

**SPATIAL VARIATION IN
THE POPULATION DYNAMICS OF *ATRIPLEX VESICARIA*
UNDER SHEEP GRAZING**

by

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TABLE OF CONTENTS

Summary	vi
Declaration	viii
Acknowledgements	ix
List of Abbreviations	x

CHAPTER 1: INTRODUCTION

BACKGROUND	1
Rangeland Ecosystems	1
<i>Nature and Importance of the World's Rangelands</i>	1
<i>Models of Vegetation Change for Rangeland Ecosystems</i>	2
<i>Ecological Basis of Management Principles and Practices</i>	4
Chenopod Shrublands	5
FRAMEWORK FOR THIS STUDY	8
Project Outline	8
Aims	9
Thesis Structure	10

CHAPTER 2: LITERATURE REVIEW

THE ECOLOGY OF BLADDER SALT BUSH, <i>ATRIPLEX VESICARIA</i>	12
Taxonomy and Morphology	12
Growth and Survival	12
Flowering, Seeding and Recruitment	14
THE NATURE OF GRAZING IN CHENOPOD SHRUBLANDS	15
Animal Distribution	15
Grazing Behaviour and Utilisation of Saltbush	16
IMPACT OF GRAZING ON SALT BUSH	17
Effect at the Individual Plant Level	17
Effect at the Population Level	19
Effect at the Landscape Level	20

CHAPTER 3: MATERIALS AND METHODS

INTRODUCTION	22
THE STUDY AREA	22
Location	22
Climate	23
Topography and Soils	23
Vegetation	24
Land Use	25
THE STUDY Paddock	27
General Description	27
Livestock and Management	27
Vegetation	28
ESTABLISHMENT OF STUDY PLOTS	28

CONDITIONS DURING THE STUDY	29
Rainfall	29
Sheep Numbers and Management	30

CHAPTER 4: PATTERNS OF SALTBUSSH DEFOLIATION BY SHEEP

INTRODUCTION	32
Background	32
Aims	34
METHODS	35
Experimental Methods	35
<i>Estimation of Defoliation Intensity</i>	35
<i>Estimation of Saltbush Biomass</i>	36
<i>Estimation of Herbage Biomass</i>	37
<i>Dung Deposition</i>	38
Statistical Analysis	38
RESULTS	39
Availability of Herbage Biomass	39
Patterns of Saltbush Defoliation	39
Saltbush Biomass	42
DISCUSSION	43
Saltbush Defoliation Patterns	43
Biomass Dynamics	45
Importance of Patterns of Grazing for Saltbush	47
Generality of Results	48
Role of Field Estimates of Defoliation	49
CONCLUSIONS	50

CHAPTER 5: POPULATION DYNAMICS AND THE EFFECTS OF GRAZING

INTRODUCTION	52
Background	52
<i>Plant Populations and Grazing Impact</i>	52
<i>Factors Affecting Grazing Impact on Plant Populations</i>	54
<i>Life-History Strategy and Dynamics of Arid Zone Perennial Plants</i>	57
<i>Plant Demographic Studies Under Grazing in Australian Rangelands</i>	58
<i>Demography of Saltbush and Grazing Impact</i>	58
Aims	60
METHODS	61
Collection of Demographic Data	61
Data Analysis	62
<i>Matrix Population Models</i>	62
<i>Analysis Procedure</i>	66
RESULTS	70
Population Sizes and Flux	70
Recruitment	72
Transition Matrices and Demographic Fate	73
Population Growth Rates and Stable Stage Distributions	76
Elasticity and LTRE Analyses	78

DISCUSSION	80
Population Changes - The Role of Grazing, Climate and Time	80
Spatial Patterns in Demographic Processes	84
<i>Recruitment</i>	84
<i>Adult Mortality</i>	85
<i>Survival and Growth of Seedlings and Juveniles</i>	86
Importance of Demographic Processes to Population Growth	89
Spatial Patterns in λ - Mechanism of Population Change	91
Small-Scale Spatial Variation	93
CONCLUSIONS	94

CHAPTER 6: TIME-VARYING POPULATION MODELS FOR SALTBUSH

INTRODUCTION	96
Background	96
Aims	97
METHODS	99
RESULTS	103
DISCUSSION	105
General Discussion of Results	105
Role of Recruitment in a Stochastic Environment	107
Importance of the Sequence of Seasons	108
Large Events and Co-occurrence of Events	110
Validity of Models	111
Further Work	113
CONCLUSIONS	114

CHAPTER 7: FLOWERING AND ASPECTS OF SEED BANK DYNAMICS UNDER GRAZING

INTRODUCTION	116
Background	116
<i>Flowering and Seed Production</i>	116
<i>Seed Banks</i>	117
Herbivory Effects on Flower and Seed Production	119
Flowering and Seed Banks in Saltbush	120
Aims	121
METHODS	123
Experimental Methods	123
<i>Flowering</i>	123
<i>Estimation of the Seed Bank</i>	123
<i>Seed Longevity</i>	126
Data Analysis	128
<i>Flowering</i>	128
<i>Seed Bank</i>	128
<i>Seed Longevity</i>	129
RESULTS	129
Flowering	129
Seed Bank	130
Seed Longevity	131

DISCUSSION	133
Spatial Patterns in Flowering and the Seed Bank	133
Seed Longevity	135
Seed Bank Dynamics	140
Importance of Low Seed Availability Under Grazing	142
CONCLUSIONS	143

CHAPTER 8: GENERAL DISCUSSION

INTRODUCTION	145
REVIEW OF STUDY	146
Reliability of Results	146
Defoliation Patterns	147
Population Dynamics and Grazing Impact	148
Seed Bank Dynamics	149
CIRCUMSTANCES LEADING TO LOCAL EXTINCTION	149
SPATIAL ELEMENT OF GRAZING AND LOCAL EXTINCTION	151
IMPLICATIONS FOR MANAGEMENT	152
A State-and-Transition Model for Grazing Management in Saltbush	154
Extrapolation to Other Paddocks	155
DIRECTIONS FOR FURTHER RESEARCH	156

REFERENCES	159
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SUMMARY

This study considered the question of whether, under continuous sheep stocking, overgrazing of *Atriplex vesicaria* Heward ex Benth. (bladder saltbush), a dominant perennial chenopod shrub in the arid rangelands of southern Australia, is confined to the immediate vicinity of water points or whether the entire population in a paddock is at risk of long-term decline. This was examined by quantifying the defoliation of saltbush at nine sites within a typical grazed paddock and investigating the effects on the species' population dynamics with the aid of matrix population models. These models were based on the fate of all plants at the nine sites, assessed at intervals of six months over 6.5 years. Aspects of the seed bank dynamics were also studied.

Heavy defoliation of saltbush by sheep at sites up to 2200 m from water for the first 18 months of the study, when conditions were dry and alternative feed was scarce, severely reduced the vigour of shrubs and led to a decline in the population at many of these sites. Projection modelling suggested that the population was at risk of local extinction at these sites. This was despite good rains and an increase in feed levels later in the study, when defoliation of saltbush was negligible. In comparison, the population was stable at sites further from water.

The decline in the saltbush population under grazing was a result of increased adult mortality and reduced recruitment. Elasticity analysis showed that poor survival of adult shrubs was the most important factor contributing to reductions in the population growth rate (λ). This reflects the importance of the survival of adults to the population growth rate in saltbush. Recruitment is less important to the population growth rate, but is more sensitive to grazing, so it is more severely reduced at greater distances from water. The seed bank studies showed that poor recruitment was likely to be a consequence of a depleted seed bank at sites up to at least 1650 m from water, and explains the poor response to good rains.

These findings suggest that saltbush is at risk of being overgrazed over large areas of paddocks under continuous grazing. Proposed management strategies to avoid this include the protection of saltbush from severe grazing during dry periods, to maintain shrub vigour and minimise the death of adults.

DECLARATION

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

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

29/5/95

Date

Leigh Hunt

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LIST OF ABBREVIATIONS

CATMOD	categorical data modelling
DSE	dry sheep equivalent
ISD	initial stage distribution
LSD	least significant difference
LTRE	life table response experiment
SAS/STAT	Statistical Analysis System, Statistical Package, Version 6.04 (SAS Institute, 1988)
SSD	stable stage distribution

λ	asymptotic population growth rate
*	$P < 0.05$
**	$P < 0.01$
***	$P < 0.001$

CHAPTER 1

INTRODUCTION



BACKGROUND

Rangeland Ecosystems

Nature and Importance of the World's Rangelands

Rangelands are some of the most important and common ecosystems, covering approximately 47% of the earth's land surface (Williams *et al.* 1968). They are characterised by at least one of the following properties; low and unpredictable rainfall, steep topography, poor soils, poor drainage or extremes of temperature, all of which limit the practice of agriculture (Box 1986, Tueller 1988). Consequently, native plant species still dominate the vegetation in many of these regions. Arid and semi-arid rangelands are the most common, covering approximately 33% of the world's land surface (Perry 1979). Despite the limitations to agriculture, arid and semi-arid rangelands directly support a large human population (estimated to be 300 million people in 1979 [Perry 1979]) by providing grazing lands for livestock production, living areas, water and wood products (Stoddart *et al.* 1975). As well, they are important wildlife habitat and a reserve of genetic diversity, while recently their use for recreation and tourism has increased. The introduction of domestic stock to arid and semi-arid rangelands has had a dramatic effect on the vegetation and soils in many areas (Box 1986) and it is their use as a grazing resource that is the main concern of this thesis.

Because of the climatic and landscape features which are typical in arid and semi-arid rangelands, standing plant biomass and growth are generally low and spatially and temporally variable, with frequent extended periods of little or no growth. This variability creates problems for people who rely on a sustained yield of product from their herds or flocks to meet their own subsistence needs or to provide income by supplying a market, regardless of whether a nomadic grazing system (as in parts of Africa and Asia) or a permanent station or ranch system (typical of Australia, USA and

South America) is employed. A consequence of this is that often the range resource will be over-utilised during periods of low rainfall and forage growth. This frequently results in some loss of productive potential because of changes ranging from undesirable shifts in plant community composition through to severe soil erosion (Walker 1979), although nomadic systems tend to be more resilient (Archer and Smeins 1991). It seems that none of the world's rangelands is free of this risk (Box 1986) but the degree of degradation does appear to be related to the time since settlement by 'pastoralists' (Walker 1979). Thus Middle-Eastern rangelands tend to be highly modified while much of Australia's rangelands, which were taken up less than 150 years ago (Wilson and Graetz 1979), are in comparatively good condition (Harrington *et al.* 1984). Given the apparent sensitivity of rangelands to over-use, the high probability of degradation and the importance of rangelands to humans, it follows that wise management of these ecosystems is essential to ensure a sustained yield of the resources.

Models of Vegetation Change for Rangeland Ecosystems

Where native plant species form the basis of livestock grazing systems, management of rangelands needs to have an ecological basis, involving the interactions between the various biotic and abiotic factors influencing the vegetation and how these might be affected by management (Wilson *et al.* 1988). The appropriateness of the models range ecologists and managers use to describe and predict the effects of disturbance on plant communities has a major bearing on the likelihood of success of management strategies that are based upon them. Traditionally the Clementsian model of plant succession (or climax theory), which was formulated for moderate rainfall, grass-dominated North American rangelands, has been the dominant paradigm utilised for understanding the effects of grazing on range vegetation (Dyksterhuis 1958, Stoddart *et al.* 1975). This model views vegetation change in an undisturbed environment as a linear successional process which leads to a stable climax community where successional forces are in equilibrium. Disturbance of the community (e.g. grazing) results in a reversal of the development process (retrogressive succession) with the magnitude of the reversal related

to the nature, degree and duration of disturbance. If the disturbance is constant a climax equilibrium establishes, but once the disturbance is removed secondary succession will proceed to re-establish the original climax vegetation (Dyksterhuis 1958). The climax community was considered to represent the potential of the site and was the benchmark against which disturbance was measured. But in recent years there has been considerable re-evaluation of these ideas (Westoby 1980, Smith 1988, Westoby *et al.* 1989, Friedel 1991, Laycock 1991), particularly in terms of their relevance to arid and semi-arid rangelands, as more examples arise of vegetation dynamics which are not compatible with or are inadequately described by climax theory. Characteristics of the dynamics of vegetation in these examples include:

- 1) the importance of large and unpredictable fluctuations in rainfall, from prolonged droughts to floods, which can bring about major and persistent changes in vegetation composition and structure. An example of this is the establishment of long-lived perennials in central Australia following large rainfall events (Griffin and Friedel 1985). This feature will particularly limit the usefulness of climax theory in Australian rangelands, which experience much greater temporal variability in annual rainfall than most of the world's rangelands (Stafford Smith and Morton 1990).
- 2) the original vegetation or 'climax' community frequently fails to return following the removal of grazing, or the return pathway does not coincide with the retrogressive pathway (Walker *et al.* 1981, Archer and Smeins 1991).
- 3) retrogressive succession in response to disturbance can be step-wise rather than linear (Archer 1989).

These observations have led range ecologists to propose non-equilibrium models (Westoby *et al.* 1989, Friedel 1991, Laycock 1991) which recognise that vegetation communities may exhibit multiple stable states, multiple pathways of vegetation change, thresholds, and transitions which are irreversible in a time-frame which is appropriate to management. Accordingly, it is not surprising that many attempts at directing vegetation

change, or preventing degradation, through the application of specific management practices derived from climax theory have failed.

Ecological Basis of Management Principles and Practices

The main aim of rangeland management is to maintain natural plant communities in a productive state so they continue to provide fodder for livestock and protect the soil from erosion (Harrington *et al.* 1984). It follows from the preceding discussion that to be successful, management practices need to be based on a sound knowledge of the ecology of key plant species present in the community. In order to be able to predict the medium- to long-term outcome of management actions demographic studies which provide an understanding of the population dynamics of these species are necessary (Noble 1986, Wilson 1986, Smith 1988). This will involve measuring, describing and explaining changes in population size in terms of the numbers of births, deaths, immigrants and emigrants for the entire life cycle of the species involved (Noble 1986). Quantification of these attributes also will facilitate the forecasting of impending changes in vegetation composition so that steps can be taken to avert undesirable shifts (Archer and Smeins 1991) or encourage desirable changes (Westoby *et al.* 1989).

It should also be recognised that the response of vegetation to grazing will be a function of the combined effects of processes operating at the various hierarchical levels of ecosystem organisation (i.e. plant, population and community). Thus, sound management practices cannot be established from a consideration of only a single level of organisation (Archer and Tieszen 1986, Brown and Allen 1989, Archer and Smeins 1991). However, population level studies should be particularly enlightening. As well as providing knowledge of population level processes, they will aid the integration of mechanistic cause and effect insights from plant level studies with community level information on shifts in species composition and biomass dynamics, to form a comprehensive information base for vegetation management in grazed systems (Briske 1991). The importance of population level studies is perhaps reflected in the recent interest in autecological studies

in many rangeland areas, following many years of concentration on plant and community studies.

Consideration of the effects of grazing at the landscape level of organisation is also crucial to understanding and managing herbivore impact (Coughenour 1991, Archer and Smeins 1991). The high degree of spatial variability inherent in rangeland ecosystems affects the availability of the resources required by livestock (e.g. water, feed and shelter) which, in turn, is important in determining the patterns of grazing impact (Coughenour 1991). Consequently, grazing is rarely spread evenly over the landscape or paddock and this must be recognised in assessing the response of vegetation to herbivory. In some situations indirect effects of grazing on the vegetation community, through processes like run-off/run-on and erosion, can be important in determining grazing consequences at a landscape scale (Stafford Smith and Pickup 1990).

To summarise the preceding discussions, it is apparent that sound management of the rangelands requires:

- 1) a full understanding of the pathways of vegetation change possible for the rangeland type in question, which will depend on,
- 2) a knowledge of the life-history characteristics of the species involved and how they interact with grazing and climatic conditions to affect the population dynamics of the species; and
- 3) a knowledge of the spatial and temporal variation in grazing impacts, the distribution of vegetation in paddocks, and the degree of spatial variation in population dynamics of the species involved.

Chenopod Shrublands

Australia's rangelands occupy 84% of the continent (Young *et al.* 1984) and include grasslands, woodlands and shrublands. An important rangeland type is the chenopod shrublands, or saltbush country, which covers 500,000 sq. km. (Graetz and Wilson

1984). These shrublands are mainly restricted to the southern arid and semi-arid regions between a latitude of 24°-35°S, and stretch across almost three-quarters of the continent from 146° to 116°E (Graetz and Wilson 1984). Rainfall is predominantly received in winter (although large falls can occur in summer) and annual totals vary from 125 mm at the western extremes of their distribution to 350 mm in the east (Wilson *et al.* 1988). As is typical of the Australian rangelands, rainfall is highly variable from year to year with a low degree of predictability. Sheep grazing for wool production on permanently¹ occupied stations is the main land-use, although some properties also graze cattle. The livestock graze in large paddocks of up to 40 sq. km. and the degree of management control is quite limited.

The vegetation of these shrublands is dominated by sclerophyllous shrubs belonging to the family Chenopodiaceae. These long-lived perennial shrubs (chiefly *Atriplex* spp. and *Maireana* spp.) occur in a number of floristic assemblages as extensive low shrublands or with a scattered overstorey of trees, which may include *Acacia*, *Eucalyptus*, *Alectryon*, *Casuarina* and *Myoporum* species. A mid-shrub layer, which includes species from genera such as *Eremophila* and *Senna*, is also frequently present. Individual chenopod shrubs are generally 1-2 metres apart or they may be clumped, with a similar spacing between clumps. Depending on the amount of rainfall in the autumn-winter period ephemeral and short-lived perennial grasses and forbs (most notably species of *Stipa*, *Danthonia*, *Astrebla*, *Enneapogon* and *Sclerolaena*) may grow between the shrubs, but often this layer is sparse or absent (Noble 1977). The shrubs are a vital component of the ecosystem having an important role in nutrient cycling (Charley and Cowling 1968) and as stabilising elements, protecting the soil from erosion (Marshall 1972). They are also considered important to the grazing industries because their ability to persist during long dry periods when little other feed is available means they are a valuable source of drought fodder (Graetz and Wilson 1984). However, there has long been concern about

¹Tenure of these stations varies between States, with some being leasehold for a defined period, others freehold. Regardless of tenure the properties can be regarded as permanently occupied as opposed to nomadic occupation.

livestock-induced degradation of the shrublands (Dixon 1892, Ratcliffe 1936, Williams and Oxley 1979) and a management strategy involving continuous grazing at conservative stocking rates of about 5.6 ha/sheep, with no more than 250-350 sheep per water point, is regarded as necessary to avoid deterioration of the resource and a loss of sustainable carrying capacity (Lange *et al.* 1984).

A consequence of livestock grazing in these shrublands is a substantial change in the plant community in the vicinity of water points. This change is apparent through the development of concentric patterns of species composition around water points, where palatable but grazing-sensitive plant species are eliminated in the vicinity of water but unpalatable or grazing-tolerant species increase (Barker and Lange 1970, Barker 1979, Andrew and Lange 1986a). These patterns, or piospheres, develop as a result of sheep needing frequent visits to water to drink, creating gradients in grazing pressure radiating out from watering points (Osborn *et al.* 1932, Lange 1969).

Bladder saltbush, *Atriplex vesicaria* Heward ex Benth, is one of the more important perennial shrubs in these rangelands, being both a dominant and widespread species, but it is also one of the first species to be removed in the area of the piosphere immediately surrounding water points (Andrew and Lange 1986a). It has been suggested that further overgrazing of saltbush is avoided by the use of 'equilibrium' stocking rates, whereby a 'natural' rotational grazing system establishes. In this 'system' the shrubs are grazed during summer and autumn when other feed is scarce but they are able to recover from grazing during winter and spring when, following winter rains, ephemeral herbage is available, which sheep graze in preference to the perennial shrubs (Graetz and Wilson 1979).

However, there is now some doubt as to the validity of this approach in maintaining viable saltbush populations. This is particularly so in the more arid parts of its range (i.e. South Australia and Western Australia), and in these areas saltbush is now

considered to be at risk of being completely eliminated from large areas of the chenopod shrublands grazed by sheep where continuous grazing regimes are practised (Wilson *et al.* 1988). This is supported by the findings of two studies in South Australia. Barker (1979) observed that paddocks with a longer grazing history had suffered a greater loss of saltbush despite the use of conservative stocking practices and Lay (1972) found substantial bush loss over a 22 year period on apparently well-managed stations, although in this case it was considered possible that other factors besides grazing, such as drought, were responsible for the reduction in shrub density.

FRAMEWORK FOR THIS STUDY

Project Outline

Given the importance of saltbush in the ecosystem and its value as drought feed, its loss from grazed paddocks is of considerable concern. To assess the risk of grazing to saltbush populations and predict future trends in the population it is essential to understand the species' population dynamics and how grazing can modify the dynamics. Thus detailed long-term studies of the population dynamics are needed. However, these studies must consider the spatial element of grazing impacts in paddocks. Studies carried out in small experimental paddocks or at only one location in a paddock will be of limited value in understanding grazing impacts at the scale of full-size paddocks. Similarly measurements of plant density alone will be inadequate to properly describe the population dynamics (Harper 1977, Noble 1986). Surprisingly, there have been very few studies of the population dynamics of saltbush which have incorporated information about paddock scale patterns of grazing.

Consequently, this project examined the issue of long-term grazing impacts over the extensive areas of sheep paddocks in chenopod shrublands by detailed study of the level of grazing of saltbush and the consequences for the population at numerous locations in a typical paddock. Since saltbush is an abundant species with a wide distribution the results

should have broad application. In addition, because saltbush is regarded as being the chenopod shrub most sensitive to grazing (Graetz and Wilson 1984) it is a useful indicator of overall grazing impact. This species should, therefore, play an important part in the making of management decisions and in determining the condition of the plant community in general. If management practices are adequate for the continued existence of the most sensitive species, there is a greater likelihood that other species are not being adversely affected (although other factors such as grazing preferences are also important).

Aims

The main purpose of this study was to enhance our knowledge of the nature and degree of spatial and temporal variation which occurs in the population dynamics of *A. vesicaria* under a continuous grazing regime. This should improve our understanding of the long-term implications of a continuous stocking regime on the species and indicate whether management practices need to be altered to maintain viable populations of saltbush under sheep grazing. An indication of the management changes necessary to achieve this should also result.

Specific aims of this study were:

- 1) to quantify the level of defoliation of saltbush by sheep and the degree to which this varies spatially across a typical paddock, and temporally between seasons and years receiving different amounts of rainfall;
- 2) to examine the spatial variation in the population dynamics of saltbush due to variations in defoliation by sheep, including the effects on recruitment and mortality, the relative importance of recruitment, growth and mortality in determining the observed population growth rates, and likely long-term population trends;
- 3) to investigate spatial variation in reproductive aspects of saltbush which might be affected by grazing or are important in determining a population's recovery from grazing, including flowering and size and longevity of the soil seed bank.

Thesis Structure

In order to put the studies presented in this thesis into context and to demonstrate their relevance to improving the management of the chenopod shrublands, a review of the literature pertaining to the ecology of saltbush, the nature of grazing and the response of saltbush to grazing is presented in Chapter 2.

Chapter 3 describes the climate, vegetation and management of the general location of the paddock chosen for this study, and presents specific information relating to the study paddock itself. This includes the location of experimental plots within the paddock which were used for most observations, seasonal conditions experienced during the study period and livestock numbers.

The question of spatial and temporal variation in the intensity of defoliation of saltbush across the study paddock is addressed in Chapter 4. The impact of this grazing on the biomass dynamics of saltbush is examined. The effects of season, livestock behaviour and herbage availability are considered in the discussion of these results. These studies provide background to help explain observed differences in the population dynamics of saltbush.

Chapters 5 and 6 consider the population dynamics of saltbush in the study paddock. Chapter 5 reports the observed dynamics during the study and presents an analysis of these dynamics using time-invariant matrix population models. This analysis helps to identify the population processes that are important for saltbush and the effects of grazing on these processes. Chapter 6 presents the results of stochastic matrix population models, which examine the likely long-term future of the saltbush population. These results are discussed in relation to variations in seasonal conditions.

The effect of grazing on saltbush flowering and seed bank levels is examined in Chapter 7. Again the variation in these factors across the study paddock is considered. A study

of the retention of a viable seed bank followed on from the investigation of seed bank levels and is reported in this chapter.

Chapter 8 discusses the overall findings of the study in terms of the implications for the population and for management. A 'state and transition' model based on the results of this work and which integrates temporal and spatial aspects of vegetation change is presented. The study is reviewed together with suggestions for further work.

CHAPTER 2

LITERATURE REVIEW

THE ECOLOGY OF BLADDER SALTBUSSH, *ATRIPLEX VESICARIA*

Taxonomy and Morphology

Atriplex vesicaria is a member of the Chenopodiaceae. It is a low, woody shrub up to 0.75m tall, but it is a highly variable species with eight recognised sub-species. Shrubs can be erect or decumbent and the mealy, pale green leaves can be elliptic, oblong, obovate or rounded with the lamina 5-25 mm long and 3-15 mm wide. Even within sub-species a high degree of polymorphism in leaf and fruiting bracteole shape is possible, and hybridisation between sub-species is also likely (Parr-Smith and Calder 1979).

The root system of *A. vesicaria* is shallow and fibrous, and is mostly confined to the upper 30 cm of the soil profile (Jones and Hodgkinson 1970). Lateral spread of roots was found to be 1m in the heavy clay soils of the Riverine Plain in NSW (Jones and Hodgkinson 1970) but 2m in more arid areas (Osborn *et al.* 1932). It has been suggested that there is a vertical zoning of root types and function in *A. vesicaria* and also in the related species *A. nummularia* (old man saltbush). Jones and Hodgkinson (1970) found that *A. vesicaria* has very fine roots in the top 5 cm of the soil profile which they suggested may be important for the uptake of nutrients, although they are possibly ephemeral roots which may die during droughts. However, these roots regrow quickly after rain and probably facilitate the rapid uptake of moisture when it is available (Osborn *et al.* 1932, Jones and Hodgkinson 1970). The majority of roots were found in the second zone to a depth of 30 cm. The third zone consisted of 'vertical exploring' roots extending to depths of 60 cm, which may be important in the acquisition of moisture during periods of moisture stress.

Growth and Survival

Saltbush is generally regarded as a long-lived shrub. Survivorship of adult saltbush fits a

negative exponential model (i.e. survival is independent of age) with a half-life of 11 years (Crisp 1978). Few individuals survive more than 25 to 30 years (Crisp 1978, Williams 1979). This is the shortest life-span amongst the dominant perennial shrubs of these rangelands (Graetz and Wilson 1984) and compares with bluebush (*Maireana sedifolia*), the longest-lived species, which has a half-life estimated to be more than 150 years (Crisp 1978). Obviously seasonal conditions and habitat will influence saltbush survival and some variation between sub-species is also probable.

A. vesicaria normally produces most growth during the wetter winter months, although it will respond to rain at any time of the year (Noble 1977). However, a minimum of 25 mm of rain, received over one to several days, is necessary to initiate a growth response (Noble 1977). Saltbush utilises the C₄ carboxylation pathway and consequently has a high level of photosynthetic efficiency. It is therefore capable of achieving high rates of growth under favourable conditions (Jones *et al.* 1970), thus gaining maximum benefit from the infrequent rainfall events. The effect of rainfall on growth has long-term effects on the standing biomass of saltbush, as the biomass dynamics of the species can be described as a growth pulse followed by a slow decline. This was illustrated by Noble (1977) who found that saltbush biomass is best correlated with rainfall received during the previous 42 months.

It is widely recognised that saltbush is a very drought tolerant species, although during drought its growth is slow (Williams 1979). Its ability to tolerate high ionic concentrations and to excrete salts onto the leaf surface to avoid extreme salt concentrations in the leaf tissue (see Jones 1970), appear to be the main adaptations for tolerating drought. During extreme droughts it sheds many of its leaves, which reduces the amount of moisture lost through transpiration and increases the chances of individual shrubs surviving the drought (Ratcliffe 1936, Graetz and Wilson 1984). Nevertheless, it has been suggested that severe drought may eventually lead to increased rates of mortality for some sub-species on certain land types (Westoby *et al.* 1989).

Flowering, Seeding and Recruitment

Saltbush plants are normally dioecious, bearing female flowers in the axils of the upper parts of stems, and male flowers in glomerules which form terminal spikes or panicles. Flowering is opportunistic and has been observed to occur at any time of the year following sufficient rainfall (Williams 1979, Briese 1982). Rainfall of 25-50 mm received over one to several days is considered necessary to initiate flowering (Williams 1979) and although flowering has been reported to occur frequently (Hall *et al.* 1964), no data on actual flowering frequency has been published. Saltbush produces a large brown seed 1.5-2.5 mm in diameter (Beadle 1952). The fruiting body is usually about 12 mm in diameter and is comprised of a single seed enclosed by two fruiting bracteoles, which may or may not have papery bladder appendages depending on the sub-species (Parr Smith 1982). These bladders are considered to facilitate dispersal of the seed by wind, although Williams (1979) found that approximately 80% of seedlings were located under female bushes while few seedlings were found under adjacent male bushes, prompting him to conclude that dispersal is minimal.

Once a seed has entered the seed bank a number of factors determine whether a reproductive plant eventually establishes from the seed. Obviously the seed must remain viable in the soil until conditions are suitable for germination, and then sufficient moisture must be available for the seedling to establish to enable it to persist through subsequent periods of low rainfall. Burbidge (1945) and Beadle (1952) established that saltbush seed would remain viable for approximately five years when stored in a laboratory. The longevity of saltbush seed in the field has not been investigated and is likely to be less than for seed stored in a laboratory. Ants are large consumers of saltbush seed, removing up to 83% of seed produced (Williams 1972, Briese 1982), and birds are also thought to consume some seed (Osborn *et al.* 1935).

Germination of saltbush seed is primarily governed by moisture availability and temperature. Laboratory investigations by Burbidge (1945) showed that saltbush seeds

germinate best at temperatures between 16°C and 20°C, suggesting that peak germination in the field could be expected during winter following sufficient rainfall. However, Beadle (1952) found that the optimum temperature for germination was between 20 and 25°C. Williams (1972) concluded that a minimum of 50 mm of rain spread over several days was necessary for germination.

Following germination, seedling establishment depends on the availability of sufficient moisture in the upper layers of the soil profile for approximately 15 days to enable the roots to penetrate to lower layers where moisture availability is more reliable (Williams 1979). Because of the low and unreliable rainfall in the chenopod shrublands seedling survival is low, with desiccation being the main cause of seedling death (Hall *et al.* 1964, Crisp 1978). Consequently, substantial establishment events can be expected only once every three to five years (Williams 1979, Graetz and Wilson 1984), although Hall *et al.* (1964) observed a greater frequency of establishment, with recruits appearing in 17 out of 36 years. Others have reported that a small amount of recruitment occurs in most years (Crisp 1978, Eldridge *et al.* 1990).

THE NATURE OF GRAZING IN CHENOPOD SHRUBLANDS

Animal Distribution

As indicated in Chapter 1, the distribution of sheep grazing in paddocks is uneven, being focussed around water points because of the need for sheep to drink regularly. Using sheep dung deposition as an index of stocking pressure, Lange (1985) showed that uneven sheep distribution could result in a large range of effective stocking rates within paddocks, from as high as six times the average paddock stocking rate down to no stocking pressure. However, sheep distribution in paddocks can also be influenced by the location of preferred vegetation types, shade, campsites and fences and the prevailing wind direction (Squires 1974, Lange 1985, Stafford Smith 1988). The importance of these factors in determining livestock distribution is governed by a hierarchy of needs of

the animals (Stafford Smith 1988), but since the relative importance of these factors varies over time, grazing patterns also will vary in time (Lange 1985, Stafford Smith 1988). For example, in winter the importance of shade and the need to visit the water point to drink are reduced, so sheep may spend more time grazing in areas of preferred vegetation than in summer. Nevertheless, the location of water generally remains the dominant factor affecting sheep distribution throughout the year.

Grazing Behaviour and Utilisation of Saltbush

In choosing their diet, herbivores are very selective. They discriminate between the class (e.g. shrub or grass), species and the various parts of plants (Arnold 1981, Stuth 1991). Within a plant, preference is for young leaf material and buds. This selection is interpreted as a strategy to maximise energy and nutrient intake and thus maximise fitness (Stuth 1991). But what is actually chosen by an animal can vary over temporal scales of hours to months depending on forage availability and the animal's physiological state (Arnold and Dudzinski 1967, Stafford Smith 1984, Stuth 1991). On a daily basis sheep tend to be less selective early in grazing periods and graze the most abundant and accessible plants so that intake is maximised. Later, as satiation approaches, the degree of selectivity increases so that material with a higher feed value is chosen, even though it may be less abundant (Stafford Smith 1984). Over a longer time-frame, as preferred feed is consumed herbivores are forced to switch to lower ranked species to maintain intake. For a more detailed discussion of foraging behaviour in livestock the reader is referred to Heitschmidt and Stuth (1991).

