is difficult to predict the behaviour of some species on the basis of their morphology. Vittadinia cuneata has a highly mobile dispersal unit due to the pappus on the achene but the three other mobile species Danthonia caespitosa, Erodium cygnorum and Stipa nitida do not have morphologies that would usually be equated with effective dispersal but rather with burying the seed. The awn facilitated the movement of these species across the ground by an erratic rolling motion.

The presence of a pappus does not necessarily ensure that the species will be dispersed long distances, as can be seen by the difference in behaviour between Vittadinia cuneata and Carthamus lanatus. The pappus of C.lanatus must be regarded as being important for this species as shown by the difference between the pappus and non-pappus forms of the seed.

The study did not demonstrate a range of differences in species response to surface irregularities. Rather it showed that two groups of species could be identified. Those whose seeds were trapped by the surface irregularities and so showed little movement comprised one group, and those which were not affected by the surface topography the other.

These results cannot be considered conclusive but rather demonstrate a trend in species response. A different result may have been obtained under stronger or lighter wind conditions. The degree of soil surface topography would also influence seed behaviour. If the study had been conducted in an area of highly disturbed soil then the movement of many more species may have been restricted. The study does, however, show that seed movement was influenced by and seed size and the possession of appendages. The seeds which did not move were either small seeds or large seeds and none possessed large appendages. The species which possessed wings, plumes or awns all moved more freely across the soil surface.

The movement of seeds along the ground surface (Phase II dispersal) can be greatly influenced by the presence of obstructions. For species with relatively immobile seeds the effect is negligible. These species tend to have smaller seeds which are trapped by irregularities in the surface that are of a scale larger than the seeds. For those species which can move more freely across the surface, the presence of obstructions reduces their ability to move. The lack of influence of the surface topography was unexpected. Limited Phase II dispersal was initially thought to be the result of surface topography. It could be however, that other factors such as the presence of twigs, litter and other plants may be more important than irregularities in the surface in restricting the dispersal of seeds.

In a dense population of annuals it could be suggested that as more seed would be produced there would be a greater chance of seeds being dispersed further from the parent plants. The results presented suggest that in a dense population of annuals there would be very limited movement of seeds. Escape may only occur from those plants near the margin of the population. The discussion is not restricted to the single species population. In a dense population of annual plants made up of numerous different species the dispersal of all species would be restricted. In years of above average rainfall there may be dense swards of annuals which effectively restrict their own dispersal. In contrast, in years when annual plants are less common, dispersal may occur to a greater extent. In terms of the success of annual plants in an arid environment restriction of dispersal may not be a disadvantage. Dispersal may be acting to maintain the population rather than expand its range or population size.

7.6 Ants

It has been reported that ants may be an important dispersal agent (Berg,1975; Ridley,1930; Pijl,1969; Davidson & Morton,1981) by collecting seed and transporting it to their nests. The ants remove elaiosomes or other structures and then discard the seed. Some species of ants collect the seed as a food source (Tevis, 1958c). In this case the ants remove the seed from the dispersal structure and discard the dispersal structure as debris around the entrance to the nest.

In the study area it was observed that there was considerable ant activity with some species collecting large numbers of seeds of different species and the entrances to the nests of some ant species are surrounded by the debris of dispersal units. On one occasion a study of seed dispersal from Danthonia caespitosa had to be abandoned because of seed removal by the ants. The ants had climbed the plants and were removing the seed from the inflorescences, including fluorescently tagged seed. With the UV lamp the ants could be easily followed carrying the fluorescent seed back to their nest.

There were three genera of ants that were recorded collecting seed. The ant genera and the species of seed that were collected are presented in Table 7.8. The ants removed a range of species of seed and there was little difference in species of seed collected by the different genera of ants. The species most commonly collected were Danthonia caespitosa, Sclerolaena obliquicuspis and Maireana sclerolaenoides. The proportions of the different species of seed around the nest varied considerably between nests and appeared to be related to the composition of the annual flora in the area around the nest. There were also changes in the seed collected with time depending upon which annual species had reached maturity.

The list of species of seed collected by the ants is incomplete. There are annual species with a dehiscent seed that has no dispersal structure. These species would not be recorded in the debris around the nests. There were also a number of species of low occurrance in the study area which were not recorded as ant-predated. In other areas where these species occur in greater numbers they may be predated by ants

The observations on ant behaviour were designed to determine whether the ants were acting as agents of seed dispersal. The observations indicate that the ants are primarily seed predators since no evidence of seed dispersal was found. This result is in contrast to that recorded by other workers (Berg,1975; Davidson & Morton,1981) who found that ants may play an important role in dispersal of some plants. The ants probably play an important role in the dynamics of the seed store of annuals through the predation of seed. Investigation of this aspect of annual dynamics was beyond the scope of this study.

7.7 Discussion and conclusions

One view of dispersal is that of Gadgil (1971) who stated:

> " In a very general way, the factor favouring evolution of dispersal would be the chance of colonising a site more favourable than the one that is presently inhabited ... An organism should disperse if the chance of reaching a better site exceeds the expected loss from the risk of death during dispersal or the chance of reaching a poorer habitat."

This view of dispersal is supported by Harper (1977). From this it would appear that there are a number of possible explanations for the behaviour of the annuals observed in this study. The first possibility is that the habitat is relatively uniform and the species obtain no advantage by the expenditure of energy upon dispersal. A second explanation could be that the habitat is highly patterned but the scale of pattern is such that the probability of a seed reaching a new habitable site is very low and the tendency to disperse is restricted. Another possible explanation could be that due to the extreme variability in the habitat, especially over time, the plants have developed other specialisations at the expense of dispersal morphologies. This view is best summarised by Went (1979) who suggested that the seed of annuals should be regarded as a survival unit rather than a dispersal unit.

In the case of Danthonia caespitosa, Stipa nitida and Erodium cygnorum it was shown previously (Chapter 5) that these species were dominant at the study site. These three species all possess a hydroscopic awn which allows the seed to be buried in response to moisture or humidity changes which cause the awn to unwind and then re-wind (Peart, 1979). In most instances the seed from these species penetrates the fine network of cracks on the surface. It may be that for these species it is more advantageous to be able to place the seed below the soil surface rather than disperse. It was also noted that Erodium cygnorum and Danthonia caespitosa were dispersed greater distances than some species which might be expected to be effectively wind dispersed. This is a consequence of Phase II dispersal being more important than Phase I in the dispersal of annual plants.

Helipterum pygmaeum is another species to which this argument may be applied. This species is a member of the Compositae and has a relatively large achene and pappus for the size of the plant. The study of this species showed very limited dispersal. This was due to a light rainfall event at the time of seed release. The achene is covered with a dense tomentum of hairs and when these are wet they release a mucilaginous substance which binds the seeds to the surface. The same applies to Plantago drummondii another species of very restricted dispersal. In the case of these species, rather than rely on dispersal to locate suitable microhabitats for germination they effectively create their own microhabitat for germination (Harper & Benton,1966).

An aspect about which little is known are the rare events of long distance dispersal. Examples which may cause this are unusually strong wind conditions at the time of seed release or when the seed is on the ground, or small, atmospheric vortexes locally termed "willy willys" which may move across the area lifting soil and plant material from the ground surface. Exceptionally wet conditions which cause flooding and sheet flow across the ground surface may also cause long distance dispersal. These rare and unpredictable events may disperse seed for considerable distances (Ridley, 1930; Pijl, 1969) although it is not feasible to actually measure the effect. They may be important for the seed and to some extent reduce the necessity of the seed to have specific adaptations for dispersal. The unpredictability of the environmental conditions may favour limited dispersal so that the seed falls near the parent population where the conditions are known to be favourable for growth and survival.

This difference in dispersal was taken into account in a model of germination and dispersal by Venable & Lawlor(1980). They suggested that there may be different germination strategies associated with the different dispersal strategies. Species that release their seed near the plant should have a high degree of innate dormancy whereas those which were dispersed to new habitats should be less rigidly controlled so that they could better utilise any suitable habitats that were located. They applied this to seed released from single species and not to the differences between species. It is however an interesting concept that there may be links between dispersal and the germination strategy.

The concept can be tied to the two different functions of dispersal described by Harper (1977). The first was the maintenance of existing populations and the second was expanding the range or population size of a species. For desert annuals the maintenance of an existing population would be represented by the release of seed near the parent plant with a high degree of innate dormancy, so that there was a sizeable seed store of dormant seed to insulate the population from unfavourable conditions. Expanding the range or population size (Harper,1977) refers to the dispersal of seed in search of new habitats suitable for colonisation. This is a much more chance related phenomenon, where the plant relies upon the chance that some seed, usually a small number, will land in a suitable habitat. These seeds will then be able to immediately utilise the habitat and produce seed.

Species	Terminal Velocity (m/sec)
Vittadinia cuneata	1.11
Helipterum pygmaeum	1.11
Stipa nitida	1.25
Danthonia caespitosa	1.42
Calotis hispidula	1.53
Erodium cygnorum	1.53
Maireana sclerolaenoides	1.66
Goodenia pusilliflora	1.66
Carthamus lanatus (plumed)	2.50
Plantago drummondii	>2.50
Carthamus lanatus (non-plumed)	>2.50

Table 7.1 Terminal Velocities for selected species. Terminal velocity was calculated by dropping seeds from a height of 2 m and timing their fall with a stop watch. The terminal velocities are the mean for 10 dispersal units for each species and repeated drops of individual seeds.

	Height(cm)			Seed no			
	mean	sd	(n)	mean	sd	(n)	
Danthonia caespitosa	18.6	± 6.3	(100)	510	± 59	(25)	e
Erodium cygnorum	3.5	± 1.0	(200)	5.2	± 3.2	(200)	c
Helipterum pygmaeum	7.7	± 1.6	(25)	4.9	± 2.1	(25)	c
Sclerolaena obliquicuspis	11.5	± 2.6	(75)	58.2	±12.6	(25)	e
Maireana sclerolaenoides	7.7	± 1.8	(75)	68.9	±20.4	(25)	e
Vittadinia cuneata	8.2	± 2.4	(25)	51.9	±17.2	(25)	e
Plantago drummondii	6.4	± 3.2	(25)	494	± 123	(25)	e
Goodenia pusilliflora	3.9	± 1.3	(25)	10.8	± 4.5	(25)	c
Stipa nitida	21.7	± 7.7	(50)	173	± 69	(25)	e

Table 7.2 Mean maximum height of seed release and the associated standard deviation obtained by measuring the heights of inflorescences in the field.n= the number of inflorescences measured. The numbers of seeds per individual was counted for some species c and estimated for the remainder e.

Wind speed (Km/hr)	Species						
	A	B	C	D	E	F	G
5	0.17	0.03	0.09	0.06	0.10	0.03	0.24
10	0.35	0.06	0.19	0.12	0.20	0.06	0.48
15	0.52	0.09	0.29	0.19	0.30	0.09	0.72
20	0.70	0.12	0.38	0.25	0.41	0.13	0.96
25	0.88	0.15	0.48	0.32	0.51	0.16	1.20
30	1.05	0.19	0.57	0.38	0.61	0.19	1.44
35	1.23	0.22	0.67	0.45	0.71	0.22	1.68
40	1.40	0.25	0.77	0.51	0.82	0.22	1.92
45	1.58	0.28	0.86	0.57	0.92	0.29	2.17
50	1.70	0.31	0.96	0.64	1.02	0.32	2.41
55	1.90	0.35	1.05	0.70	1.12	0.35	2.65
60	2.11	0.38	1.15	0.77	1.23	0.39	2.89
65	2.28	0.41	1.25	0.83	1.33	0.42	3.13
70	2.46	0.44	1.34	0.90	1.43	0.45	3.37

Table 7.3 The predicted distances (m) seeds of 7 species would move through the air (Phase I dispersal) for different wind speeds. The species are A. *Danthonia caespitosa* B. *Erodium cygnorum* C. *Helipterum pygmaeum* D. *Maireana sclerolaenoides* E. *Vittadinia cuneata* F. *Goodenia pusiliflora* G. *Stipa nitida*.

	RADIAL DISTANCE (Metres)						
	0.2	0.4	0.6	0.8	1.0	2.0	Max
Erodium cygnorum	10.0	26.6	36.6	40.0	53.3	79.9	4.2
Danthonia caespitosa	24.5	51.9	73.1	87.2	92.9	99.8	2.2
D.caespitosa B	13.1	34.0	52.7	68.4	80.6	98.6	2.6
Sclerolaena obliquicuspis	61.1	86.9	95.0	99.1	99.5	100.0	1.1
S.obliquicuspis B	40.6	66.6	79.9	84.7	94.2	100.0	1.8
Maireana sclerolaenoides	34.8	70.7	85.5	91.1	94.0	98.6	2.1
Helipterum pygmaeum	90.3	94.9	94.9	99.5	100.0	100.0	0.9
M.pyramidata	6.1	49.5	67.8	72.2	79.1	90.4	5.4

Table 7.4 The percentage of the seed found within areas of increasing radius and the maximum distance at which a seed was relocated for 6 different species.

Species	A	C	r^2
Erodium cygnorum	-0.53	1.11	0.99
Danthonia caespitosa(A)	-1.77	3.90	0.99
Danthonia caespitosa(B)	-1.36	3.40	0.98
Sclerolaena obliquicuspis(A)	-2.87	3.00	0.96
Sclerolaena obliquicuspis(B)	-2.27	3.20	0.93
Maireana sclerolaenoides	-2.60	3.40	0.97
Helipterum pygmaeum	-6.46	3.30	0.87
Maireana pyramidata	-1.51	3.90	0.75

Table 7.5 The values of the constants A (slope) and C (intercept) and the significance of the regression equations for log density versus distance from the seed source for species discussed in Section 7.4.

WEIGHT OF WHOLE DISPERSAL UNITS

Species	Weight (gm)
Calotis hispidula	1.002×10^{-3}
Plantago drummondii	1.087×10^{-3}
Danthonia caespitosa	1.298×10^{-3}
Stipa nitida	1.396×10^{-3}
Vittadinia cuneata	1.438×10^{-3}
Helipterum pygmaeum	2.490×10^{-3}
Sclerolaena obliquicuspis	4.428×10^{-3}
Erodium cygnorum	16.250×10^{-3}
Erodium cygnorum (de-awned)	5.648×10^{-3}
Maireana sclerolaenoides	8.330×10^{-3}
Carthamus lanatus (plumed)	26.290×10^{-3}
Carthamus lanatus (non-plumed)	21.880×10^{-3}

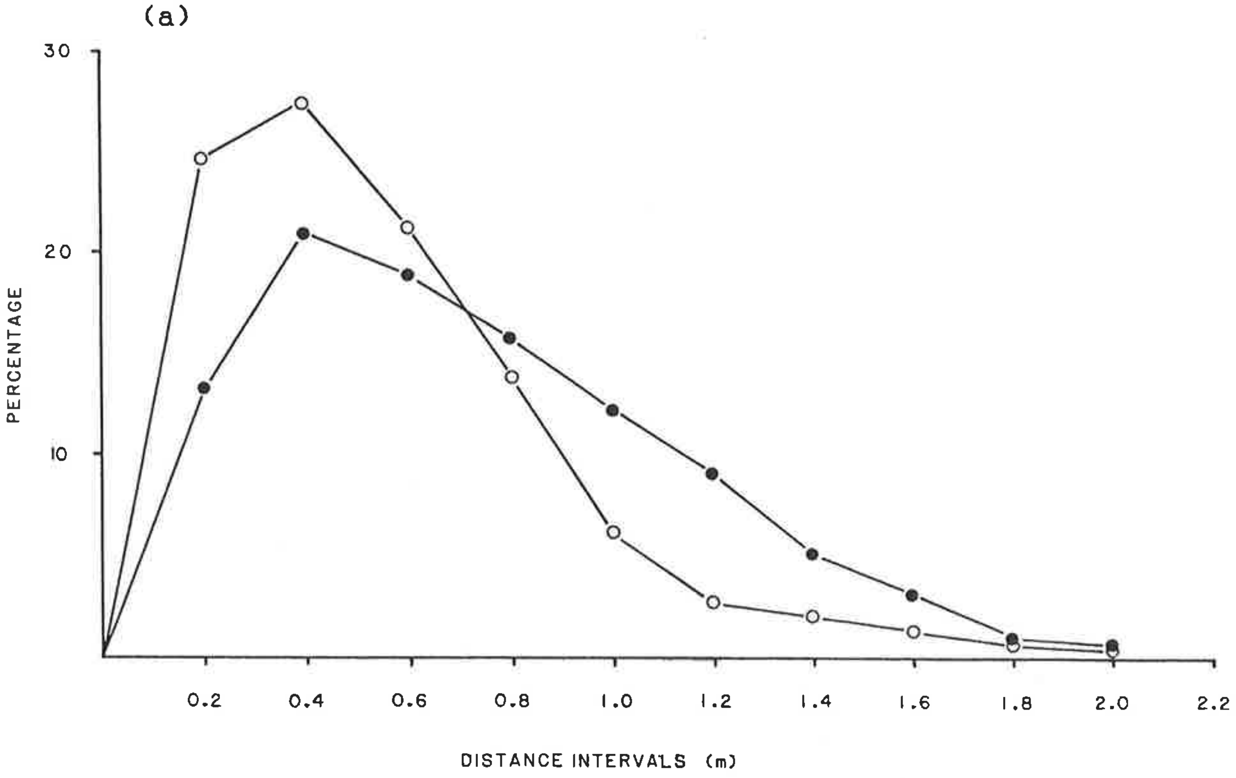
Table 7.6 The weights (gm) of whole dispersal units for 10 species. Weights were calculated by weighing 5 batches of 25 dispersal units for each of the species. The batches were weighed on a Metler analytical balance.