In the chenopod shrublands high levels of salts in saltbush and other perennial shrubs reduce their acceptability, making them a less preferred source of forage (Knowles and Condon 1951, Graetz and Wilson 1984). Instead, diet studies have shown that sheep prefer to graze the short-lived herbaceous species and grasses when available, only switching to the perennial shrubs when the herbage has been consumed or the grasses have flowered and hayed off (Leigh and Mulham 1966, Graetz and Wilson 1980, Graetz

and Wilson 1984, Graetz 1986). In western NSW, studies using fistulated sheep have shown that the proportion of saltbush in the diet of the animals varied from 0-99% over a three year period, with the highest proportions being recorded in late summer when short-lived feed was scarce (Graetz 1986). This variation in the utilisation of saltbush is the basis of the 'in-built' rotational grazing system suggested by Graetz and Wilson (1984), in which perennial shrubs may escape grazing for a time. However, sheep may consume considerable quantities of the perennial shrubs early in daily grazing periods even when other feed is available (Stafford Smith 1984).

Of the common perennial chenopod shrubs (including bluebush, *Maireana sedifolia*, and blackbush, *M. pyramidata*) saltbush is the most preferred forage. Together with its moderate protein content and digestibility (15% and 53% of dry weight respectively), this makes saltbush an important source of drought feed (Graetz and Wilson 1979). Sheep have been shown to maintain their body weight or record a slight weight gain when fed a diet of saltbush, provided that good quality water is available (Wilson 1966). The high concentration of salts in the leaves of saltbush increases the water requirements of sheep, because of the need for the salts to be excreted by the animal for it to maintain a favourable osmotic balance (Graetz and Wilson 1984).

IMPACT OF GRAZING ON SALTBUSH

Effect at the Individual Plant Level

Saltbush populations are considered to be easily degraded by grazing because of the inability of adults to tolerate defoliation. However, the severity of defoliation is important in determining the consequences of grazing for individual plants. While heavy grazing results in substantial bush mortality, moderate grazing appears to have little effect on plant survival (Osborn *et al.* 1932, Carrodus and Specht 1965). The effect of heavy grazing in causing bush death was clearly shown in a study by Wilson *et al.* (1969) on the Riverine Plain in N.S.W. in which the consequences of different levels of sheep

grazing were examined. All plants heavily defoliated by sheep had died within 23 months of the onset of heavy grazing (2.5 sheep/ha) while at the lightest stocking rate (0.6 sheep/ha) only 1% had died over the same period. Importantly, protection of shrubs from grazing following heavy defoliation failed to reduce bush mortality. Further work by Leigh and Mulham (1971) to more accurately define the response of saltbush to grazing produced similar results. They grazed sheep on saltbush plots for 10 days to achieve various levels of defoliation, with one group of plots being irrigated, and found that plants with fewer than 40 leaves remaining had increased rates of mortality (70-80% compared to 10-15% on ungrazed controls). Irrigated plants had lower mortality, but completely defoliated shrubs recorded mortality rates of 100% irrespective of soil moisture treatment.

In comparison, moderate grazing levels reduce the size (height and diameter) and biomass of shrubs (Graetz 1978, Graetz 1980), but Eldridge *et al.* (1990) reported that most shrubs rapidly recover following rainfall which is sufficient to initiate growth. In other studies, moderate levels of grazing have been reported to increase the vigour of shrubs (Osborn *et al.* 1932, Andrew and Lange 1986b), while Knowles and Condon (1951) considered occasional heavy grazing to be beneficial since the removal of the terminal buds was found to increase the production of lateral shoots.

The reasons for poor survival of saltbush following heavy defoliation are not clear and a number of possible explanations have been advanced. Leigh and Mulham (1971) attributed it to the inability of saltbush to initiate new growth from old woody stems, arguing that saltbush has most buds located on the young terminal shoots which are generally removed by heavy grazing. Hodgkinson and Baas Becking (1977) observed the slowing and cessation of root growth following defoliation of saltbush and suggested that this may be responsible for the poor survival of defoliated plants because of reduced water and nutrient uptake. A further explanation came from Coleman (1982) who suggested the lack of, or inability of saltbush to mobilise, stored carbohydrates at certain

times could contribute to the low tolerance of saltbush to defoliation.

Effect at the Population Level

In some studies grazing has been found to cause a variety of changes in saltbush populations, while in others no effects have been detected. These differences in the response of a population to grazing appear primarily to be a function of the grazing pressure applied, although comparisons between the numerous studies are made difficult by the assortment of experimental designs (from grazing gradient to small plot studies) used by different workers and the varying duration of the studies.

The high sensitivity of individual bushes to defoliation has been implicated as the main reason for changes in the structure of saltbush populations under grazing. The most dramatic effect is the reduction in the density of saltbush due to increased mortality rates of established shrubs (Barker and Lange 1969, Graetz 1978). A less obvious effect is an increase in the proportion of small shrubs due to the direct effects of grazing on size of established plants (Graetz 1978, Graetz 1980). Grazed saltbush populations also tend to have a greater proportion of male plants than ungrazed populations (Graetz 1978, Williams *et al.* 1978). This occurs because female shrubs are more heavily utilised and consequently suffer greater rates of mortality than males, since sheep apparently dislike grazing the granular male flowers (Graetz 1978). Because male flowers are borne in terminal spikes it is difficult for sheep to avoid them if grazing a male shrub. However, Graetz (1978) did not regard this shift in sex ratio as being of any consequence for the saltbush population. Grazing has also been found to reduce the proportion of shrubs in flower (Andrew and Lange 1986b).

Results contrasting with those above were obtained in an eight year study of the effects of grazing on the population dynamics of saltbush at 1200-1500 metres from water (Eldridge *et al.* 1990). Here it was found that there were no significant differences in population density, recruitment or mortality between grazed transects and those which were protected

from grazing for the period of the study. The interpretation of these results is made difficult though, because the defoliation intensity experienced by shrubs on the grazed treatment was not specified. In another study involving sheep grazing on 50 hectare plots at two stocking rates (0.16 and 0.24 sheep/ha), grazing for two years had no effect on the proportion of seedlings, juveniles, adults, senescent adults and dead shrubs in the population (Graetz 1986). The stocking rates in the grazed treatments were then increased and after a further two years of grazing there was a significant suppression of adults and an increase in the proportion of juveniles on the highest stocking rate treatments (0.4 and 0.6 sheep/ha). Graetz (1986) concluded that little or no grazing favoured senescence of saltbush, while heavy grazing encouraged the recruitment of juveniles by eliminating some adults and releasing seedlings from competitive suppression by adults.

A further effect of sheep grazing on saltbush populations concerns the palatability of the shrubs. By offering sheep a pasture composed of shrubs which originated from populations with varying grazing histories, Pearson *et al.* (1990) found that grazing over a period of many years can decrease the palatability of saltbush populations. This suggests a change in the genetic make-up of the population, but the ecological significance of this and the implications for pastoralism are not known.

Effect at the Landscape Level

Because the chenopod shrublands are a fairly uniform range type, the consequences of grazing for the whole landscape are essentially determined by the arrangement of paddocks and waters over a region. This provides a convenient basis for stratifying the landscape when examining the broad-scale impact of grazing, particularly since it is also at the scale of paddocks and water points that grazing management decisions operate (Stafford Smith and Pickup 1990). Consequently, vegetation change at this scale is generally described in terms of the piosphere.

As might be expected, the changes in saltbush population structure that occur as a result of grazing are distributed around water points in a piosphere pattern because of the gradients in grazing pressure focussed on water points. Osborn *et al.* (1932) were the first to describe this pattern of grazing impact, distinguishing four zones surrounding water points in which the condition of saltbush varied. Close to the water shrubs were small and sparsely foliated and plant density was low, while further away shrub size, condition and density were greater. They also commented that light to moderate levels of grazing in the second zone from water appeared to have increased plant vigour judging from the amount of young leaf tissue on the shrubs, as I discussed earlier. Subsequent more detailed studies by Barker and Lange (1969) and Graetz (1978) supported the early conclusions that shrub size, biomass and density were markedly reduced in the vicinity of water due to heavy grazing and the effect of grazing on the shrubs decreased as distance from water increased. This relationship between distance from water and shrub density, size, biomass and the sex ratio of shrubs was shown to be described by the sigmoid population growth curve (Graetz and Ludwig 1978). However, in considering entire paddocks, areas of high grazing impact and others of low impact which are unrelated to distance from water can be found and may be related to other factors affecting sheep grazing patterns such as wind direction or campsites (Graetz 1978).

The aforementioned studies were of long-established piospheres but Andrew and Lange (1986b) showed that a long grazing history is not necessary for these patterns to become evident. In their study of the initial impact of sheep stocking around a new water point in shrublands that were previously little affected by grazing, they observed piosphere patterns after only two years of grazing. These effects were in variables that reflect contemporary circumstances, including the proportion of saltbush plants in flower and the defoliation of individual shrubs. A piosphere pattern in shrub survival, which reflects the cumulative effects of conditions over a longer time frame, was detected following re-assessment of the site after eight years of stocking.

CHAPTER 3

MATERIALS AND METHODS

INTRODUCTION

As discussed in Chapter 1, the aim of this study was to examine the potential long-term impact of sheep grazing on saltbush populations over the extensive areas of sheep paddocks in the chenopod shrublands. It was decided that the best approach to achieve this aim was to investigate in detail the population dynamics of saltbush throughout a single typical paddock grazed by sheep. With limited resources it was not considered practical to replicate the study by examining more than one paddock. However, in view of the unpredictable and erratic nature of rainfall in the Australian arid zone (Stafford Smith and Morton 1990), it was considered necessary for the study to continue for as long as possible to ensure a good range of seasonal conditions was encountered. Consequently the study continued for 6.5 years, from October 1987 to March 1994.

This chapter describes the general location of the study, the paddock used and the rainfall and stocking rates during the study. Specific information concerning the experimental procedures for the various components of this study are presented in the relevant chapters.

THE STUDY AREA

Location

This study was carried out on Katunga Station (32.44 S, 137.08 E) in the north-eastern region of the Eyre Peninsula, South Australia (Figure 3.1). Katunga Homestead is approximately 50 km north-west of Whyalla, on the outskirts of Iron Knob. The property runs south from Iron Knob towards Iron Baron covering approximately 365 sq. km. and adjoins the western boundaries of the well-studied Middleback and Roopena Stations, the former being the site of the University of Adelaide's Middleback Field Centre.



Figure 3.1. The location of the study site on north-eastern Eyre Peninsula in South Australia.

Climate

The distinguishing features of the climate of the region are its semi-arid to arid nature, the highly erratic and unpredictable rainfall, and the long, hot summers. Mean annual rainfall for Iron Knob (1911-1992) is 221 mm (Commonwealth Bureau of Meteorology data), while for Middleback Station, 20 km east of Katunga, the mean for the years 1925-1992 is slightly less at 211 mm. The total annual rainfall is highly variable from year to year, and is biased towards lower totals, with a median for Iron Knob of 202 mm. However, there are rare years of very high rainfall. Annual rainfall totals recorded for Iron Knob range from 83 mm (in 1957) to 545 mm (in 1974). There is little evidence of seasonality in rainfall amount at Iron Knob, with average monthly rainfall being uniformly distributed throughout the year (Figure 3.2). However, rainfall events in winter tend to be smaller but more frequent than in summer when fewer heavy falls can be expected (mean of 5.3 rain days per month in winter but 2 rain days per month in summer). Like the yearly rainfall, monthly rainfall is highly erratic and is skewed towards lower totals, as indicated by the lower median values (Figure 3.2). Average annual evaporation in the region is high, being approximately 2200-2400 mm or ten times the mean annual rainfall (Laut *et al.* 1977). Temperatures at Whyalla in January (summer) are high, with a mean daily maximum of 28.8°C, while winters are cool, with a mean daily minimum of 7.3°C in July (Figure 3.3). Temperature records for Iron Knob are not available.

Topography and Soils

The main topographic feature in the region is the Middleback Range, a line of low hills (relief <250 m) running south from Iron Knob just to the west of Katunga. Apart from this range the topography is mostly a low undulating system of interfluvial slopes and plains with washes and basins (Laut *et al.* 1977). Katunga is located on the gentle eastern slopes of the Middleback Ranges and extends onto the surrounding plains.

The soils in the area are derived from alluvial and aeolian sedimentary parent material

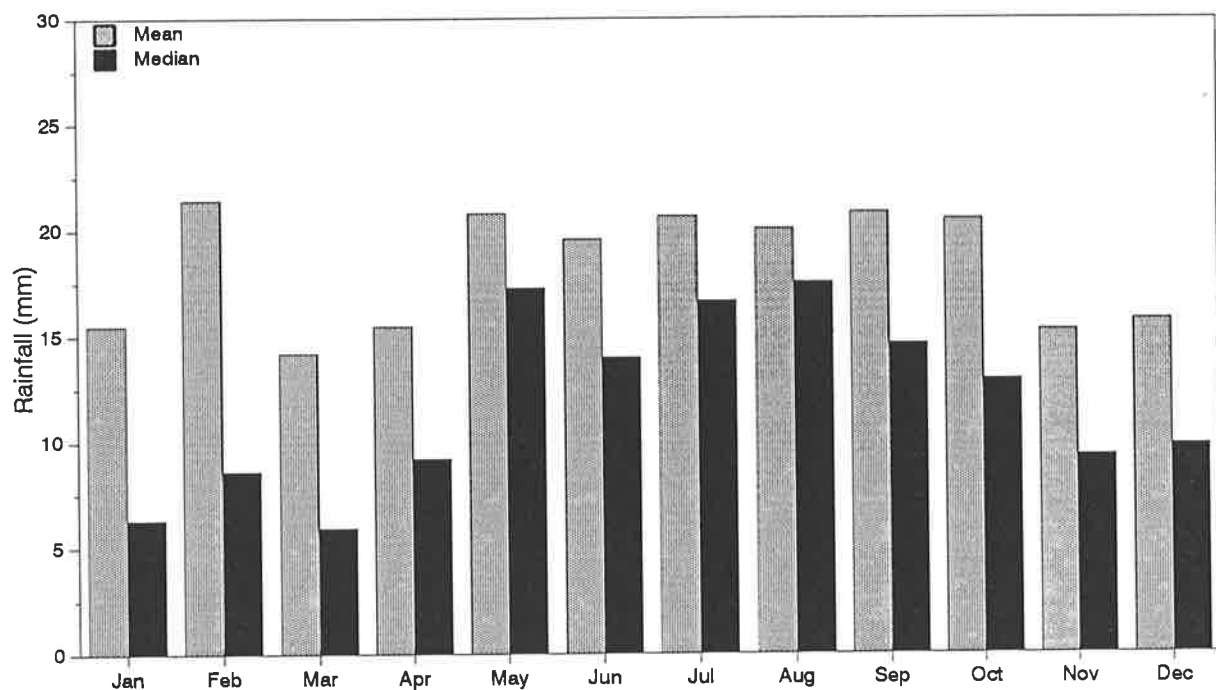


Fig. 3.2. Mean and median monthly rainfall (1911-1992) at Iron Knob (Commonwealth Bureau of Meteorology 1994).

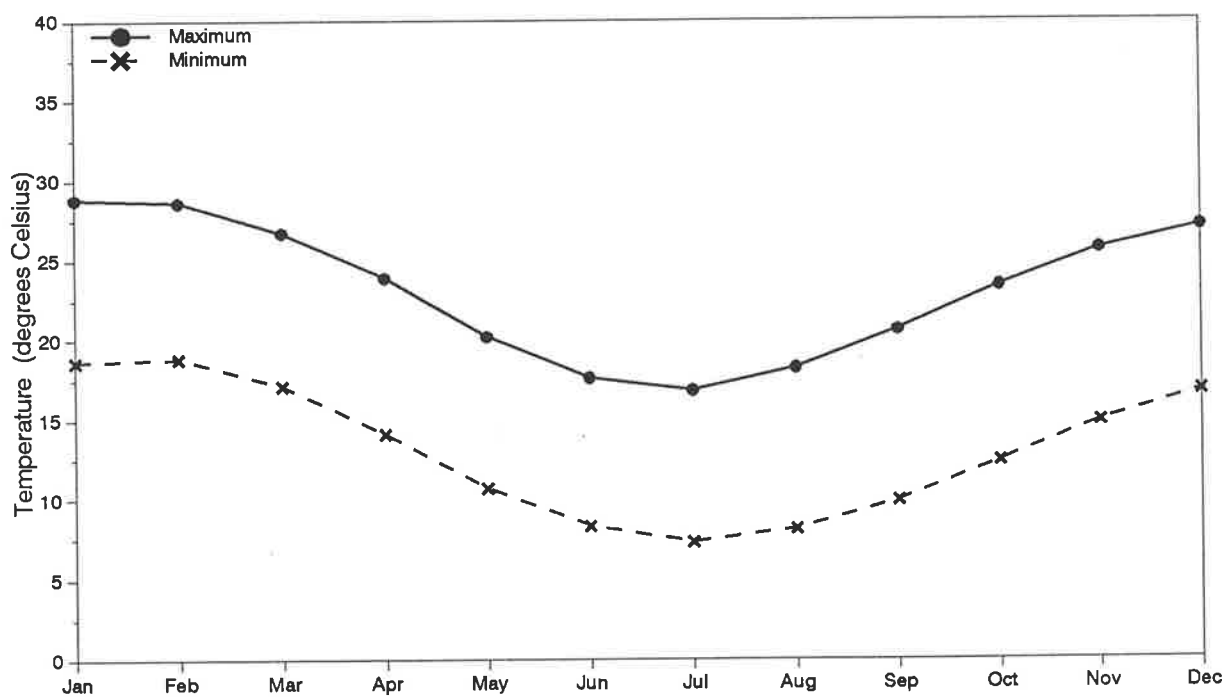


Fig. 3.3. Mean daily maximum and minimum temperatures for each month at Whyalla, 50 km south-east of Iron Knob (Commonwealth Bureau of Meteorology 1994).

(Jessup and Wright 1971) and are predominantly red-brown calcareous earths with a clay-loam texture (Gc 1.12 and Gc 1.22; Northcote 1968), although in some areas the texture is distinctly sandy. Soil texture in the profile is gradational, with the clay fraction increasing with depth, and a marked layer of calcium carbonate nodules occurs at depths of between 20-50 cm (Northcote 1968). Soils are generally well-drained but in the washes and basins, less well-drained crusty duplex soils (Dr 1.43) predominate (Wright 1985).

Vegetation

Crocker (1946) classified the vegetation of north-eastern Eyre Peninsula into two edaphic complexes. One of these is an *Acacia papyrocarpa* - *Casuarina cristata* complex, which is essentially the chenopod shrublands covering the entire Middleback and Katunga area and extending to the north. The other is a *Eucalyptus oleosa* - *E. gracilis* - *E. dumosa* complex which is the mallee eucalypt woodlands found to the south and west of Katunga (Wotton 1993). Within the *Acacia papyrocarpa* - *Casuarina cristata* complex Crocker identified four associations:

- 1) *Acacia papyrocarpa* - *Myoporum platycarpum*
- 2) *Casuarina cristata* - *Maireana sedifolia*
- 3) *Atriplex vesicaria* - *Maireana sedifolia*
- 4) *Maireana sedifolia*.

These are similar to the three main vegetation associations identified in the Middleback area by Reid (1984) which are also typical of the vegetation on Katunga. These associations are:

- 1) **Chenopod low open-shrubland.** Generally, these plant communities are dominated by bluebush (*Maireana sedifolia*) and saltbush (*Atriplex vesicaria*). Both species occur together on the interfluvial slopes and plains and saltbush dominates in the low lying washes and basins. In heavily grazed areas *Maireana pyramidata* (blackbush) dominates the washes and basins and bluebush dominates the plains and slopes. *Rhagodia ulicina* and *Lycium australe* are two shrub

species also common in these communities.

2) **Western myall low open-woodland.** This is a common vegetation association, occurring over much of the area. It consists of a scattered but dominant overstorey of *Acacia papyrocarpa* (western myall) with an understorey of bluebush, saltbush and blackbush in various proportions. Lower lying areas have a higher tree density, and tall shrub and other tree species, including *Eremophila scoparia*, *Alectryon oleifolius* (bullock bush) and *Myoporum platycarpum* (sugarwood), may also be locally dominant in these areas. Under the canopies of the larger trees (e.g. western myall and sugarwood) *Enchylaena tomentosa* and *Rhagodia spinescens* dominate.

3) **Black oak low woodland.** This association is comprised of quite dense groves of black oak (*Casuarina cristata*) trees, which result from the clonal nature of the species. Groves generally range in size from about one to one hundred hectares and are normally found on deeper sandier soils. Species in the understorey can include saltbush, bluebush, blackbush, *Enchylaena tomentosa* and *Rhagodia spinescens*.

Land Use

The two major land uses in the region are sheep grazing for wool production, with most land in the region being allocated for this purpose, and iron ore mining, which is restricted to the Middleback Ranges. Initial attempts to run sheep in this region in the 1850s and 1860s failed because of poor water supplies and recurring drought, which resulted in the land being abandoned on several occasions (Richardson 1925). Land in the Katunga and Middleback area was first taken up in small runs by various people between 1868 and 1877, but it was not until more reliable water supplies were established in the early 1900s that permanent pastoral occupation was possible. An important part of the development of Middleback and Roopena Stations involved the construction of an extensive water piping system to distribute water from one major reliable well to locations throughout the properties (Lange *et al.* 1984). In addition to underground

water, pastoralism in the area relies on an extensive series of surface catchment dams which retain water for varying periods. Some properties also have access to water piped more than 200 km from the River Murray in the east of the State.

Land is occupied for sheep pastoralism in this area, as it is in the majority of the SA rangelands, under a leasehold system administered by the State Government. Lease agreements are initially issued for 42 years. They include covenants imposing maximum stock numbers for each lease and a requirement that the vegetation resources of the lease be maintained at least in the condition existing at the time of the granting of the lease (South Australia 1989). A system of range condition monitoring and assessment is implemented by the government.

Pastoral enterprises in the region are large, ranging from 150 to 1000 sq. km. The majority of pastoralists in the region implement the Waite/Nicolson pastoral management model (Lange *et al.* 1984). This involves the sub-division of a property into small paddocks (less than 2000 ha), with one or more permanent water points per paddock, no more than 350 sheep per water and an overall stocking rate not exceeding 5.6 ha/sheep. These stocking rates are conservative in comparison to general industry standards (Lange *et al.* 1984) and because of these low rates destocking or spelling of the country is not considered necessary, even in drought. Despite several changes of ownership, Katunga has been managed for many years in accordance with these principles. Since 1986 the property has been managed by the Nicolson families from Middleback and Roopena Stations. They have continued to use stocking rates similar to those used by the previous owner (A.D. Nicolson pers. comm.), who had run the property since the early 1970s.

THE STUDY Paddock

General Description

A 1100 ha paddock named Yanaby was selected for the study. In most aspects, including its size, vegetation composition and condition, water availability for livestock and management, Yanaby is a typical paddock for the region. It is an almost rectangular paddock, approximately 5 km $\times$ 2 km, aligned north - south (Figure 3.4). It contains one water point, a surface catchment dam, on the eastern fence line slightly to the northern end of the paddock. This is a reliable water supply which has only dried up twice (in 1970 and 1983) in recent years. The dam is believed to have been constructed in the 1920s (A.D. Nicolson pers. comm.). Another water supply, fed from the River Murray pipeline, has been installed in the north-west corner of the paddock but this is not used unless the dam runs dry.

Livestock and Management

The paddock is usually stocked with 120 ewes. These are introduced to the paddock in late March - early April each year following shearing. The ewes lamb in June-July and apart from being removed for a few days during October for crutching, the ewes and lambs remain in the paddock until shearing in the following March. In addition to sheep, western grey kangaroos, *Macropus fuliginosus*, (estimated to number 100-200) and rabbits, *Oryctolagus cuniculus*, were present in the paddock.

Yanaby was sub-divided to its current size in the early 1970s, when a road was constructed connecting Iron Knob and Iron Baron. Prior to then it was part of a larger paddock which included land to the west of the current paddock. The original paddock was stocked with 300 ewes and although there was another dam in the western part of the original paddock the sheep mainly watered at Yanaby dam, apparently preferring to avoid the denser tree overstorey near the western dam (A.D. Nicolson pers. comm.). It therefore seems likely that the vegetation in Yanaby has experienced higher levels of grazing in the past than now.



Figure 3.4. The layout of the study paddock, Yanaby, showing the main vegetation associations, the location of the water point (W) and the location of the nine permanent study sites (indicated by the letters A-I).

Vegetation

The vegetation in the paddock includes the three common associations identified by Reid (1984) which were described earlier. A map of the distribution of the vegetation, prepared from an examination of aerial photos and from surveys through the paddock, is shown in Figure 3.4. The main features are the low open shrubland covering most of the northern end of the paddock and the western myall low open-woodland to the south. A large area of black oak woodland is on the western fence. Consequently, the most common species in the paddock were *M. sedifolia*, *Atriplex vesicaria*, *Acacia papyrocarpa*, *Alectryon oleifolius* and *C. cristata*. Saltbush (*Atriplex vesicaria*) occurs in all three associations, either mixed with bluebush (*M. sedifolia*) in various proportions or as the only chenopod shrub. However, saltbush is more common in the southern part of the paddock, and past grazing has eliminated the species from an area extending about one kilometre out from the water point.

Other common perennial shrub and tree species in the paddock include *Senna* spp. (occurring as individuals or as small stands scattered throughout the paddock), *Eremophila scoparia*, *Myoporum platycarpum*, *Santalum spicatum* and *Pittosporum phylliraeoides* (all occurring as individuals scattered throughout the paddock), *Lycium australe* and *Nitraria billardiarei* (occurring in low lying areas, mainly near the dam) and *Maireana georgei* (chiefly in the heavily grazed areas near the water point). The grass and herbage layer which appeared after good rains included *Stipa nitida* and *Danthonia caespitosa* (short-lived perennial grasses), *Schismus barbartus*, *Erodium cygnorum* and *Tetragonia tetragonioides* (annual/ephemeral grasses and forbs) and *Sclerolaena obliquicuspis* (a short-lived chenopod sub-shrub).

ESTABLISHMENT OF STUDY PLOTS

Permanent study plots were established at nine sites spread across Yanaby during winter 1987 (Figure 3.4). These plots formed the basis of the majority of the field work in this

study, including the defoliation of saltbush by sheep and the population dynamics and flowering of saltbush, while samples for the estimation of the saltbush soil seed bank were collected from areas in the vicinity of the plots. The sites were selected to include a good range of saltbush 'populations' from as many areas in the paddock as possible. At each site four 20 m $\times$ 10 m plots were selected which appeared by eye to be representative of the saltbush population (in terms of shrub density and biomass) in the area and which also appeared as similar to each other as possible. The four plots for each site were chosen so they were all within 500 m of each other, and preferably 300 m of each other. Once selected one of the four plots at each site was randomly chosen to be an exclosed plot and a 90 cm high cyclone mesh fence was constructed around it. This fence prevented access to the plot by sheep but kangaroos could enter the plot by going over the fence and rabbits could easily pass through the wire mesh. The remaining three plots at each site constituted replicates of the grazed treatment and were simply marked with small wooden pegs.

CONDITIONS DURING THE STUDY

Rainfall

The study period, from October 1987 to March 1994, was characterised by typically variable rainfall. Annual totals for Iron Knob for the seven years from 1987 to 1993 were 202, 162, 265, 165, 186, 468 and 223 mm, respectively. These totals are within rainfall deciles 5, 3, 8, 3, 5, 10 and 7, respectively, indicating that the study period could not be considered to be unusually dry and only the high rainfall of 468 mm in 1992 could be regarded as a rare event. However, annual totals are misleading since there was substantial variability in rainfall within years, as indicated by the monthly rainfall totals (Figure 3.5). This within year variability resulted in poor rainfall for a lengthy period beginning just before the study commenced. For the 12 months from March 1987 to February 1988 rainfall was 136 mm (decile 2) and for the subsequent 12 months to February 1989 a total of 153 mm (decile 3) was received. This period culminated in two

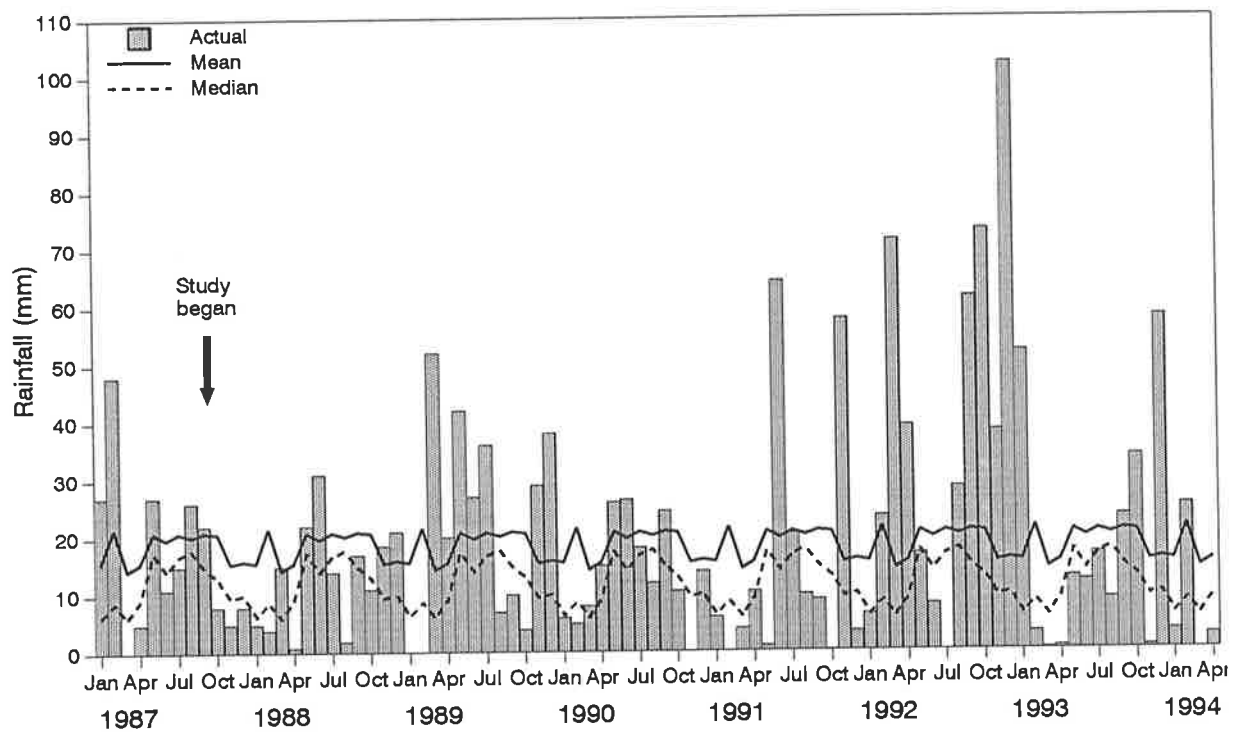


Fig. 3.5. Actual monthly rainfall at Iron Knob during the study and monthly means and medians (Commonwealth Bureau of Meteorology 1994).

months without rain followed by 52 mm in March 1989. In contrast, a lengthy period of good rains extended from June 1991 until January 1993. This period began with isolated months receiving rains of around 60 mm and finished with a period of five consecutive months each with rain greater than 38 mm, and one month in this period receiving 102 mm.

Rainfall was also measured in the paddock using a storage gauge, which was read on each visit to the paddock. From these readings it appeared that rainfall was similar to the official recordings at Iron Knob. The data from Iron Knob has been used in this study as it was recorded daily.

Sheep Numbers and Management

Normal management procedures were adhered to during this study, including the stocking of the paddock at most times with the usual rate of 120 ewes. Numbers varied from this on occasions due to some sheep escaping through a collapsed fence (i.e. December 1988-February 1989), or short-term increases in numbers during mustering for shearing when sheep from adjacent paddocks were held in Yanaby for from 1 to 14 days. Information on the dates the paddock was stocked, the number of sheep and the dates the sheep were removed from the paddock, was supplied by the managers. Detailed data were obtained for only the first three years of the study (November 1987 - November 1990). Because the paddock was stocked with breeding ewes which produced lambs during each year, the physiological status and metabolic requirements of the sheep varied, so the number of sheep and lambs in the paddock was converted to dry sheep equivalents (DSE) on a weekly basis, using the conversions published by Reid (1981).