	Plants	Twigs/ litter	Bare soil	Mean distance(cm)
D.caespitosa				
Dense	64	32	4	36.5
Bare	-	74	26	78.1
S.obliquicuspis				
Dense	17	8	75	27.6
Bare	-	43	57	41.3
M.sclerolaenoides				
Dense	42	49	9	59.3
Bare	-	94	6	140
V.cuneata				
Dense	77	17	6	62.5
Bare	-	85	15	560
P.drummondii				
Dense	0	0	100	1.5
Bare	-	0	100	1.5
E.cygnorum				
Dense	62	16	22	160
Bare	-	83	17	290
H.pygmaeum				
Dense	8	14	78	18.2
Bare	-	7	93	19.7
G.pusilliflora				
Dense	5	6	89	14.9
Bare	-	0	100	14.1
S.nitida				
Dense	66	21	13	97.2
Bare	-	76	24	160

Table 7.7 The effects of obstructions upon seed movement. The numbers in the table are the percentage of the released fluorescently tagged seed which were identified as trapped by plants, twigs/litter or remained on bare soil. The two categories "Dense" and "Bare" refer to two different areas where the experiment was conducted. The "Dense" area had a dense covering of annual plants. The "Bare" area had no annual plants.

	Meloporus sp	Pheidole spp	Chelaner spp
Danthonia caespitisa	*	*	*
Atriplex vesicaria	*	*	*
A.stipitata	*	*	-
Daucus glochidiatus	*	-	-
Stipa nitida	*	*	*
Maireana excavata	*	-	-
M.pyramidata	*	-	-
M.sedifolia	*	*	*
M.sclerolaenoides	*	*	*
Tetragonia eremaea	*	*	*
Calotis hispidula	*	*	-
Isoetopsis graminifolia	*	-	-
Vella annua	*	*	-
Sclerolaena obliquicuspis	*	*	*
S.patenticuspis	*	*	*
Erodium cygnorum	*	*	*
Sclerochlamys brachyptera	-	*	-
Omphalolappula concava	-	-	*
Plantago drummondii	-	-	*
Vittadinia cuneata	-	*	-
Sida intricata	-	*	-

Table 7.8 Species of seed which were recorded being harvested by three genera of ants in the period 1979 - 1983. This table was compiled by observation of ants in the field and recording the seeds the ants were collecting. Additional information was obtained by collecting the debris from around the entrance to nests and inspecting it under a binocular microscope to identify the species of seed that had been collected.



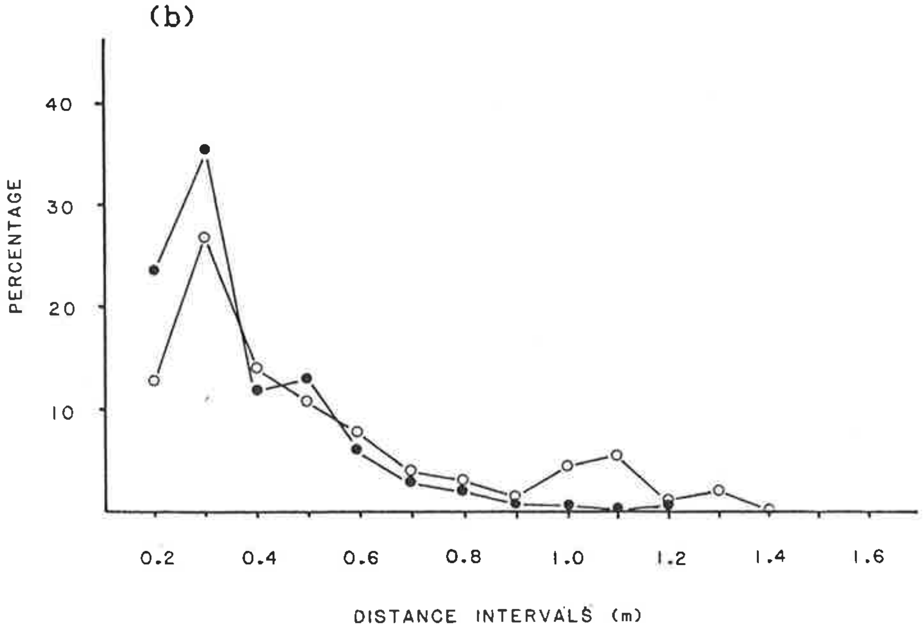


Figure 7.1 (a) Dispersal pattern from *Danthonia caespitosa* for two different areas (●) low density; (○) high density.
(b) Dispersal pattern from *Sclerolaena obliquicuspis* (●) first reading; (○) second reading.

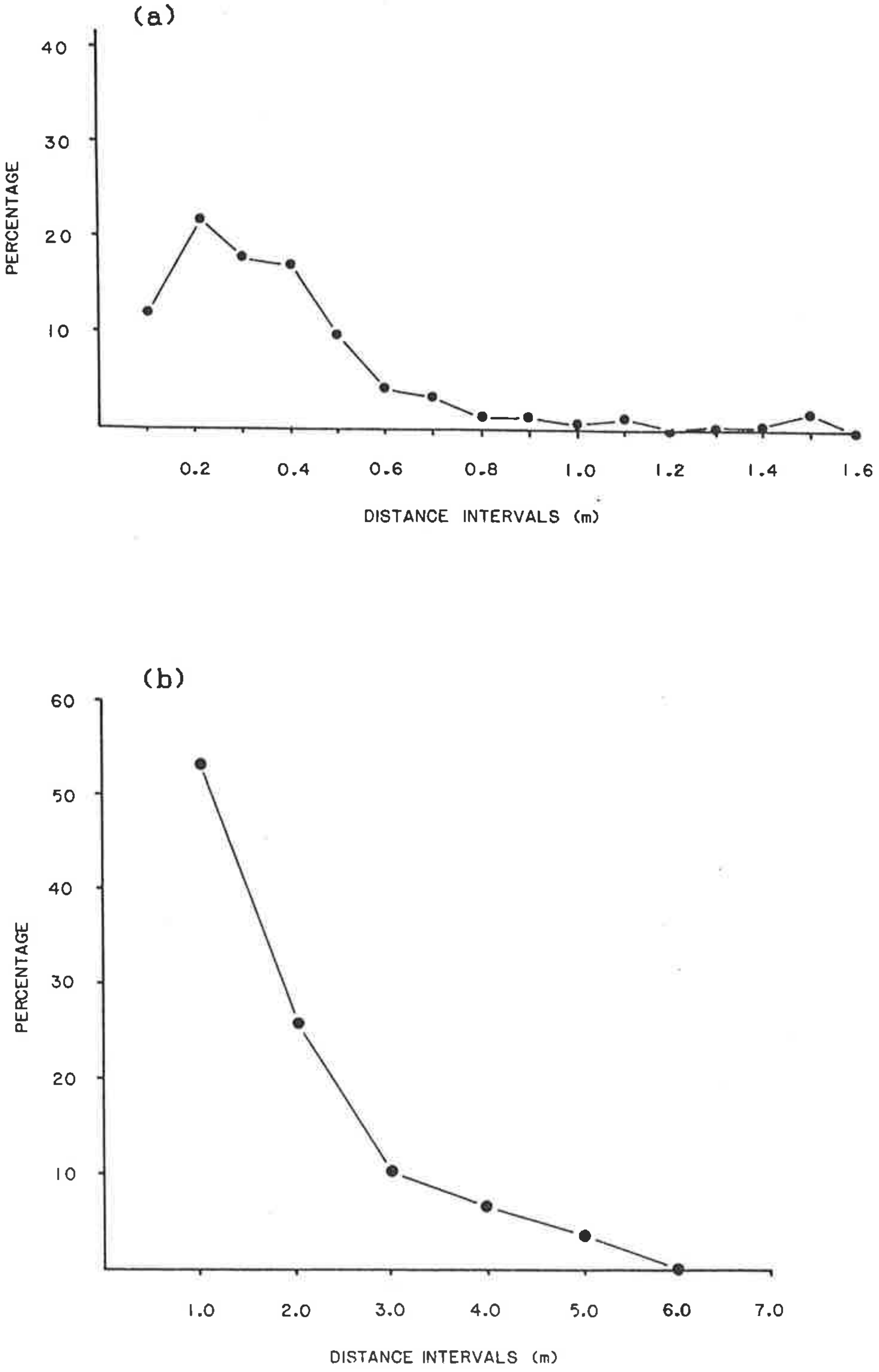
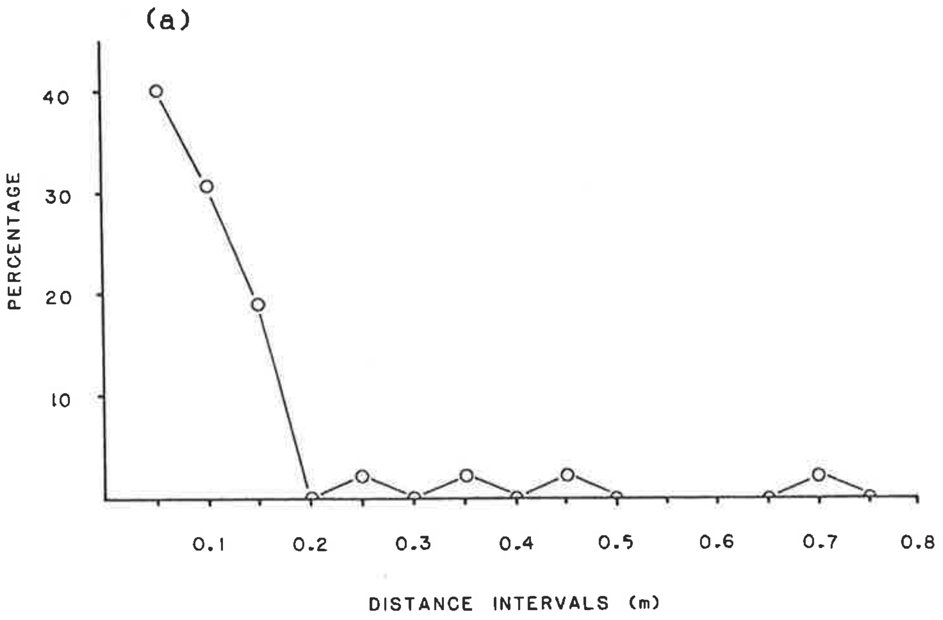


Figure 7.2 (a) Dispersal pattern from *Maireana sclerolaenoides*
(b) Dispersal pattern from *Erodium cygnorum*



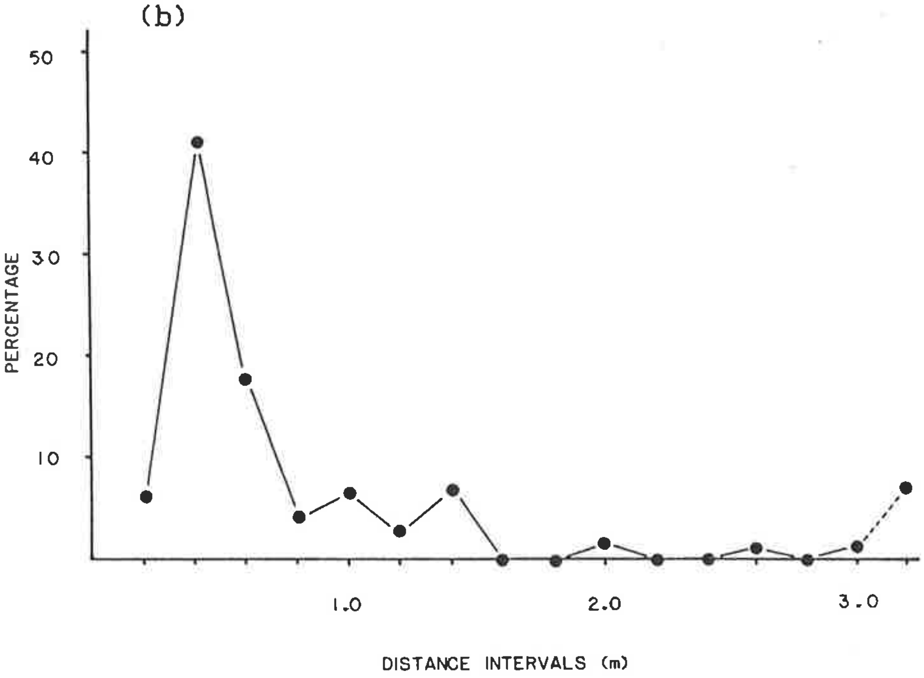


Figure 7.3 (a) Dispersal pattern from *Helipterum pygmaeum*
(b) Dispersal pattern from *Maireana pyramidata*

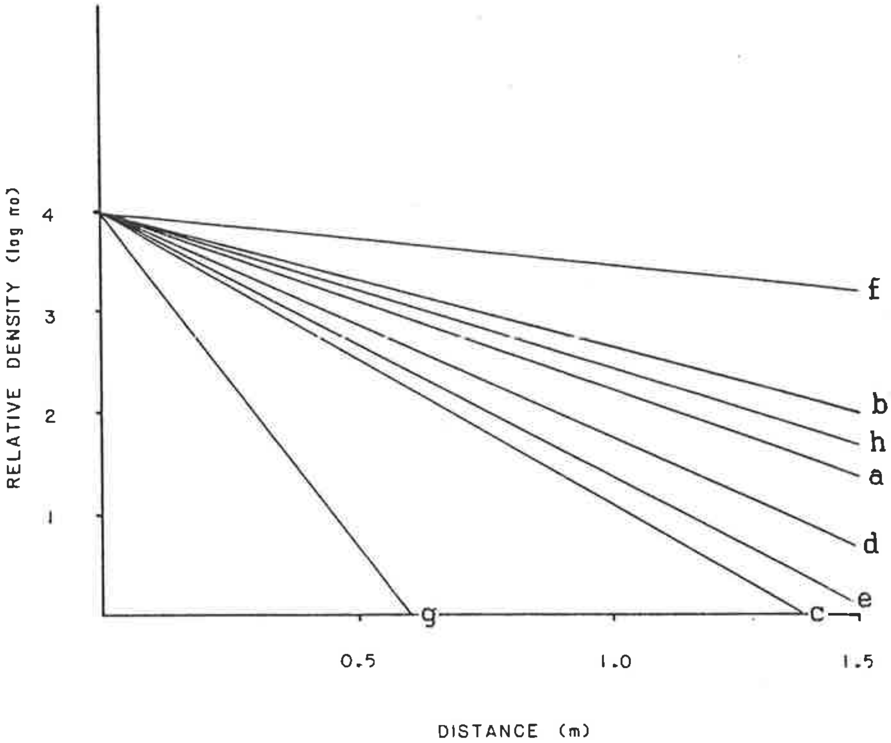


Figure 7.4 The relationship between the log of density seed fall and distance from the plant: The graph is drawn using the same intercept value for all species, this allows comparison in the rate of decrease of relative seed density between the species. All regressions were significant (Table 7.5) (a) Danthonia caespitosa 1 (b) D.caespitosa 2 (c) Sclerolaena obliquicuspis 1 (d) S.obliquicuspis 2 (e) Maireana sclerolaenoides (f) Erodium cygnorum (g) Helipterum pygmaeum (h) Maireana pyramidata.