Actual stocking pressure generally varied within each year from a low of 120 DSE in April (excluding times of destocking at shearing and crutching) to a high of 220-250 DSE over spring and summer, unless sheep numbers were adjusted downwards slightly following crutching in spring (Figure 3.6). The mean number of sheep (DSEs) per week

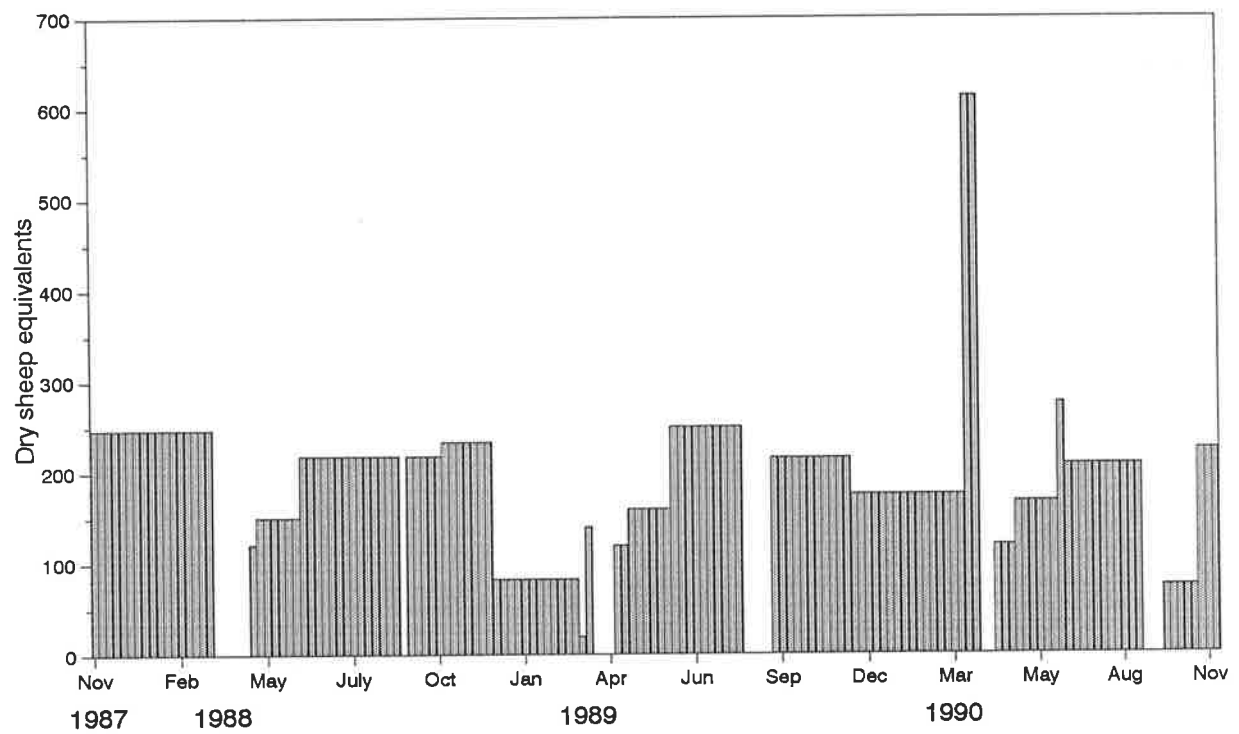


Fig. 3.6. Stocking pressure (in dry sheep equivalents) in Yanaby for each week of the first three years of the study.

in the paddock between November 1987 and November 1990 (again excluding destocked periods) was 194.8 which is equivalent to an overall stocking rate for the paddock of 5.4 ha/DSE. Sheep numbers for the second half of the study from December 1990 to March 1994 followed a similar pattern to the first three years, but following substantial sheep losses due to blow-fly strike in spring 1992 the number of ewes introduced to the paddock after shearing was reduced to approximately 100.

CHAPTER 4

PATTERNS OF SALTBUSH DEFOLIATION BY SHEEP

INTRODUCTION

Background

Defoliation can affect plants by altering rates of growth, reproduction and mortality (Jameson 1963, Archer and Smeins 1991, Huntly 1991). However, the focus of much of the large body of literature on the effects of large herbivores on plants has been on the question of biomass production and, in particular, whether plants can compensate or even over-compensate for the loss of tissue to herbivores. This question has been the centre of considerable debate (see Belsky 1986, McNaughton 1986) but the conflicting findings of many studies can be reconciled by recognising the differing scales of interest in the studies (i.e. plant or community, short- or long-term, and aboveground, belowground or total plant biomass) (Brown and Allen 1989, Milchunas and Lauenroth 1993). The environmental conditions (e.g. moisture and nutrient availability, presence of competitors) under which a study is performed are also important in determining the observed effects of grazing (Trlica and Rittenhouse 1993). Most investigations have also been carried out on grasses under controlled and somewhat artificial conditions where defoliation treatments are applied by hand clipping of plants or by short-term intensive grazing by herbivores (Hart and Norton 1988). Nonetheless, these studies have revealed some important effects of defoliation on plants.

The immediate effects of herbivory are a reduction in photosynthetic leaf area, the removal of active meristems from which new leaf tissue is produced and which are sinks for photosynthates, and a loss of nutrients stored in the removed tissue (Noy-Meir 1993). As a consequence the rates of physiological processes such as photosynthesis, carbon allocation and storage are altered (Briske 1991, Chapin 1991, Turner *et al.* 1993), generally resulting in a decline in plant growth rate (Noy-Meir 1993). In the longer term the intensity, frequency and timing (in relation to phenological stage or environmental

conditions) of defoliation will be important in determining the consequences of defoliation for a particular plant (Bosch and Tainton 1988, Archer and Pyke 1991, Chambers and Norton 1993). The intensity of defoliation (i.e. how much tissue is removed) determines the amount of plant tissue and meristems that remain undamaged for use in recovery (Brown and Stuth 1993), while the frequency of defoliation (i.e. how often tissue is removed) determines the length of time for recovery and thus the degree to which carbohydrate reserves are regained (Turner *et al.* 1993). These factors play a fundamental role in the recovery of a plant from defoliation (Menke and Trlica 1983, Briske 1991, Brown and Stuth 1993). Doak (1992), however, pointed out that the intensity and frequency of defoliation will interact to determine the impact on a plant since they are not separate processes with distinct effects. Thus, for example, chronic grazing (i.e. the repeated removal of small amounts of tissue) can have severe negative effects on plants despite the amount of tissue being removed at each defoliation being so small as to have little effect on the plant if defoliation was less frequent.

In the field, the level of defoliation experienced by plants of a particular species will depend on many factors. These include the amount of plant biomass available relative to herbivore numbers, the location of the plants relative to other factors which affect herbivore distribution (such as water, shade and wind), the feed quality and palatability of the plant, the availability of other plant species and the physiological state of the animal (Arnold 1981, Coughenour 1991, Stuth 1991).

Having an appreciation of the patterns of defoliation in the field is vital to understanding and managing the impact of herbivores on plants (Gammon and Roberts 1978, Graetz and Wilson 1979, Hodgkinson 1980, Coughenour 1991, Stuth 1991). Measurements of defoliation will clarify the roles of various factors in causing observed changes in plant populations. These factors include grazing by domestic stock and wild herbivores and climatic fluctuations, especially drought. The effects of grazing and drought on plant populations are often similar (e.g. reduced growth, reproduction and survival), so it is

important to distinguish their respective impacts (Hart and Norton 1988, Coughenour 1991). A detailed knowledge of grazing patterns will also identify limitations in management practices and serve as a basis for the development of improved management recommendations. However, it is rare for quantitative measurements of defoliation to be made in grazing studies even though the usual qualitative estimates are often inaccurate (Milchunas and Lauenroth 1993). Indeed, Gammon and Roberts (1978) noted that a lack of knowledge of actual patterns of defoliation can lead to conflicting management recommendations, even where there is general agreement on the desired level of defoliation.

Aims

The level of grazing of saltbush by sheep in large full-scale paddocks has not been quantified. Dung deposition patterns and direct observation of sheep have shown that usage of paddocks varies spatially and temporally (see Chapter 2). Together with diet selection studies, this suggests defoliation of saltbush by sheep is also likely to vary spatially and temporally. However, dung accumulation and time spent at a site are poor indicators of grazing pressure on plants (Taylor *et al.* 1987). The lack of data on the actual severity of defoliation of saltbush is one limitation in our ability to effectively manage the entire saltbush population in a particular paddock. A knowledge of the patterns of defoliation in relation to the various population processes will facilitate the development of management strategies to ensure population survival.

The aims of this study, therefore, were to:

- 1) quantify the severity of saltbush defoliation due to sheep at nine sites spread throughout the study paddock under a range of seasonal conditions.
- 2) quantify the effects this grazing has on the levels and fluctuation of saltbush biomass.
- 3) examine the temporal and spatial variation in defoliation in relation to herbage availability, distance from water and sheep distribution patterns.

METHODS

Experimental Methods

Estimation of Defoliation Intensity

I chose to measure defoliation by monitoring the loss of discreetly tagged leaves on bushes on both the grazed and ungrazed plots at the nine permanent study sites located throughout the paddock. I tagged a leaf near the shoot apex on ten shoots spread over the outer canopy of each of 20 bushes for each treatment per site. The 20 bushes were randomly selected, but for the grazed treatment they were shared over the three grazed plots at each site, with two plots having seven marked bushes and one with six. The leaves were tagged by applying small dots (< 2 mm diameter) of yellow acrylic paint, with a red identification band painted around the base of the tagged shoots to aid re-inspection. This tagging method has no effect on the selection of shoots by sheep, and over grazing intervals of about a week the loss of the tags is correlated with the loss of shrub foliage biomass (Lange 1984). For much of the study low foliage biomass on shrubs on the grazed treatment at the site closest to the water point meant that it was only possible to tag five shoots per shrub for that treatment. Leaf age in saltbush is approximately 12 months (Charley 1971), which facilitates the use of leaf-marking in estimating defoliation by herbivores.

For the long observation periods in this study it is necessary to assume that little or no plant growth occurs, so that the tag to leaf ratio remains constant. If this assumption holds, the method provides an estimate of the percentage loss of the initial standing crop of leaf tissue over the entire period that a set of leaf-tags is followed, as well as the progressive loss for each six week period. Similarly, this method can provide an estimate of the percentage of initial foliage biomass at the time of tag application which remains at the end of the period, again assuming no growth occurs. However, leaf-marking does not provide an absolute measure of the weight of biomass removed during each interval or remaining at the end of the period. In addition, since initial standing biomass varied between sites and shrubs and also between the occasions when new tags were applied, the

loss of the same percentage of initial standing crop on different shrubs or at different times could represent varying weights of biomass. Therefore, presentation of this data as a rate (percent biomass loss per day) best demonstrates the temporal patterns of grazing pressure experienced by the shrubs.

The level of defoliation of saltbush was quantified for the first three years of the project. A new set of leaves was tagged on eight occasions during the period from November 1987 to November 1990 and counts of the number of tags remaining usually were made at intervals of six weeks. While the intention was to apply a new set of tags when the number of tags at any site fell below 10% of the initial number, this proved difficult to achieve since tag loss on grazed plots at many sites was much more rapid than expected. Together with the considerable amount of time required to apply a set of tags, and with limited resources, this meant that it was not possible to apply new tags as originally intended. I minimised potential problems with rapid growth of the shrubs by tagging a new set of shoots following each period of growth, and on one occasion (winter 1990) tags were not counted because of rapid shrub growth during the grazing interval. For many grazing intervals the assumption of negligible growth held.

In view of the limitations of this method, better estimates of saltbush defoliation by sheep may have been obtained by actual measurements of standing foliage biomass every six weeks. However, the large amount of work required to obtain accurate estimates of shrub biomass (Andrew *et al.* 1981) was considered prohibitive in a large-scale study such as this. Despite the limitations of leaf-marking in measuring defoliation, I believe that this method gave sufficiently accurate results for the purposes of my study.

Estimation of Saltbush Biomass

To provide a general measure of the effects of grazing on saltbush foliage biomass, estimates of shrub biomass were made approximately every six months, usually in April and October in each of the three years of the defoliation study and for a further 2.5 years

following that. The estimates were made using a shrub dimension technique (Andrew *et al.* 1981). This involves measuring the height, length and maximum width normal to the length vector of the experimental bushes and then constructing a calibration regression using the measurements and biomass of shrubs harvested from outside the experimental area. On each plot I measured all saltbush and bluebush shrubs within a 10×5 metre sub-section of the plot. After harvesting, the calibration shrubs (normally 15 shrubs on each occasion, harvested from the paddock adjoining Yanaby) were stripped of all leaf and soft stem material which was then oven-dried at 80°C for 48 hours and weighed. Woody material was excluded from the estimates. On each occasion a number of simple regressions were tried, using the shrub measurements both alone and in combination (e.g. cross-sectional area, volume), to find the best predictor of biomass. Mean shrub biomass and biomass per unit area were then calculated.

Estimation of Herbage Biomass

Herbage biomass (i.e. the biomass of ephemeral and short-lived perennial forbs and grasses) was estimated from colour 'landscape view' photographs of each $20 \text{ m} \times 10 \text{ m}$ plot using a 'comparative yield' method. Photographs were taken from a standing position at one corner of each plot, with the camera field of view focussed on the centre of the plot. These were taken each time the tags were counted. From the complete set of photos a subset of 11 photostandards was selected which represented the range of herbage biomass present during the study, in increments of approximately 10%, from 0-100%. These standards were then used to give all other photos a score from zero to ten. The photostandards were calibrated by comparison with twelve photos of known herbage biomass, assuming a linear relationship between biomass score and actual dry weight (as in Noble 1977). The calibration photos were taken on two occasions from four locations in Yanaby, to represent a wide range of herbage yields. For each of the calibration photos the herbage in a $40 \times 0.1 \text{ m}$ strip extending away from the point of photography was harvested, dried at 80°C for 48 hours and weighed.

Dung Deposition

Collections of sheep, kangaroo and rabbit dung were made from each plot to ascertain the potential grazing pressure of each species on each plot. Collections were made from a 30 m $\times$ 2 m belt transect superimposed over each of the grazed plots and from a 20 m $\times$ 2 m transect on each of the exclosed plots. Collections were generally made the week prior to the tag counts (i.e. every six weeks). On returning to the laboratory the dung was sorted by species, oven-dried for 48 hours at 80°C and weighed. Weights for the exclosed plots were then adjusted to account for the smaller size of the transect.

Statistical Analysis

The main interest in the analysis of this data was the severity of sheep grazing of saltbush and the degree of variation in grazing between different parts of the paddock.

Differences between sites and grazing treatment (i.e. sheep grazed or exclosed) in the proportion of initial shrub biomass remaining at the end of each six week observation period were compared using mean score analysis. This is a weighted least squares method as suggested by Bhapkar (1968) for the analysis of contingency tables with a quantitative response. This analysis was performed on the tag counts using the CATMOD (categorical data modelling) procedure in the SAS/STAT statistical analysis software package (SAS Institute 1988). This procedure tests the homogeneity of mean scores, and I used it first to test the overall site $\times$ grazing treatment interaction for each observation period. The contingency table was then broken down to examine the effect of site and grazing treatment separately. The inflated probability of Type I errors when the number of comparisons is high, was ignored. The rate of biomass loss (i.e. tag loss) between observation periods was compared between sites, treatments and dates using analysis of variance.

The regression option in the CATMOD procedure was used to test for linear relationships between mean score and cumulative sheep dung deposition and distance from water. Similarly, simple linear regressions were used to test for linear relationships between

defoliation rate (percentage biomass loss per day due to sheep grazing) and dung deposition, distance from water and saltbush biomass. These regressions were performed using the Statistix software package (Analytical Software 1991). However, these models were invariably poor and are not presented.

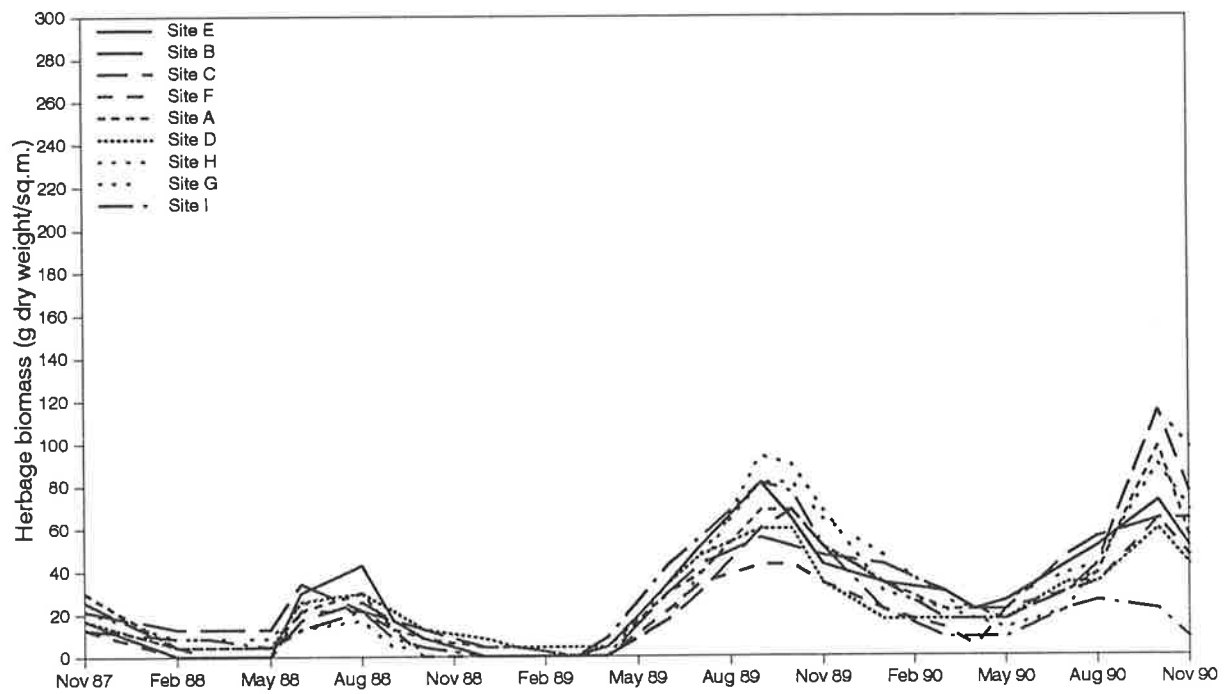
RESULTS

Availability of Herbage Biomass

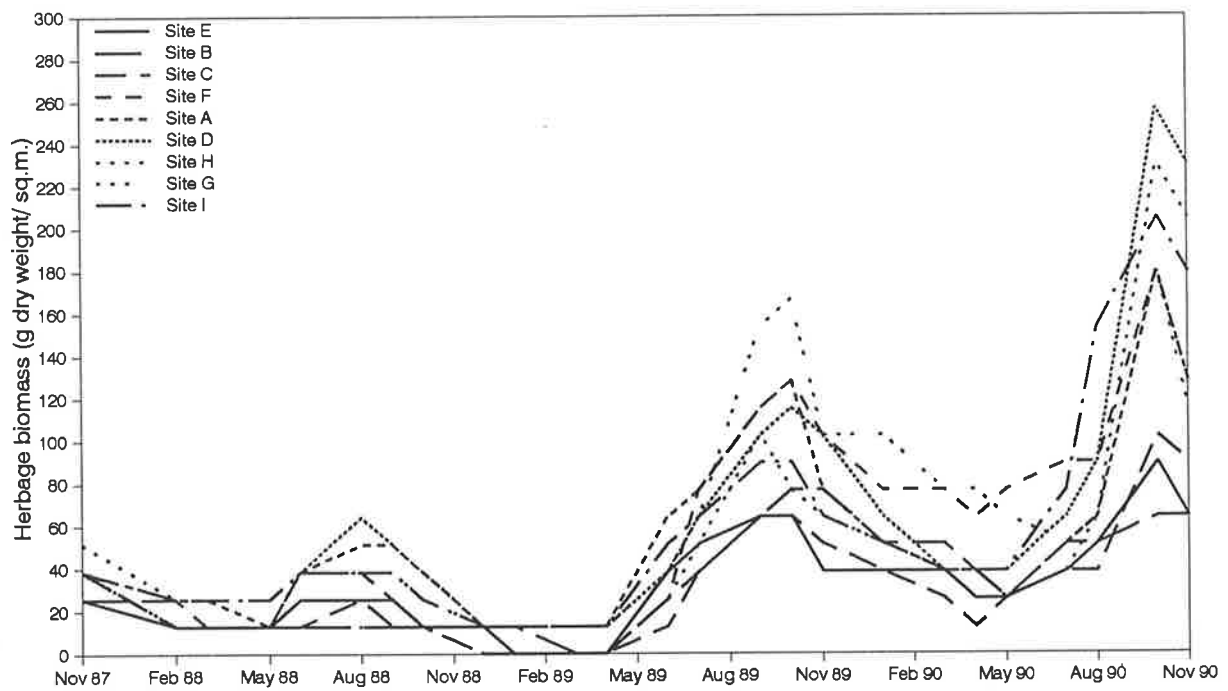
Herbage biomass fluctuated seasonally, peaking in winter or spring each year and bottoming out in autumn (Figure 4.1). The abundance of herbage biomass also varied between years depending on rainfall (compare Figure 4.1 with rainfall chart, Figure 3.5), with peak levels in the first year (1988) being at least half those of the following two years. With poor herbage growth during winter in 1988, herbage levels were negligible on grazed plots for about four months during the subsequent summer and early autumn. In general, the exclosed plots had higher herbage biomass than the grazed ones. The maximum herbage biomass recorded was approximately 260 g dry weight/sq. m. on the exclosed plot at site D in October 1990, while during the dry period prior to April 1989, herbage levels were negligible on most grazed plots.

Patterns of Saltbush Defoliation

The study was characterised by two distinct periods which had markedly different patterns of saltbush defoliation. The intensity of defoliation on grazed plots was surprisingly high at most sites during the first 12-18 months of the study (up to April 1989), with as little as 2% of initial foliage biomass remaining on some shrubs after 6-12 weeks (Figure 4.2). In contrast, the exclosed plots recorded significantly lower levels of defoliation during this period (see Table 4.1 for the results of the mean score analysis), although an increase was observed towards the end of 1988. The mean score analysis also showed that the site $\times$ grazing treatment interaction was significant on all assessment dates ($P < 0.001$). The two grazed treatments furthest from the water point (site G at 2800 m and site I at 3400



(a) Grazed plots.



(b) Exclosed plots.

Fig. 4.1. Herbage biomass on grazed and exclosed plots at nine sites in Yanaby during the period that saltbush defoliation estimates were made. The values for the grazed treatment are the means of three plots.

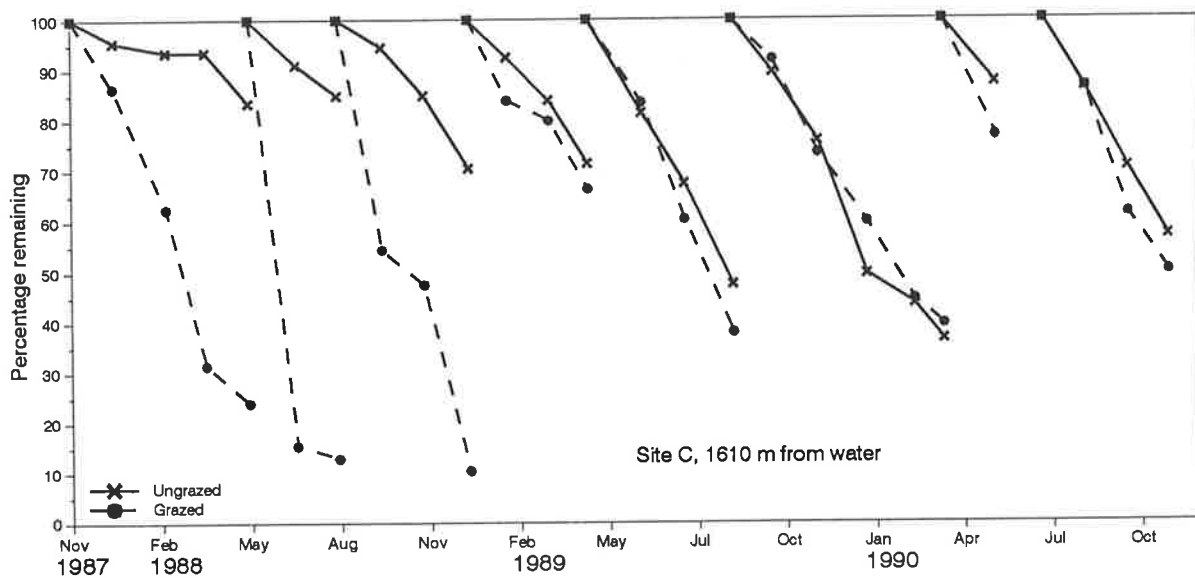
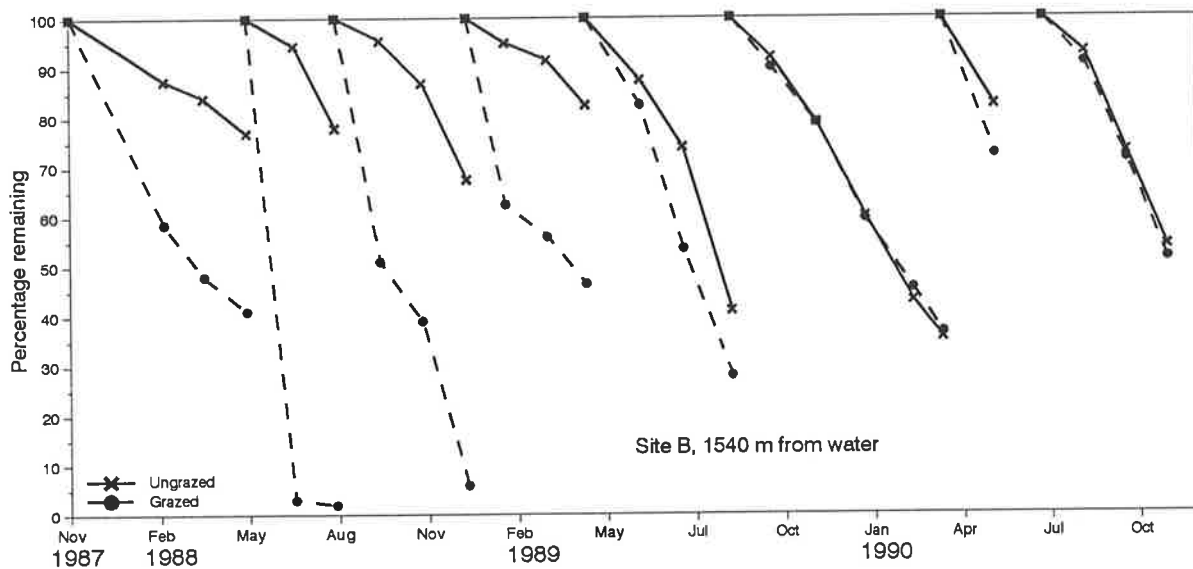
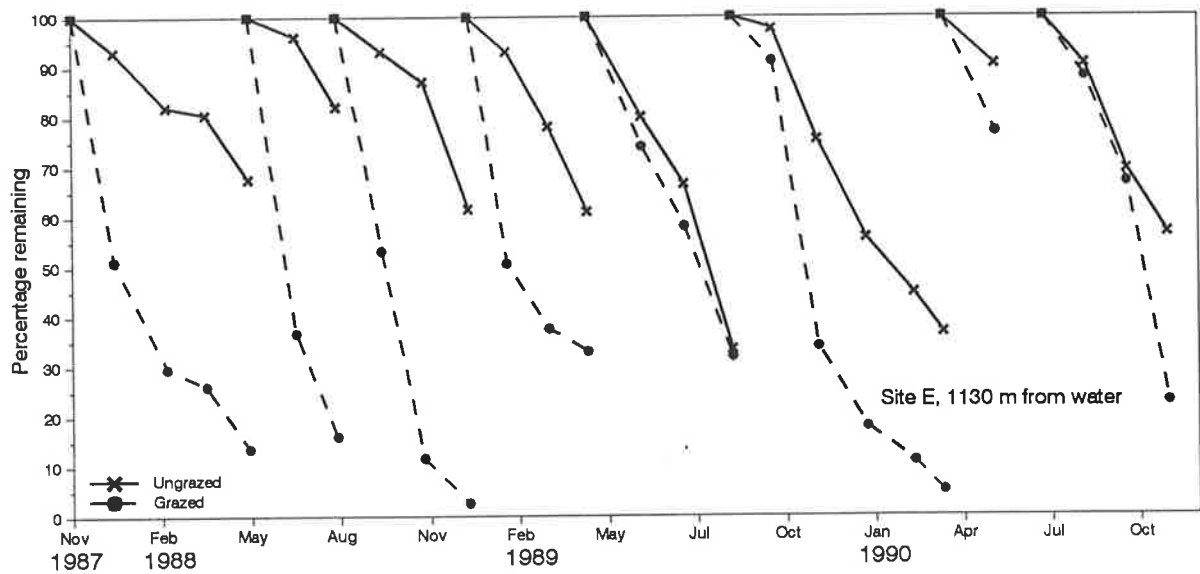


Fig. 4.2. The percentage of initial foliage biomass remaining on saltbush shrubs over eight periods at nine sites in Yanaby. Values are means of 20 shrubs. See text for further explanation. Graphs are in order of increasing distance from water. Continued over the page.

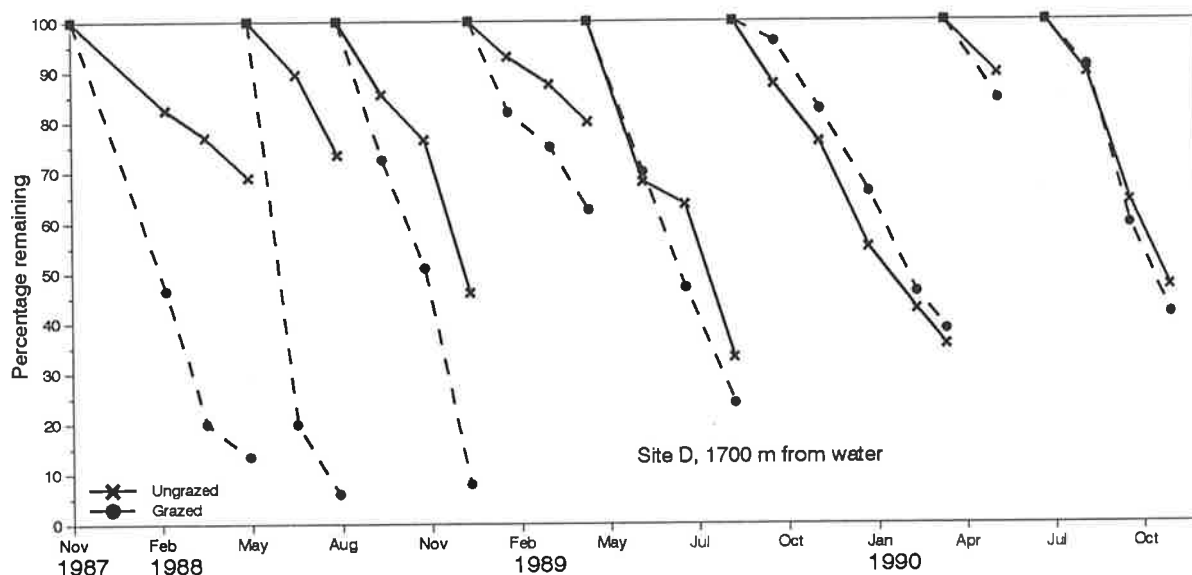
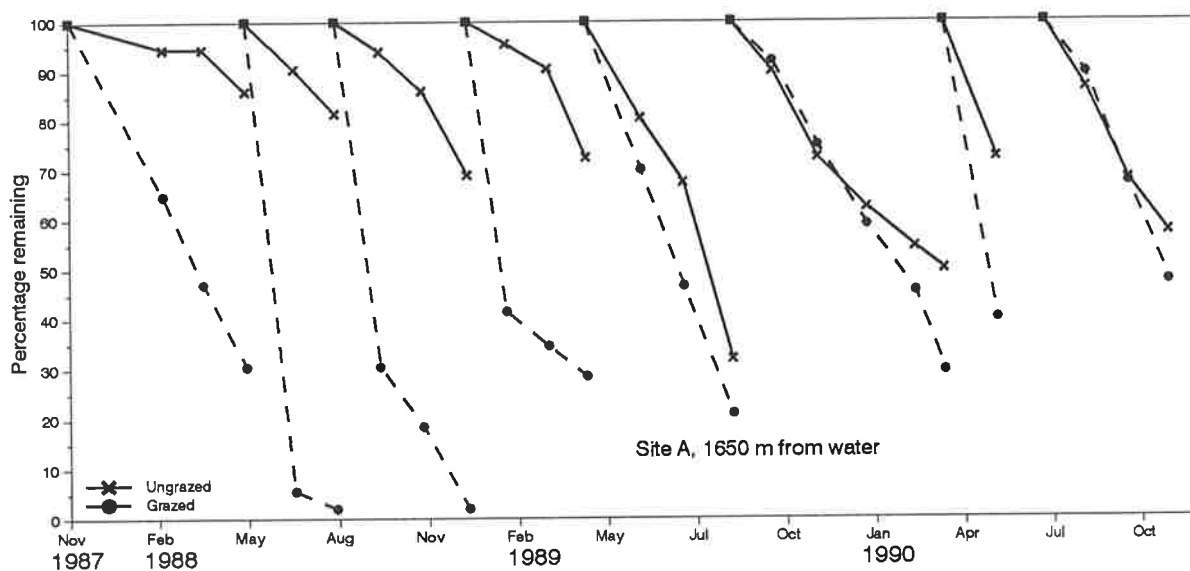
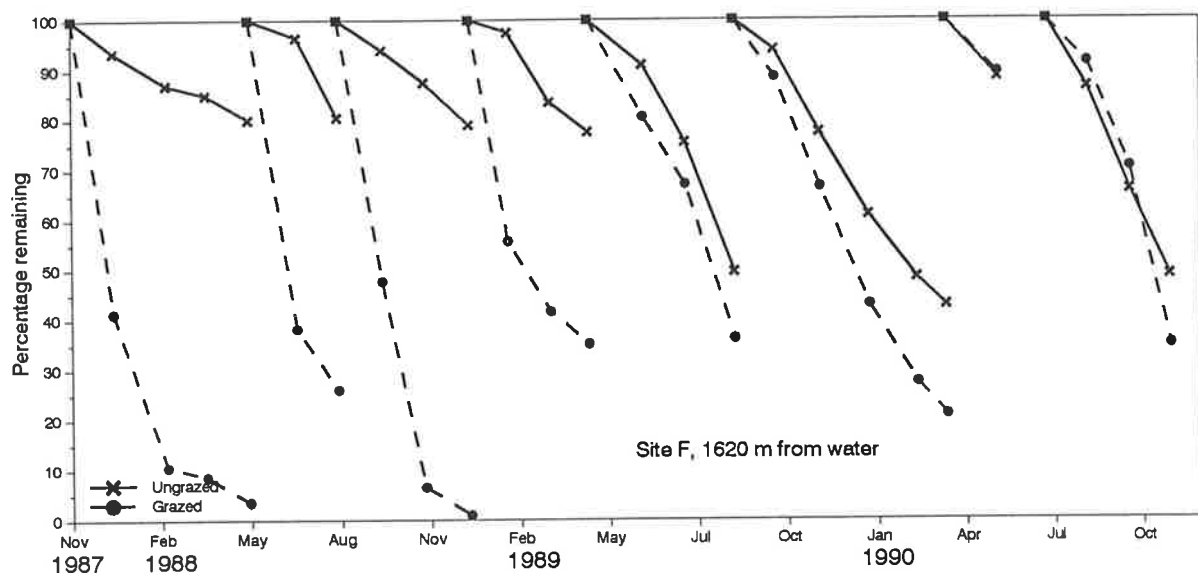


Fig. 4.2. (continued). The percentage of initial foliage biomass remaining on saltbush shrubs over eight periods at nine sites in Yanaby. Values are means of 20 shrubs. See text for further explanation. Graphs are in order of increasing distance from water. Continued over the page.