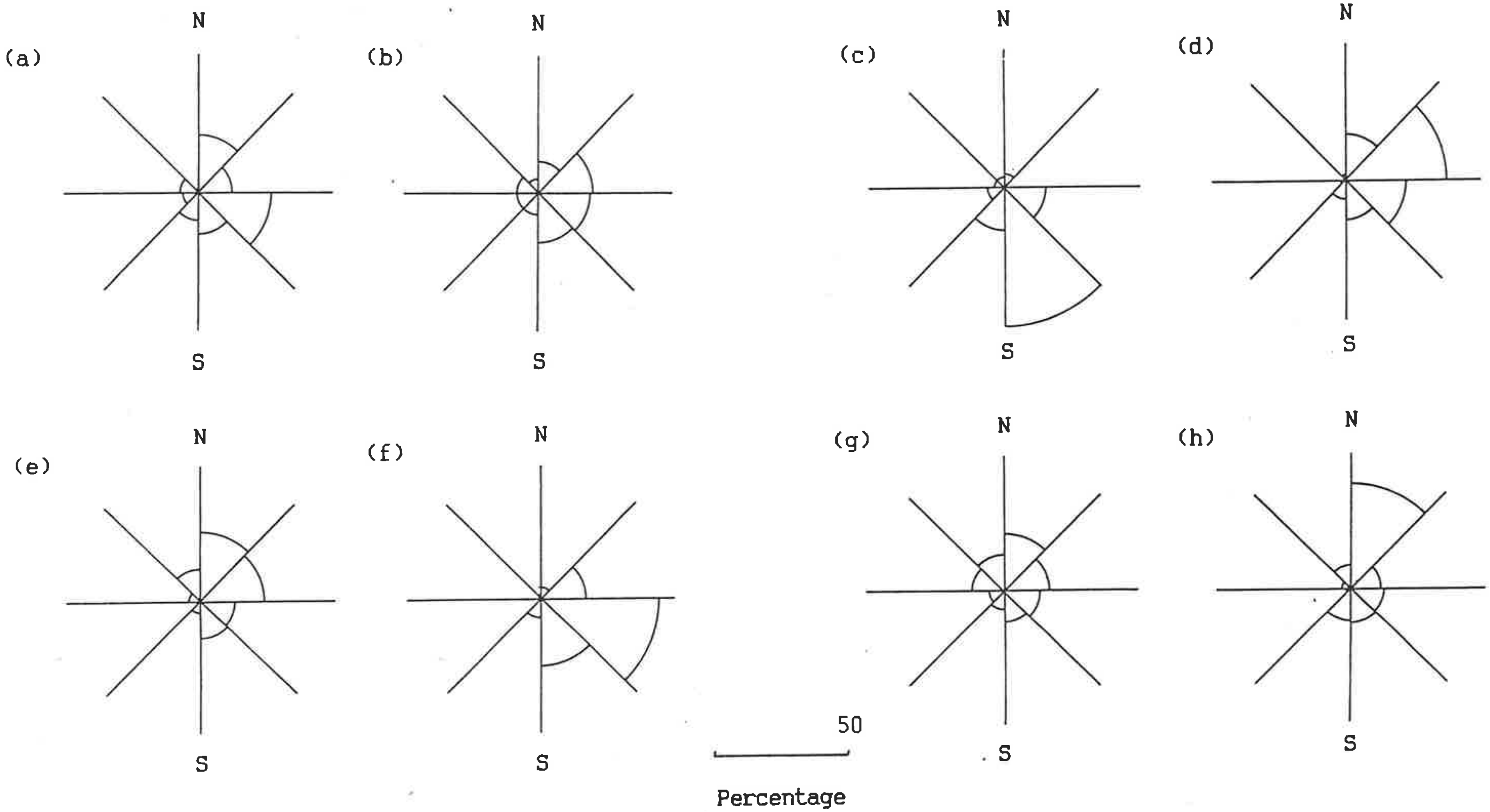


Figure 7.5 The percentage of seed found in eight directions around the plants: (a) Sclerolaena obliquicuspis, first reading. (b) S.obliquicuspis, second reading. (c) Erodium cygnorum (d) Maireana pyramidata (e) M.sclerolaenoides (f)Helipterum pygmaeum (g) Danthonia caespitosa A (h) D.caespitosa B

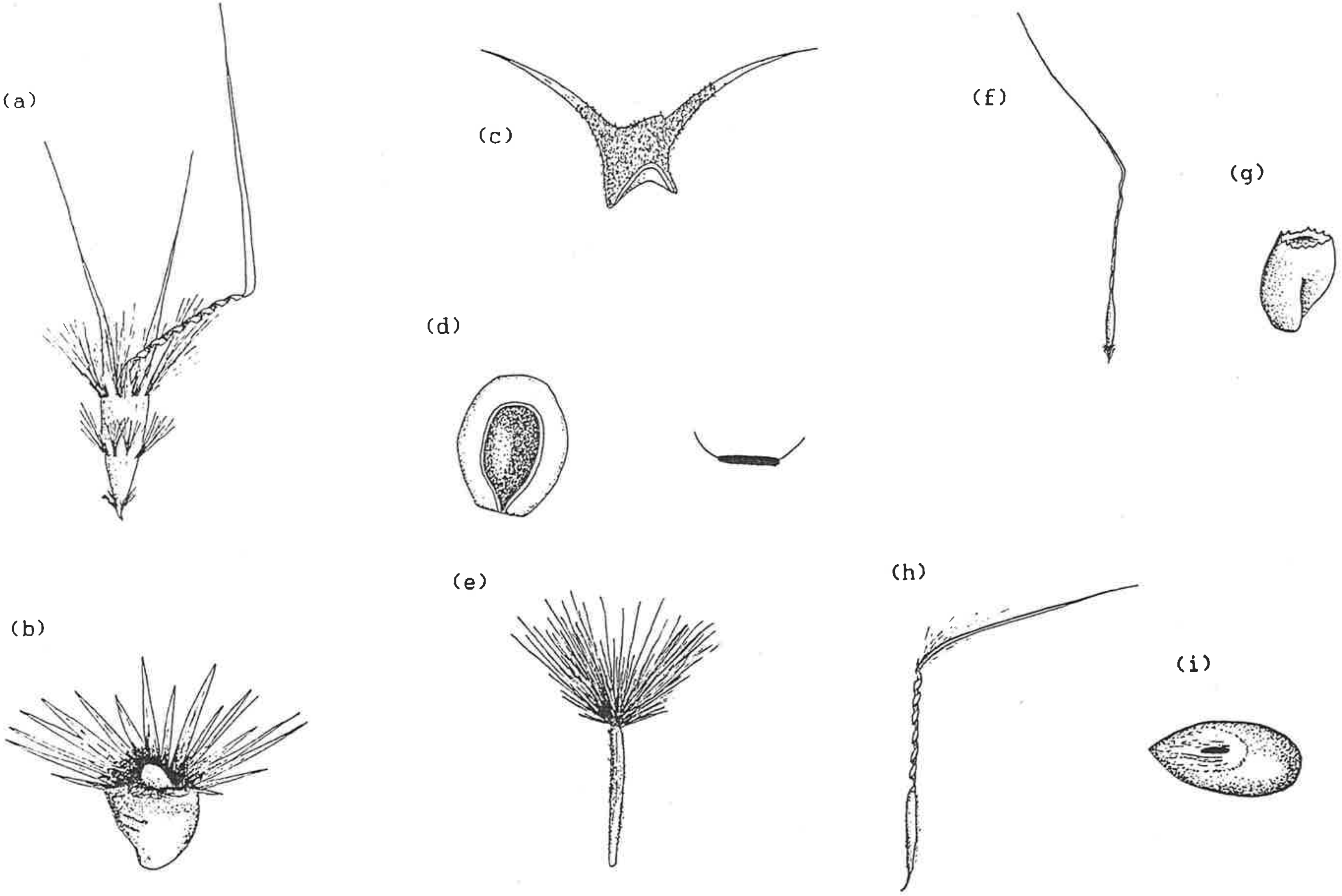


Figure 7.6 Drawings of the dispersal units of some of the species considered in this chapter (a) Danthonia caespitosa (b) Carthamus lanatus (plumed) (c) Sclerolaena obliquicuspis (d) Goodenia pusilliflora (e) Vittadinia cuneata (f) Stipa nitida (g) Carthamus lanatus (non-plumed) (h) Erodium cygnorum (i) Plantago drummondii.

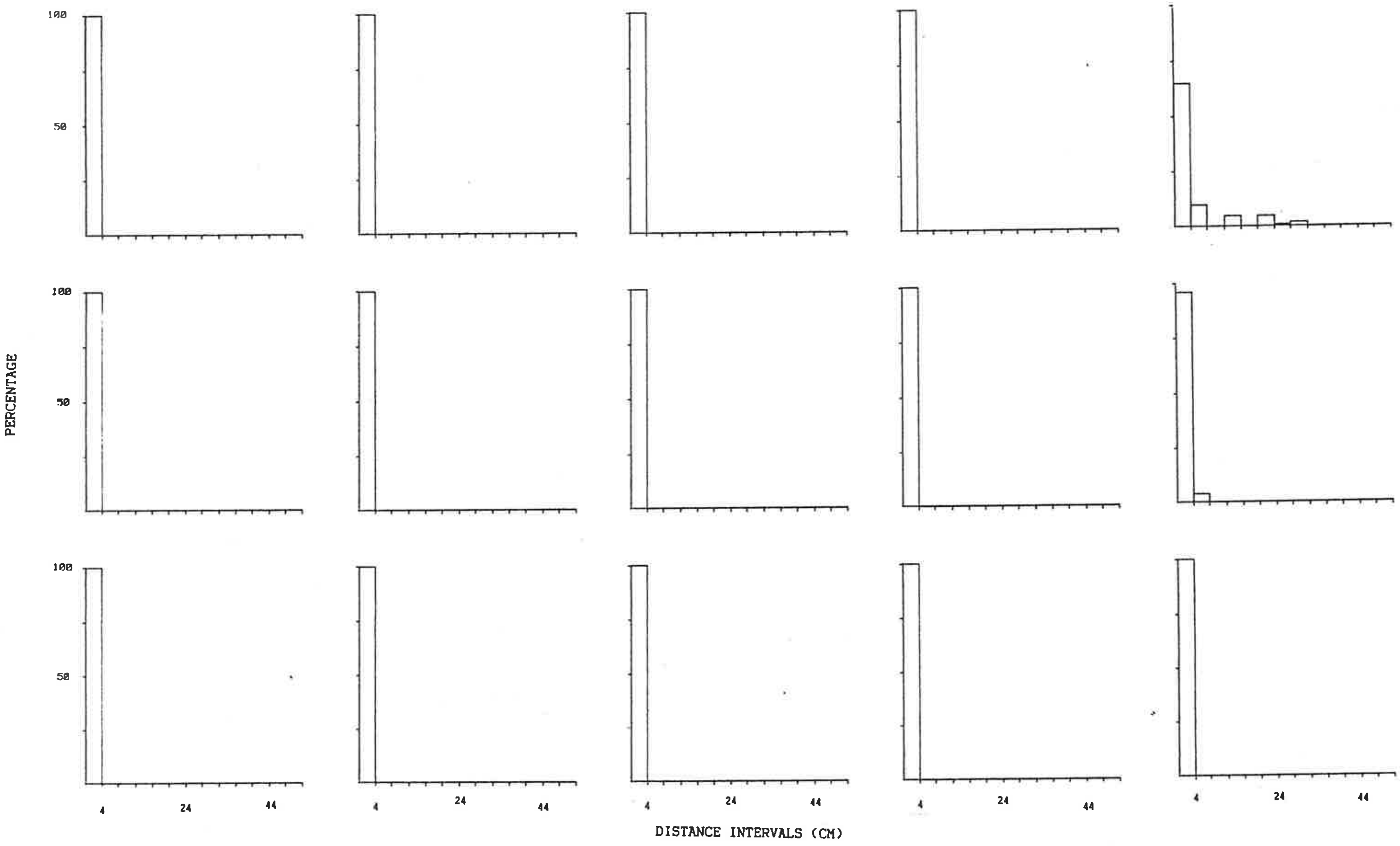


Figure 7.7 The movement of seeds of *Plantago drummondii* across three surfaces of different texture at five different wind speeds. Surface texture increases from fine to coarse down the page and wind speed increases from left to right across the page.

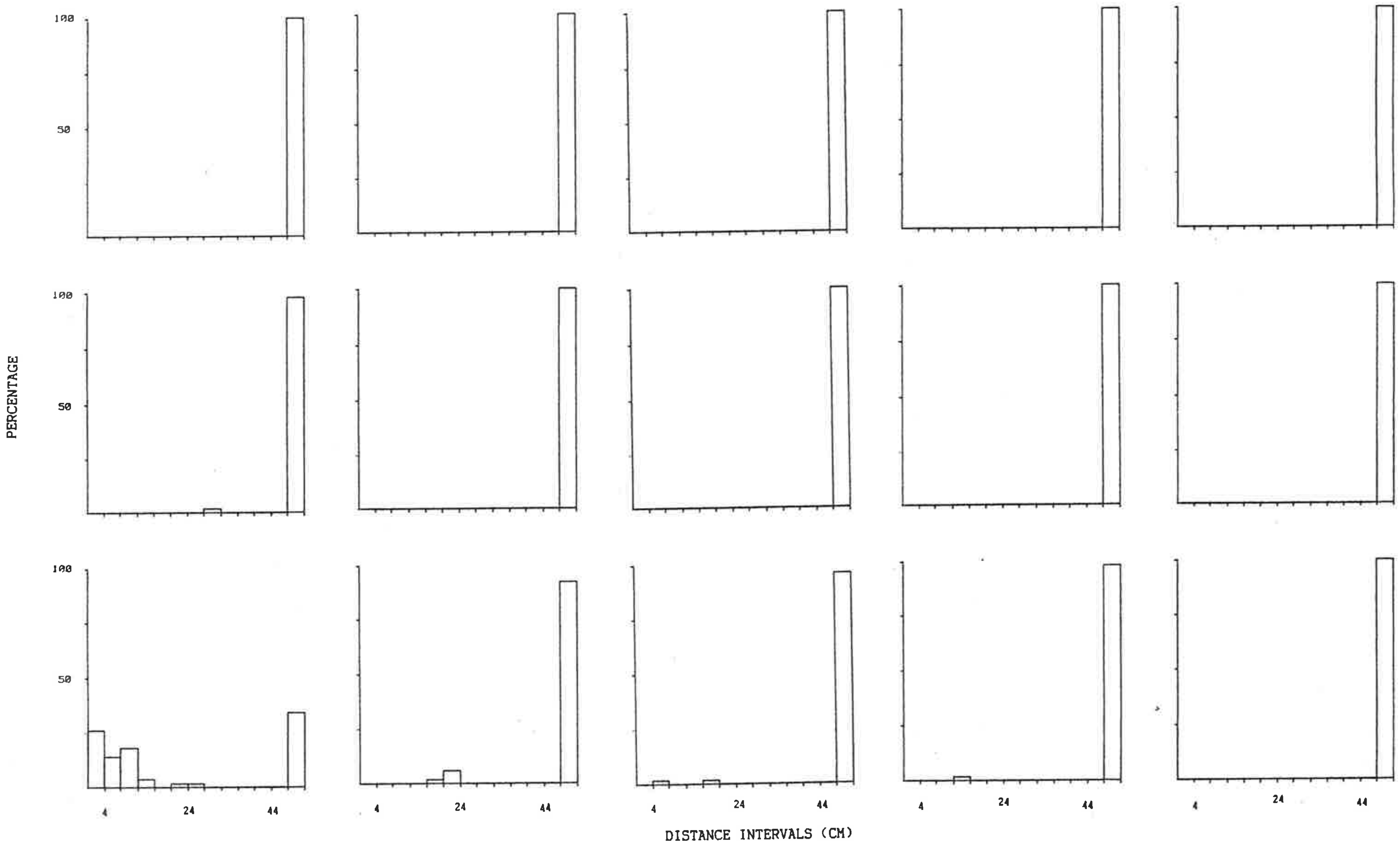


Figure 7.8 The movement of seeds of *Danthonia caespitosa* across three surfaces of different texture at five different wind speeds. Surface texture increases from fine to coarse down the page and wind speed increases from left to right across the page.

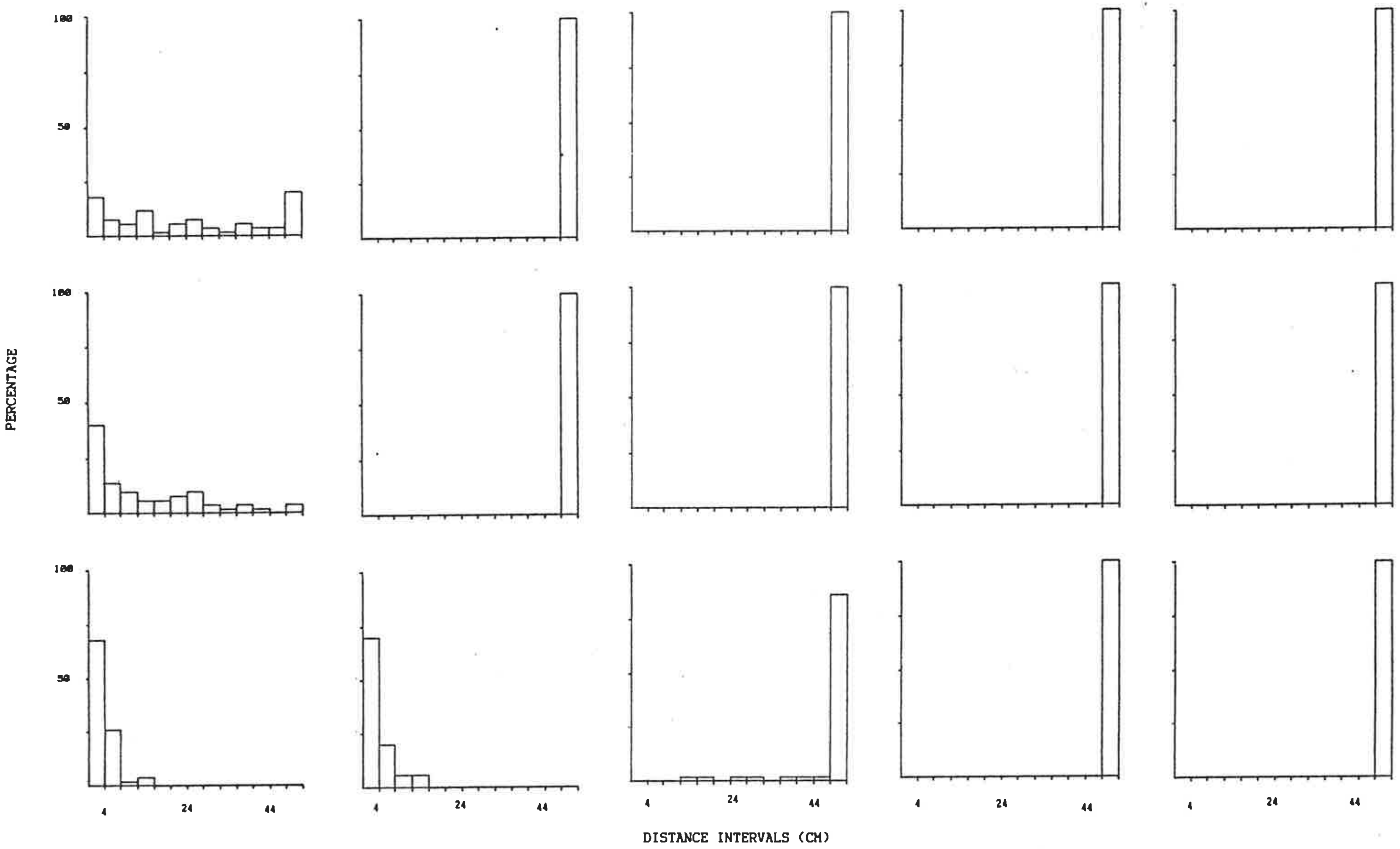
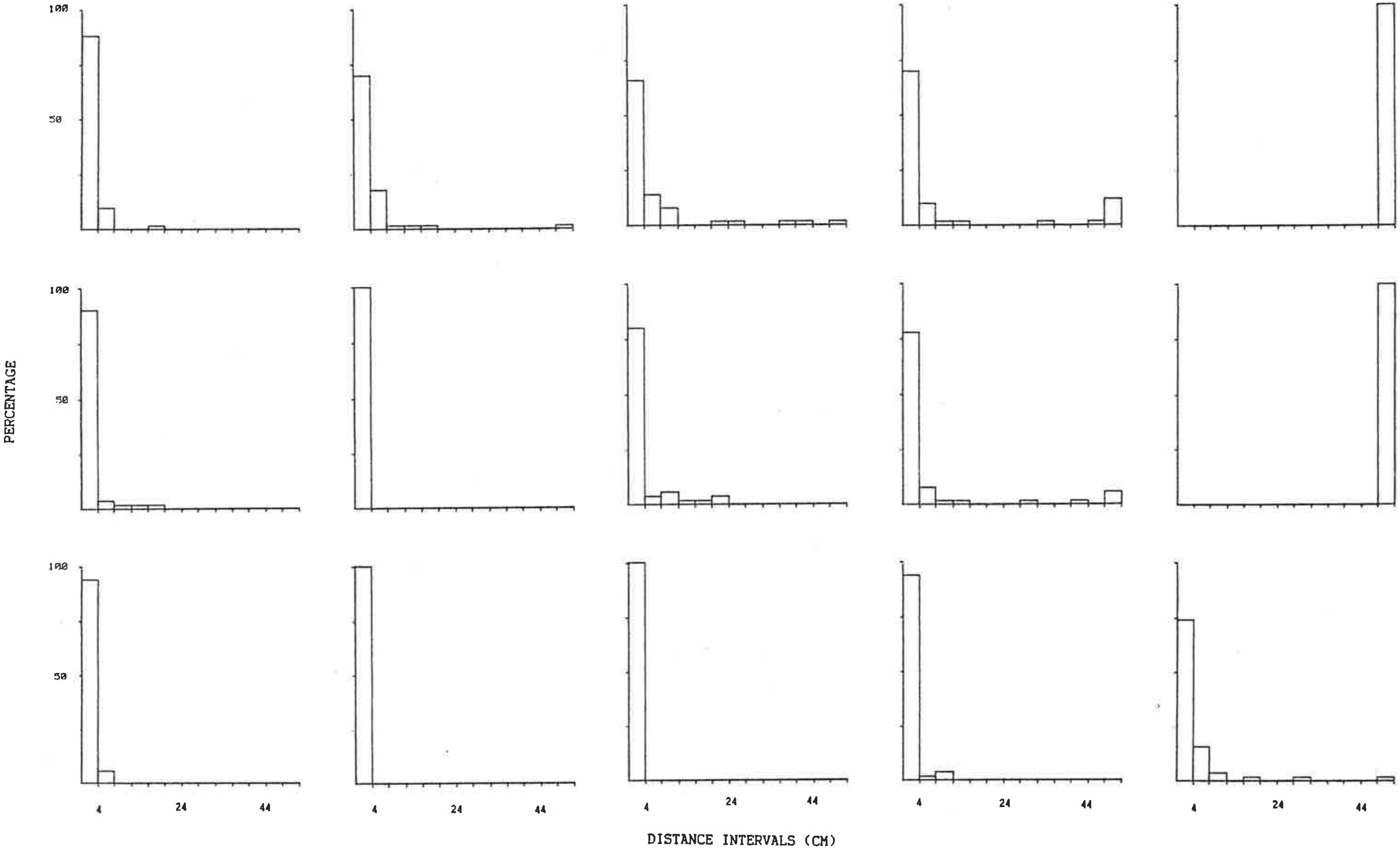


Figure 7.9 The movement of seeds of *Erodium cygnorum* across three surfaces of different texture at five different wind speeds. Surface texture increases from fine to coarse down the page and wind speed increases from left to right across the page.



<u>Figure 7.10</u> The movement of seeds of <u>Sclerolaena</u> <u>obliquicuspis</u> across three surfaces of different texture at five different wind speeds. Surface texture increases from fine to coarse down the page and wind speed increases from left to right across the page.

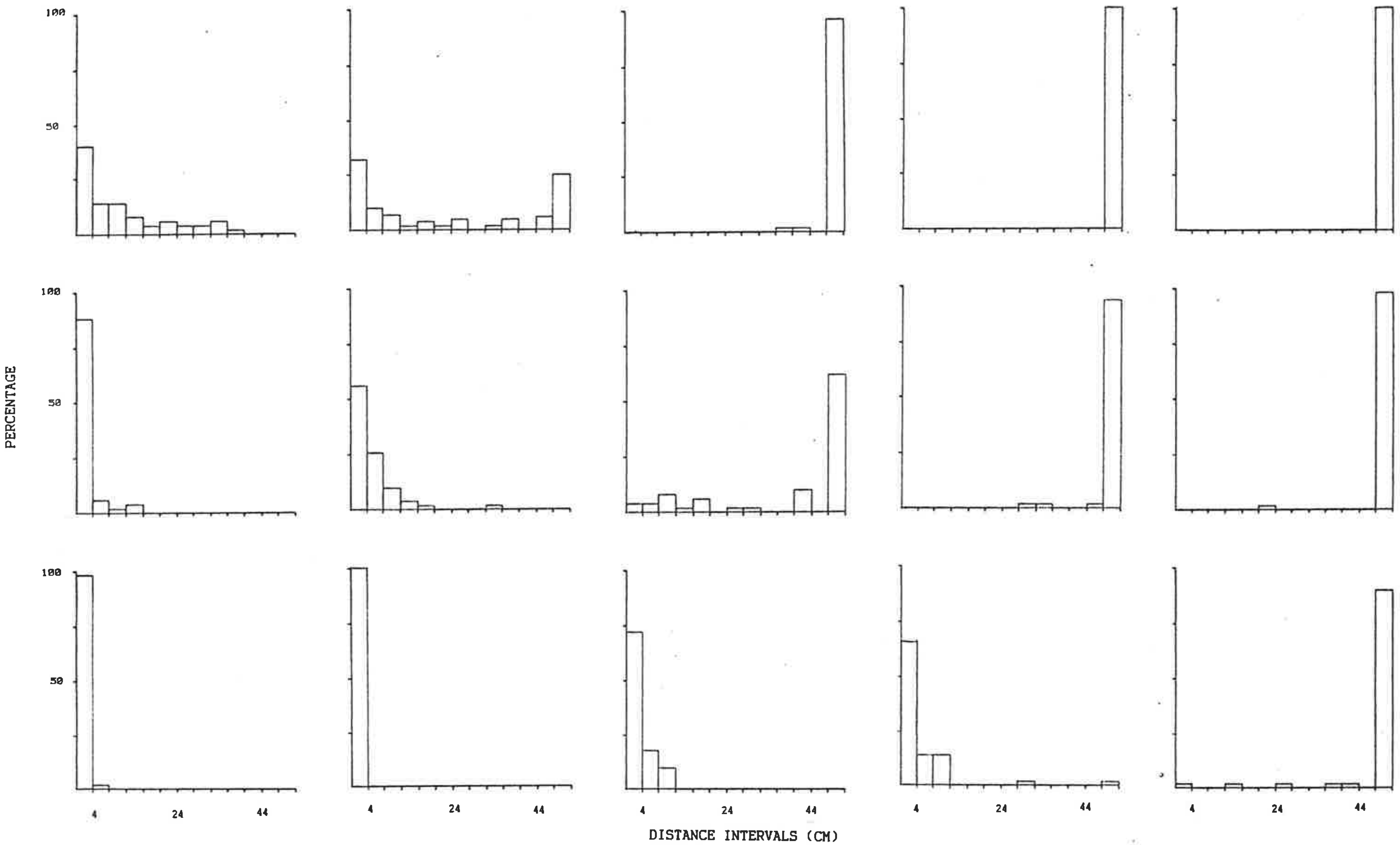


Figure 7.11 The movement of seeds of *Carthamus lanatus* (plumed) across three surfaces of different texture at five different wind speeds. Surface texture increases from fine to coarse down the page and wind speed increases from left to right across the page.

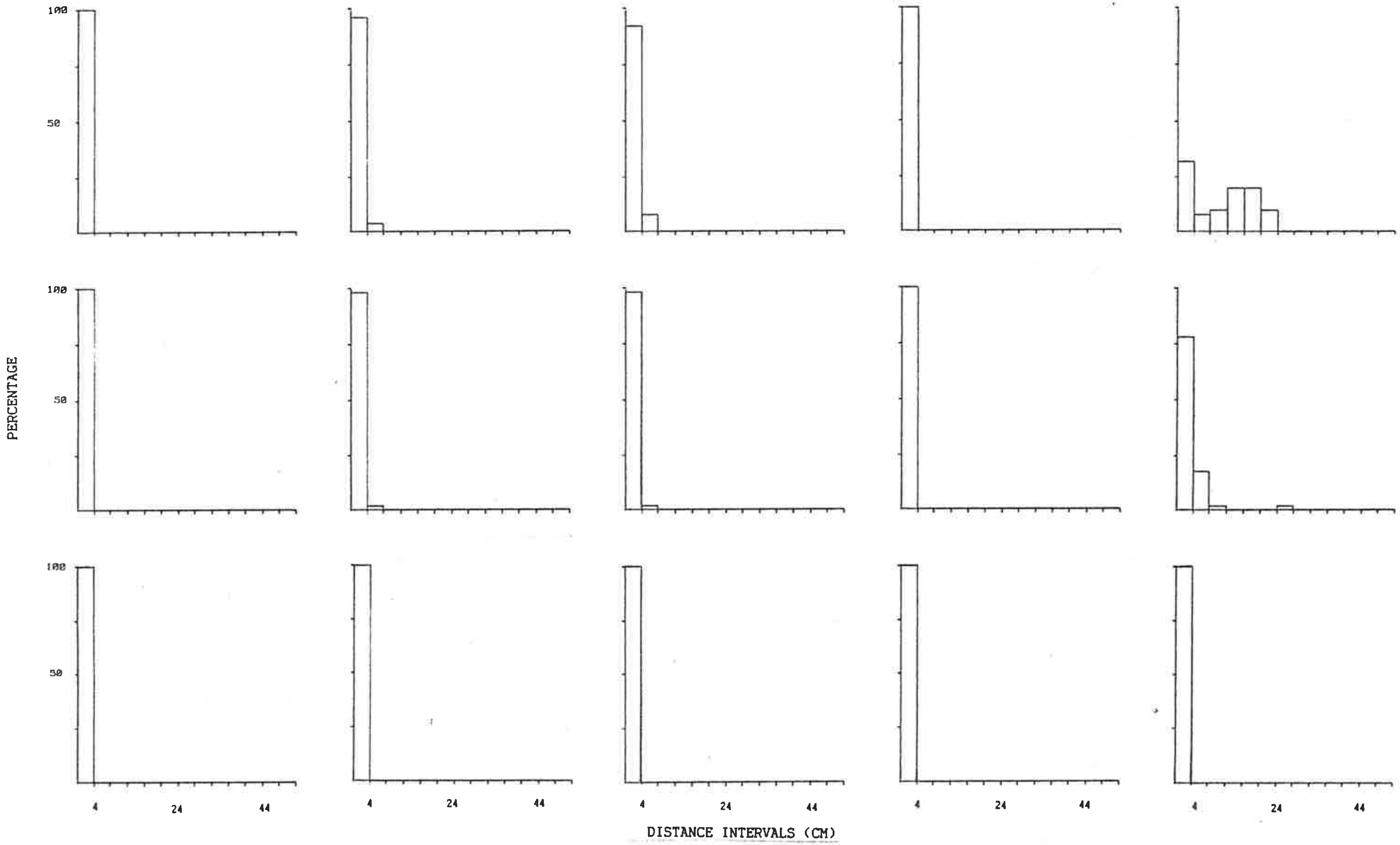


Figure 7.12 The movement of seeds of *Carthamus lanatus* (non-plumed) across three surfaces of different texture at five different wind speeds. Surface texture increases from fine to coarse down the page and wind speed increases from left to right across the page.