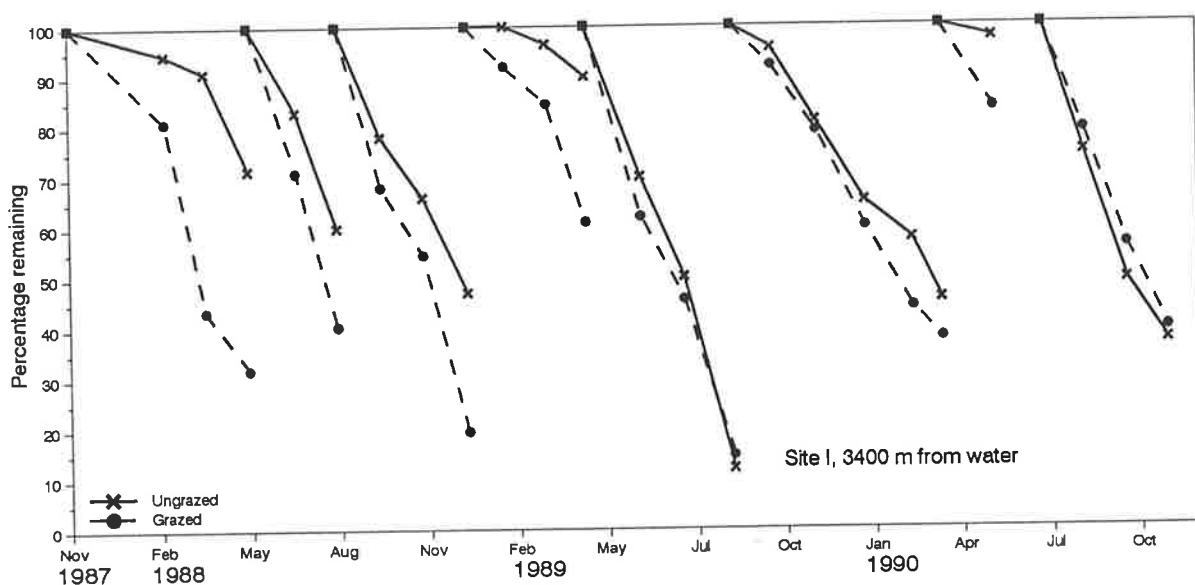
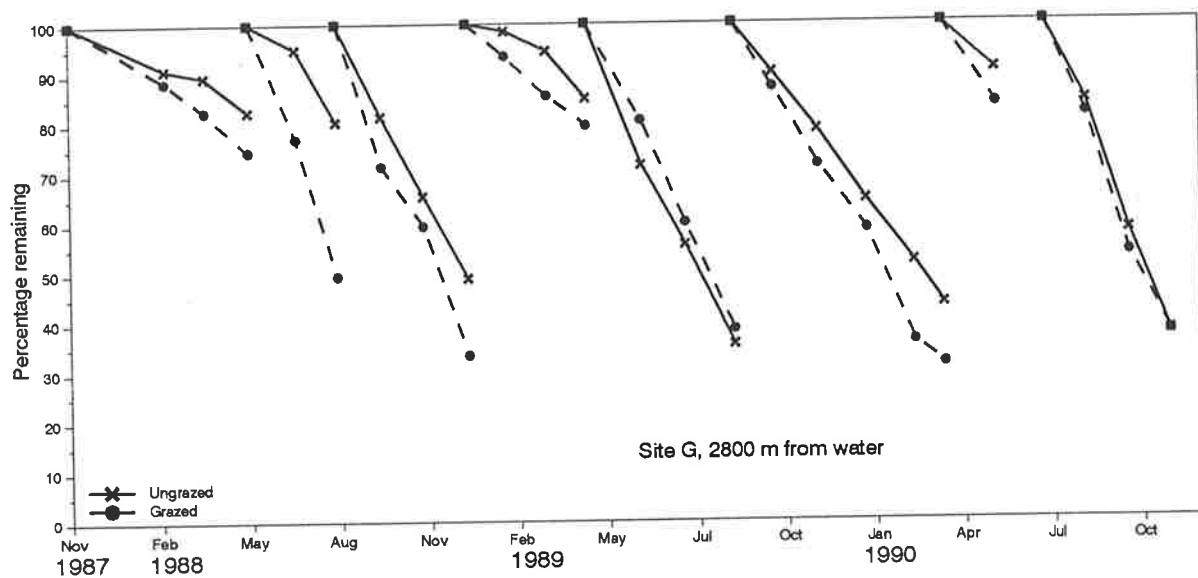
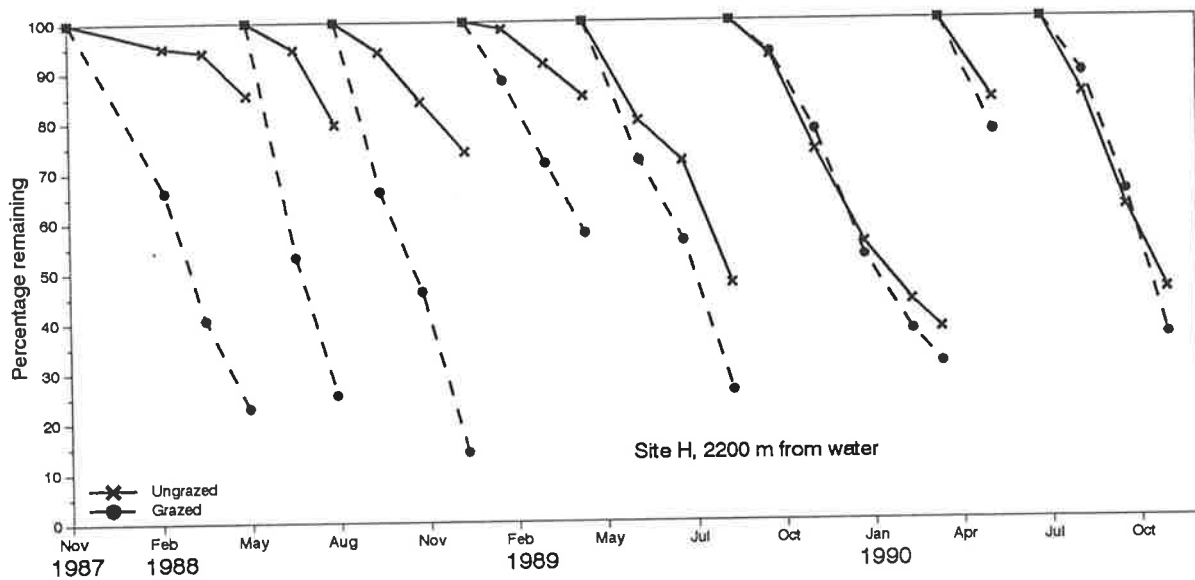


Fig. 4.2. (continued). The percentage of initial foliage biomass remaining on saltbush shrubs over eight periods at nine sites in Yanaby. Values are means of 20 shrubs. See text for further explanation. Graphs are in order of increasing distance from water.

Table 4.1. X² values and significance for the mean score analysis, testing for homogeneity of the mean number of tagged leaves remaining on saltbush shrubs. Results are presented for the overall site * grazing treatment interaction, for the effect of site within grazing treatment, and for the effect of grazing treatment within site. Sites are arranged in order of increasing distance from water. The increased probability of Type one errors with a large number of comparisons has been ignored. Vertical lines in the table indicate when new leaf tags were applied. Cells marked by a dash could not be tested because of a lack of variation between replicate shrubs on the ungrazed plot at site I. * P<0.05, ** P<0.01, *** P<0.001, d.f. is degrees of freedom. The table is continued on the following page.

Source			d.f.	Feb '88	Mar '88	May '88	June '88	Aug '88	Sept '88	Oct '88	Dec '88	Jan '89	Mar '89	Apr '89
Site * Grazing treat.			8	168.90***	125.44***	146.01***	236.29***	100.36***	88.13***	241.05***	144.36***	-	91.58***	51.57***
Site														
Ungrazed			8	28.16***	40.76***	41.94***	21.75**	23.43**	34.69***	46.33***	72.53***	-	43.97***	47.40***
Grazed			8	265.39***	189.97***	315.75***	291.02***	166.62**	65.40***	264.67***	157.71***	148.98***	175.38***	128.10***
Grazing Treatment														
Site	E	1	48.75***	48.74***	71.87***	85.64***	272.25***	41.99***	297.08***	115.74***	40.33***	31.10***	17.23***	
	B	1	15.27***	23.14***	23.56***	1952.71***	395.62***	34.63***	57.60***	150.46***	21.47***	27.80***	30.80***	
	C	1	25.24***	138.40***	127.18***	331.65***	318.04***	61.60***	45.82***	184.85***	3.26	0.65	0.69	
	F	1	311.50***	309.85***	413.95***	90.21***	61.32***	41.47***	722.98***	360.00***	72.97***	44.91***	46.69***	
	A	1	34.88***	32.10***	55.56***	805.01***	796.25***	172.04***	183.44***	338.79***	73.13***	101.24***	43.93***	
	D	1	20.07***	54.56***	75.89***	141.08***	199.51***	2.93	12.60***	47.34***	4.51*	4.38*	8.40**	
	H	1	14.15***	36.72***	84.73***	23.50***	70.31***	28.61***	34.88***	172.25***	5.27*	9.58**	15.69***	
	G	1	0.29	2.07	2.95	5.37*	18.14***	2.88	0.95	8.55**	4.33*	6.76*	1.59	
	I	1	7.09**	35.48***	26.93***	2.97	7.08**	3.16	2.85	32.47***	-	5.67*	20.54***	

Table 4.1. (continued).

Source		d.f.	Jun '89	Jul '89	Sep '89	Oct '89	Nov '89	Jan '90	Mar '90	Apr '90	May '90	Aug '90	Oct '90	Nov '90
Site * Grazing		8	10.44	11.99	16.73•	14.33	49.08***	41.50***	29.04***	35.17***	18.84•	4.69	4.85	16.26•
Site														
Ungrazed		8	29.12***	19.58•	129.44***	23.84••	4.27	8.42	11.29	11.04	49.35***	21.38••	17.95•	17.97•
Grazed		8	24.60••	17.25•	38.55***	12.62	69.46***	86.06***	49.93***	91.82***	56.08***	10.36	12.85	25.30••
Grazing Treatment														
Site	E	1	0.73	1.14	0.04	4.07•	47.92***	38.0***	33.31***	50.44***	5.02•	0.31	0.09	19.56***
	B	1	1.29	13.63***	5.01•	0.51	0.00	0.01	0.16	0.02	2.64	0.36	0.08	0.17
	C	1	0.20	0.93	1.76	0.50	0.21	1.21	0.02	0.14	3.50	0.00	2.81	1.13
	F	1	3.43	1.15	3.65	1.22	3.18	7.90••	7.53••	8.96••	0.07	1.96	0.55	3.83
	A	1	2.49	11.29***	3.04	0.29	0.19	0.26	1.82	11.93***	16.27***	0.65	0.01	2.03
	D	1	0.05	3.80	1.27	6.21•	1.59	2.60	0.25	0.18	1.62	0.08	0.40	0.65
	H	1	1.74	7.01••	9.31••	0.03	0.53	0.10	0.49	0.82	1.75	1.84	0.19	0.94
	G	1	2.43	0.37	0.22	0.56	1.31	0.96	4.03•	2.47	3.19	0.24	0.33	0.00
	I	1	1.48	0.38	0.52	1.24	0.14	0.45	3.06	0.82	12.58***	0.51	0.76	0.12

m) were lightly defoliated, often with no significant difference in mean score between the grazed and exclosed plots. The loss of tagged leaves on grazed plots declined in April 1989. After this time, the loss of tagged leaves was similar on both grazed and ungrazed treatments, with no significant difference between treatments at most sites on most occasions. However, two sites in the vicinity of the water point (site E, the closest to water at 1130 m, and site F at 1620 m) registered significantly greater ($P < 0.01$) defoliation on grazed plots than ungrazed plots during the 1989-90 summer. The significance of the site $\times$ grazing treatment interaction during much of this period reflects this spatial variation in saltbush defoliation.

Although there were no differences between treatments for most sites in the later part of the study, both treatments did record increases in the loss of tagged leaves. This reflects an increase in the natural loss of leaves from the shrubs, probably because old leaves were being replaced by new growth. Because of this increase in natural leaf loss the percentage of tags remaining is a poor indicator of the percentage of initial biomass remaining on shrubs for this part of the study. This natural leaf turnover might also have masked a small grazing effect on the grazed plots, although there was little evidence of grazing on the shrubs at most sites during this period.

Because the data on the severity of defoliation is cumulative over the life of a set of tags, it is difficult to examine the temporal variation in defoliation pressure. This is best investigated by calculating the rate of defoliation for each observation interval (i.e. relative to the biomass available at the beginning of each six week period) within a set of tags. This was calculated as an overall rate for all marked shrubs on a plot. These results show that although there was some short-term fluctuation between observation periods, defoliation rates generally remained high on grazed plots for the early part of the study for most sites (Figure 4.3). Defoliation rates in the order of 1.4%/day of standing biomass were common. Naturally these results reflect the general trends seen in the defoliation severity data, so again it was only at the two sites which were well away from

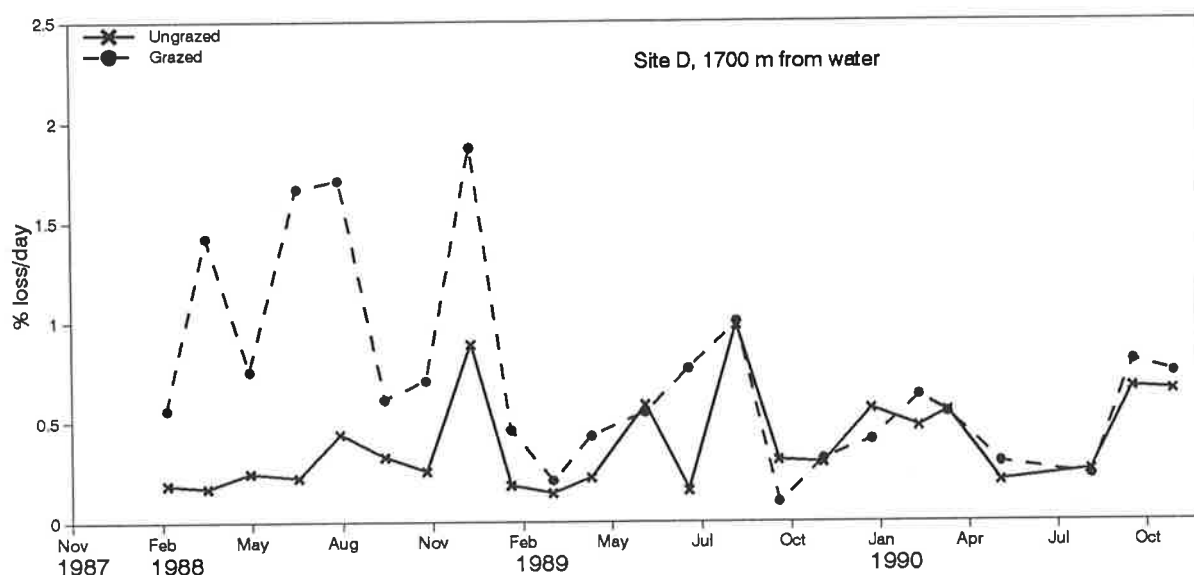
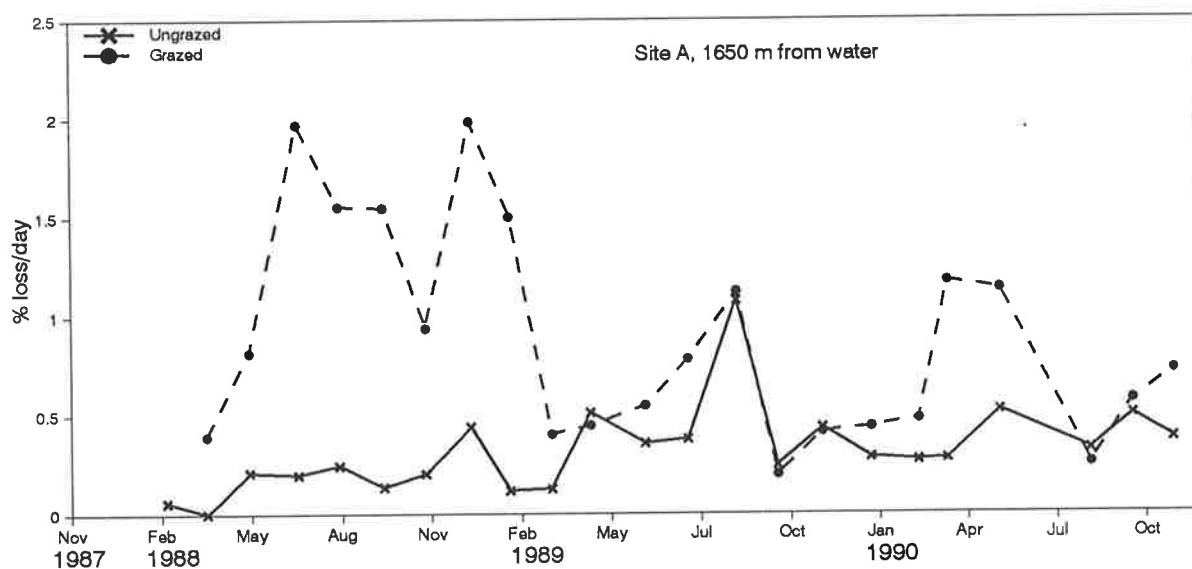
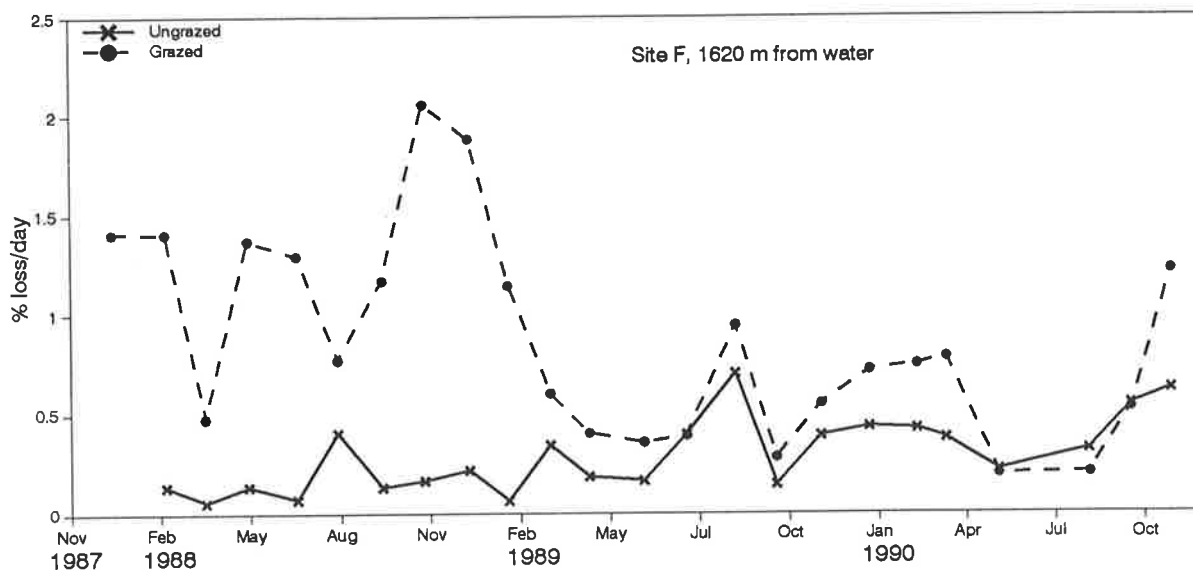


Fig. 4.3. (continued). The rate of standing foliage biomass loss from saltbush shrubs on grazed and exclosed plots at nine sites in Yanaby. Graphs are in order of increasing distance from water. The figure is continued on the following pages.

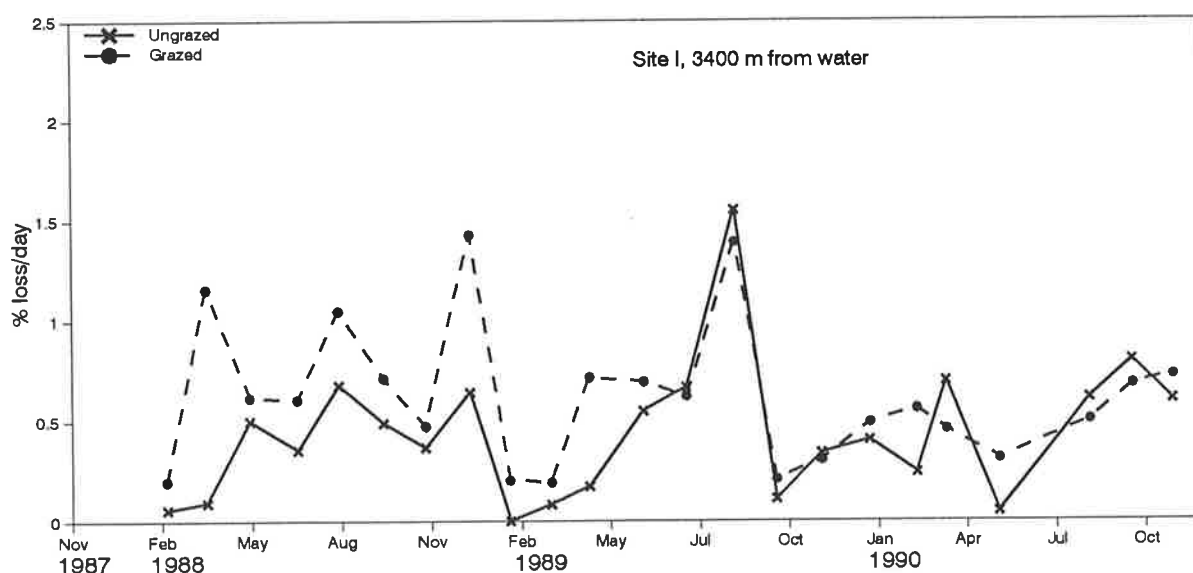
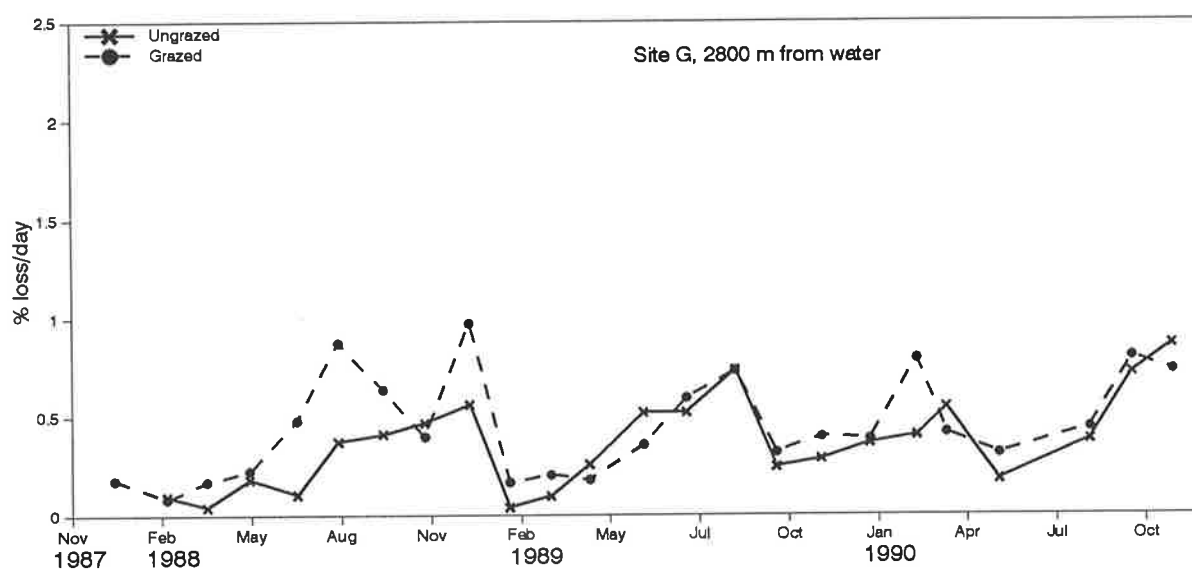
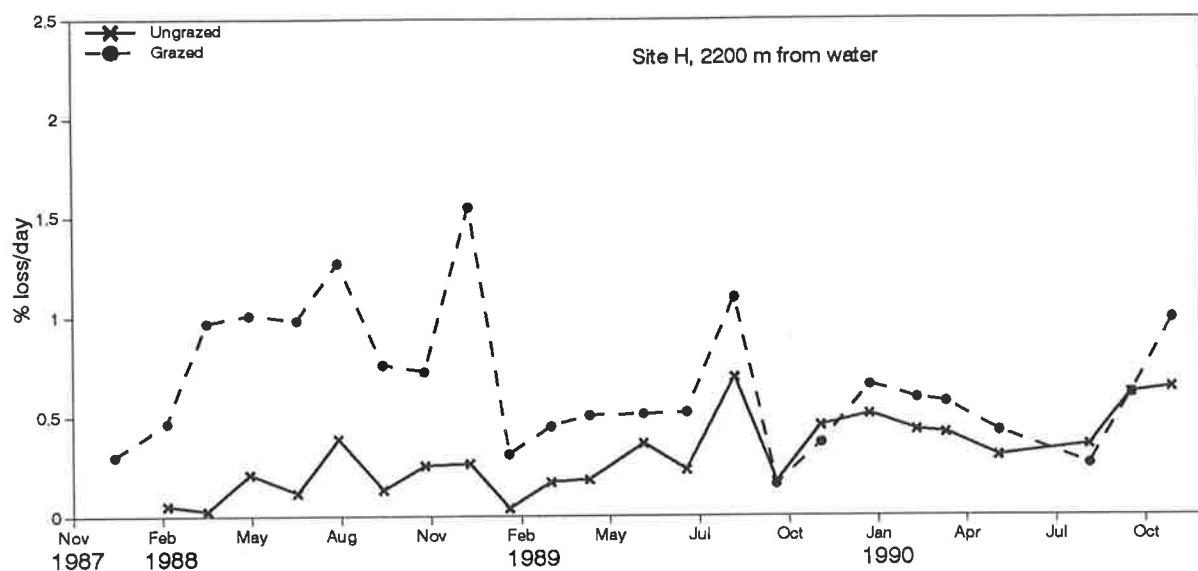


Fig. 4.3. (continued). The rate of standing foliage biomass loss from saltbush shrubs on grazed and exclosed plots at nine sites in Yanaby. Graphs are arranged in order of increasing distance from water.

the water that defoliation rates were similar on grazed and exclosed plots. Site E (and to a lesser extent site F) was notable for a consistently higher defoliation rate on the grazed treatment than the exclosed treatment for all but about 10 months of the 36 month study. Analysis of variance of the defoliation rate data showed that site, grazing treatment and observation period were all significant ($P < 0.001$), as were the site $\times$ treatment and treatment $\times$ observation period interactions (Table 4.2).

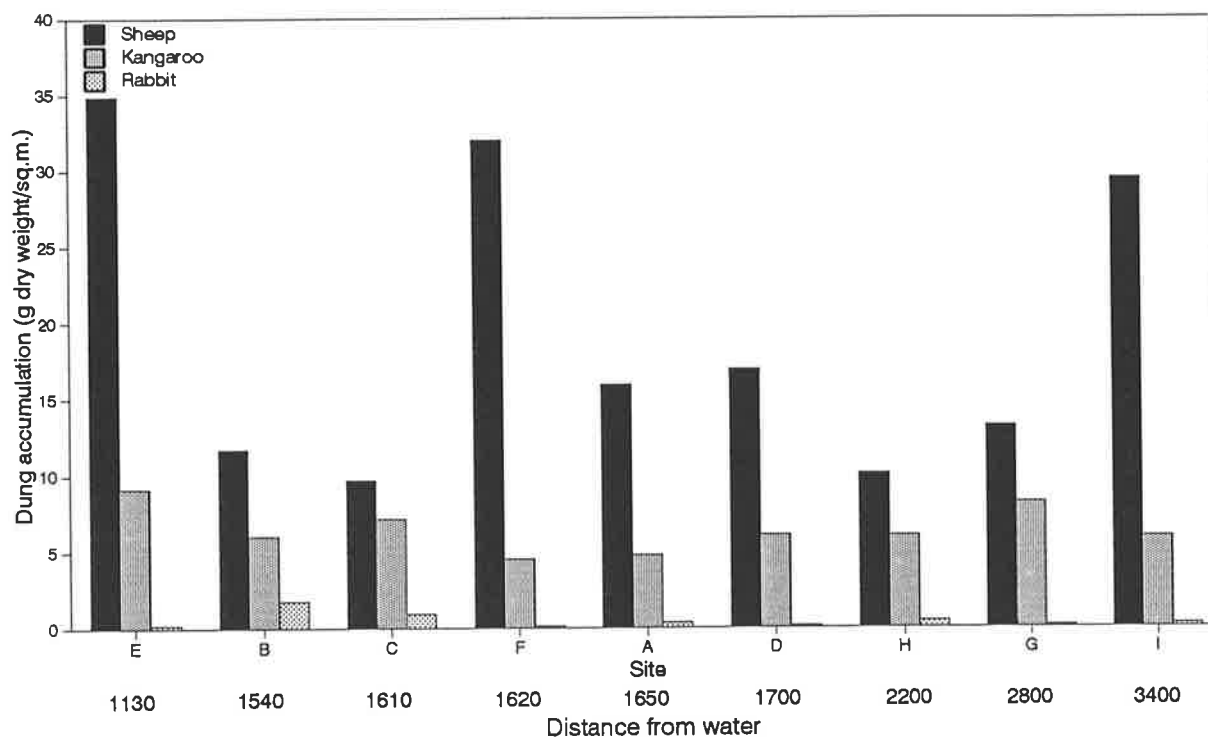
The differences between the grazing treatments suggest sheep were the main cause of defoliation of saltbush. This is supported by the dung data. Large amounts of sheep dung were recovered from grazed plots over the life of the study but no fresh sheep dung was found on exclosed treatments (Figure 4.4). In contrast, considerable amounts of rabbit and kangaroo dung were collected from both grazed and exclosed plots at certain times during the study. It should be noted that there was a reduced number of sheep (approximately one third of the normal DSE rate) in the paddock during the last 4 months of the period up to April 1989 (see Figure 3.6), as a result of sheep escaping from the paddock, and probably contributed to lower defoliation intensity at certain sites at that time.

The availability of herbage biomass appeared to be primarily responsible for temporal variation in the level of saltbush defoliation during the study. The heavy defoliation of saltbush at many sites in the period of the study up to April 1989 was associated with the lack of alternative preferred feed for sheep. Following increases in the availability of herbage after April 1989 there was a decrease in saltbush defoliation, and although herbage biomass fluctuated during the later part of the study, saltbush defoliation remained relatively low. Sites E, F and A (1130, 1620 and 1650 m from water, respectively) were the only sites to record increased levels of saltbush defoliation on grazed plots as herbage levels declined during this later period.