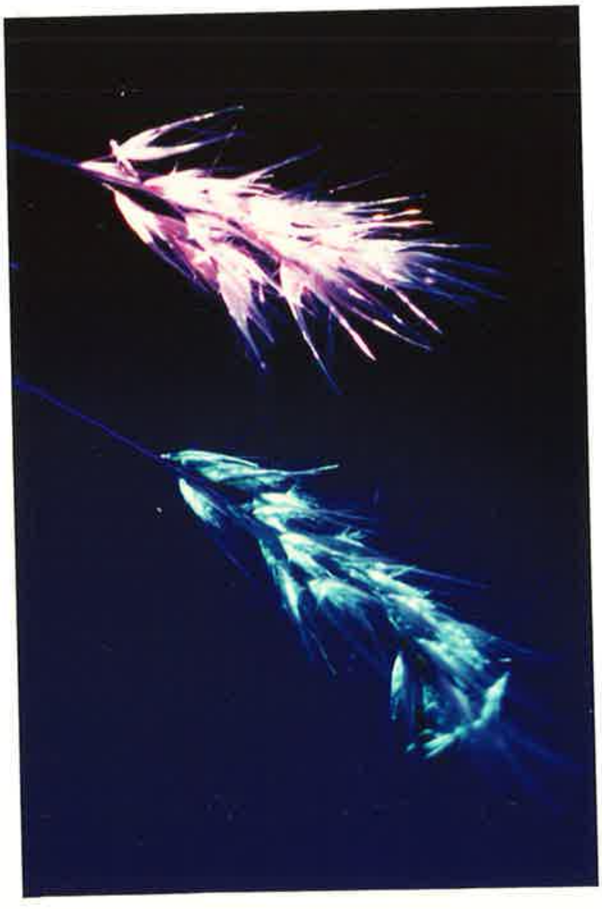
PLATE 3

(1) Inflorescences of *Danthonia caespitosa* with fluorescent dye applied, under natural light.

(2) The same inflorescence illuminated with UV light.

(3) An individual of *Danthonia caespitosa* tagged with orange fluorescent dye in the field.

(4) A fluorescently tagged dispersal unit of *Danthonia caespitosa* on the ground.



8. DISCUSSION AND CONCLUSIONS

8.1 Introduction

The aim of this study, described in detail in Chapter 1 of this thesis, was to investigate pattern in populations of annual plants in the Middleback area. The behaviour of annual plants in the Middleback area was in some aspects similar to those reported from other arid regions (Went,1948,1949; Beatley,1967,1974; Tevis,1958a,b; Mott,1972a; Loria & Noy-Meir,1980). There were however some aspects which had not previously been reported.

The studies described in this thesis can be broadly separated into two types; (1) investigations of the temporal patterns of species occurrence and abundance, (2) investigations of the spatial patterns exibited by the annual species during the periods of germination and growth. Initially it was proposed to investigate predominantly spatial patterns, however, as the study progressed it became evident that the factors that were influencing the temporal patterns were also influencing the spatial patterns. The results of studies on the spatial pattern of annual plants indicated that there were changes, in spatial pattern through time. To some extent these changes and hence the patterns themselves, were the result of the temporal influence on annual populations. For this reason the initial discussion centres around the factors that influence the appearance of annual plants and following on from this, is a consideration of how they may also influence spatial pattern.

8.2 Temporal patterns

The factors that lead to the spatial and temporal patterns of annual plants observed in this study can perhaps be best considered through the factors which affect annuals throughout their life cycle. The life cycle of an annual is essentially the same as that of a perennial plant that reproduces from seed. The main difference between the annual and perennial life cycle is the time taken for completion of the life cycle. In the case of annuals seed set usually preceeds the immediate death of the individual. The changes in temporal and spatial patterns of annual plants can be explained in terms of the relative importance of the different stages of the life cycle. There are stages in the life cycle of both annual and perennial plants which can be identified as being important to the development of spatial patterns.

A generalized life cycle of an annual plant is shown in Figure 8.1. The factors which influence the seasonal occurrence of annuals are those early in the life cycle, specifically those that affect germination. There are a number of studies which suggest that the floristic composition of the annual vegetation is determined at germination (Went,1948,1949). The subsequent factors such as competition and mortality during the growth phase appear to be less important. This is in direct contrast to perennial plants where competition, both interspecific and intraspecific, is a major factor influencing the floristic composition of the vegetation over long periods of time. In the case of annual plants, if the floristic composition is determined at germination then to a large extent the spatial pattern will also be determined at germination. If the pattern of annuals is largely determined at germination then the distribution of seed in the soil will also play an important role in the determination of spatial pattern.

The factors that influence germination can be divided into two groups. The first are environmental factors and the second are inherent seed characteristics, for example seed dormancy. This discussion is centered on the environmental influences as these are the factors that change from season to season and from one germination event to the next. The three environmental influences considered here as being of major importance are rainfall, temperature and microsite. These three factors can be considered as a set of filters. A seed must have its requirements satisfied at each filter before it has the potential to germinate. The filters themselves can be considered as differential filters, excluding some species but allowing other species to pass through for any given set of conditions.

Studies of the autecology of species have often concentrated upon the specific requirements of the species for germination, growth and flowering. The assumption is that by understanding the species requirements and responses then it allows a better understanding of the species behaviour in the field situation. This is undoubtably true but an aspect often not considered, especially in arid areas, is that the environmental conditions are highly variable. It is not often that "optimum" conditions for germination, growth and flowering occur. This is of particular importance when considering a complete annual flora rather than just individual species. The resultant annual vegetation may be the sum of the species responses to conditions that are not "optimal" for any individual species in the annual vegetation.

The primary requirement for the germination of annuals is available moisture, however, available moisture does not exert an "all" or "none" response for germination. Available moisture is the amount of moisture in the soil and it cannot exceed the field capacity of the soil. There is a great deal of evidence that the amount of available moisture influences the success of germination. Many species are highly susceptible to changes in the available moisture at germination. Moore (1946,1958) found that allowing soil moisture levels to drop to less than 60 % of field capacity before re-watering reduced the level of germination in Danthonia. McWilliams and Phillips (1971) also found that the germination of Danthonia and Astrebla, both arid zone species, was greatly reduced at osmotic potentials less than - 10.0 bars. Mott(1972) also found similar results for three arid zone species in Western Australia. Mott compared his results to two pasture species and concluded that desert ephemerals are poorly adapted to germination under moisture stress.

The consequence of a differential germination response of species to moisture stress is that if all other factors were unchanged, the available moisture alone has the potential to cause changes in the floristic composition of the annual vegetation. This may not play an important role in a climatic system which has predictable heavy rainfall events which raise the soil moisture to field capacity regularly from year to year. In a system where rainfall is erratic and there are numerous rainfalls which do not saturate the soil, floristic compostion may be determined partially by the intensity and duration of rainfall.

Throughout this thesis there has been a tendency to compare the later annual vegetation to that obtained in 1979 and 1980. There was considerable disappointment when the annual vegetation in subsequent years was less diverse and at much lower density. In reality the annual vegetation in those first two years of this study was exceptional. An annual vegetation of such diversity and density is an unusual event, caused by a progression of heavy rainfall events that saturated the soil and maintained high soil moisture levels for extended periods of time. In those two years it is unlikely that the differential effect of moisture stress was a major determinant of the floristic composition whereas it may have had a major effect on the later populations of annuals studied.

Another major factor, besides rainfall, that will influence the appearance and abundance of annual plants in a population, is the temperature both at the time of the initiating rainfall event and in the days immediately following the rainfall. The temperature can have a selective effect upon the species that germinate and the quantity of germination that occurs for each species. It is well recognised that different species have different temperature requirements for germination (Mayer & Poljakoff-Mayber, 1978). In his studies in Western Australia Mott (1972a) showed that summer and winter annuals possessed different temperature optima for germination, (the optimum germination temperature being that at which the highest percentage of seed of the species germinated). The percentage of seeds that germinate then declines either side of the optimum temperature. Mott(1972a) also showed that the shapes of the germination curves differed for summer and winter annuals. The winter germinating annual Helipterum had an optimum germination temperature of 15° C but still showed some germination at temperatures as high as 30° C. In contrast the summer annual Aristida showed optimum germination at 30° C but germination was still recorded at temperatures as low as 10° C. Obviously a summer rainfall event accompanied by high temperatures will cause considerable germination of Aristida and little of Helipterum. A winter rainfall would cause a reverse trend in the relative dominance of the two species.

In the Middleback region although distinct seasonal floras were not found there were species which showed trends in seasonal occurrance. Species such as Daucus glochidiatus and Brachycome lineariloba were mainly recorded during the cooler months and species such as Erodium cygnorum, Danthonia caespitosa and Stipa nitida showed a tendency towards greater germination in the warmer months. In general however, most species were recorded to some degree from late summer to winter.

When considering seasonal germination of annuals it is usually assumed that rainfall events in summer are followed by high temperatures and that rainfall events in winter are followed by low temperatures. This may not always be the case. The temperature data presented in Chapter 2 for Whyalla shows that the summer temperatures may vary considerable. A lower daily temperature at the time of the initiating rainfall event might be expected to produce a different germination pattern to a higher temperature. This would partially explain the differences in the floristic composition of the annual vegetation from year to year. Rainfall events may occur in the same month of different years but differences in daily temperature may cause germination of different species or different quantities of germination of the species.

The situation is further complicated by the nature of the rainfall itself. If a very heavy rainfall event occurs and is then followed a few days later by subsequent falls, different species may germinate depending upon the daily temperature. Under these conditions a highly diverse and extensive annual flora may develop. It is suggested that this is what occurred in 1979 and 1980 and gave rise to the very extensive annual vegetation in those two years.

The daily temperature at the time of the rainfall event can have a secondary influence through soil moisture. If a rainfall event occurs in summer when the temperatures are high then the soil surface may dry very rapidly. It was observed on a number of occasions after summer rainfall events that on the following day, if high temperatures occurred, the soil surface dried within a period of a few hours. The effect was to restrict the germination of many species which germinate on the soil surface.

It is possible to model the soil moisture (Noble, 1975) from temperature and rainfall data. The application of such models is appropriate to the prediction of the growth of plants but it is not possible to predict germination responses of individual species. The problem arises due to the scale of the models. In the case of the soil moisture model used in this study (Noble,1975) the smallest zone discriminated was the top 10 cm of the soil surface. For germination, the scale that will affect the seed will be much smaller, for seed buried in the soil it may be the top 1 - 2 cm of the soil surface and for seeds on the surface it may be only the top few millimetres. To date there appear to be no models that can accurately predict what occurs in such germination zones under field conditions.

8.3 Spatial Patterns

The results of the investigations of the spatial pattern of annual plants were more difficult to interpret. The initial study on the broad scale patterns of annuals indicated that the majority of annual species did not show any preference for particular perennial communities. The study indicated that the habitat factors which influence the distribution of the dominant perennial chenopods did not influence the distribution of the majority of the annual species.

The factors which influence the distribution of annual plants appear to be different to those that influence or control the distribution of the perennial vegetation communities in the study region. In many ecosystems the distribution of perennial species can be related to habitat features such as soil type and other edaphic factors. It has been suggested however, that in rangelands, the soil texture and low availability of moisture tends to influence the growth of plants more than does soil nutrients variation (Noy-Meir, 1974). The difference in behaviour of annuals and perennials is largely a consequence of their different life histories. Most plants can grow in a wide range of habitats (Kooper, 1927). The reason why many plants are not found over a wider range of habitats is usually due to the cumulative outcome of competitive interactions between species over many growing periods rather than the species inability to grow in that habitat. In the case of annuals there appears to be little mortality due to competitive stress. As previously mentioned the floristic composition and pattern in annual vegetation may be determined at the time of germination and competition may only have an indirect influence through seed production (Inouye et al.,1980). Annual distribution is more likely to be influenced by factors such as seed dispersal and the suitability of microhabitats for germination.

This is supported by a number of the results from this study. The dominant annual species all possess a common feature; the presence of a hygroscopic awn. The function of this morphological feature is assumed to be to bury the seed so that it germinates below the ground surface. In this manner the seed is actively locating a suitable microhabitat for germination. It is not relying upon the chance event of locating a suitable microhabitat for germination through dispersal. Those species which do not possess this feature in many cases dominate the southern sides of bushes (Chapter 6). This is a habitat where they can germinate on the surface or beneath litter where the rate of soil moisture loss is lower. The factor that influences the distribution of the species appears to be the occurrence of suitable sites for germination.

The comments on the relationship between annuals and perennials applies only in the context of the perennial communities considered in the study. There are numerous areas within the region which represent quite different habitats and which also may support annual species not recorded in this study. The two most obvious habitats to which this applies are the swamps that occur around many of the dams and the range of rocky hills in the northern part of Middleback Station. In these areas annual species can be found which are not found in any other habitats. These habitats were not investigated in this study. The habitats selected were those most commonly represented in the study area.

8.4 Change in spatial patterns of annuals

The discussion so far presented has concentrated upon the aspects which can cause changes in species abundance in time but has not considered how these factors may influence the changes in spatial pattern. The changes in spatial pattern require that another factor be considered, that is, the heterogeneity of the environment or soil surface. There is a tendency to think of the soil environment as being stable in the short term. Over a period of a year the soil environment may change considerably, especially if there are herbivores such as sheep present. The soil may also develop in response to the presence of different plant species. A fact not considered is that there may be fluctuations in the soil environment due to environmental factors.

The soil surface is highly heterogeneous when considered at the scale of a seed. The soil surface consists of a mosaic of microhabitats, small rises and depressions, cracks in the surface, litter on the surface, areas that are shaded and different surface textures. There is a great range of surface characteristics that are important to the germination of seeds. The important question is however whether these microhabitats are stable over time, and how important they are under different conditions. For example, a very heavy rainfall event followed by smaller subsequent rainfall events may keep the soil surface saturated for a period of time that allows the germination of many different species. Moisture is not a factor limiting germination under these conditions. If, however, the rainfall event was of a smaller magnitude then only some of the microhabitats are suitable for seeds to germinate. In areas where there is insufficient soil moisture germination does not occur.

The situation can be considered as a progression. Light falls of rain may present only a few microhabitats for germination. A heavier rainfall may open up further microhabitats for germination until the extreme condition is reached where virtually all microhabitats were available for germination. The spatial arrangement of these microhabitats will then determine the species spatial patterns under any set of rainfall conditions.

Many species actively create or locate suitable microhabitats. Examples of this are *Danthonia caespitosa* , *Stipa nitida* , *Erodium cygnorum*, *Plantago drummondii*, *Helipterum pygmaeum* and *Goodenia pusilliflora*. These species possess two quite different attributes both of which assist in their success. The first three species all possess a hygroscopic awn. When the awn becomes wet, either through direct moisture contact or from increased relative humidity, the awn begins to uncurl. As it dries it then re-curls and this has two effects. The first is to move the seed across the ground until it becomes lodged against an obstruction and the second is that if the sharp callus becomes wedged in a crack the winding and uncurling motion of the awn bores the seed into the soil surface. Following rainfall events when seeds of these species are on the ground the awns can be seen projecting from cracks in the surface with the seed buried up to 1 cm below the surface. In this way these species place their seed below the soil surface where they are probably better protected from predation, and when rainfall events occur they are less likely to suffer desiccation than species which are restricted to germinating on the soil surface. It is interesting to note also that these three species are the most dominant ephemerals in the study region, suggesting that they do have some feature which gives them an advantage over other species.

The other three species mentioned above *Plantago drummondii*, *Helipterum pygmaeum* and *Goodenia pusilliflora* all possess a different mechanism for locating a suitable habitat for germination. These species when wet release a mucilaginous substance which binds the seed closely to the soil surface. It has been well demonstrated that if the seed can increase its surface area contact with the soil surface then this increases its chance of germination.

The discussion so far has considered the availability of "safe sites" for germination and establishment and the appropriate conditions. Another situation which can also exist is if "safe sites" are available but there is no seed to utilise the sites. An assumption which is often made in ecological studies (often without being mentioned) is that there is an even distribution of seed in the soil. This assumption is sometimes made because of the difficulties involved in determining the distribution of seed in the soil. Studies of the seed bank are often conducted to determine its floristic composition but not to measure any spatial heterogeneity in seed distribution. In this study rather than determine the distribution of seed in the soil the dispersal patterns of some species were determined.

8.5 Dispersal of annuals

The dispersal patterns from the selected annual species were different to those expected. It was found that dispersal was very restricted for all the species investigated. The restriction in the movement of the dispersal units could largely be attributed to the height of release of the dispersal units from the parent plants. Species like Helipterum pygmaeum and Vittadinia cuneata possess a pappus on the achene, a morphology which is usually assummed to indicate wind dispersal (Ridley,1930; Pijl,1969). The annual plants in the study region are generally small and the wind does not carry the dispersal units far before they reach the ground and so the flight phase of dispersal is small. The restricted dispersal of the species suggests that their survival is not dependent upon their ability to escape to new habitats.

The most efficient dispersal method of the annuals studied was for those species whose dispersal units exhibited a rolling motion across the ground surface. Examples of this were Danthonia caespitosa and Erodium cygnorum. The morphology of these two species does not appear to be adapted for dispersal. It would appear that there may be too great an emphasis placed upon describing the mode of dispersal (Ridley,1930; Pijl,1969) simply on the basis of the morphology of the dispersal unit. In the case of the annual plants investigated in this study it was not possible to predict the efficiency of dispersal based upon morphology.

Not only does the dispersal distance vary from species to species but also the directions the seeds move may differ. In a mixed population of annual plants the different species flower and fruit at different times of the year. The species release their seed under different wind conditions and so the dispersal units may move different distances and directions. Dispersal patterns from a single species may also vary from one year to the next.

If there is a non-homogeneous distribution of seed on the soil surface as the result of dispersal then it may be expected that the distribution of seed in the soil may also be far from uniform. The distribution of seed in the soil is the result of more than one factor. The effects of dispersal events from previous populations and the effect of seed predators will also influence the distribution of seed in the seed store. It would be expected that the seed store in the soil would be patterned and this to some degree will influence the distribution of plants in the annual vegetation, although to exactly what degree is difficult to determine.

One aspect of dispersal which had not previously been considered was the influence of the population of plants upon dispersal distance. In the case of the annual plants in this study, where dispersal occurred predominantly on the ground surface, the density of the population influenced the distance seeds moved. In a dense population the individual plants and litter on the ground act as a barrier to seed movement. In a population of lower density the seeds can move greater distances before being trapped by an obstruction. The same could be applied to the annual vegetation in different years. In years when there is a dense annual population dispersal may be restricted when compared to those years when a less dense annual population is present.

8.6 Effect of grazing on annuals

The discussion in the previous sections has concentrated on the effects of variable climatic conditions upon the distribution and abundance of annual plants in both space and time. Another aspect which should be mentioned in relation to some of the sudies is the effect of herbivores. In the studies described in this thesis herbivores such as sheep were excluded from areas where they previously had grazed. The exclusion from grazing may have influenced the pattern of annual plants. Williams (1969) reported a range of responses of annual plants to grazing. In that study he found that the following species were encouraged by grazing: *Tripogon loliiformis*, *Crassula colorata*, *Calotis hispidula*, *Carthamus lanatus*, *Actinoble uliginosum*, *Spergularia rubra*, *Goodenia pusilliflora*, *Isoetopsis graminifolia*, *Helipterum pygmaeum*, *Daucus glochidiatus* and *Brachycome lineariloba*. Species which were favoured by protection from grazing were *Bulbine bulbosa*, *Vittadinia cuneata*, *Convolvulus erebescens*, *Sonchus oleraceus*, *Whalenbergia gracilentia*, *Hypochoeris glabra* and *Erodium cicutarium*. Species with a response intermediate between these two groups were *Oxalis corniculata* and *Medicago minima*.

All of the above ephemeral species occur in the Middleback area and many were recorded at the Overland paddock study site (Chapter 5). Some of the changes in the spatial pattern and abundance of the species described in that chapter could be the result of protection from grazing; superimposed on the fluctuations caused by climatic variability there may be changes due to a differential response to an absence of grazing. The influence of this factor is difficult to judge due to the magnitude of natural variation from year to year. A comprehensive study over an extended period of time would be required to determine the extent of the grazing effect upon annual vegetation. It is well recognised that sheep and kangaroos graze annuals but there have been few studies on the effect upon opportunistic populations of plants like annuals.

8.7 Implications for the pastoral industry

Studies on the Riverine Plain of New South Wales on *Atriplex vesicaria* - *Danthonia caespitosa* communities have shown that if the community is extensivley grazed then the *A.vesicara* component of the community is removed. Once this has occurred then a *D.caespitosa* disclimax community may be obtained. The disclimax community is considered more productive for sheep grazing and so the elimination of *A.vesicara* from the pasture has become an accepted management practice in that area. The results presented in this thesis suggest that this would be an unacceptable management practice in the Middleback region.

The herbaceous species described in this study, including *Danthonia caespitosa*, rely upon rainfall for their survival and when heavy rainfall events do not occur the herbaceous community declines very rapidly. Through the years of 1981, 1982 and 1983 there would have been insufficient herbaceous growth to sustain a grazing flock. In the Middleback region if the perennial bush component of the vegetation is removed a disclimax grassland is not achieved. Past experience (A.D. &

D.A. Nicolson, pers comm.) in the region has shown that if overgrazing sufficient to remove the perennial component occurs then there may be severe degradation of the soil through wind erosion. When the area is then released from grazing it takes a long period for the area to become sufficiently vegetated to be productive for grazing. Often the result is that the area may become dominated by numerous weedy species which are less palatable. There are good examples of this in the north of Middleback Station. The area around an old well, Wizzo Well, was severely overgrazed but now has not been grazed for over 50 years. In good years this area has an extensive ephemeral vegetation but in average and below average years there is very little available forage.

8.8 Conclusions

The spatial patterns or more specifically the changes in spatial pattern over time which were observed in this study may be closely related to the temporal variability in the climatic factors, especially rainfall and temperature. Harper et al. (1965) used the term "safe site" to describe the specific conditions of the soil surface which permit seeds to escape all the hazards of the pre-germination phase and to overcome dormancy.

When considering germination the scale of heterogeneity in the environment that will influence germination will be at the scale of the size of the seed. Differences in the size, shape and dormancy requirements of seeds when considered relative to the heterogeneity of the surface environment would be sufficient to cause differences in germination of seeds. The different species of seeds will all require a different "safe site".

The availability of "safe sites" for germination and establishment must be considered in relation to variation in the climatic conditions. A very heavy rainfall event that saturates the soil surface may cause the germination of many species because there are a large number of "safe sites" available for germination of those species. A smaller rainfall event may only make available "safe sites" for certain species. There may be an interaction between the amount of rainfall and the surface characteristics to determine the floristic composition of the germinating flora.

It is suggested that this is a possible cause of the changes that occur in spatial patterns of annual plants. In Chapter 5 it was suggested that changes in association from one reading to the next may be the result of transient factors. It can be seen from the preceding discussion that there may be a very complex interaction between, (a) the conditions required for germination of a species, (b) the amount of rainfall, (c) the temperature at the time of the rainfall event and (d) the availability of "safe sites" for germination.

The changes in pattern in this study are probably the result of different conditions at the time of germination, opening different microsites suitable for the germination of different species. If the study was extended for a period of decades then it would probably be found that the spatial patterns are stable and are repeated at various intervals when similar climatic conditions occur.

Throughout this thesis there has been a deliberate avoidance of trying to associate patterns in the annual vegetation with "stable" habitat factors such as soil nutrients, soil texture and microtopographical features, because of the instability of pattern. This instability of pattern has been observed in previous studies (Fatchen,1975) but has received little attention. In the case of short lived plants like desert annuals in an unpredictable environment, the pattern of the vegetation and the floristic compostion is the result of a set of conditions which may not be repeated for many generations.

It would appear from the results obtained that great care should be taken when surveying arid annual plant distribution. Unlike perennial plants the pattern observed may be only a short term pattern, the consequence of one years climatic conditions. It may require surveys over extended periods of time, much longer than this study, to determine if there are identifiable communities of annual plants which are related to habitat factors in the same manner as many perennial communities. It is even difficult to compare annual vegetation in different regions in the short term.

There are major implications for vegetation analysis as a result of the studies on annual pattern described in this thesis. The changes in patterns of annual plants over time have not been considered in studies of community pattern. Studies of pattern usually represent a one-off, that is they represent a picture of what is present and the spatial pattern at a single point in time. Often on the basis of these studies conclusions are made on the factors that are controlling the distribution of the plants. The most frequent factors implicated are edaphic factors, such as differences in soil type, soil nutrients or topographic factors such as slope and aspect. In the case of perennial plants these assumptions may be correct. The situation for annuals however may be quite different.

It would appear that any conclusions on the distribution of annuals, based on one observation only, could be questioned. It is possible that a different pattern of annual plants is obtained each year. As was discussed in the previous sections the distribution of annuals may be dependant upon transient factors which are difficult to identify in the mature population. This interpretation should not under any circumstances be construed to suggest that annuals do not have habitat preferences and are not influenced by edaphic and topographic factors. The suggestion is that if generalisations concerning an annual pattern are made on the basis of one observation only then they may be incorrect. Under different conditions the population may show a quite different pattern. A similar observation was made by Fatchen (1975) on the distribution of ephemerals in arid South Australia in response to grazing. He found that pattern changed over time. Other studies however (Barker,1972) make no reference to the possibility of non stable patterns.

The problem of attempting to identify the causes of pattern in a population is complex. The problem was well stated by Harper (1977) who suggested that:

> "The causal events that determine whether a seed forms a seedling or not are usually intraceable when the plant has developed and the real causes of distribution and abundance will often be missed when mature vegetation is studied."

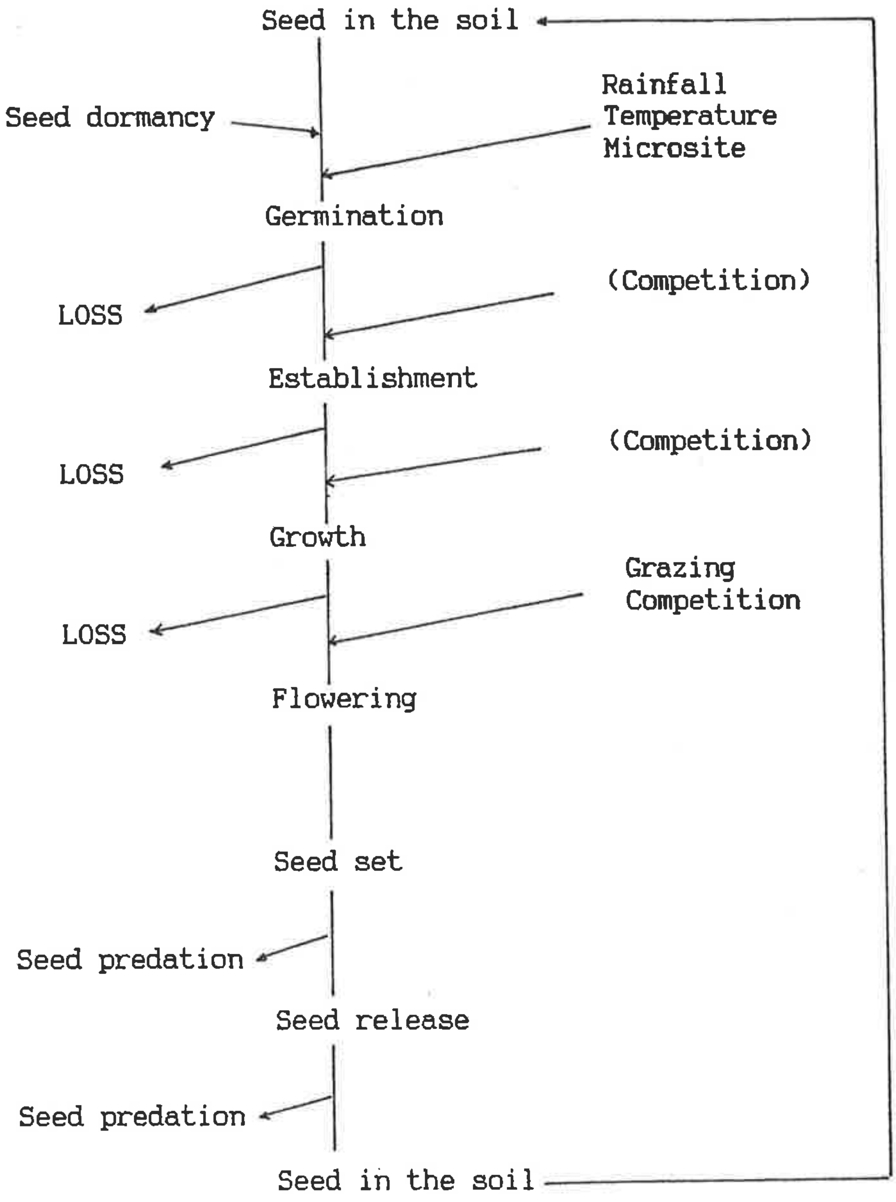


Figure 8.1 Schematic representation of the generalized life cycle of an annual plant. Influences enclosed in parentheses are considered less important.

APPENDIX I

MIDDLEBACK EPHEMERAL FLORA

Introduction

This section is designed as an introduction to selected annual and ephemeral species of the Middleback region for the reader not familiar with the flora. A list of all species of the study area (annual and perennial) refered to in this thesis is also provided. A brief description of some of the species most often refered to in this thesis is also given.

Danthonia caespitosa

This species is highly variable and extends over a considerable range in south-eastern Australia, (Hodgkinson & Quinn, 1976,1978). In most instances it is considered as a perennial species, (Williams,1970; Williams & Roe,1975). In the Middleback region it may behave as an annual or an ephemeral depending upon the prevailing conditions. It is described by Black (1947) as 20 - 90 cm high, usually with 10 - 30 spiklets per panicle. At Middleback station the annual form may be as small as 5 cm high with only 5 - 10 spiklets. Under more favourable conditions the plants may grow much larger and flower profusely (see plate 1). There is considerable literature on D.caespitosa particularly from the Riverine plain of New South Wales where it is a valuable fodder plant, (Williams,1955,1956,1961,1968,1970; Williams & Roe,1975; Hodgkinson & Quinn,1976,1978).

Stipa nitida

Stipa nitida is an erect perennial with stiff glabrous leaf blades. The panicle is dense and 12 - 30 cm long, (Black,1947). As with Danthonia caespitosa this species may behave as an annual with small individuals up to 10 cm high with a single panicle. Osborn et al (1931) found that this species usually germinated after late summer rains, grew through autumn and winter, flowered in spring and set seed in summer. Wood (1936) concluded that it germinated best after early winter rains. Crisp (1975) found that S.nitida germinated from January to April and Noble and Crisp (1979) concluded from the long term Koonamore records that germination usually occured in autumn to winter and the plants had a life span of nine months. Only 9% survived to a second year.