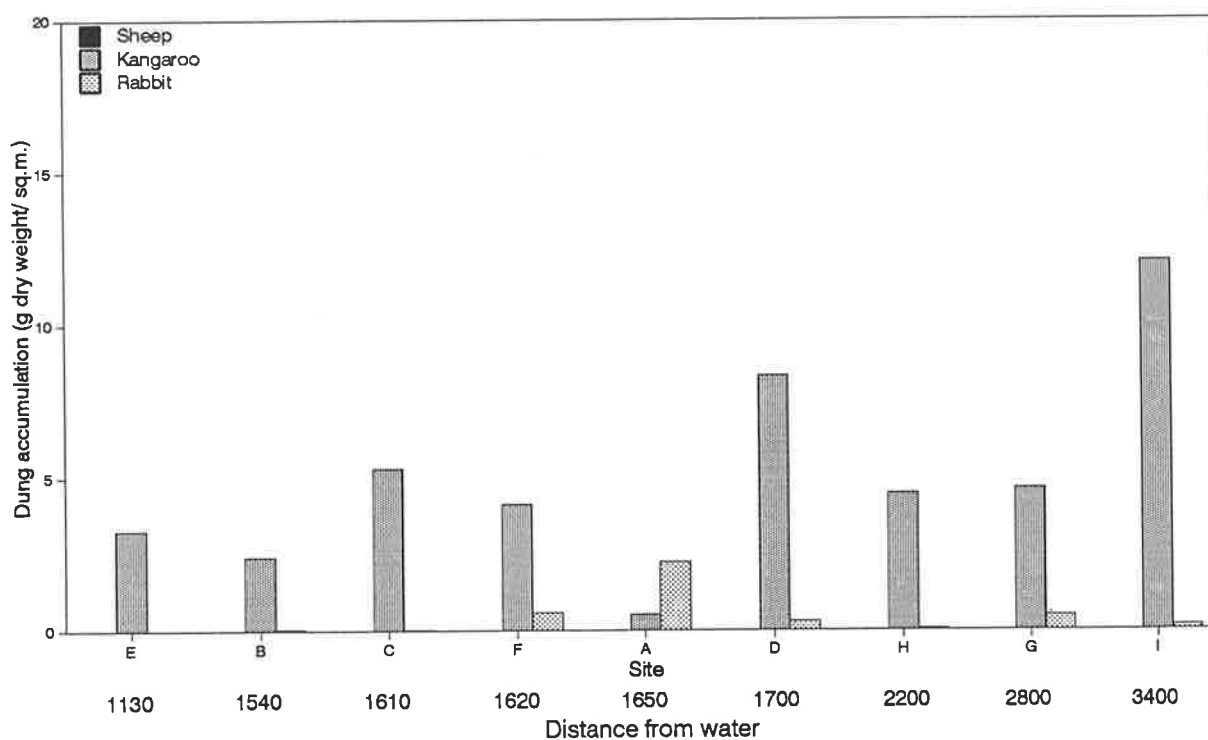
Despite the lack of a significant linear relationship between defoliation and distance from

Table 4.2. Analysis of variance of the daily rate of saltbush defoliation (i.e. loss of tagged leaves). The analysis is for 23 measurement periods (each of approximately six weeks duration) over three years for grazed and ungrazed treatments at nine sites in Yanaby. The rate of defoliation was calculated as an overall rate for the marked shrubs on a plot.

Source	DF	SS	MS	F	P
Site (A)	8	1.919	0.239	4.88	0.0000
Treatment (B)	1	13.941	13.941	283.33	0.0000
Period (C)	22	18.783	0.854	17.35	0.0000
A*B	8	2.523	0.315	6.41	0.0000
A*C	176	10.328	0.059	1.19	0.1222
B*C	22	12.030	0.547	11.11	0.0000
A*B*C	175	8.611	0.049		
Total	412	68.134			
Grand Average	1	115.36			



(a) Grazed plots.



(b) Exclosed plots.

Fig. 4.4. The accumulation of sheep, kangaroo and rabbit dung on grazed and exclosed plots at nine sites in Yanaby. The data are the total weight of dung (g dry weight/sq. m.) accumulated in the period from November 1987 to November 1990, with collections being made at intervals of six weeks. Note the different scale for the ordinate in each graph.

water, the differences in defoliation of saltbush between sites were associated with a general trend of reduced saltbush defoliation on grazed plots as distance from water increased. Throughout the study the two most distant sites experienced much lighter defoliation than closer sites or were not grazed at all. Also, as mentioned above, the grazed plots closer to water experienced grazing on a more frequent basis than other sites which were further from water.

Saltbush Biomass

Figure 4.5 shows the foliage biomass of saltbush (on a per plant and a per unit area basis) at all sites for the period during which defoliation was measured and for a further 2.5 years up until April 1993. Although the initial biomass levels were similar between treatments within a site, during the course of the study mean shrub biomass (i.e. per plant) became increasingly greater on the plots protected from sheep grazing compared to the grazed plots for many sites. There was a general decline in biomass per plant on the grazed plots during the first 18 months of the study but after April 1989, apart from seasonal fluctuations, there was a trend of increasing shrub biomass. In many cases, shrub biomass in April 1993 was greater than at the beginning of the study. On plots protected from sheep grazing shrub biomass remained similar to initial levels in the early part of the study and then increased later, in line with the increase on the grazed plots, but to a greater extent. The two sites furthest from water (sites G and I) were exceptions to this general trend with the grazed plots being little different to the exclosed treatment. The estimates for mean shrub biomass during the study ranged from approximately 2 to 40 g dry weight/plant on grazed plots and 5 to 49 g dry weight/plant on the exclosed plots. Biomass per unit area showed similar trends to mean shrub biomass, although at sites B, D, and E available biomass on the grazed plots did not increase after April 1989 as it did at other sites, reflecting a decrease in shrub density.

Biomass also varied between sites. At the start of the study there was a significant linear trend of increasing shrub biomass (i.e. per plant) with distance from water, which was

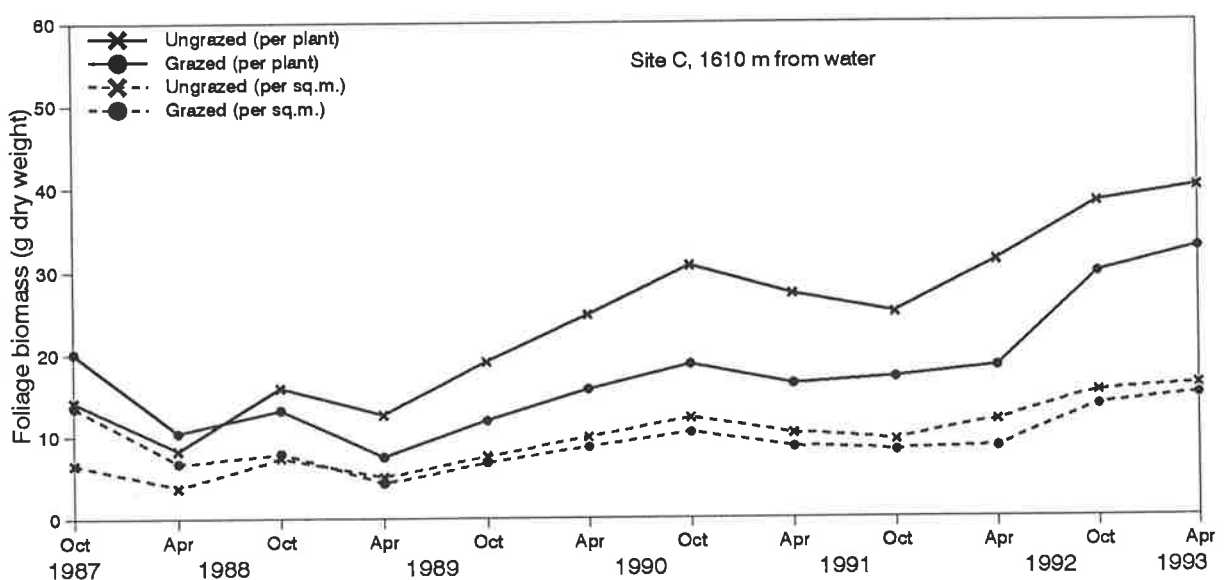
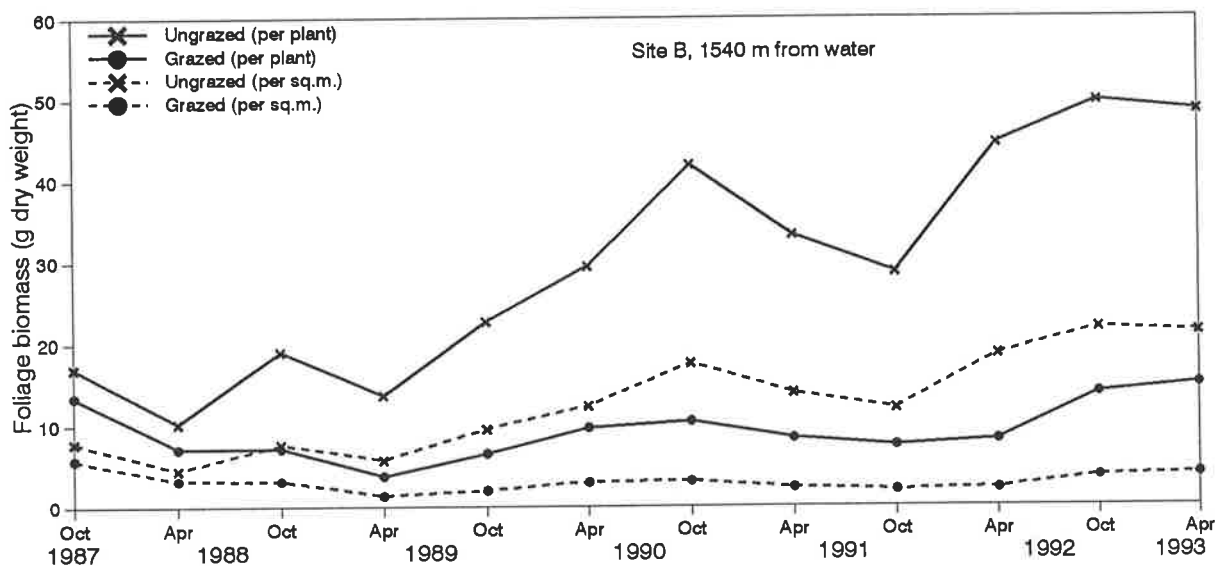
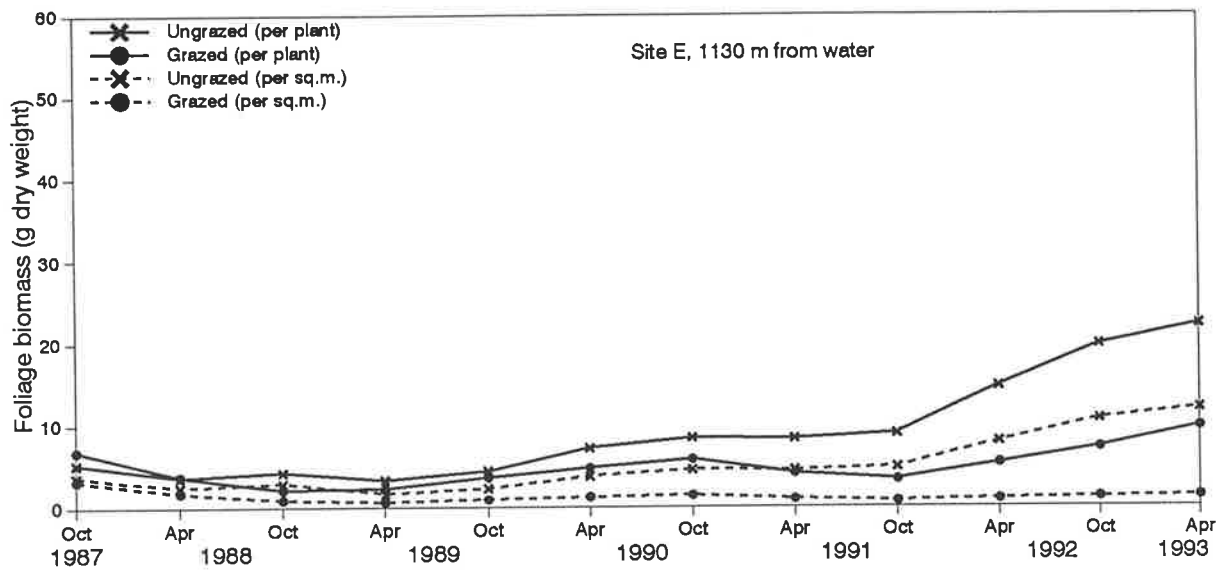


Fig. 4.5. Foliage biomass of saltbush on grazed and excluded plots at nine sites in Yanaby. The values for the grazed treatment are the means of two plots. Graphs are arranged in order of increasing distance from water. The figure is continued on the following pages.

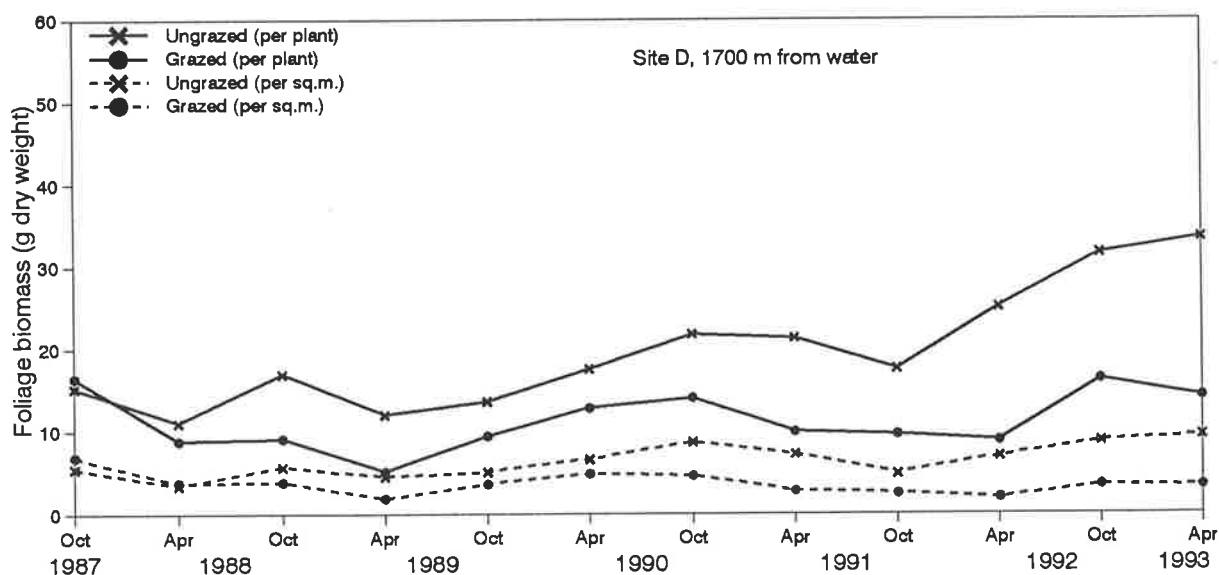
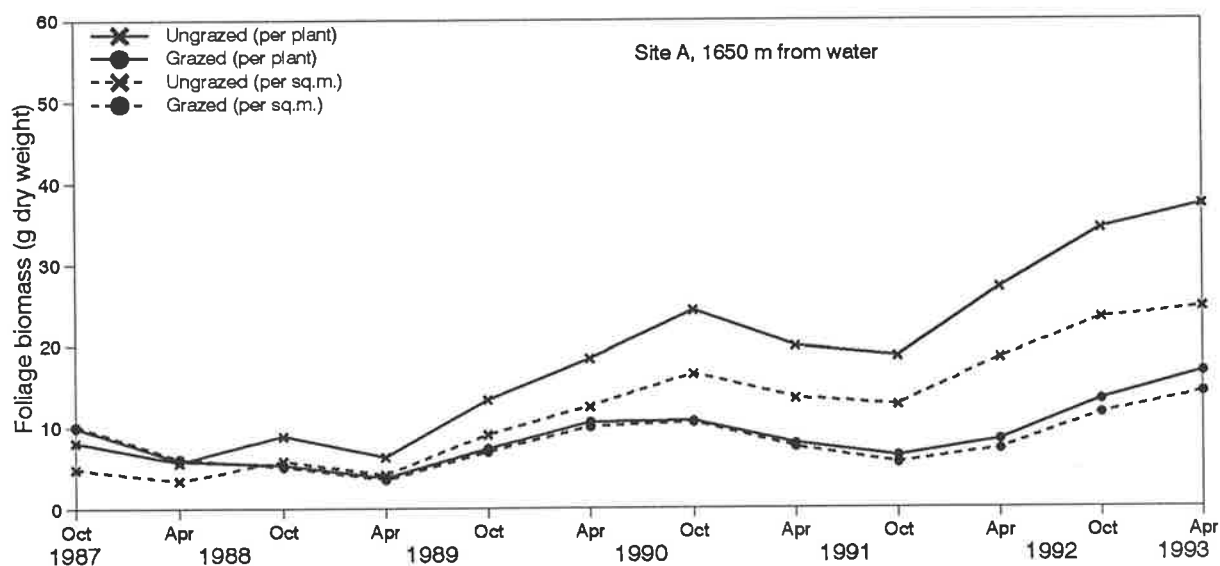
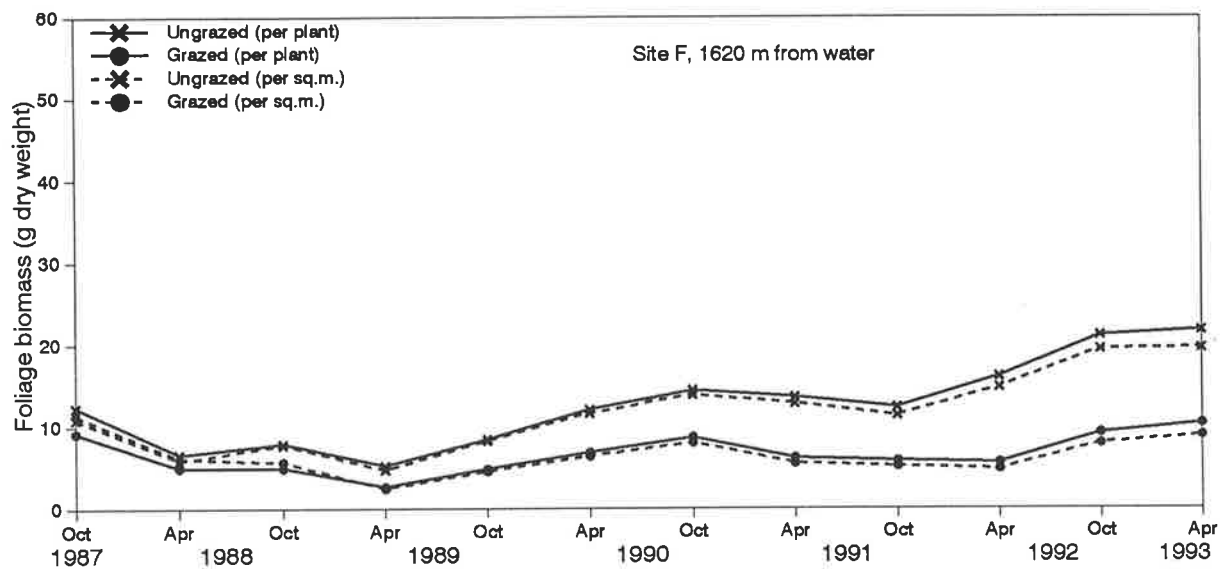


Fig. 4.5. (continued). Foliage biomass of saltbush on grazed and exclosed plots at nine sites in Yanaby. The values for the grazed treatment are the means of two plots. Graphs are arranged in order of increasing distance from water. The figure is continued on the following page.

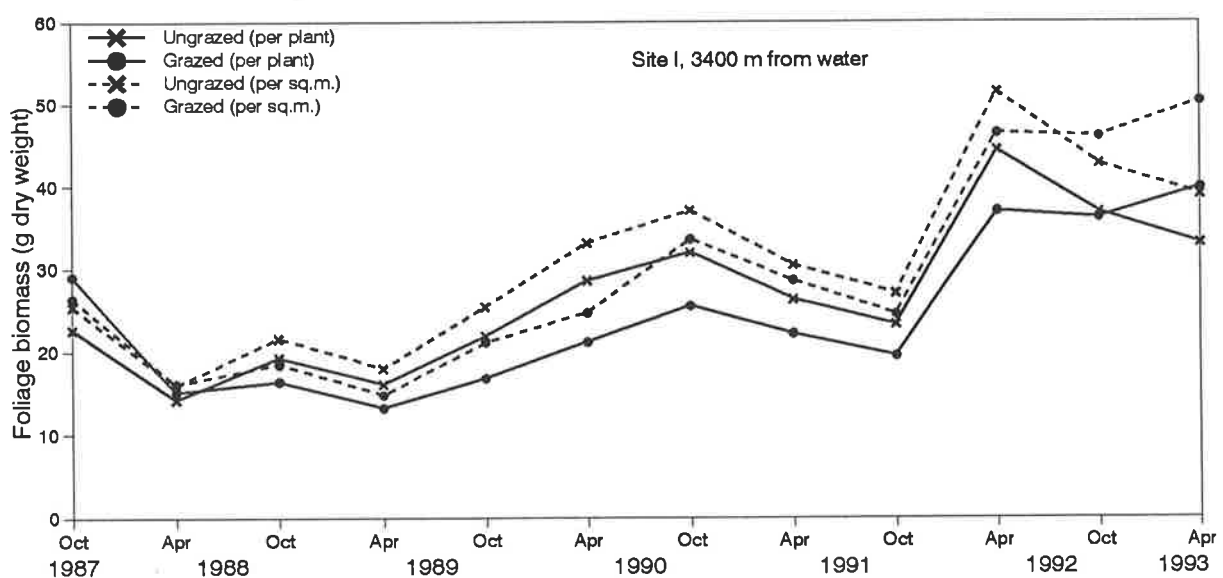
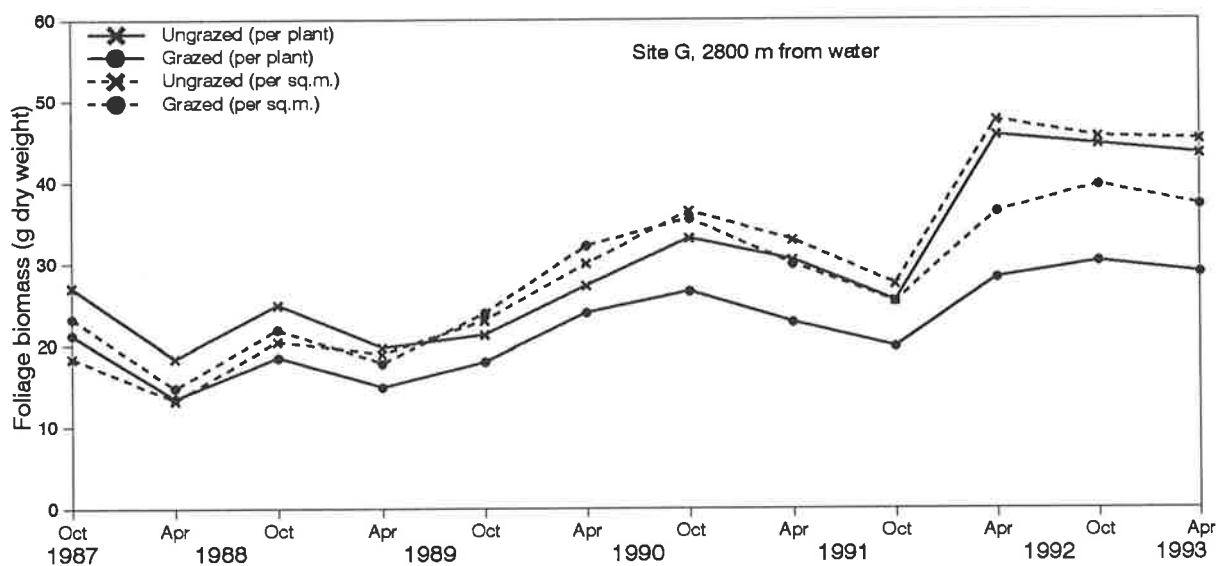
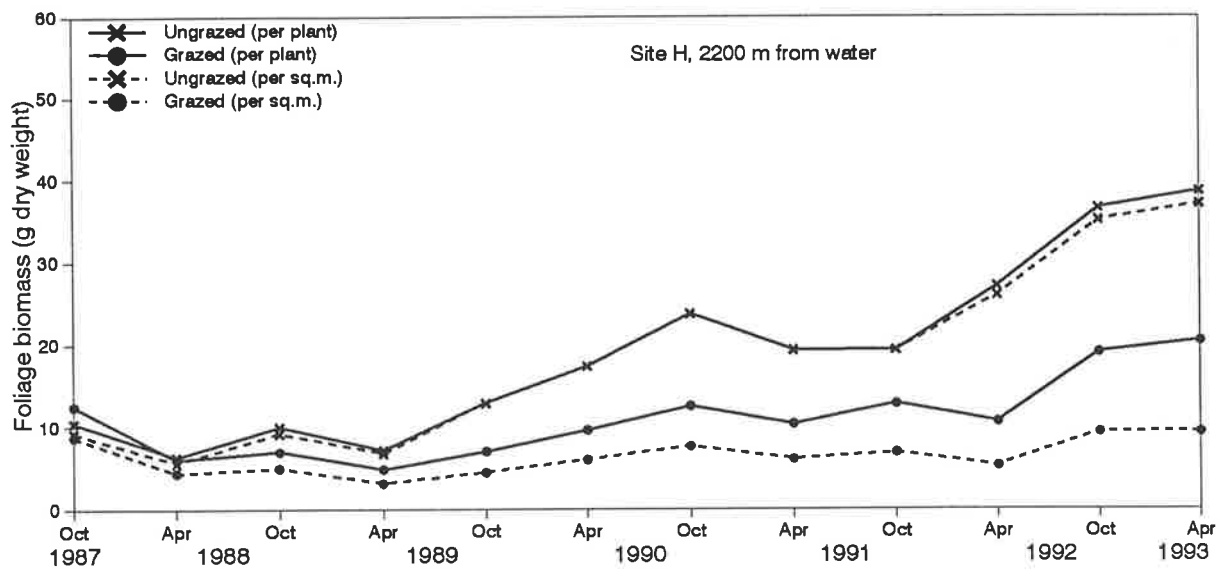


Fig. 4.5. (continued). Foliage biomass of saltbush on grazed and exclosed plots at nine sites in Yanaby. The values for the grazed treatment are the means of two plots. Graphs are arranged in order of increasing distance from water.

maintained on grazed plots throughout the study (biomass per plant = $-0.21 + 0.012^* \cdot$ distance (m); $R^2=0.58$, at the final estimate in March 1993). There was no such relationship on the exclosed plots at the end of the study. A similar trend occurred on a per sq.m. basis (biomass per sq.m. = $-10.4^{***} + 0.01^{***} \cdot$ distance (m); $R^2=0.678$, over all dates).

DISCUSSION

Saltbush Defoliation Patterns

The heavy defoliation of saltbush at times during this study can be attributed almost solely to the grazing activities of sheep. The fact that there were considerable quantities of kangaroo and rabbit dung deposited in the exclosures at various times without large rates of saltbush defoliation being recorded on these plots, suggests that these herbivores did little grazing of this species. These findings are consistent with earlier reports.

Western grey kangaroos typically consume graminoids, but may resort to chenopods and other shrubs at times of low grass availability (Barker 1987). In my study it is likely kangaroos browsed the foliage of western myall trees during the period of low herbage levels prior to April 1989. This has been frequently observed in the Katunga area during periods of low feed availability (D. Nicolson pers. comm.), and is supported by the high browse lines on many myalls. Rabbits also do not graze saltbush, apparently because of the high level of salts in the tissue (Ratcliffe 1936, Hall *et al.* 1964). This is consistent with the difficulty rabbits have in maintaining a suitable internal moisture balance in the arid zone (Cooke 1982, Wood and Lee 1985).

The defoliation of saltbush by sheep in this study varied both temporally and spatially. Temporal variations in defoliation were mainly due to fluctuations in the availability of herbage. The period of heavy grazing during the first 18 months of the study was associated with a low availability of herbage, which was a consequence of poor rainfall. It was only when abundant herbage was available following good rains that the overall

level of saltbush defoliation by sheep was low. These results are supported by the findings of earlier diet studies (Graetz and Wilson 1979) and graze-down experiments (Short 1985), which showed that sheep graze the perennial shrubs only after the short-lived herbage species have been depleted. However, the importance of my results rests in the severity and duration of the periods of saltbush defoliation which were observed. Rather than the grazing of saltbush being confined to summer and autumn of each year when herbage biomass is often low, as was reported by Graetz (1986), low rainfall and poor growth of herbage during winter in 1988 resulted in an extended period of heavy saltbush defoliation. Rates of defoliation of 1-2% of standing foliage biomass per day continued for 18 months, from early autumn in 1988 to late autumn in the following year. During this period, casual leaf counts when grazing of the shrubs was most severe (site E, March 1989) indicated a minimum leaf number per shrub of approximately 50. Therefore, in this study the failure of the winter rains meant that there was not an annual 'natural rotational grazing system' as suggested by Graetz and Wilson (1984) and consequently, no easing of the grazing pressure on saltbush. Although there was temporal variation in the grazing of saltbush, the time-scale for this variation was greater than the literature suggested.

Grazing of saltbush by sheep also varied spatially, irrespective of the availability of herbage at the time. As expected, the water point was the focus of grazing activity. While sites closer than approximately 2200 m to water were consistently and heavily grazed when herbage levels were low, the two sites greater than 2200 m from water (sites G and I) experienced a more variable grazing pressure, including no grazing, light grazing or a rare bout of heavy grazing. The ability of sheep to graze at these locations would have been limited by the distance to water and the need for them to frequently return to the water point to drink (Squires 1974, Graetz and Wilson 1984). Despite the water point being the general focus of sheep grazing activity, significant linear regressions between the defoliation of saltbush by sheep and distance to water were not obtained. This may reflect the influence of other less obvious factors on sheep

distribution which have been found to be important, such as shade, camp sites or wind (Stafford Smith 1984).

In my study, an important effect of the focussing of sheep activity around the water point was the heavy grazing of saltbush on several plots near the water point in spite of high herbage availability. As well as being heavily grazed during the period of low rainfall, shrubs on grazed plots at site E were grazed for seven months from October 1989 to May 1990, so that there were only eight months of the study during which site E shrubs were not grazed. It was only during the months when green herbage was available (i.e. mainly the winter months in 1989 and 1990) that shrubs at site E were not grazed. It is not clear why this occurred, particularly given the low availability of saltbush biomass on these shrubs, which suggests it would have required more effort by the sheep to seek it out. However, since this did not occur when green feed was available, it may reflect the decline in palatability of the grasses after they have flowered (Noble 1975).

Biomass Dynamics

Grazing by sheep and temporal variation in rainfall appeared to be the main determinants of the fluctuating levels of saltbush biomass during the study. The decline in mean shrub biomass on most grazed plots during the first 18 months of the study was a result of heavy defoliation during a period of poor growth of saltbush, due to low rainfall.

Although subsequent good rains (see rainfall chart, Figure 3.5) resulted in increases in shrub biomass on both the grazed and exclosed plots, at the heavily grazed sites the response was much greater on the exclosed plots (Figure 4.5). There was little grazing of saltbush on many plots during this period, suggesting that earlier heavy defoliation on the grazed plots had reduced the ability of the shrubs to respond to rain. Four years after the end of severe grazing this effect continued, with shrubs on grazed plots having approximately half the foliage shrub biomass of the exclosed ones (although at most sites grazed shrub biomass was equal to or greater than levels at the start of the study). It was only at the sites which were lightly grazed during the initial dry period (sites G and I)

that the growth response was similar on both grazed and exclosed plots.

The effects of grazing and rainfall on shrub biomass are generally consistent with other studies. Noble (1977) and Wellard (1987) reported that grazing and rainfall are both important in determining shrub biomass in chenopod shrublands, but rainfall is the overriding factor. While the temporal fluctuations in the biomass of saltbush plants in this study were chiefly determined by rainfall, actual shrub biomass at a particular site was determined by previous and present grazing pressure.

In view of the severe and prolonged defoliation of saltbush near the water point, the depression of shrub biomass and the reduced ability of shrubs to respond to rain were not surprising. A similar depression of shrub biomass was obtained by Coleman (1982) in a study examining the possible mechanisms for the poor tolerance of saltbush to defoliation, while Cook and Child (1971) found that desert shrubs from the United States had not fully recovered seven years after being moderately defoliated. Despite a considerable amount of work on the problem, it is still not clear what mechanism/s is/are responsible for the sensitivity of saltbush to defoliation, although a ~~of~~ lack of buds, death of roots due to grazing and the lack of carbohydrate reserves or an inability to mobilise them have all been suggested (Leigh and Mulham 1971, Hodgkinson and Baas Becking 1977, Coleman 1982). In the early part of the period of heavy grazing I frequently observed new lateral shoots on heavily grazed plants, but often these too were soon grazed. Later in this period the production of these laterals was less noticeable. This observation, although only a casual observation, and the long-term depression of shrub biomass, lend support to the hypothesis that a shortage of resources in the plant, either carbohydrates or other compounds, may be important in reducing saltbush growth after heavy grazing. The long-term depression of shrub biomass also suggests that the ability of shrubs to recover adequately from the effects of prolonged heavy grazing during subsequent more favourable times when grazing is low, will largely depend on the frequency of the periods of grazing. My results contrast with those of Eldridge *et al.* (1990). They reported that

the size of saltbush shrubs at 1200-1500 m from water declined more rapidly during drought on grazed plots than on ungrazed ones, but following falls of rain that were sufficient to initiate growth the difference disappeared as the grazed shrubs rapidly recovered.