Erodium cygnorum

Erodium cygnorum is one of the common annual species in the Middleback region. It can germinate throughout much of the year but the most prolific germination occurs after late summer and autumn rains,(Biddiscome et al,1954). In the Middleback region it most often occurs as a small rosette of leaves, and produces 2 - 3 flowers. In favoured sites it may spread across the ground and flower profusely. Biddiscome et al (1954) report that it can produce an almost exponential increase in green forage between the months of May and September. In some areas it is regarded as a valuable fodder plant, (Beadle,1948). This species is variable in its flowering time. Onset of drought conditions appears to initiate flowering even though individuals may be very small with only two or three leaves.

Sclerolaena obliquicuspis

This species is a short lived perennial which may behave as an annual under certain climatic conditions. The size of the species is variable depending upon the prevailing conditions. It usually grows 10 - 20 cm high but in favoured habitats such as beneath penennial bushes it may produce long straggly branches that climb through the perennials. This species is a member of the Chenopodiaceae, has small succulent leaves and produces a spiny fruiting perianth in the axis of the leaves. Although the leaves are succulent the spines tend to discourage grazing. The fruiting perianth remains attached to the dead skeleton of the plant and is not easily dislodged.

Goodenia pusiliflora

A small prostrate annual species with a rosette of leaves. The flower stalks are procumbent up to 10 cm long terminating in a small yellow flower. The dispersal unit of this species consists of the seed surrounded by a small stiff wing. When the wing becomes wet it releases a mucilagenous substance which causes the dispersal unit to adhere to the ground surface.

Helipterum pygmaeum

Helipterum pygmaeum is a small annual species usually less than 10 cm high. It is a member of the Asteraceae and produces a considerable

ADDITIONS TO SPECIES LIST

AIZOACEAE

Tetragonia eremaea Ostenf.

CHENOPODIACEAE

Chenopodium cristatum (F.Muell.) F. Muell.
Maireana turbinata Paul G. Wilson
Sclerochlamys brachyptera F. Muell.

CONVOLVULACEAE

Convolvulus erubescens Sims

GRAMINEAE

Tripogon loliiformis (F.Muell.) C.E. Hubb.

LEGUMINOSEAE

Acacia papyrocarpa Benth.
Cassia nemophila Cunn. ex J. Vogel

MYOPORACEAE

Eremophila scoparia (R.Br.) F. Muell.
Myoporum platycarpum R.Br.

POLYGONACEAE

Emex australis Steinh.

SANTALACEAE

Exocarpos aphyllus R.Br.
Santalum acuminatum (R.Br.) A.DC.

SAPINDACEAE

Heterodendrum oleaefolium Desf.

SOLANACEAE

Lycium australe F. Muell.

number of large achenes with a large pappus. The achene is covered by long hairs which when wet release a mucilaginous substance which causes the achene to adhere strongly to the ground.

LIST OF SPECIES OF THE MIDDLEBACK FLORA REFERRED TO IN THIS THESIS

ASTERACEAE

Actinobole uliginosum (A.Gray) H.Eichler

Brachycome lineariloba (DC) Druce

Calotis hispidula (F.Muell) F.Muell.

*Carthamus lanatus L.

Gnephosis burkittii Benth. = Angianthus burkittii (Benth.) Black

Helipterum floribundum DC.

Helipterum pygmaeum (DC) Benth.

*Hypochoeris glabra L.

Isoetopsis graminifolia Turcz.

Ixiochlamys nana (Ewart & Jean White) Grau. = Podocoma nana Ewart & Jean White

Senecio quadridentatus Labill.

*Sonchus oleraceus L.

Vittadinia cuneata DC.

AIZOACEAE

Galena pubescens (Ecklon & Zeyher) Druce

Mesembryanthemem crystallinum L. = Gasoul crystallinum (L.) Rothm.

Mesembryanthemem nodiflorum L. = Gasoul nodiflorum (L.) Rothm.

AMARANTHACEAE

Ptilotus obovatus (Gaudich.) F.Muell.

BORAGINACEAE

Echium plantagineum L. = Echium lycopsis L.

Omphalolappula concava (F.Muell.) Brand

BRASSICACEAE

Allyssum linifolium Stephan ex Willd.

*Carrictera annua (L.) DC. = Vella annua L.

Geococcus pusillus J.L.Drumm. ex Harvey

*Sisymbrium erysimoides Desf.

*Sisymbrium irio L.

CAMPANULACEAE

Whalenbergia gracilis (Forster f.) Schrad.

CARYOPHYLLACEAE

*Herniaria hirsuta L.

*Spergularia rubra (L.) J.S. & C.Presl.

Stellaria multiflora Hook

CASUARINACEAE

Casuarina cristata Miq.

CHENOPODIACEAE

Atriplex spongiosa F.Muell.

Atriplex stipitata Benth.

Atriplex vesicaria Heward ex Benth.

Dissocarpus biflorus F.Muell.

Dissocarpus paradoxus (R.Br.) F.Muell. ex Ulbr.

Enchylaena tomentosa R.Br.

Maireana sclerolaenoides (F.Muell) Paul G. Wilson

Maireana excavata (J.Black) Paul G. Wilson

Maireana pyramidata (Benth.) Paul G. Wilson

Maireana sedifolia (F.Muell.)Paul G. Wilson

Malacocera tricornis (Benth.) R.Anderson

Rhagodia spinescens R.Br.

Rhagodia ulicina (Gand.) Paul G. Wilson

Salsola kali L.

Sclerolaena obliquicuspis (R.Anderson) Ulbr.

Sclerolaena patenticuspis (R.Anderson) Ulbr.

CRASSULACEAE

Crassula colorata (Nees) Ostenf.

Crassula sieberana (Schultes & Schultes f.) Druce

EUPHORBIACEAE

Euphorbia drummondii Boiss.

Euphorbia tannensis Sprengel ssp. eremophila (Cunn.) Hassall var. eremophila = Euphorbia eremophila Cunn. ex Hook.

GERANIACEAE

*Erodium cicutarium (L.)L Her. ex Aiton

Erodium cygnorum Nees ssp. glandulosum Carolin

GOODENIACEAE

Goodenia pusilliflora F.Muell.

GRAMINEAE

Aristida contorta F.Muell.

*Avena barbata Pott. ex Link

Danthonia caespitosa Gaudich.

Eragrostis dielsii Pilger.

*Hordeum leporinum Link

*Lamarckia aurea L.

Lophochloa pumila (L.) N. Hylander

*Schismus barbatus (L.) Thell.

Stipa nitida Summerh. & C.E. Hubb.

Triraphis mollis R.Br.

LEGUMINOSEAE

*Medicago minima (L.) Bartal. var. minima

*Medicago polymorpha L. var. polymorpha

Swainsona oliveri F.Muell.

Lotus cruentus Court

LILIACEAE

Bulbine semibarbata (R.Br.) Haw.

Thysanotus baueri R.Br.

MALVACEAE

Sida intricata F.Muell.

ONAGRACEAE

*Oenothera stricta Ledeb. ex Link

OXALIDACEAE

Oxalis corniculata L. ssp. corniculata

PLANTAGINACEAE

Plantago drummondii Decne.

PORTULACACEAE

Calandrinia eremaea Ewart

UMBELLIFERAE

Daucus glochidiatus (Labill.) Kischer, C.Meyer & Ave Lall.

ZYGOPHYLLACEAE

Zygophyllum aurantiacum (Lindley) F.Muell.

Zygophyllum crenatum F.Muell.

Zygophyllum ovatum Ewart & Jean White

APPENDIX 2

This appendix contains the Analysis of Variance tables for the density data for the study of broad scale pattern (Chapter3). The appendix is divided into 3 three sections. 1. Untransformed data 2. Logarithmic transformation 3. Square root transformation

1. Untransformed data

Daucus glochidiatus

	df	Sum Sq	MS	F
Between grp	5	796.95	159.39	
Within grp	54	2511.9	46.5167	3.42651
Total	59	3308.85		

Crassula colorata

	df	Sum Sq	MS	F
Between grp	5	1934.88	386.977	
Within grp	54	10767.7	199.402	1.94069
Total	59	12702.6		

Brachycome leariloba

	df	Sum Sq	MS	F
Between grp	5	7.68333	1.53667	
Within grp	54	81.3	1.50556	1.02066
Total	59	88.9833		

Crassula sieberana

	df	Sum Sq	MS	F
Between grp	5	1760.93	352.187	
Within grp	54	11559.8	214.07	1.64519
Total	59	13320.7		

Plantago drummondii

	df	Sum Sq	MS	F
Between grp	5	3800.55	760.11	
Within grp	54	21049.1	389.798	1.95001
Total	59	24849.7		

Lopochloa pumila

	df	Sum Sq	MS	F
Between grp	5	1938.55	387.71	
Within grp	54	25194.3	466.561	.830995
Total	59	27132.9		

Senecio quadridentatus

	df	Sum Sq	MS	F
Between grp	5	8.08333	1.61667	
Within grp	54	58.5	1.08333	1.49231
Total	59	66.5833		

Calandrinia eremaea

	df	Sum Sq	MS	F
Between grp	5	.15	.03	
Within grp	54	2.7	.05	.6
Total	59	2.85		

Tetragonia eremaea

	df	Sum Sq	MS	F
Between grp	5	80.6	16.12	
Within grp	54	748.8	13.8667	1.1625
Total	59	829.4		

Actinobole uliginosum

	df	Sum Sq	MS	F
Between grp	5	.733333	.146667	
Within grp	54	9	.166667	.88
Total	59	9.73333		

Schismus barbatus

	df	Sum Sq	MS	F
Between grp	5	16526.7	3305.34	
Within grp	54	126016	2333.62	1.4164
Total	59	142542		

Sonchus oleraceus

	df	Sum Sq	MS	F
Between grp	5	5.73333	1.14667	
Within grp	54	73	1.35185	.848219
Total	59	78.7333		

Erodium cygnorum

	df	Sum Sq	MS	F
Between grp	5	2.73333	.546667	
Within grp	54	16	.296296	1.845
Total	59	18.7333		

Sclerolaena obliquicuspis

	df	Sum Sq	MS	F
Between grp	5	14.1333	2.82667	
Within grp	54	78.6	1.45556	1.94199
Total	59	92.7333		

Vittadinia cuneata

	df	Sum Sq	MS	F
Between grp	5	77.1333	15.4267	
Within grp	54	484.6	8.97407	1.71903
Total	59	561.733		

Atriplex spongiosa

	df	Sum Sq	MS	F
Between grp	5	1.08333	.216667	
Within grp	54	9.9	.183333	1.18182
Total	59	10.9833		

Emex australis

	df	Sum Sq	MS	F
Between grp	5	167.333	33.4667	
Within grp	54	989.4	18.3222	1.82656
Total	59	1156.73		

Calotis hispidula

	df	Sum Sq	MS	F
Between grp	5	2.15	.43	
Within grp	54	25.1	.464815	.9251
Total	59	27.25		

Danthonia caespitosa

	df	Sum Sq	MS	F
Between grp	5	15.95	3.19	
Within grp	54	75.3	1.39444	2.28765
Total	59	91.25		

Goodenia pusilliflora

	df	Sum Sq	MS	F
Between grp	5	12.8833	2.57667	
Within grp	54	63.7	1.17963	2.1843
Total	59	76.5833		

Hernaria hirsuta

	df	Sum Sq	MS	F
Between grp	5	16.0833	3.21667	
Within grp	54	104.1	1.92778	1.66859
Total	59	120.183		

Stipa nitida

	df	Sum Sq	MS	F
Between grp	5	2.73333	.546667	
Within grp	54	37.6	.696296	.785107
Total	59	40.3333		

Gnephosis burkitii

	df	Sum Sq	MS	F
Between grp	5	.35	.07	
Within grp	54	2.5	.0462963	1.512
Total	59	2.85		

Oxalis corniculata

	df	Sum Sq	MS	F
Between grp	5	.35	.07	
Within grp	54	2.5	.0462963	1.512
Total	59	2.85		

Helipterum pygmaeum

	df	Sum Sq	MS	F
Between grp	5	2	.4	
Within grp	54	7.4	.137037	2.91892
Total	59	9.4		

2. LOG TRANSFORM

Daucus glochidiatus

	df	Sum Sq	MS	F
Between grp	5	17.8796	3.57592	
Within grp	54	59.126	1.09493	3.2659
Total	59	77.0057		

Crassula colorata

	df	Sum Sq	MS	F
Between grp	5	16.1139	3.22279	
Within grp	54	98.4762	1.82363	1.76723
Total	59	114.59		

Brachycome lineariloba

	df	Sum Sq	MS	F
Between grp	5	1.05176	.210352	
Within grp	54	9.46877	.175348	1.19963
Total	59	10.5205		

Crassula sieberana

	df	Sum Sq	MS	F
Between grp	5	14.4433	2.88865	
Within grp	54	69.9411	1.29521	2.23027
Total	59	84.3844		

Plantago drummondii

	df	Sum Sq	MS	F
Between grp	5	36.4525	7.2905	
Within grp	54	58.383	1.08117	6.74318
Total	59	94.8355		

Lopochloa pumila

	df	Sum Sq	MS	F
Between grp	5	7.06645	1.41329	
Within grp	54	91.2241	1.68933	.836596
Total	59	98.2905		

Senecio quadridentatus

	df	Sum Sq	MS	F
Between grp	5	1.70938	.341876	
Within grp	54	11.3418	.210033	1.62772
Total	59	13.0512		

Calandrinia eremea

	df	Sum Sq	MS	F
Between grp	5	.072068	.0144136	
Within grp	54	1.29722	.0240227	.6
Total	59	1.36929		

Tetragonia eremaea

	df	Sum Sq	MS	F
Between grp	5	3.73371	.746742	
Within grp	54	36.5155	.676213	1.1043
Total	59	40.2492		

Actinobole uliginosum

	df	Sum Sq	MS	F
Between grp	5	.168159	.0336317	
Within grp	54	2.16204	.0400378	.84
Total	59	2.3302		

Schismus barbatus

	df	Sum Sq	MS	F
Between grp	5	28.6294	5.72588	
Within grp	54	96.8735	1.79395	3.19176
Total	59	125.503		

Sonchus oleraceus

	df	Sum Sq	MS	F
Between grp	5	.611568	.122314	
Within grp	54	7.31798	.135518	.902563
Total	59	7.92955		

Erodium cygnorum

	df	Sum Sq	MS	F
Between grp	5	.868768	.173754	
Within grp	54	5.62242	.104119	1.6688
Total	59	6.49119		

Sclerolaena obliquicuspis

	df	Sum Sq	MS	F
Between grp	5	2.7255	.545099	
Within grp	54	13.2264	.244933	2.2255
Total	59	15.9519		

Vittadinia cuneata

	df	Sum Sq	MS	F
Between grp	5	2.79632	.559265	
Within grp	54	17.827	.33013	1.69407
Total	59	20.6234		

Atriplex spongiosa

	df	Sum Sq	MS	F
Between grp	5	.480859	.0961719	
Within grp	54	4.15299	.0769072	1.25049
Total	59	4.63385		

Emex australis

	df	Sum Sq	MS	F
Between grp	5	4.32481	.864961	
Within grp	54	14.234	.263593	3.28143
Total	59	18.5588		

Calotis hispidula

	df	Sum Sq	MS	F
Between grp	5	.561147	.112229	
Within grp	54	6.91267	.128012	.876708
Total	59	7.47381		

Danthonia caespitosa

	df	Sum Sq	MS	F
Between grp	5	1.83943	.367886	
Within grp	54	6.57106	.121686	3.02323
Total	59	8.41049		

Goodenia pusilliflora

	df	Sum Sq	MS	F
Between grp	5	2.28516	.457032	
Within grp	54	10.7604	.199267	2.29356
Total	59	13.0456		