Moderate levels of grazing have been reported to result in grazing-induced vigour in saltbush (Osborn *et al.* 1932, Andrew and Lange 1986b) and other arid zone shrubs (McConnel and Smith 1977, Price *et al.* 1989). This occurs because removal of the apical meristem by grazing releases lateral shoots from apical dominance. Andrew and Lange (1986b) found that this resulted in shrub biomass often being significantly greater on grazed shrubs than ungrazed ones. As mentioned above, although I initially observed the production of lateral shoots following grazing, these shoots were subsequently grazed and shrub biomass on grazed treatments remained less than on the corresponding exclosed plots. Price *et al.* (1989), working in New Mexico, have reported a similar effect in *Atriplex canescens* (fourwing saltbush) grazed continuously by cattle.

Importance of Patterns of Grazing for Saltbush

Temporal variation in the defoliation of saltbush by sheep in response to changes in herbage availability is thought to provide a rest period for saltbush under a continuous grazing regime, enabling it to recover from the negative effects of grazing (Graetz and Wilson 1984). However, because of the nature of the temporal and spatial patterns of sheep grazing in this study, saltbush shrubs were heavily grazed in parts of the paddock for an extended period, resulting in a long-term decline in shrub biomass. Thus it would also appear that conservative stocking rates are less effective at avoiding severe grazing of saltbush under continuous stocking than is normally suggested.

The frequency of these extended periods of heavy grazing pressure will be important in determining the implications of grazing for the population, since adequate recovery of heavily grazed saltbush shrubs would appear to require several favourable years. In these

rangelands where rainfall is erratic and unreliable, episodes of grazing similar to that observed in this study may happen frequently, given that some herbage grew in 1988, and in many years little herbage is produced. In the chenopod shrublands, the amount of herbage biomass at a particular time is determined by the rainfall received in the preceding 6 to 12 months (Noble 1977). In my study, the rainfall received during the two 6 month periods prior to spring in 1988 (when herbage levels were low and grazing of saltbush was heavy) was equivalent to decile 2 and 4 respectively (or decile 1 for the entire 12 month period). Thus while there is a low frequency of having two consecutive 6 month periods of poor rainfall similar to those encountered in this study, the frequency of having rainfall equivalent to that received during autumn and winter, which are favourable times for herbage growth, is much greater. Extended periods of saltbush defoliation similar to that observed in this study may therefore occur as often as four times in ten years.

The timing of periods of grazing are also important. Defoliation of saltbush was most severe during a dry spell when shrubs were also likely to be moisture stressed.

Reductions in root growth following defoliation have been reported for many species (Davidson and Milthorpe 1966, Crawley 1983), while defoliation of saltbush can lead to the death of roots (Hodgkinson and Baas Becking 1977). Obviously this will exacerbate the problem of obtaining sufficient water during times of moisture stress and reduce the ability of plants to cope with moisture stress.

Generality of Results

The fact that the severity of defoliation in this paddock was much greater than expected raises the question of the generality of the results. I have already dealt with the nature of seasonal conditions during the study, but the characteristics of the paddock may have contributed to 'unusual' results. Yanaby was chosen as the study paddock because it was a typical commercial paddock which was also of a manageable size for such a study. Consequently, there is nothing to suggest that Yanaby is different in any way that might

result in abnormal grazing patterns. Naturally the actual patterns of grazing in other paddocks will depend on paddock layout including water point location, vegetation distribution and paddock shape and size, saltbush abundance relative to other fodder species and numerous other factors. However, casual observations in nearby paddocks suggested that the general patterns and severity of defoliation were similar in most paddocks during the study.

Role of Field Estimates of Defoliation

The patterns of defoliation observed in this study have further highlighted both the limitations of the methods commonly used in the study of defoliation impacts on plants and the need for large-scale field studies of grazing impact. As discussed earlier, many studies examine the effects of defoliation on plants by either simulating grazing by clipping or hand stripping of plants either in the laboratory or field or, if experimental plants are grazed by animals it is only in small study plots with high animal intensities (Hart and Norton 1988). These approaches have a number of shortcomings which limit the application of the results to field situations (Trlica and Rittenhouse 1993), particularly where the life-time impact of grazing on plants is of prime concern (Doak 1992).

Apart from environmental factors which may affect plant growth (e.g. nutrient cycling effects from dung and litter accumulation or competition from neighbouring plants [Archer and Detling 1984]), perhaps one of the major factors which is frequently overlooked in many defoliation studies is the temporal nature of grazing patterns of individual plants in the field. Defoliation treatments often are applied as discrete events, with a limited number of combinations of defoliation intensity, frequency and timing. This inadequately represents the normal grazing process, particularly in rangelands where paddocks are large and continuous grazing practices are common, since defoliation in the field is not a regular event of defined intensity and frequency occurring for a specified period.

A short-term study of the effect of grazing on saltbush, in which small plots of saltbush

were subjected to a high grazing intensity over a period of ten days, found that saltbush was killed by a single complete defoliation (Leigh and Mulham 1971). Despite high levels of defoliation in the present study, on no occasion were any individual shrubs seen to be completely defoliated (minimum leaf number approximately 50). Also, grazing of shrubs occurred over much longer periods than ten days. If sheep utilise an optimal foraging strategy to maximise energy intake, as has been suggested for many herbivores (Stuth 1991), then it is unlikely they will continue to graze a particular plant once the marginal return of grazing the plant has fallen below some threshold, particularly when other shrubs are available. In saltbush, it appears that this threshold occurs at a point when some biomass remains on a plant, although as feed becomes scarce overall this level may fall. Repeated grazing of the shrubs, so that they are maintained at this threshold level for long periods, may be the more likely manner in which grazing has a long-term negative impact on the population in the field than complete defoliation. Clearly, without knowledge of the grazing patterns occurring in the field, care is needed in applying the results of small-scale studies to the field situation.

Despite this, I am not aware of any other studies which have attempted to quantify the defoliation of plants in the rangelands on as large a scale as this study. Most investigations have been confined to much smaller paddocks and shorter time frames (e.g. Hodgkinson 1980, Bosch and Dudzinski 1984). Notwithstanding the difficulties associated with measuring defoliation in extensive grazing systems, a knowledge of defoliation patterns in the field is a necessary part of developing management practices for vegetation in rangeland ecosystems.

CONCLUSIONS

- The defoliation of saltbush by sheep in large paddocks under a continuous grazing regime can vary substantially, both temporally and spatially.

- Saltbush shrubs over large areas of these paddocks can be severely defoliated at times, with some shrubs in the study paddock being almost completely defoliated.
- Temporal variations in the defoliation of saltbush are a response to fluctuations in rainfall, because of its effect on herbage availability. Sheep graze saltbush more heavily when herbage is unavailable or of poor quality. Because of the low and erratic rainfall in these rangelands, extended dry periods when there is little herbage available are likely to be frequent but unpredictable. This can lead to extended periods of heavy grazing of saltbush by sheep.
- Spatial variation in grazing patterns due to the location of water points results in shrubs nearer the water point experiencing heavier grazing than those elsewhere in the paddock. However, these shrubs, by virtue of their location nearer the water point, also suffer grazing on a more sustained basis, often being grazed even when other feed is available. They are also the first shrubs to be grazed when other feed declines in availability.
- These patterns of defoliation have a marked effect in reducing the biomass of saltbush shrubs, and lower their ability to produce new growth following rainfall.
- The study of the actual rates of defoliation of forage plants in the field is a critical part of the development of effective grazing management practices.

CHAPTER 5

POPULATION DYNAMICS AND THE EFFECTS OF GRAZING

INTRODUCTION

Background

Plant Populations and Grazing Impact

The size of a population is essentially determined by the balance between the number of births, deaths, immigrants and emigrants (Harper and White 1974), and there are a range of demographic processes that constitute the life-cycle of an organism that contribute to this. For plants these include seed production, germination, establishment, vegetative propagation (for certain species), growth and mortality (Caswell 1989, O'Connor 1993). Variations in the rates of these processes determine the dynamics of a plant population, which are often summarised as the population growth rate (Caswell 1989, O'Connor 1993). These processes are regulated by an array of factors including population density, climate, competition, soil conditions, pathogens and grazing, which interact to determine the balance between recruitment and mortality, and hence the size of the plant population (Watkinson 1986).

In order to gain insights into the likely long-term impact of a disturbance such as grazing on a plant population, a detailed study of the species' population demography and how it is modified by the disturbance is needed (Harper and White 1974, Silander 1983, O'Connor 1993). It is only through studying the way demographic processes are altered by disturbance that an understanding of the mechanisms that control or regulate population size will be achieved (Harper 1977, Williams 1977, 1978, Crisp 1978, Jones and Mott 1980).

Grazing of plants may increase or, more commonly, decrease population size, or have little effect. Grazing activity can result in alterations to the population dynamics of a

species through the direct effects of defoliation or trampling on plants and indirect effects such as the modification of microclimate, soil physical and chemical properties and plant competitive interactions (Archer and Smeins 1991, Andrew and Lange 1986a, Charley and Cowling 1968, Louda *et al.* 1990). Grazing may also alter the timing of phenological events, for example, delaying senescence and mortality in semelparous plants by inhibiting flowering (Crawley 1983).

The direct effects of grazing reported in the literature are many and varied. Grazing may reduce the flowering of plants (O'Connor 1991, Milton 1994), the production of seed (Milton and Dean 1990, Bastrenta 1991, Hodgkinson 1991), seed size (Marshall *et al.* 1986), the survival of seedlings (Silander 1983, Gardiner 1986, Owens and Norton 1992), growth of plants (Crawley 1983, Louda *et al.* 1990, Milchunas and Lauenroth 1993, Milton 1994) and the survival of adults (Chambers and Norton 1993).

Other studies have reported examples where many of these demographic processes are unaffected or increased by grazing. Seed production increases in response to grazing have been observed in woody shrubs (Roundy and Ruyle 1989), grasses (Orr and Evenson 1991) and biennial species (Paige and Whitham 1987). Trampling by livestock may increase seedling establishment by burying seed (Hart and Norton 1988). Both Milton (1994), working on shrubs in South Africa, and Bastrenta (1991), who studied a rosette-forming legume (*Anthyllis vulneraria*) in France, reported that grazing made no impression on adult and seedling survival. Norton (1978) came to a similar conclusion concerning the effect of grazing on recruitment and survival in winterfat (*Ceratoides lanata*), a woody desert shrub in the United States, even though utilisation of the shrubs was more than 70%. He suggested three possible reasons for this, which were: 1) low population turnover, so the grazing treatments had not had the opportunity to express themselves; 2) grazing levels were within the carrying capacity of winterfat; or 3) extreme utilisation was avoided in drought years by adjusting stock numbers.

Indirect effects of grazing can be both beneficial or detrimental to plants. For example, the modification of inter-specific competitive relationships can often favour weedy or undesirable species. Heavy grazing increased the emergence and survival of seedlings of the thistle *Cirsium vulgare* in English pastures because selective grazing of the dominant grasses created gaps in the canopy and probably reduced competition from the grasses (Bullock *et al.* 1994). In contrast, compaction of the soil by the hooves of grazing animals can reduce water infiltration and thus reduce plant growth (Thurow 1991).

Factors Affecting Grazing Impact on Plant Populations

The diversity in the direct effects of grazing partly reflects life-form and species differences in the ability to cope with grazing (Chambers and Norton 1993, Van Duivenbooden 1993). It is well-known that grasses and many herbaceous dicots have a greater tolerance of grazing than most woody shrubs (Archer and Tieszen 1986). This was highlighted in a study by West *et al.* (1979) in North America. They found that grazing by sheep reduced the longevity of the woody shrub *Artemisia tripartita* (sagebrush) but increased the longevity of grasses. The ability to cope with grazing is associated with mechanisms that ensure rapid recovery of leaf area and carbohydrate reserves¹ following damage. These mechanisms can be physiological, such as compensatory photosynthesis (Gifford and Marshall 1973, Caldwell *et al.* 1981, Nowak and Caldwell 1984) and increased allocation of carbon to above ground parts (Detling *et al.* 1979, Bilbrough and Richards 1993), and/or morphological, like protected or dormant meristems (Briske 1986).

Obviously different intensities and frequencies of defoliation will be important in determining the effects of grazing, but the timing of defoliation experienced by the plants is also important (Dirzo 1984) and could contribute to the range of effects observed in the various studies. Defoliation of plants when they are physiologically active tends have a

¹Although the role of carbohydrate reserves in regrowth following defoliation is now thought to be of minor importance and that regrowth may be limited by a lack of other compounds (e.g. proteins) or trace elements (Caldwell 1986, Briske 1991, K. Hodgkinson pers. comm.), adequate energy reserves will be necessary before substantial growth, flowering and seed production occurs.

greater effect in increasing mortality and reducing recruitment than grazing at other times (Chambers and Norton 1993).

The influence of the intensity and timing of defoliation in determining the effects on plant populations is linked to the sensitivity of the various demographic processes to grazing. Certain processes appear to be more sensitive to grazing than others, so that not all processes are equally affected by grazing. Seed production is usually highly sensitive to grazing and is one of the first processes to be disrupted when plants are stressed by defoliation (Crawley 1983). For example, Hodgkinson (1991) observed this in several palatable arid zone perennial grasses; seed production was negligible at a level of grazing approximately half that at which a survival threshold was crossed and substantial mortality of established plants occurred. It has also been suggested that it is unusual for mature plants to be killed by herbivory, partly because only a percentage of the total leaf material is normally taken (Williams 1977, Dirzo 1984, Watkinson 1986). This implies that adult plant survival is reasonably tolerant of some levels of grazing. In contrast, seedlings are particularly vulnerable to defoliation because of their low biomass and low reserves of carbohydrates (Crawley 1983). Thus there is often a reduction in the sensitivity to grazing of a plant species with an increase in plant size (Silander 1983, Bullock *et al.* 1994).

Climatic conditions can interact with grazing to influence the outcome of herbivore activity on plant populations. Chambers and Norton (1993) reported that grazing increased mortality and decreased natality of *Artemisia spinescens*, a palatable, grazing sensitive species in salt desert shrubland in Utah, and these effects were intensified by drought. They also observed that *Atriplex confertifolia*, a species of low palatability which normally increases under grazing but is drought sensitive, suffered much higher adult mortality on grazed treatments during drought because of greater browsing of the shrub by sheep. Thus the effects of grazing or drought on plant populations can be amplified or modified by the effects of the other. However, grazing can have positive effects on plants during drought: *Ceratoides lanata* in Utah and *Maireana sedifolia* in

Australia have both shown enhanced tolerance of drought when grazed because the reduced leaf area results in more efficient use of soil moisture by the plants (Chambers and Norton 1993, Trumble and Woodroffe 1954).

A change in the abundance of a certain plant species under herbivory can also depend on the relative effects of herbivory on the demographic processes of the range of plant species present (Fox and Morrow 1986, O'Connor 1994). Inter-specific competition has been regarded as important in mediating changes in plant abundance due to herbivory in mixed communities, because the species least tolerant of defoliation would have a reduced competitive ability and would become less abundant (Jameson 1963, Crawley 1983, Westoby 1989, Louda *et al.* 1990). These interactions will depend to some extent on the availability of nutrients and other resources (Maschinski and Whitham 1989), so that competition in resource-rich areas will be less important. However, more recently it has been proposed that herbivore selectivity through its effect on differential defoliation intensity between co-occurring species, rather than defoliation tolerance, is the predominate factor determining changes in the abundance of a plant species in a mixed community (Brown and Stuth 1993).

The degree to which a change in the rate of a particular demographic process will determine changes in population size is dependent on the contribution the demographic process makes to the population growth rate. The relative importance of each of the demographic processes to the population growth rate varies between species, reflecting differences in the life-form and life-history strategies of species (Caswell 1986, de Kroon *et al.* 1986, Silvertown *et al.* 1993). Thus, for example, short-lived herbaceous species have a high contribution to the population growth rate from seedling recruitment, while survival of established plants is most important in long-lived species and woody plants (O'Connor 1993, Silvertown *et al.* 1993). The alteration of a demographic rate by grazing may have, therefore, only a minor impact on the population if it is a process which contributes little to the population growth rate. Often this aspect of population demography is overlooked, even though it can facilitate a greater understanding of

population changes and is useful in identifying optimum management strategies (e.g. Crouse *et al.* 1987). A good example of this is provided by O'Connor (1993, 1994), who studied the influence of grazing and rainfall on the demography of a number of savanna grasses in Africa. He found that reductions in the population growth rate were mainly due to differences in the survival of larger plants and changes in recruitment had little effect on population growth, because this process only contributed <5% to the growth rate.

Life-History Strategy and Dynamics of Arid Zone Perennial Plants

Arid zone perennial plants are generally long-lived. They have stable populations with a low turnover of individuals, where new individuals in the population are replacements for those that die (Harper and White 1974; Beatley 1974, Milton 1994). However, there is a diversity of demographic strategies within this plant life-form (Westoby 1980). Many studies have demonstrated that the population dynamics of these plants are dominated by rainfall (Williams 1970, Noble 1986b, Turner 1990), which is low and unpredictable with irregular, very dry periods and infrequent pluvial periods. These plants are characterised as 'stress-tolerators', possessing life-history strategies and morphology that confer an ability to cope with drought (Grime 1977, 1979, Westoby 1980, Stafford Smith and Morton 1990). Nevertheless, extremely dry periods are associated with increased mortality of adults (Turner 1971, Crisp 1978). Recruitment occurs infrequently (Beatley 1974, Grubb 1977) and seedlings are poor competitors and slow growing. Therefore establishment often relies on a series of good rains (Stafford Smith and Morton 1990, Griffin and Friedel 1985). In common with long-lived species from more mesic environments, seedling survival is low (Harper 1977, Owens and Norton 1989), with most seedlings dying as a result of desiccation (Beatley 1974, Hennessy *et al.* 1984, Auld 1990, Harrington 1991). Seedling mortalities of up to 100% after 12 months have been reported for *Acacia victoriae* and *Cassia* spp. (syn. *Senna*) in western New South Wales (Grice and Westoby 1987). Consequently, the survival of established plants tends to be very important to these populations and makes a large contribution to the population

growth rate¹ while recruitment and the survival of seedlings are generally less important (Silvertown *et al.* 1993, O'Connor 1993).

Plant Demographic Studies Under Grazing In Australian Rangelands

Historically, studies of plant population dynamics in many of the world's ecosystems have been rare (Harper and White 1974, Franco and Silvertown 1990) even though the need for studies of the mechanisms of population change under grazing (and other disturbance) has been recognised (Crisp 1978, Williams 1978, Jones and Mott 1980). In Australian rangelands the most comprehensive demographic studies have examined the effects of grazing on the population dynamics of several important pasture grasses. Williams (1968, 1970) focussed on *Danthonia caespitosa* (wallaby grass) on the Riverine Plain of NSW and Orr (1991) and Orr and Evenson (1991a,b) studied *Astrebla* spp. (mitchell grasses) in sub-tropical Queensland. These studies have shown that moderate levels of grazing can be beneficial to both species. A long-term study of the effects of grazing on the population dynamics of perennial grasses in the semi-arid mulga woodlands of NSW is currently underway (K. Hodgkinson pers. comm.).

Demography of Saltbush and Grazing Impact

A number of studies have examined particular aspects of the demography of saltbush but often the results vary between studies and are contradictory. Mortality of ungrazed mature saltbush shrubs is usually low. Saltbush populations at Koonamore Vegetation Reserve in north-eastern South Australia exhibited negative exponential survivorship of mature plants when ungrazed and recovering from a period of severe overgrazing, indicating the rate of mortality (6%) was constant with age (Crisp 1978). However, high mortality can occur in extreme droughts (Crisp 1978, Westoby *et al.* 1989, Eldridge and Westoby 1991) and maximum longevity is reported to be approximately 30 years (Crisp

¹Although I imply it here, note that a correspondence between the demographic approach to life-history strategy (using measures of fecundity, growth and survival and their contribution to the population growth rate) and the Competitive, Stress-tolerant and Ruderal (CSR) classification (Grime 1977) has not been demonstrated (Silvertown *et al.* 1992, 1993), despite a superficial similarity between their classifications.

1978, Williams 1979). At Middleback, Andrew and Lange (1986b) recorded a mean mortality rate for ungrazed saltbush of 37% over a period of 8 years (1975-1983), which included a severe drought.

Reports on the frequency of recruitment in saltbush vary. Some workers have suggested that major recruitment events occur sporadically, averaging about once every three to five years in association with periods of heavy rainfall (Williams 1979, Graetz and Wilson 1984), although Hall *et al.* (1964) observed a greater frequency, with recruits appearing in 17 out of 36 years. In contrast, Crisp (1978) and Eldridge and Westoby (1991) reported that recruitment occurred in most years but seedling survival was low (as low as 25% per month; Eldridge and Westoby 1991). Also, Eldridge *et al.* (1990) suggested that rather than being stable, populations of the species are highly dynamic with annual turnover rates of up to 54% for entire populations and 20% for that part of populations greater than 9 cm tall. Consequently young plants (less than 2 years old) constituted an average of 60% of the population at any time. They stated that the density of saltbush populations cannot be expected to be constant even in the absence of grazing, presumably because of climatic fluctuations. Graetz (1986), on the other hand, observed that sexually mature adults made up approximately 90% of the population suggesting a much lower turnover rate.

Despite the chenopod shrublands, and saltbush in particular, being the subject of a considerable amount of ecological research over the years there has been no study that has investigated the effects of grazing on the whole life cycle of saltbush. A few studies have examined grazing effects on particular demographic processes, but most information on these changes has been deduced from the analysis of changes in population structure under grazing. Saltbush is generally unable to recover from severe defoliation, so heavy grazing results in the death of adult shrubs. Moderate levels of grazing, on the other hand, have been reported to have little effect on plant survival (Osborn *et al.* 1932, Carrodus and Specht 1965, Wilson *et al.* 1969, Leigh and Mulham 1971, Graetz 1978, 1980). This was probably the situation in the study carried out by Eldridge *et al.* (1990).

In their study of grazing effects at a single distance from water they found no difference in recruitment or the survival of both seedlings and adults on grazed and ungrazed plots. No clear indication was given of the level of defoliation experienced by the shrubs in this study and the results possibly reflect a moderate level of grazing. Knowles and Condon (1951) suggested that saltbush seedlings are selectively grazed by sheep, so they considered careful management to be necessary when seedlings are present to prevent their elimination. In contrast, Lange *et al.* (1992) found that saltbush seedlings were spared by sheep in small experimental plots with high stocking rates. In another study Williams *et al.* (1978) concluded that trampling by sheep could increase seedling mortality. Heavy grazing has been reported to increase recruitment because the removal of adult plants by grazing favours seedlings through reduced competition from adults (Graetz 1980, 1986). However, Graetz (1980) suggested that rainfall has a greater influence on seedling fate than grazing.

Aims

Despite spatial variation in the rates of demographic processes in plant populations being ubiquitous, most plant demographic studies fail to recognise this variation or incorporate it into models of population dynamics, as recently pointed out by Bullock *et al.* (1994). The spatial and temporal patterns of defoliation observed in Yanaby (Chapter 4) could be expected to have a number of possible long-term consequences for the saltbush population, depending on the location within the paddock. This variation will have important implications for management of the population. Previous studies of grazing impacts on saltbush populations have either examined some of the demographic processes under grazing and ignored the spatial variation or, alternatively, considered the spatial variation in population structure under grazing but not the controlling mechanisms. Since an understanding of the impact of grazing on population processes is necessary for effective management, and given that this impact will vary across a paddock, a full demographic study of the saltbush life cycle across an entire grazed paddock should provide useful information for the development of improved management practices.

The aims of this study, therefore, were to:

- 1) examine how recruitment, survival and growth of saltbush varied over a paddock due to the patterns of defoliation of saltbush by sheep, for a period of 6.5 years.
- 2) quantify the changes in population size as a result of these impacts and assess population stability with the aid of matrix population models.
- 3) use the matrix models to identify the demographic processes which are most critical in the saltbush life cycle and which are most influential in causing changes in the population dynamics under grazing.

METHODS

Collection of Demographic Data

A census of the saltbush populations at each of the nine study sites in Yanaby was taken at intervals of approximately six months (April and October each year), in conjunction with the estimates of shrub biomass presented in Chapter 4. Thus the first records were from October 1987 and the latest results presented here are from March 1994. It was not possible to collect data in October 1993, so the March 1994 data represents population changes over a full year rather than six months. On each occasion all saltbush plants on the 10×5 m sub-section of each 20×10 m plot were located, measured, sexed (if possible) and charted. The plots were carefully searched to find all seedlings at all stages of growth, and great care was taken to avoid trampling seedlings during sampling. This process was extremely time-consuming so it was only possible to sample two grazed plots and the exclosed plot at each site. Plants were classified using a modified version of the scheme used by Barker (1979). Seedlings were classified into two size categories, those below 4 cm tall and those 4 cm tall or higher. Juvenile shrubs were defined as being less than 10 cm tall and with a woody stem greater than 3 mm basal diameter. Woody plants greater than 10 cm tall were deemed adults. By mapping and classifying plants in this way the fate of individual plants could be followed through time.

Data Analysis

Matrix Population Models

Matrix population models were used to analyse much of the population dynamics data. These models (sometimes referred to as population projection matrices) are a powerful tool for analysing the demography of organisms and are becoming increasingly popular for examining the effects of disturbance on populations and as a tool in the management of populations. With these models it is possible to calculate the population growth rate and determine the contribution of each of the demographic processes to this rate (Caswell 1989). These models were first used for the analysis of age-based life-tables (Leslie 1945) but they also are readily applied to both plants and animals where the rates of life-cycle processes (reproduction, survival and growth) are associated with size classes or developmental stages of the organism. A number of examples of their use exist in the literature which include the analysis of population data for clonal (Huenneke and Marks 1987) and non-clonal plants (Werner and Caswell 1977, Caswell and Werner 1978, Silva *et al.* 1991), marine algae (Ang and De Wreede 1990), insects (Lefkovitch 1965), rabbits (Smith and Trout 1994) and sea turtles (Crouse *et al.* 1987).

Much of the power of matrix population models arises from the utilisation of the stage or size structure of a population to define the fates of individuals in the population. The models thus permit the integration of the impact of the environment on vital rates throughout the life cycle. Stage or size structure of a population is often employed rather than age structure because for many plants, and in particular perennial species, stage or size is a much better descriptor of plant performance or fate than age (Harper and White 1974). Furthermore, age is often difficult to determine in long-lived plants (Harper and White 1974, Caswell 1989). However, the use of such models for long-lived perennial plants is still rare (Enright and Watson 1991) even though much could be learnt about the dynamics of such species through the application of these models.

Matrix population models take the form of the simple difference equation

$$\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t) \quad (5.1)$$

where $\mathbf{n}(t)$ is a column vector whose elements, $n_i(t)$, represent the size/stage class distribution of the population at time (t) and $\mathbf{A}$ is a square matrix whose components (a_{ij}) represent the transition probabilities for the fate of individuals in the population. These fates include surviving and remaining in the same size/stage class (stasis), surviving and growing to the next size/stage class (progression) and surviving but declining in size-class (retrogression). The transition matrix also includes values for stage-specific fecundity. Multiplying the population vector (size/stage class distribution) by the transition matrix yields the predicted population size and structure after a single time period has elapsed.

By repeated multiplication the population can be projected for any number of time periods, k , which is equivalent to:

$$\mathbf{n}(t+k) = \mathbf{A}^k \mathbf{n}(t) \quad (5.2)$$

At increasing values of k the predicted population size/stage class distribution approaches what is known as the stable stage distribution (SSD), where the proportion of individuals in each class remains constant from one time period to the next. The SSD is equivalent to the dominant right eigenvector ($\mathbf{w}$) of the transition matrix, which can be calculated algebraically.

The rate of population growth over each projection interval must also be stable once the population stage distribution has converged at the SSD and is represented by λ , the asymptotic population growth rate (or the finite rate of natural increase), where

$$\lambda = \mathbf{n}(k)/\mathbf{n}(k-1) \quad (5.3)$$

and $\mathbf{n}(k)$ represents the projected stage distribution vector after k time-periods given that a stable stage distribution has been reached. When $\lambda = 1.0$ population size remains constant through time. A value > 1.0 indicates an increasing population, and a value < 1.0 indicates a declining population. The population growth rate λ is also given by the dominant eigenvalue of the transition matrix and is related to the intrinsic rate of natural

increase r :

$$r = \ln \lambda. \quad (5.4)$$

Matrix population models fall into two main classes; time-invariant and time-varying models. In time-invariant models the transition probabilities or vital rates are constant for each population so that the transition matrix is deterministic. Thus, unless the population is stable, population growth or decline will be exponential so that predictions of future population size quickly become unrealistic and meaningless. However, time-invariant models are useful in the analysis of demographic data since they reveal information about present conditions, and the performance of populations growing under different environmental conditions can be assessed by comparing λ and SSD for each set of circumstances (e.g. Werner and Caswell 1977, Bullock *et al.* 1994). The sensitivity of λ to changes in individual transitions (i.e. survival, growth and reproduction for each stage) can also be examined by using elasticity analysis, where the elasticity e_{ij} is the proportional change in λ resulting from a proportional change in a_{ij} (de Kroon *et al.* 1986, Caswell 1986). The elasticity of λ with respect to a transition a_{ij} is given by

$$e_{ij} = \frac{a_{ij}}{\lambda} \frac{\partial \lambda}{\partial a_{ij}} \quad (5.5)$$

$$= \frac{a_{ij}}{\lambda} \frac{v_i w_j}{\langle \mathbf{w}, \mathbf{v} \rangle} \quad (5.6)$$

where v_i is the i th element of the left eigenvector $\mathbf{v}$, w_j is the j th element of the right eigenvector $\mathbf{w}$, and $\langle \mathbf{w}, \mathbf{v} \rangle$ is the scalar product of $\mathbf{w}$ and $\mathbf{v}$. The elasticities e_{ij} also represent an estimate of the relative contribution of each transition to the population growth rate, so it is possible to examine the degree to which population growth depends on survival, growth and reproduction at different stages in a species' life cycle (de Kroon *et al.* 1986, Caswell 1989). Elasticity analysis, therefore, is also a useful tool in comparative demographic studies of life history strategies (see Enright and Ogden 1979, Enright and Watson 1992, Silvertown *et al.* 1993, Svensson *et al.* 1993). Another important function of elasticity analysis is that it provides an indication of the effect of

errors in the estimation of matrix elements on λ , where errors in elements with high elasticity have the greatest influence. This can serve to indicate the part of the life cycle where extra effort is needed or an alternative experimental design is required in subsequent studies to improve the precision of the model.

An extension of elasticity analysis, life-table response experiment (LTRE) analysis (Caswell 1989), can be used to identify the differences in vital rates between populations which are important in causing differences in population growth rate between populations existing under different environmental conditions, or subjected to different experimental treatments. This involves decomposing the effect of the environment or treatment on λ into contributions from the different demographic rates. This is achieved by taking the mean of the matrices for the two populations of interest and for each matrix element multiplying the difference in transition probability between each population matrix and the mean matrix by the sensitivity of λ to the respective matrix element, to give the contribution of each transition to the difference in λ . The sum of these contributions for each matrix gives an approximation for the overall effect $\alpha^{(i)}$ of the conditions or treatment on the population growth rate $\lambda^{(i)}$ compared to the growth rate for the average projection matrix $\lambda^{(\cdot)}$, i.e.

$$\lambda^{(i)} = \lambda^{(\cdot)} + \alpha^{(i)} \quad (5.7)$$

where $\alpha^{(i)}$ is approximated as

$$\bar{\alpha}^i = \sum_{k,l} (a_{kl}^{(i)} - a_{kl}^{(\cdot)}) \left. \frac{\partial \lambda}{\partial a_{kl}} \right|_{\frac{1}{2}(A^{(i)} + A^{(\cdot)})} \quad (5.8)$$

and $A^{(i)}$ is the population matrix for treatment i , $A^{(\cdot)}$ is the mean matrix and a_{kl} the (k,l) entry of a matrix. The sensitivity is assessed at a matrix midway between the two matrices being compared. The contributions can be summed for each fate (survival, growth and reproduction) for each stage class and compared to identify the differences in the fates for each stage class between the populations which are contributing most to the difference in the population growth rate between the populations.

In time-varying models the transition probabilities vary between projection intervals, representing temporal change in vital rates due to climate or other factors. These models generally do not converge to a stable stage distribution but instead population size and structure fluctuate in response to the conditions represented by the transition matrices (Caswell 1989). These models are useful for projecting what the population may be like in the future, for estimating expected population growth rates in stochastic environments and estimating the probability of, and time to, extinction (Tuljapurkar and Orzack 1980). Time-varying models of saltbush dynamics are dealt with in Chapter 6.

Analysis Procedure

A time-invariant size/stage classified model with a six month time step was used in the analysis of the data. The transition matrix structure (Table 5.1) was derived from the life cycle graph shown in Figure 5.1. The size-classes, although chosen arbitrarily, attempted to represent differences in survival and fecundity, with the probability of survival increasing for each size-class from size-class one through to size-class four. Plants in size-class four were the only ones considered capable of reproduction. These decisions were based on the high rates of seedling and small shrub mortality reported for saltbush (Crisp 1978, Eldridge and Westoby 1991) and my casual observations of saltbush. The existence of thresholds in plant size before flowering occurs has been reported for many other species (Samson and Werk 1986).

The model was parameterised by constructing transition frequency tables (Caswell 1989) from the raw data for each site and grazing treatment for each six month observation interval. These tables yield maximum likelihood estimates of the transition probabilities (Bishop *et al.* 1975) for growth (i.e. transition to another size-class) and survival elements of the transition matrix. The survival, growth and death probabilities for each stage class sum to one, so the rate of mortality of individuals within stage class j during time interval t , d_{jt} , can be determined from the matrix, i.e.

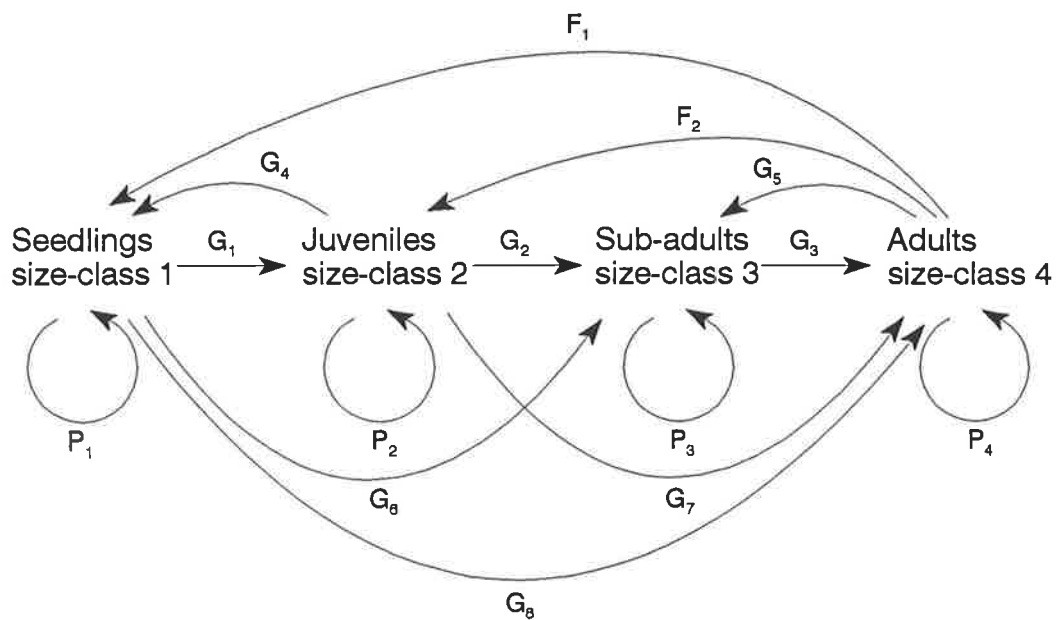


Figure 5.1. The life cycle graph that was used as the basis for the size-structured matrix population models for saltbush. This graph describes the transitions between size-classes that were considered possible for saltbush over a transition interval ($t, t+1$) of six months. P = survival, G = growth, F = fertility (i.e. reproduction). Note that although transition G_8 was defined as being possible over a six month transition period, it was a very rare transition. See Methods section in text for the criteria used to allocate plants to size-classes.

Table 5.1. The structure of the transition matrix, derived from the life cycle graph.

Size-class at census $t+1$	Size-class at census t			
	1	2	3	4
1	P_1	G_4	-	F_1
2	G_1	P_2	-	F_2
3	G_6	G_2	P_3	G_5
4	G_8	G_7	G_3	P_4

$$d_{jt} = 1 - \sum_i a_{ijt} \quad (5.9)$$

Fecundity was estimated as the ratio of recruits to reproductive adults at each census. Although saltbush is dioecious, reproductive values were based on the total number of adults in size-class four, both male and female, since it was difficult to reliably sex the shrubs on many occasions. These estimates assume there is no migration of seed into the population and that a persistent seed bank does not develop. While the latter supposition is dubious the former is supported by evidence that the majority of seeds remain within close proximity of the parent plant (Williams 1979).

The slow rates of change and the limitations to the sample size that could be obtained meant that many transitions were rare, so it was necessary to estimate the transition matrix over the entire study period for each plot. This can be accomplished by summing the transition frequencies for each census for each plot before determining the probabilities (Caswell 1989). However, since my data consisted of separate transition frequency tables for summer and winter periods (i.e. April and October), a yearly matrix was created by multiplying the summer and winter matrices resulting from summing all the summer transition frequency tables and all the winter frequencies respectively. To include the data from March 1994, which already represented changes over a year, a weighted average matrix was calculated for each plot, based on the number of six month periods contributing information to the matrices. This is described by the equation:

$$C = 11/13(C_{ij})_p + 2/13(C_{ij})_y \quad (5.10)$$

where C is the overall annual matrix, $(C_{ij})_p$ is the product matrix for summed winter and summer transitions and $(C_{ij})_y$ is the yearly matrix for March 1994. In this way all of the available information was able to be included and the seasonal variation in transitions was utilised in a realistic way, although it meant differences between seasons/years could not be examined analytically. Separate matrices were constructed and analysed for the two replicate grazed plots at each site because of considerable variation in the data between the plots at certain sites. These replicate plots are indicated in the results by a letter

representing the site and their replicate number (e.g. E1).

The power method (Caswell 1989), which employs equation (5.3), was used to calculate the population growth rate, λ , and the dominant left and right eigenvectors (v and w) of the matrix for each plot. Using the methods described earlier, elasticities were calculated for each matrix to determine the sensitivity of λ to the various demographic processes and LTRE analysis was performed to examine the demographic processes which were contributing most to the differences in λ between sites at different distances from water.

To test for differences between matrices, the demographic fate of individuals was compared between sites and grazing treatments using log-linear analysis (Bishop *et al.* 1975). This analysis was carried out on the summer and winter transition frequency tables summed over the first 5.5 years (i.e. data for March 1994 was excluded). The counts used for the grazed treatment were the mean values of the two grazed plots at each site. Tables were collapsed to the following three demographic fates to ensure adequate sample size: (1) plants remaining in the same stage class; (2) plants moving up one or more stage classes; and, (3) plants moving down a stage class or dying. All cells of the contingency tables, apart from structural zeros, had 0.5 added to avoid problems with too many expected frequencies near zero (as in Caswell 1989). Since recruitment is a different class of transition (i.e. it is not a true fate of an individual) and it is confined to adult shrubs, it was analysed separately. This analysis simply tested for an effect of the interaction between site and treatment on the number of recruits on each plot during the entire study.

The null hypothesis for the main analyses was that the fate (F) of an individual was independent of location (L) (i.e. site) and grazing treatment (T) conditional upon its initial size-class (S). Models were fitted sequentially and a significance level of 0.05 was used. If the first model (SF, STL) did not fit, then location, grazing treatment or both had an effect on fate. If the next model (SFT, STL) did not fit, then location had an effect, and similarly, treatment had a significant effect if the model SFL, STL did not fit. If none of

the models fitted, then location and grazing treatment both had effects. The model STL, SFT, SFL was then fitted to test whether location and grazing treatment interacted to affect fate; if the model did not fit then the interaction was significant. To dissect out the significant effects apparent in the overall analysis, the main table was decomposed into the two grazing treatments and then to the plant size-classes within treatments. Marginally significant effects in the results of this decomposition need to be treated with caution, since the probability of Type I errors is inflated as the number of comparisons increases (Sokal and Rohlf 1981). Calculations were performed using the Statistix software package (Analytical Software 1991).

Separate log-linear analyses were carried out to test for an effect of location (L) (i.e. site) and grazing treatment (T) on mortality, for the data grouped in three ways, i.e. all size-classes pooled, seedlings pooled with juveniles and sub-adults pooled with adults. Because of the low rates of mortality on some plots and the low numbers of individuals on others, these analyses were performed on data summed for the whole study, so time effects could not be tested. Two fates (F) were defined; mortality of the individual during the study or survival until the end of the study. Fitting the model LT, LF, TF against LT, LF tests whether mortality was independent of grazing treatment once the effects of location have been included (i.e. it tests the TF term). Similarly, fitting LT, LF, TF against LT, TF tests whether mortality was independent of location once the effects of grazing treatment have been included. The probability for the model LT, LF, TF indicates the significance of the LTF interaction (following Caswell 1989). The analyses were performed using the Statistix software package (Analytical Software 1991). Trends in certain demographic parameters with distance from water were examined using linear regression, while temporal trends were examined by graphical comparison.

RESULTS

Population Sizes and Flux

Initial population sizes at each site reflected the already established piosphere pattern (due to a long history of grazing; see Chapter 3), with lower plant numbers nearer to water, due to the impact of sheep grazing for approximately the past 60 years. Two sites near the water point had approximately 20 plants on each 50 sq. m. plot while those sites furthest from water (sites G and I) had plant numbers around 110-120 per plot (Figure 5.2). The number of plants per plot increased with distance from water in a linear fashion (regression, $\text{plant number} = -18.9 + 0.03^{***} \cdot \text{distance(m)}$, $R^2=0.61$). Despite attempts to choose plots with similar plant density when establishing the sites, there were differences between plots within certain sites in initial plant numbers, although the foliage biomass levels on these plots were similar (see Chapter 4).

Several patterns were apparent in the changes in saltbush numbers during the study, depending on the location in the paddock and the grazing treatment (Figure 5.2). Rainfall appeared to be important in determining the fluctuations in plant numbers at sites furthest from water, whereas grazing appeared to be the main factor controlling plant number at sites nearer to the water point. The number of plants fluctuated most at the sites furthest from water (sites G and I), in response to variability in rainfall, but the magnitude of the changes differed between these two sites. An initial decline in numbers on most plots at these sites during the 18 months from October 1987 until April 1989 reflected the dry conditions over the period (see Figure 3.5). Following good rainfall (184 mm) in autumn and winter in 1989, numbers increased, particularly at site G which recorded a substantial increase in numbers (26-39 plants per 50 sq. m plot; see Figure 5.2). Gains were much smaller at site I (4-11 plants per plot). Numbers then declined during summer 1990, again reflecting low rainfall, but increased at both sites following good rains in winter 1991. On this occasion the increase at site I was more substantial than the first rise (31-141 plants per plot) while at site G it was similar. A slow decline then ensued during 1992 and continued until the final census in March 1994, despite excellent rains for much of this period. Although there were small differences in the nature of these fluctuations

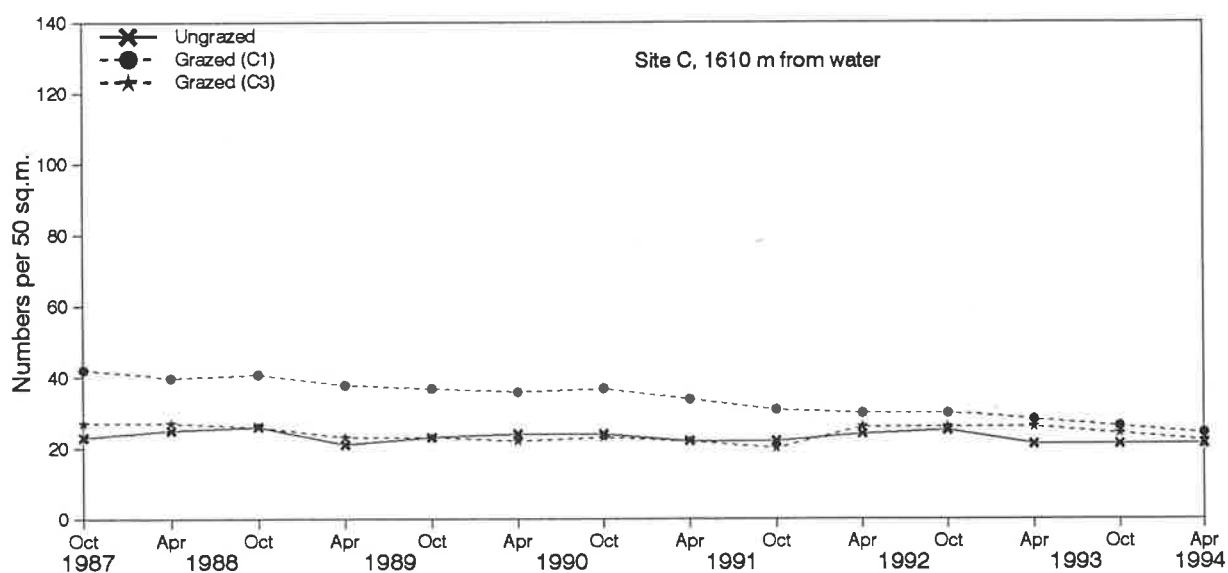
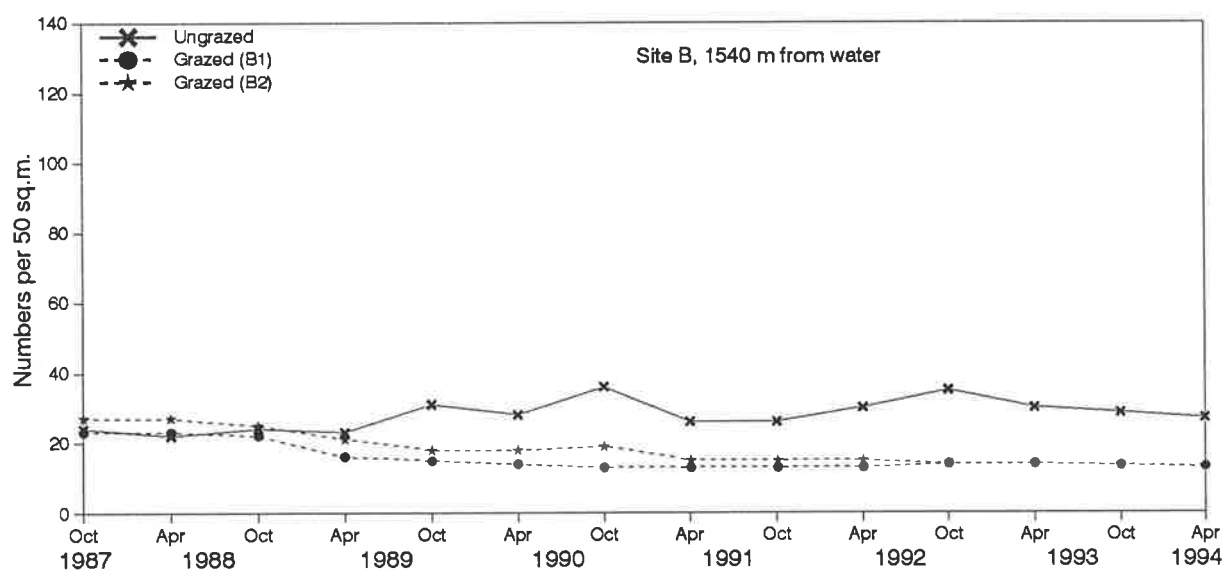
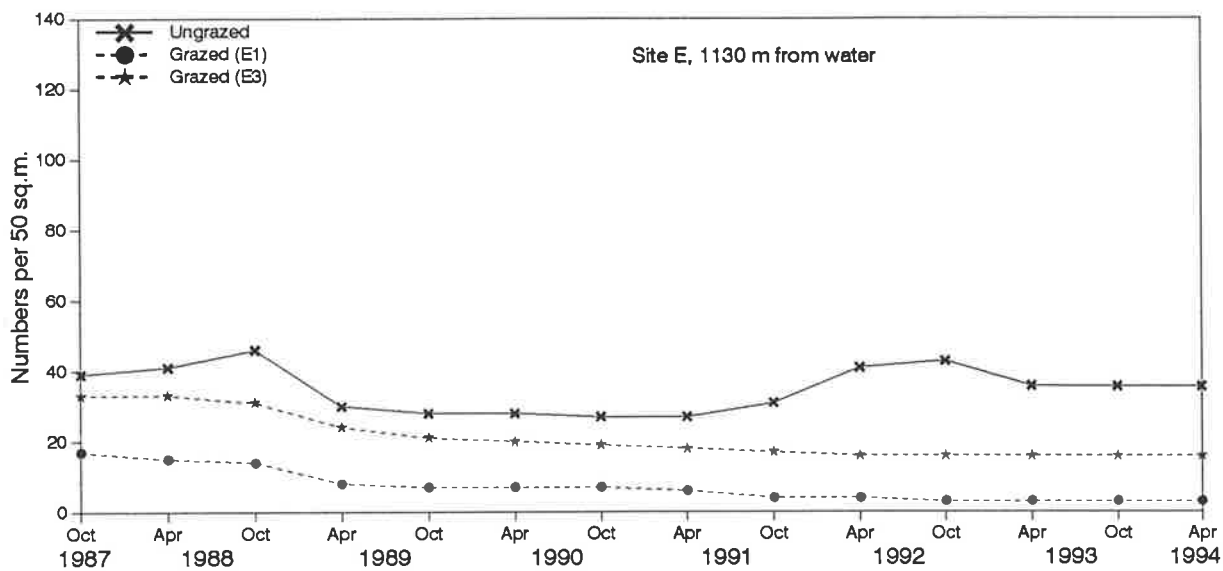


Fig. 5.2. Saltbush numbers on two grazed and a single exclosed plots at nine sites in Yanaby. Graphs are arranged in order of increasing distance from water. The figure is continued on the following pages.

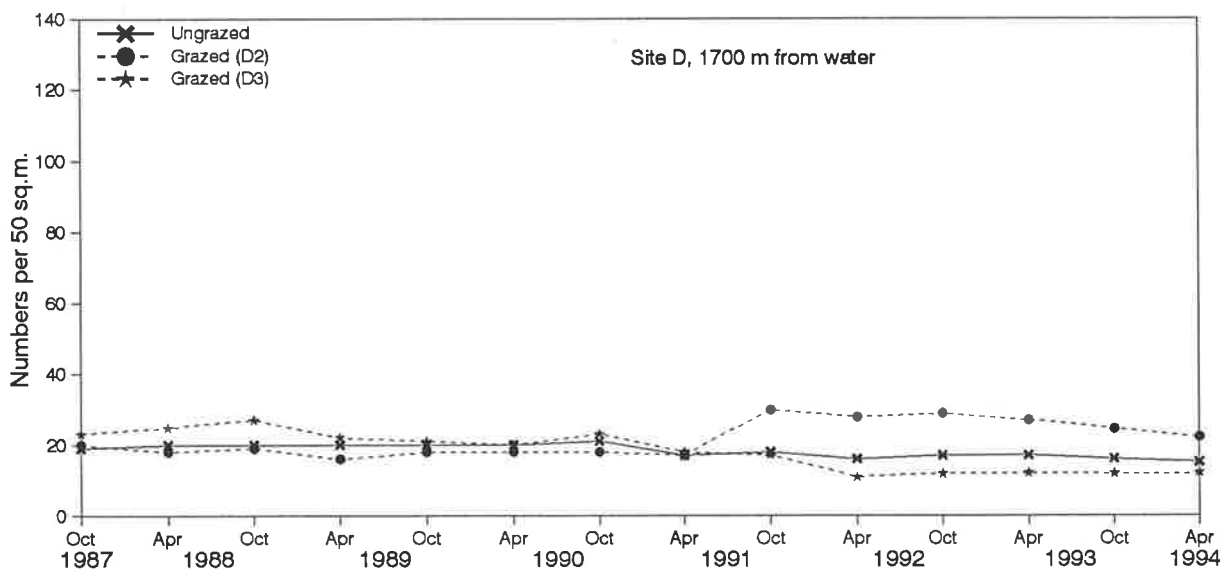
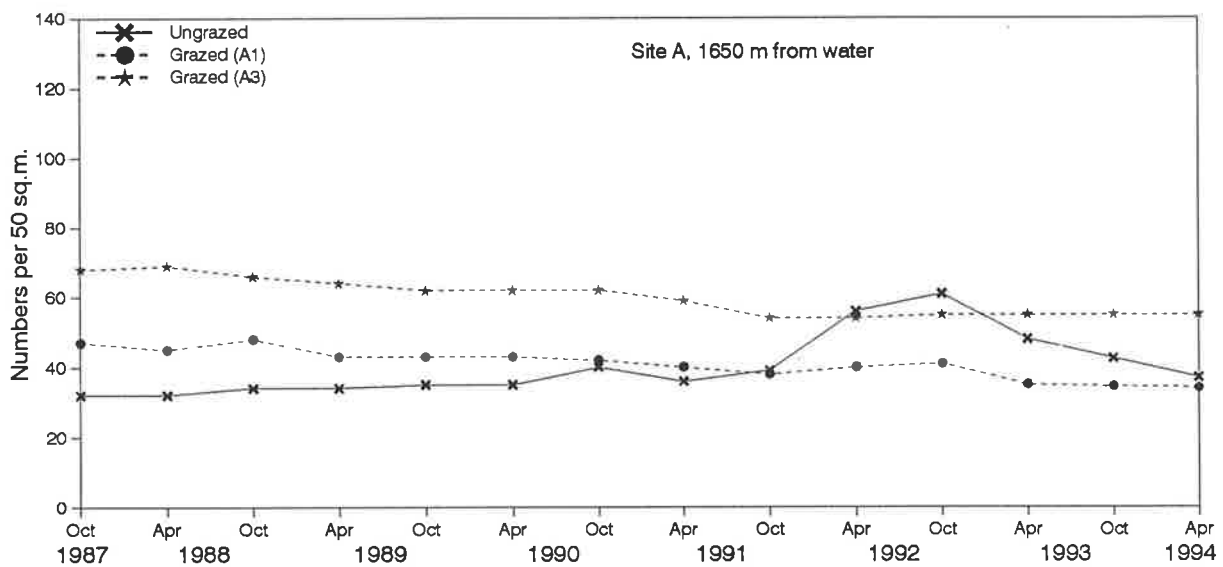
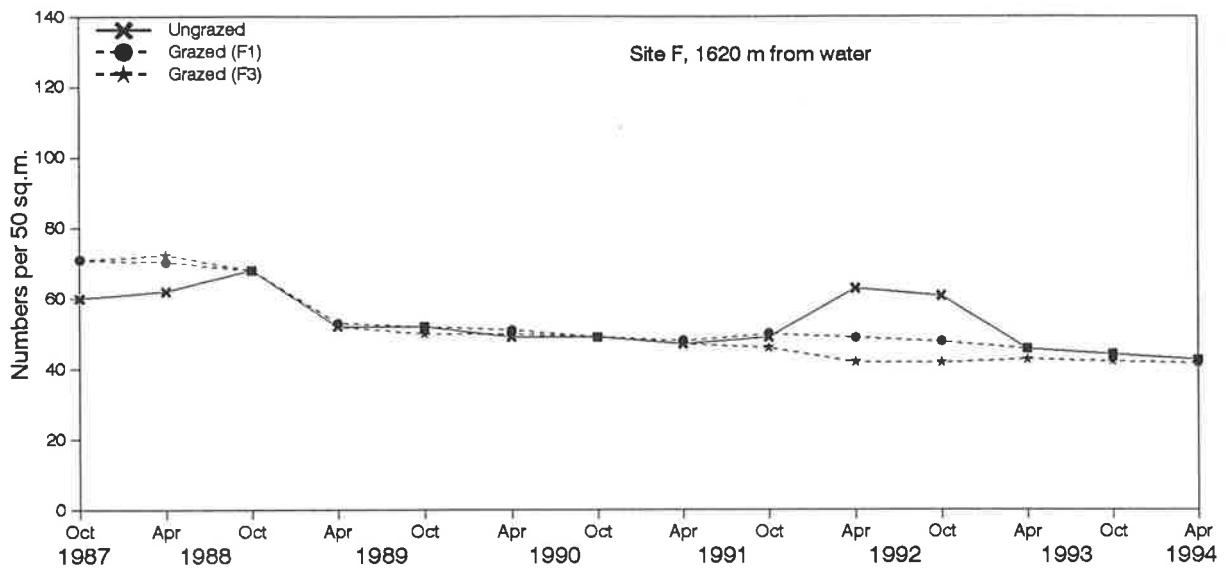


Fig. 5.2. (continued) Saltbush numbers on two grazed and a single exclosed plots at nine sites in Yanaby. Graphs are arranged in order of increasing distance from water. The figure is continued on the following page.

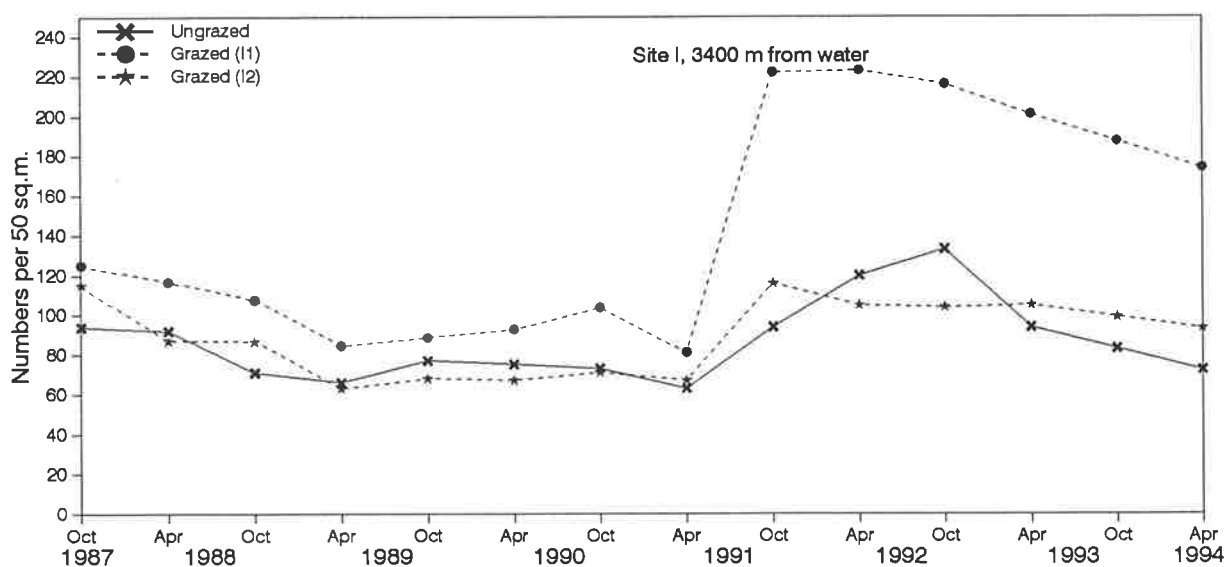
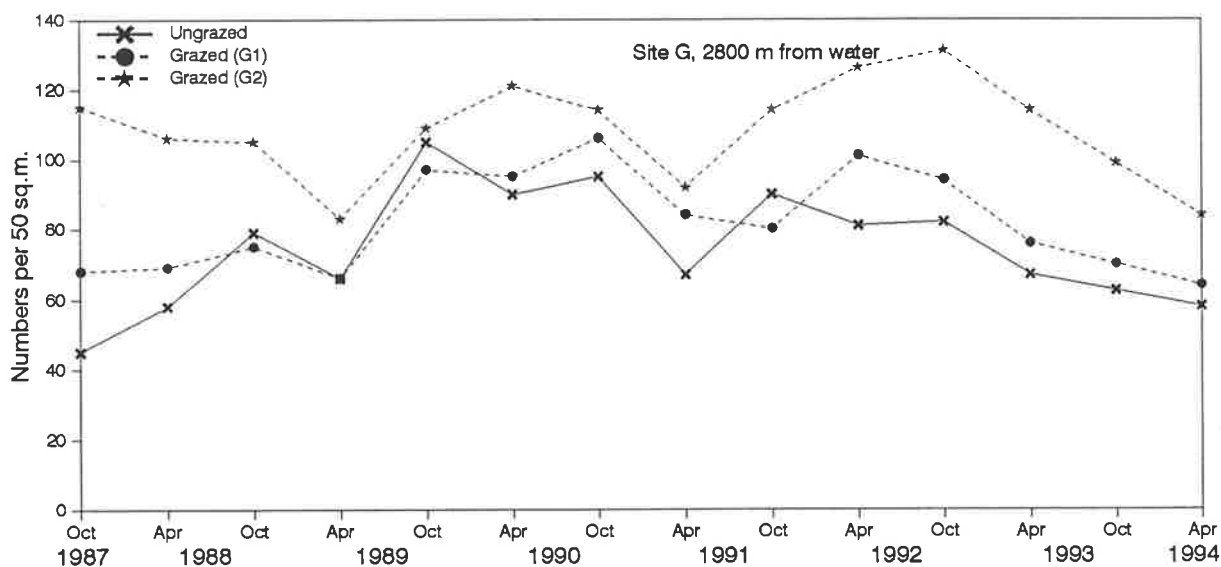
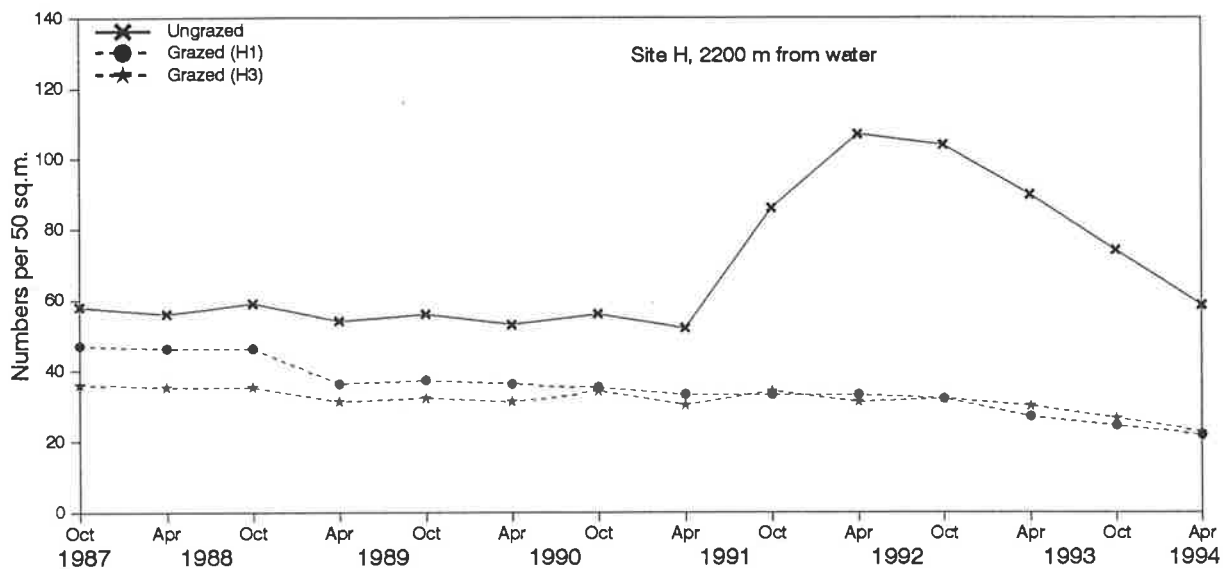


Fig. 5.2. (continued) Saltbush numbers on two grazed and a single exclosed plots at nine sites in Yanaby. Graphs are arranged in order of increasing distance from water. Note the change in scale of the ordinate for site I.

between the exclosed and grazed treatments at each of these sites, the general patterns were similar, suggesting the light grazing experienced by the shrubs on the grazed plots was having little effect on population size.

At most other sites differences were apparent between grazing treatments in the fluctuations in numbers, particularly following the good rains in winter 1991. Early in the study numbers showed no change, a decline or a slight rise, but during the very dry summer of 1988-89 numbers declined on most grazed plots, with some showing marked reductions. Most exclosed plots also showed this decline in numbers during this period but there were several exceptions where numbers were maintained (sites A, B and D). The rains in April 1989 had little immediate effect on numbers on both grazed and exclosed plots, except at Site B which recorded a modest increase on the exclosed plot 6-7 months after the rains. Numbers changed little on the remaining plots during the next 18 months apart from a very gradual decline on most grazed plots. In contrast to the 1989 rains, the winter and spring rains in 1991 caused increases on several exclosed plots (sites A, B, E, F and H) and on a grazed plot at site D but there was only a minor response, no change or a continued slow decline on the grazed plots at other sites. On the plots where numbers did increase a decline followed, mainly during summer 1992-93. In summary, the overall patterns at these sites for the duration of the study were of a decline in shrub numbers on the grazed plots, with little fluctuation in numbers, and stable or declining numbers on the exclosed plots initially, but with increases late in the study. This, together with the patterns observed at the more distant sites, suggests grazing was having a negative impact on plant numbers on grazed plots at these sites during this study. Changes in plant number during the study sustained the piosphere pattern (regression: $\text{plant number} = -55.9^{**} + 0.05^{***} \cdot \text{distance(m)}$, $R^2 = 0.7$).

Population turnover (the proportion of plants present at the beginning of the study in October 1987 which had died prior to the census in April 1994) was variable between sites and grazing treatments (Table 5.2). Turnover ranged from 10% (site A, exclosed) to 83% (site D, grazed plot D3). There was no consistent spatial pattern in turnover

Table 5.2. Population turnover in saltbush between October 1987 and April 1994 for grazed and ungrazed plots at nine sites in Yanaby. Population turnover is the proportion of plants (%) present at the beginning of the study which died prior to the final census in April 1994. Sites are arranged in order of increasing distance from water.

Site	Plot	Turnover (%)
E	ungrazed	49
	grazed (E1)	77
	grazed (E3)	55
B	ungrazed	21
	grazed (B1)	48
	grazed (B2)	60
C	ungrazed	26
	grazed (C1)	44
	grazed (C3)	42
F	ungrazed	37
	grazed (F1)	45
	grazed (F3)	44
A	ungrazed	10
	grazed (A1)	38
	grazed (A3)	37
D	ungrazed	37
	grazed (D2)	35
	grazed (D3)	83
H	ungrazed	18
	grazed (H1)	54
	grazed (H3)	50
G	ungrazed	20
	grazed (G1)	29
	grazed (G2)	47
I	ungrazed	45
	grazed (I1)	55
	grazed (I2)	49

across the paddock. However, in comparing grazing treatments turnover was generally lower on exclosed plots than on the corresponding grazed plots.