Hernaria hirsuta

	df	Sum Sq	MS	F
Between grp	5	1.67389	.334778	
Within grp	54	10.5981	.196261	1.70577
Total	59	12.272		

Stipa nitida

	df	Sum Sq	MS	F
Between grp	5	.36433	.0728661	
Within grp	54	5.26289	.0974609	.747644
Total	59	5.62722		

Gnephosis burkittii

	df	Sum Sq	MS	F
Between grp	5	.168159	.0336317	
Within grp	54	1.20113	.0222432	1.512
Total	59	1.36929		

Oxalis corniculata

	df	Sum Sq	MS	F
Between grp	5	.168159	.0336317	
Within grp	54	1.20113	.0222432	1.512
Total	59	1.36929		

Helipterum pygmaeum

	df	Sum Sq	MS	F
Between grp	5	.669443	.133889	
Within grp	54	2.49133	.0461358	2.90206
Total	59	3.16078		

3. SQUARE ROOT TRANSFORM

Daucus glochidiatus

	df	Sum Sq	MS	F
Between grp	5	28.282	5.65641	
Within grp	54	85.585	1.58491	3.56892
Total	59	113.867		

Crassula colorata

	df	Sum Sq	MS	F
Between grp	5	35.6465	7.1293	
Within grp	54	208.747	3.86569	1.84425
Total	59	244.394		

Brachycome lineariloba

	df	Sum Sq	MS	F
Between grp	5	.842735	.168547	
Within grp	54	8.00384	.148219	1.13715
Total	59	8.84658		

Crassula sieberana

	df	Sum Sq	MS	F
Between grp	5	31.6517	6.33033	
Within grp	54	167.076	3.094	2.046
Total	59	198.728		

Plantago drummondii

	df	Sum Sq	MS	F
Between grp	5	68.8446	13.7689	
Within grp	54	173.791	3.21835	4.27826
Total	59	242.635		

Lopochloa pumila

	df	Sum Sq	MS	F
Between grp	5	18.4002	3.68004	
Within grp	54	249.292	4.61651	.797148
Total	59	267.692		

Senecio quadridentatus

```
              df          Sum Sq          MS              F
Between grp    5            1.19053       .238106
Within grp    54            8.15578       .151033         1.57651
Total         59            9.34631
```

Calandrinia erenaea

```
              df          Sum Sq          MS              F
Between grp    5           .0401917       8.03833E-03
Within grp    54           .723469        .0133976        .599984
Total         59           .76366
```

Tetragonia eremaea

```
              df          Sum Sq          MS              F
Between grp    5           4.2244         .844881
Within grp    54           39.2397        .72666          1.16269
Total         59           43.4641
```

Actinobole uliginosum

```
              df          Sum Sq          MS              F
Between grp    5           .115101        .0230202
Within grp    54           1.45998        .0270367        .85144
Total         59           1.57508
```

Schismus barbatus

```
              df          Sum Sq          MS              F
Between grp    5           98.5463        19.7093
Within grp    54           528.268        9.78275         2.0147
Total         59           626.815
```

Sonchus oleraceus

```
              df          Sum Sq          MS              F
Between grp    5           .526093        .105219
Within grp    54           6.52511        .120835         .870759
Total         59           7.0512
```

Erodium cygnorum

```
              df          Sum Sq          MS              F
Between grp    5           .540012        .108002
Within grp    54           3.39698        .0629071        1.71686
Total         59           3.937
```

Sclerolaena obliquicuspis

	df	Sum Sq	MS	F
Between grp	5	1.96229	.392458	
Within grp	54	9.84412	.182299	2.15283
Total	59	11.8064		

Vittadinia cuneata

	df	Sum Sq	MS	F
Between grp	5	3.61402	.722803	
Within grp	54	21.9943	.407301	1.77462
Total	59	25.6083		

Atriplex spongiosa

	df	Sum Sq	MS	F
Between grp	5	.272972	.0545944	
Within grp	54	2.39231	.0443021	1.23232
Total	59	2.66529		

Emex australis

	df	Sum Sq	MS	F
Between grp	5	6.10736	1.22147	
Within grp	54	25.528	.472741	2.58381
Total	59	31.6354		

Calotis hispidula

	df	Sum Sq	MS	F
Between grp	5	.369083	.0738167	
Within grp	54	4.46694	.0827211	.892356
Total	59	4.83602		

Danthonia caespitosa

	df	Sum Sq	MS	F
Between grp	5	1.56896	.313792	
Within grp	54	6.05312	.112095	2.79934
Total	59	7.62207		

Goodenia pusilliflora

	df	Sum Sq	MS	F
Between grp	5	1.70098	.340195	
Within grp	54	8.06031	.149265	2.27914
Total	59	9.76129		

Hernaria hirsuta

	df	Sum Sq	MS	F
Between grp	5	1.46313	.292626	
Within grp	54	9.04356	.167473	1.7473
Total	59	10.5067		

Stipa nitida

	df	Sum Sq	MS	F
Between grp	5	.288425	.0576851	
Within grp	54	4.17127	.0772457	.746774
Total	59	4.45969		

Gnephosis burkittii

	df	Sum Sq	MS	F
Between grp	5	.0937805	.0187561	
Within grp	54	.66988	.0124052	1.51196
Total	59	.76366		

Oxalis corniculata

	df	Sum Sq	MS	F
Between grp	5	.0937767	.0187553	
Within grp	54	.66988	.0124052	1.5119
Total	59	.763657		

Helipterum pygmaeum

	df	Sum Sq	MS	F
Between grp	5	.411018	.0822037	
Within grp	54	1.52363	.0282154	2.91343
Total	59	1.93465		

APPENDIX 3

Table 1

Mean number of plants per subquadrat beneath *Maireana sedifolia*

	S-SE	SE-S	E-NE	NE-N	N-NW	NW-W	W-SW	SW-S
Danthonia	15.5	18.5	8.7	2.5	2.0	1.5	6.0	11.0
S.obliquicuspis	7.0	7.7	13.5	4.5	5.5	12.0	8.2	8.2
Eriochiton	2.0	7.7	4.5	7.0	4.2	6.5	4.2	4.7
Daucus	27.7	5.5	7.7	0.7	4.0	1.7	4.5	24.7
Brachyscome	26.5	10.5	1.2	0.5	1.0	1.5	7.0	24.7
Helipterum	1.5	0.0	0.0	0.0	0.0	0.2	0.2	0.2
Erodium	3.0	2.5	1.7	4.0	5.5	6.2	6.2	4.5
Swainsona	0.2	0.0	0.0	0.0	0.2	0.0	0.0	0.0
Isoetopsis	2.7	0.0	0.0	0.0	0.2	1.0	1.5	1.2
Plantago	0.2	1.0	0.0	0.0	0.0	1.2	1.2	2.0
Whalenbergia	7.5	4.2	2.2	1.5	1.2	4.5	5.7	6.0
Sonchus	3.2	2.5	1.7	1.7	3.5	1.2	1.2	4.2
Carthamus	0.0	0.7	0.7	0.5	0.2	0.7	0.2	1.0
Tetragonia	6.7	8.0	16.0	9.7	3.5	9.2	11.5	7.0
Hypochoeris	0.0	0.2	0.2	0.0	0.0	0.2	0.0	0.0
Atriplex	0.2	0.5	0.2	1.0	0.5	1.2	1.0	1.2
Chenopod sp.	0.2	0.0	0.2	0.2	0.2	0.2	0.2	0.2
Omphalolappula	0.5	2.2	3.7	1.0	2.0	3.0	1.7	2.2
Zygophyllum	0.0	0.2	1.5	0.2	0.7	2.5	0.0	0.2
Euphorbia	0.0	0.0	0.0	0.0	0.5	0.5	0.0	0.0
Goodenia	0.0	0.0	0.0	0.0	0.0	0.0	0.7	1.7
Stipa	0.0	0.0	0.0	0.2	0.0	0.2	0.0	1.2
Calotis	3.2	0.2	0.0	0.0	0.0	0.0	0.0	0.2
Vittadinia	0.0	0.0	0.0	0.0	0.2	0.0	0.2	0.2
Senecio	0.5	0.0	0.0	0.0	0.0	0.0	0.0	1.0
Medicago	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2
Hernaria	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2
Alyssum	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0
Means	108.7	72.5	64.2	35.5	35.5	55.7	62.2	108.5

Table 2

Standard deviations for the mean number of plants per subquadrat beneath *Maireana sedifolia* (Table 1)

	S-SE	SE-S	E-NE	NE-N	N-NW	NW-W	W-SW	SW-S
Danthonia	7.6	8.4	10.6	3.7	2.4	1.1	3.6	5.2
S.obliquicuspis	6.5	4.5	15.7	4.3	3.5	13.9	7.1	10.4
Eriochiton	1.5	6.6	2.5	4.1	3.4	3.9	2.8	1.2
Daucus	34.8	4.1	9.5	0.8	6.9	1.2	3.2	23.5
Brachyscome	23.2	11.4	1.2	0.8	1.7	1.1	4.3	20.0
Helipterum	1.6	0.0	0.0	0.0	0.0	0.4	0.4	0.4
Erodium	3.3	1.6	2.4	1.7	3.6	3.7	6.4	4.7
Swainsona	0.4	0.0	0.0	0.0	0.4	0.0	0.0	0.0
Isoetopsis	2.7	0.0	0.0	0.0	0.4	1.2	1.5	1.2
Plantago	0.4	1.2	0.0	0.0	0.0	1.2	1.6	3.4
Whalenbergia	8.2	3.2	2.8	2.0	1.2	4.0	7.7	1.7
Sonchus	2.4	0.5	1.4	1.7	4.0	1.2	1.2	1.4
Carthamus	0.0	1.2	1.2	0.8	0.4	0.8	0.4	1.2
Tetragonia	5.8	5.7	12.9	8.5	1.8	6.4	11.9	7.8
Hypochoeris	0.0	0.4	0.4	0.0	0.0	0.4	0.0	0.0
Atriplex	0.4	0.5	0.4	1.7	0.5	1.6	1.2	0.4
Chenopod sp.	0.4	0.0	0.4	0.4	0.4	0.4	0.4	0.4
Omphalolappula	0.8	2.4	3.5	1.7	2.9	4.6	2.0	1.4
Zygophyllum	0.0	0.4	2.5	0.4	0.8	4.3	0.0	0.4
Euphorbia	0.0	0.0	0.0	0.0	0.8	0.8	0.0	0.0
Goodenia	0.0	0.0	0.0	0.0	0.0	0.0	0.8	2.0
Stipa	0.0	0.0	0.0	0.4	0.0	0.4	0.0	1.0
Calotis	5.6	0.4	0.0	0.0	0.0	0.0	0.0	0.4
Vittadinia	0.0	0.0	0.0	0.0	0.4	0.0	0.4	0.4
Senecio	0.8	0.0	0.0	0.0	0.0	0.0	0.0	1.7
Medicago	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4
Hernaria	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4
Alyssum	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0

Table 3

Mean number of plants per subquadrat beneath *Atriplex vesicaria*

	S-SE	SE-S	E-NE	NE-N	N-NW	NW-W	W-SW	SW-S
Danthonia	6.5	6.7	8.2	2.7	3.5	4.5	4.5	7.0
S.obliquicuspis	2.5	0.5	1.2	1.0	0.0	0.0	0.2	1.2
Eriochiton	0.7	1.0	0.5	2.2	0.7	0.7	1.0	2.0
Daucus	24.0	22.5	18.7	6.0	6.7	5.0	13.0	12.0
Brachyscome	2.2	2.5	2.5	2.0	0.7	1.7	1.7	3.2
Helipterum	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Erodium	0.7	2.2	1.7	1.5	6.0	4.2	3.2	1.5
Swainsona	0.0	0.2	0.2	0.2	0.2	0.0	0.0	0.2
Isoetopsis	3.5	3.5	5.0	3.2	4.2	4.7	3.0	1.0
Plantago	2.0	3.5	2.5	3.0	2.0	4.5	6.2	3.5
Whalenbergia	0.2	3.0	4.5	0.7	1.2	1.2	4.5	2.0
Sonchus	2.7	4.0	3.5	2.2	1.7	2.0	2.7	1.5
Carthamus	0.0	0.0	1.2	1.7	0.7	0.2	0.2	0.5
Tetragonia	1.5	3.0	4.7	1.2	0.7	0.5	1.2	1.7
Hypochoeris	0.2	0.0	0.0	0.0	0.2	0.0	0.2	0.5
Atriplex	1.0	0.7	0.7	0.0	0.0	0.0	0.2	0.5
Chenopod sp.	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0
Omphalolappula	3.7	2.2	5.0	1.7	1.2	0.2	0.5	2.0
Zygophyllum	0.0	0.2	0.0	0.0	0.0	0.0	0.2	0.2
Euphorbia	0.0	0.2	0.0	1.5	1.2	1.2	0.2	0.0
Goodenia	2.2	0.7	1.0	0.0	0.7	2.0	1.2	0.2
Stipa	0.5	1.0	0.0	1.0	0.7	0.5	0.7	1.0
Calotis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Vittadinia	0.5	0.2	0.0	0.0	0.0	0.2	0.2	0.0
Senecio	0.2	0.5	0.0	0.0	0.0	0.0	0.2	0.0
Medicago	0.2	0.0	0.0	0.0	0.0	0.0	0.2	0.5
Hernaria	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Alyssum	0.0	0.0	0.0	0.0	0.5	0.0	1.0	0.0
Means	55.7	58.7	61.7	32.2	33.5	33.7	47.0	42.5

Table 4

Standard deviations for the mean number of plants per subquadrat beneath *Atriplex vesicaria* (Table 3)

	S-SE	SE-S	E-NE	NE-N	N-NW	NW-W	W-SW	SW-S
Danthonia	3.7	4.2	5.7	1.4	1.6	2.6	2.6	3.0
S.obliquicuspis	3.2	0.8	0.4	1.0	0.0	0.0	0.4	0.4
Eriochiton	1.2	1.2	0.5	2.2	0.4	0.8	0.7	1.2
Daucus	23.8	19.0	16.3	4.6	9.9	7.5	13.1	14.4
Brachyscome	1.7	2.2	3.2	2.4	0.8	2.0	2.0	1.7
Helipterum	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Erodium	1.2	2.8	2.4	2.0	3.5	5.1	3.2	1.1
Swainsona	0.0	0.4	0.4	0.4	0.4	0.0	0.0	0.4
Isoetopsis	3.7	5.5	8.0	3.2	5.7	6.6	3.6	1.7
Plantago	1.5	2.0	3.7	2.1	1.2	2.0	9.1	1.5
Whalenbergia	0.4	3.0	2.8	0.8	1.6	0.8	5.1	2.9
Sonchus	1.2	5.2	2.6	1.0	0.4	0.7	3.2	1.1
Carthamus	0.0	0.0	2.1	2.4	1.2	0.4	0.4	0.8
Tetragonia	1.5	2.5	2.9	1.6	0.8	0.8	1.0	1.9
Hypochoeris	0.4	0.0	0.0	0.0	0.4	0.0	0.4	0.5
Atriplex	1.0	0.8	0.8	0.0	0.0	0.0	0.4	0.5
Chenopod sp.	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0
Omphalolappula	3.7	1.9	4.1	1.0	1.2	0.4	0.5	1.2
Zygophyllum	0.0	0.4	0.0	0.0	0.0	0.0	0.4	0.4
Euphorbia	0.0	0.4	0.0	1.5	1.0	1.6	0.4	0.0
Goodenia	1.7	0.8	0.7	0.0	0.8	0.7	0.8	0.4
Stipa	0.5	1.2	0.0	0.7	0.8	0.8	0.4	1.2
Calotis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Vittadinia	0.5	0.4	0.0	0.0	0.0	0.4	0.4	0.0
Senecio	0.4	0.8	0.0	0.0	0.0	0.0	0.4	0.0
Medicago	0.4	0.0	0.0	0.0	0.0	0.0	0.4	0.5
Hernaria	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Alyssum	0.0	0.0	0.0	0.0	0.8	0.0	1.7	0.0

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