Recruitment

Recruitment of seedlings fluctuated in time and varied between sites and grazing treatments (Figure 5.3). Site and treatment were not independent ($G^2=158.12$, $P<0.001$) with respect to the number of recruits. Compared to grazed plots, exclosures generally recorded greater recruitment. The exceptions to this were at sites further than 2200 m from the water point (sites G and I) where, overall, recruitment was higher but similar between treatments. Low numbers of recruits in many years precluded a full analysis of temporal fluctuations. Early in the study recruitment was similarly low on both grazing treatments at sites near the water and higher at distance. Later in the study the general level of recruitment increased. However, at a number of sites nearer the water (sites A, B, E, F, H) a difference in recruitment developed between the grazing treatments, with greater recruitment occurring on the exclosed plots than on grazed ones, where recruitment remained negligible. The total number of recruits recorded on grazed plots during the study increased linearly with distance to water (regression: $\text{recruits} = -138.52^{***} + 0.09^{***} \cdot \text{distance(m)}$, $R^2=0.9$).

Seasonal differences in the amount and timing of rainfall between years appeared to be the chief cause of temporal variation in the number of recruits (Figure 5.4). The two main recruitment events occurred in winter, one in 1989 and the other in 1991, following good autumn-winter rains. In each of these years at least one month during these seasons received rainfall in excess of 50 mm. One other recruitment event (recorded in April 1992) occurred over the summer months and was initiated either by good rains in the preceding spring, since 58 mm of rain fell in November 1991, or by 63 mm of rain which fell on the last day of February 1992. The latter option is most likely because of the small size of the seedlings at the time of field work in April. Large rainfalls did not inevitably lead to major recruitment events. Despite good rains between August 1992 and January 1993, which included four months each with rainfall of more than 50 mm, there

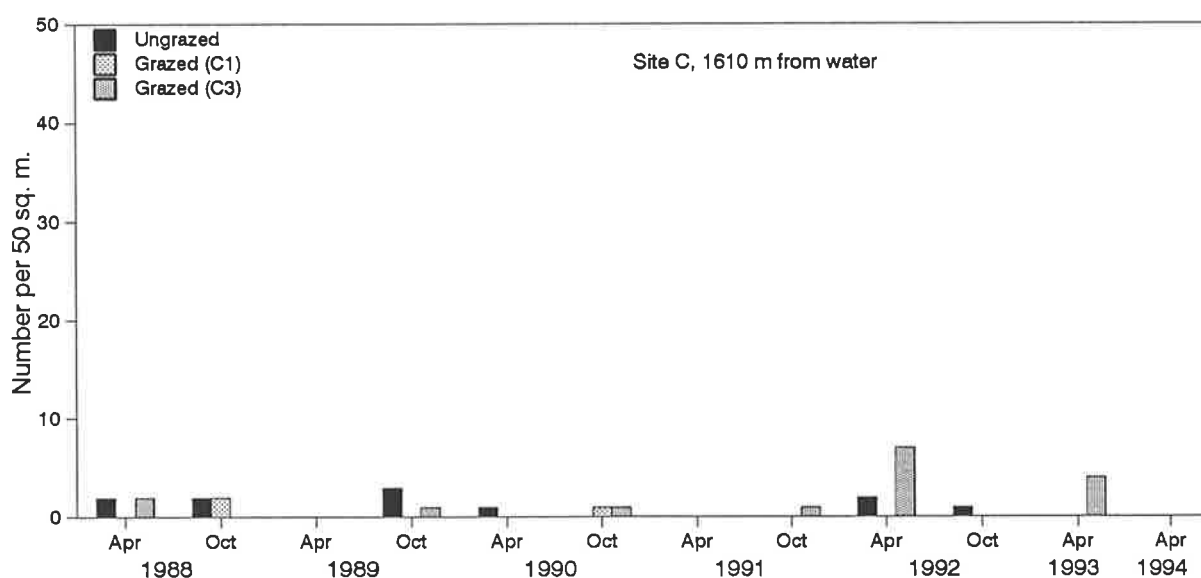
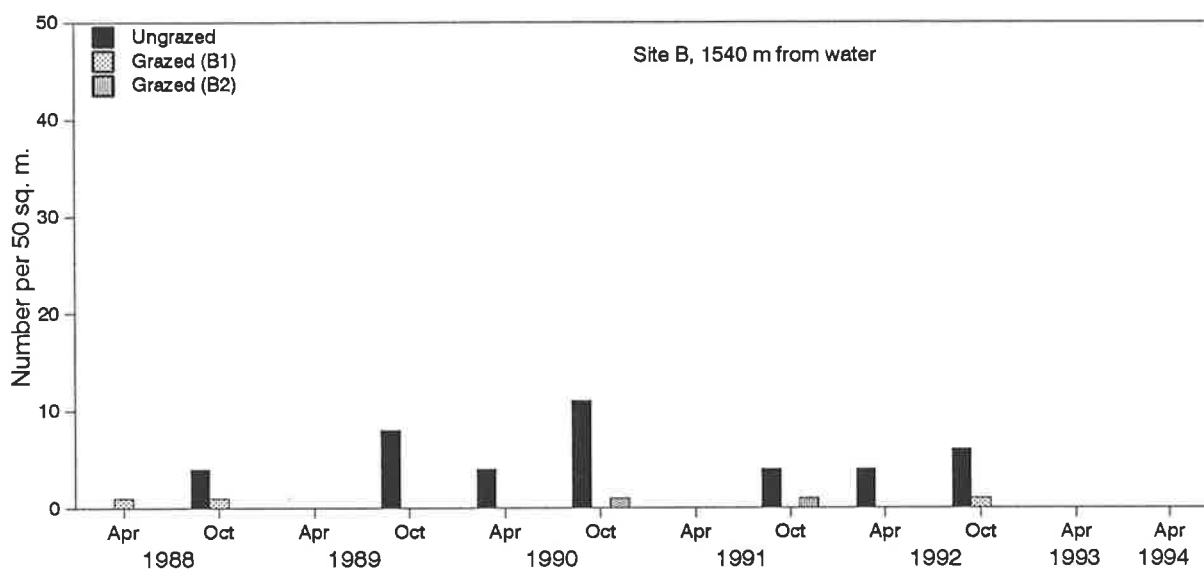
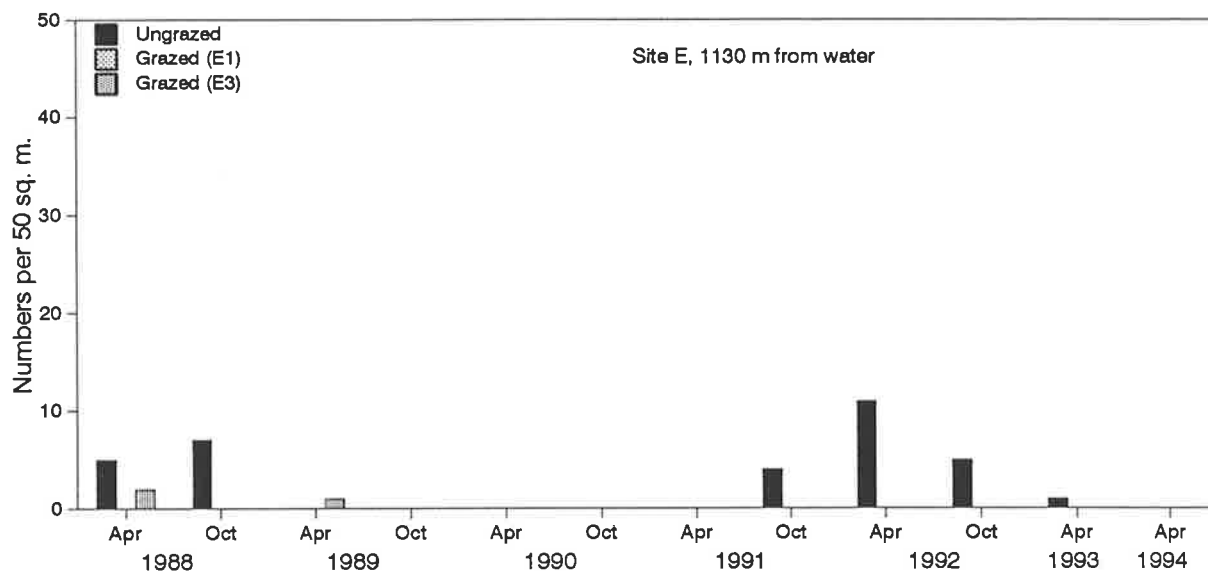


Fig. 5.3. Recruitment on a single exclosed and two grazed plots at nine sites in Yanaby. Note that the data for April 1994 is for a 12 month census period, not the usual 6 months. Graphs are arranged in order of increasing distance from water. The figure is continued on the following pages.

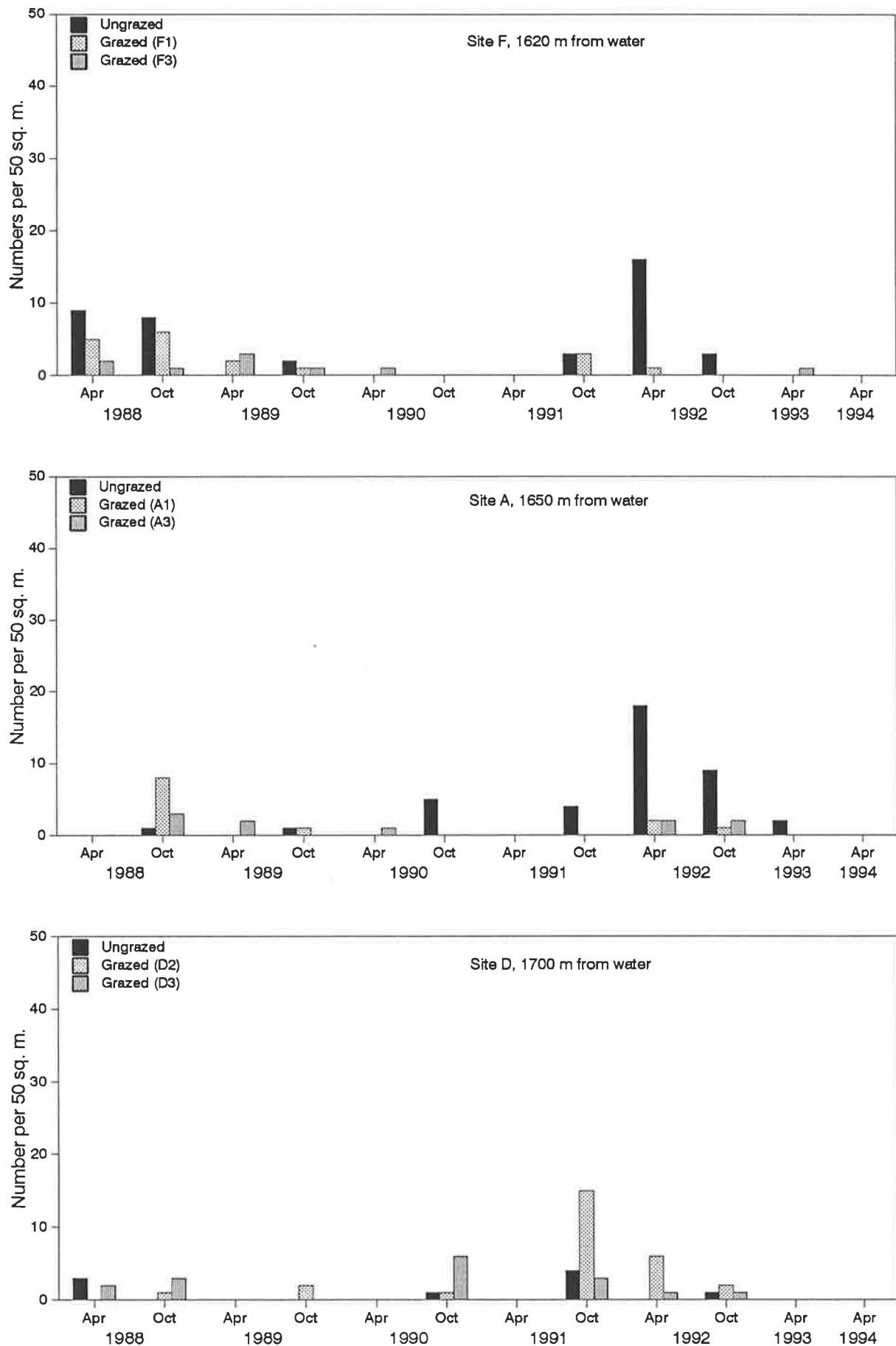


Fig. 5.3. (continued). Recruitment on a single exclosed and two grazed plots at nine sites in Yanaby. Note that the data for April 1994 is for a 12 month census period, not the usual 6 months. Graphs are arranged in order of increasing distance from water. The figure is continued on the following page.

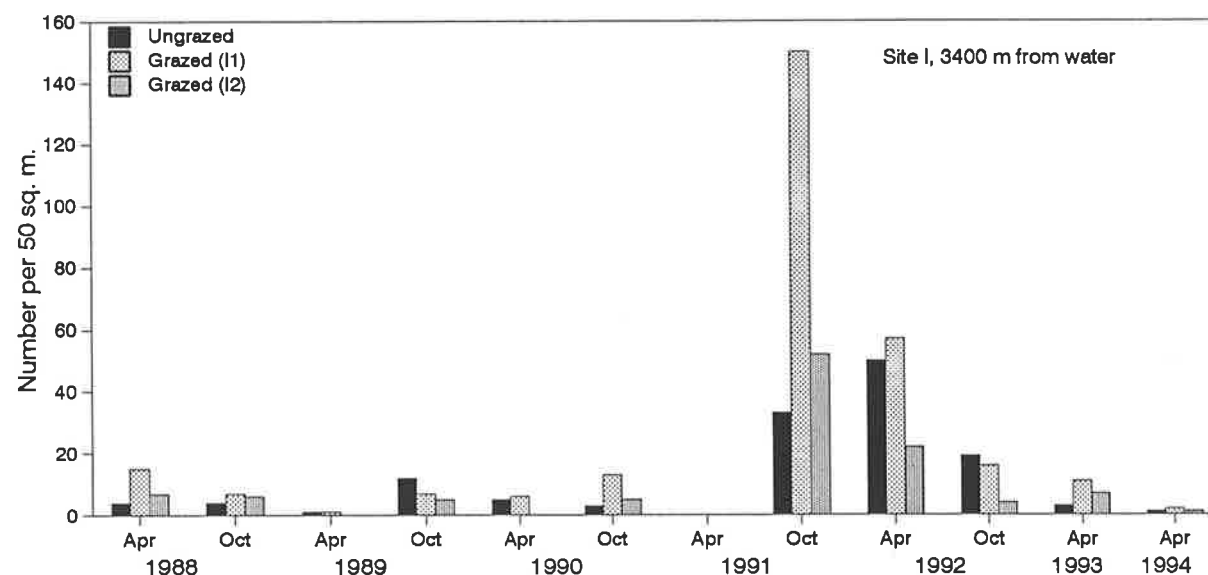
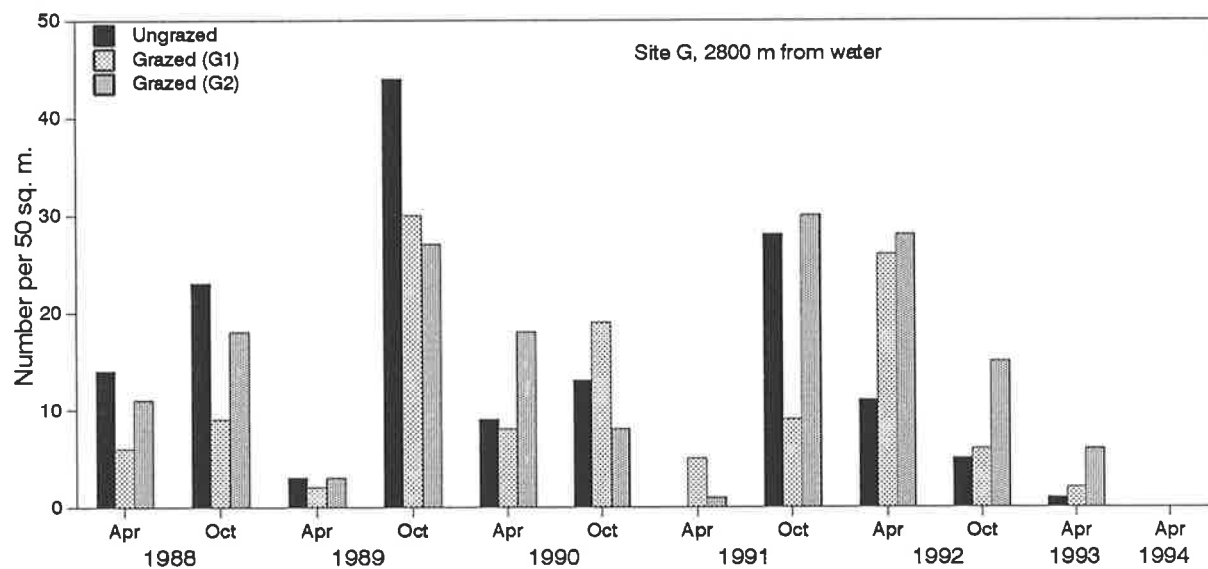
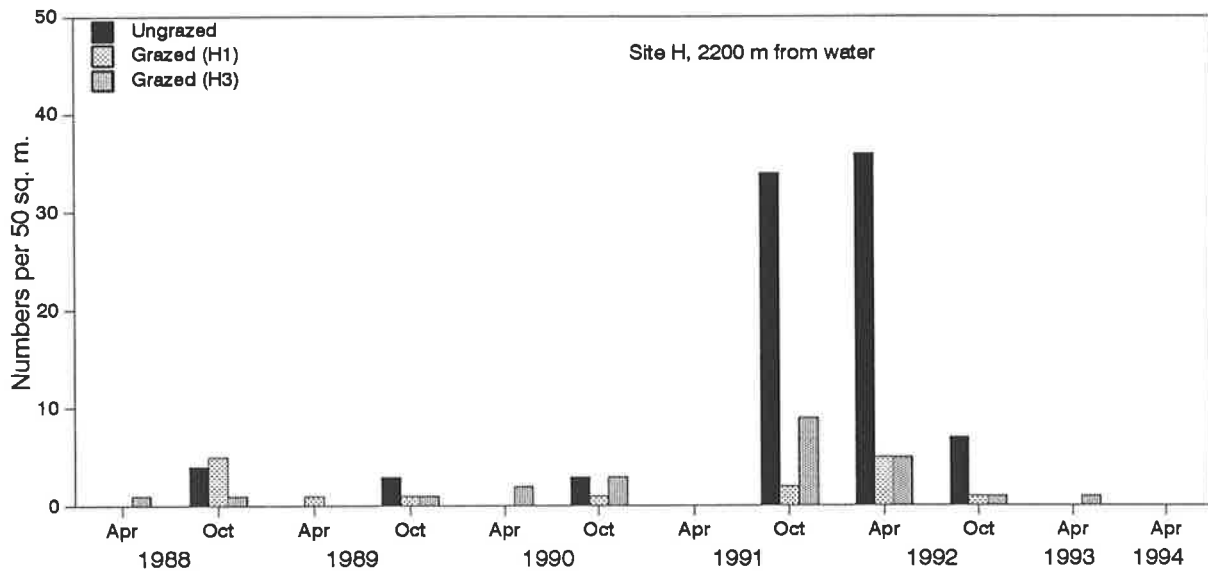


Fig. 5.3. (continued). Recruitment on a single exclosed and two grazed plots at nine sites in Yanaby. Note that the data for April 1994 is for a 12 month census period, not the usual 6 months. Graphs are arranged in order of increasing distance from water. Also note the change in scale of the ordinate for site I.

was little recruitment recorded. Lower rainfall in 1988 and 1990 resulted in only a small amount of recruitment at some of the more distant sites. The highest monthly rainfall during these two years was 31 mm in June 1988. Overall, the largest recruitment event was in response to the winter 1991 rains, although this varied across the paddock and even between the two grazed plots within sites. For the exclosed plots at sites close to the water the highest recruitment was that recorded in April 1992.

Transition Matrices and Demographic Fate

The transition matrices (Table 5.3) were highly variable amongst plots. Nonetheless, stasis of size-class four (adults) was the most common transition on all plots except plot E3 (a heavily grazed plot near the water point), where stasis of size-class three (sub-adults) was most common. Both the diagonal elements of the matrices, which represent stasis (plants surviving and remaining in the same size-class for the interval), and the sub-diagonal elements, representing growth, were common transitions. However, for seedlings (size-class 1) mortality was high on all plots and usually exceeded the individual probability of other fates (indicated by subtracting the sum of the elements in the first column from one, which gives a value for mortality; also see mortality data later). Growth rates of seedlings and juveniles varied (since these matrices were determined using data from six years this mostly represents temporal variation during the study rather than differences between individuals) with some individuals passing through two and three size-classes over a year, although seedlings in most cases advanced only to the next size-class. Juveniles frequently advanced to adults, missing the sub-adult stage.

As these yearly matrices are product matrices, each element in the matrices includes contributions from other transitions in the parent six monthly matrices. Thus, for example, the contributions of reproduction from the six monthly matrices are spread out across the yearly matrix rather than being confined to the first two rows in the last column, as they were in the six monthly matrix. For this reason, plants in size-class 3 (sub-adults), which were deemed to be non-reproductive, are shown as being reproductive over a one year transition interval (the elements on the first and second rows of the third

Table 5.3. Transition matrices for saltbush on ungrazed (U) and grazed (G) plots at nine sites in Yanaby, pooled over all transition periods from October 1987 to April 1994. Sites are arranged in order of increasing distance from water. Continued on the following pages.

	Size-class	1	2	3	4		1	2	3	4
Site E	1	0.23	0.02	0.06	0.13	Site B	0.07	0.01	0.05	0.11
U	2	0.28	0.12	0.00	0.03	U	0.31	0.31	0.01	0.05
	3	0.09	0.29	0.18	0.07		0.03	0.02	0.00	0.00
	4	0.01	0.27	0.56	0.87		0.03	0.20	0.84	0.97
G (E1)	1	0.00	0.00	0.00	0.00	G (B1)	0.15	0.00	0.00	0.02
	2	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00
	3	0.00	0.00	0.37	0.15		0.00	0.00	0.57	0.03
	4	0.00	0.00	0.24	0.62		0.00	0.00	0.26	0.89
G (E3)	1	0.21	0.00	0.01	0.02	G (B2)	0.00	0.00	0.00	0.00
	2	0.07	0.28	0.00	0.00		0.00	0.44	0.00	0.01
	3	0.17	0.00	0.62	0.28		0.00	0.23	0.42	0.11
	4	0.03	0.00	0.28	0.58		0.00	0.02	0.45	0.78
Site C						Site F				
U	1	0.24	0.00	0.01	0.04	U	0.09	0.03	0.05	0.08
	2	0.20	0.56	0.00	0.02		0.09	0.14	0.00	0.01
	3	0.02	0.07	0.42	0.00		0.02	0.19	0.15	0.01
	4	0.05	0.25	0.40	0.96		0.01	0.36	0.59	0.95
G (C1)	1	0.00	0.00	0.00	0.00	G (F1)	0.14	0.08	0.01	0.03
	2	0.00	0.00	0.00	0.00		0.13	0.32	0.00	0.01
	3	0.00	0.00	0.17	0.01		0.05	0.19	0.20	0.03
	4	0.00	0.00	0.49	0.91		0.03	0.14	0.73	0.90
G (C3)	1	0.25	0.02	0.00	0.09	G (F3)	0.19	0.12	0.01	0.02
	2	0.17	0.48	0.00	0.01		0.21	0.32	0.00	0.01
	3	0.00	0.00	0.42	0.00		0.05	0.02	0.27	0.18
	4	0.01	0.30	0.42	0.93		0.03	0.29	0.44	0.75

Table 5.3. (continued). Transition matrices for saltbush on ungrazed (U) and grazed (G) plots at nine sites in Yanaby, pooled over all transition periods from October 1987 to April 1994. Sites are arranged in order of increasing distance from water. Continued on the following page.

	Size-class	1	2	3	4		1	2	3	4
Site A	1	0.23	0.11	0.03	0.12	Site D	0.00	0.01	0.00	0.03
U	2	0.09	0.62	0.00	0.02	U	0.48	0.37	0.00	0.03
	3	0.03	0.00	0.42	0.00		0.00	0.00	0.42	0.01
	4	0.01	0.14	0.37	0.99		0.24	0.47	0.42	0.93
G (A1)	1	0.10	0.00	0.00	0.02	G (D2)	0.38	0.00	0.00	0.15
	2	0.29	0.24	0.00	0.01		0.20	0.13	0.00	0.05
	3	0.00	0.09	0.26	0.04		0.00	0.00	0.00	0.00
	4	0.16	0.45	0.45	0.90		0.00	0.00	0.00	0.94
G (A3)	1	0.27	0.00	0.00	0.02		0.05	0.01	0.01	0.07
	2	0.33	0.46	0.00	0.01		0.23	0.34	0.01	0.06
	3	0.20	0.18	0.49	0.04		0.00	0.10	0.19	0.01
	4	0.03	0.17	0.30	0.90		0.08	0.42	0.48	0.82
Site H						Site G				
U	1	0.34	0.01	0.05	0.19	U	0.20	0.01	0.07	0.25
	2	0.14	0.55	0.00	0.03		0.15	0.39	0.01	0.04
	3	0.01	0.03	0.14	0.00		0.02	0.18	0.20	0.01
	4	0.02	0.20	0.70	0.98		0.03	0.21	0.63	0.96
G (H1)	1	0.17	0.04	0.01	0.04	G (G1)	0.13	0.04	0.07	0.15
	2	0.00	0.15	0.00	0.01		0.16	0.37	0.01	0.04
	3	0.06	0.21	0.39	0.05		0.02	0.03	0.18	0.00
	4	0.00	0.01	0.20	0.88		0.01	0.18	0.59	0.95
G (H3)	1	0.24	0.00	0.01	0.07	G (G2)	0.27	0.05	0.08	0.30
	2	0.07	0.67	0.00	0.04		0.10	0.59	0.00	0.04
	3	0.00	0.04	0.38	0.04		0.03	0.11	0.48	0.03
	4	0.00	0.12	0.34	0.88		0.01	0.11	0.47	0.96

Table 5.3. (continued). Transition matrices for saltbush on ungrazed (U) and grazed (G) plots at nine sites in Yanaby, pooled over all transition periods from October 1987 to April 1994.

	Size- class	1	2	3	4
Site I U	1	0.22	0.04	0.11	0.22
	2	0.09	0.41	0.00	0.04
	3	0.00	0.05	0.16	0.00
	4	0.00	0.11	0.68	0.98
G (I1)	1	0.33	0.03	0.10	0.46
	2	0.20	0.60	0.01	0.16
	3	0.00	0.10	0.39	0.02
	4	0.00	0.12	0.55	0.96
G (I2)	1	0.16	0.02	0.04	0.11
	2	0.19	0.41	0.01	0.07
	3	0.01	0.06	0.24	0.01
	4	0.01	0.09	0.54	0.99

column of the transition matrix). While it is feasible that a plant beginning in size-class 3 would be able to grow into size-class 4 (adult), produce seed and have that seed germinate within the same 12 month period, the probability of this transition is small. These entries however, and those for reproduction in the first two lines of column four of the product matrices, are not confounded with declines in size of adult and sub-adult shrubs to seedlings and juveniles (which would otherwise have occurred in the product matrices) because these transitions are not possible. Similarly, the entries on the first row of columns one and two include a component of reproduction, but the production of recruits by seedlings and juveniles within a year is very unlikely to occur. This was normally a very small contribution in the matrices. Instead, these elements were due primarily to individuals remaining in the smallest size-class (in the first column) or individuals declining in size and so retrogressing from size-class two to size-class one. These transitions were observed to occur over the six monthly observation intervals and are possible over 12 months.

Log-linear analysis showed the fate of individuals, conditional upon their initial size-class, was dependent on site (called location in the analysis) and grazing treatment (Table 5.4). There was also a strong interaction ($P=0.0006$) between site and grazing treatment. Decomposing the main table into the two grazing treatments revealed that for both treatments, site and fate were not independent ($P<0.0001$ for both treatments). However, for the grazed treatment site had a significant ($P<0.0001$) effect only on the fate of size-class four plants (i.e. adults). For the exclosed treatment, site had a significant effect on the fate of seedlings, juveniles and adults (all $P<0.001$). The tables were not broken down to examine differences between treatments for two reasons; firstly, residual effects from previous grazing on the exclosures early in the study reduced the value of these comparisons and secondly, to reduce the chance of making Type I errors.

The mortality of individuals was affected by site ($P<0.0001$), but treatment and the interaction between site and treatment were not significant (Table 5.5). However, it is somewhat misleading to consider mortality rates for all size-classes together and for data

Table 5.4. Log-linear analysis of the dependence of fate (F) of an individual saltbush, conditional on its initial size (S), on location (L) (i.e. site in paddock) and grazing treatment (T) for nine sites in Yanaby. Results are presented for the overall analysis, for the separate grazing treatments and for size-classes within grazing treatments. See Methods section in text for interpretation of the analysis results.

Model	G ²	degrees of freedom	P
SF, STL	410.59	120	<0.0001
SFT, STL	332.81	112	<0.0001
SFL, STL	191.33	56	<0.0001
SFT, SFL, STL	85.91	48	0.0006
<u>Grazed plots</u>			
SF, SL	172.32	56	<0.0001
<i>Size-class</i> (model F, L)			
1	15.64	16	0.4785
2	10.14	16	0.8592
3	15.83	16	0.4648
4	130.71	8	<0.0001
<u>Ungrazed plots</u>			
SF, SL	160.49	56	<0.0001
<i>Size-class</i> (model F, L)			
1	47.49	16	0.0001
2	41.18	16	0.0005
3	19.16	16	0.2604
4	52.66	8	<0.0001

Table 5.5. Log-linear analysis of the influence of location (L) (i.e. site in paddock) and grazing treatment (T) on the mortality (F) of saltbush plants for nine sites in Yanaby. Results are presented for the overall analysis, for adults and sub-adults pooled and for seedlings pooled with juveniles. See Methods section in text for interpretation of the analysis results.

Term	G ²	degrees of freedom	P
<u>Overall</u>			
TF	2.29	1	0.1302
LF	49.20	8	<0.0001
LTF	12.41	8	0.1339
<u>Adults and sub-adults</u>			
TF	26.39	1	<0.0001
LF	55.70	8	<0.0001
LTF	13.98	8	0.0823
<u>Seedlings and juveniles</u>			
TF	14.93	1	0.0001
LF	27.03	8	0.0007
LTF	28.25	8	0.0004

pooled over the entire study. Separate log-linear analyses of seedling and juvenile mortality pooled over all censuses (Table 5.5), and sub-adult and adult mortality pooled (Table 5.5), revealed that both site and treatment had significant (all $P < 0.001$) effects on mortality for these plant sizes. In the case of the smaller plants there was a significant interaction ($P = 0.0004$) between site and treatment. The mortality data for seedlings/juveniles and sub-adults/adults are presented in Table 5.6. Seedlings and juveniles accounted for the majority of mortality on many exclosures and plots furthest from water (sites G and I had in excess of 90% due to seedlings) while the heavily grazed plots near water had as low as 9% of mortality due to these smallest size-classes (Table 5.6). Mortality of adults/sub-adults on grazed plots was linearly related to distance from water (regression: $\text{mortality} = 78.6^{***} - 0.02^{**} \cdot \text{distance(m)}$, $R^2 = 0.72$), but there was no such trend for the exclosed plots.

These analyses, together with an examination of the data, indicate the following trends. On the grazed treatment the mortality of adults and the rate of retrogression of adults to the sub-adult stage were greater near the water. Adult mortality was also higher near the water point on the exclosed treatment but this was less than on the corresponding grazed plots (although note that the site $\times$ treatment interaction term was not significant; $P > 0.05$, Table 5.5). There appeared to be no difference in adult mortality between grazing treatments at distant sites. Seedling and juvenile survival was higher on exclosed plots near the water than on the exclosures further from water and also higher than on the corresponding grazed plots near the water.

Temporal variation in mortality was observed in addition to the spatial trends. The rate of mortality varied in time on most plots (from no mortality to $> 40\%$ in some cases), with some plots recording high mortality early in the study (up to April 1989) associated with the dry conditions during this period. Others experienced peaks in mortality in the later part of the study (Figure 5.5). There were also differences in mortality between grazed and exclosed plots at certain sites at individual censuses, but these differences varied over the study. For example, sites A and D had little mortality on exclosed plots

Table 5.6. Mortality in saltbush, pooled over all population censuses from October 1987 to April 1994, for grazed and ungrazed plots at nine sites in Yanaby. The size-classes have been reduced to two groups as shown. No seedlings were recorded on plot E1. The proportion of total mortality which was due to seedlings and juveniles is also shown (only the mean for the grazed plots is presented). Sites are arranged in order of increasing distance from water.

Site	Plot	Adult and sub-adults (%)	Seedlings and juveniles (%)	Proportion due to seed/juv. (%)
E	ungrazed	39	54	53
	grazed (E1)	82	-	9
	grazed (E3)	52	75	
B	ungrazed	19	79	87
	grazed (B1)	43	67	21
	grazed (B2)	54	50	
C	ungrazed	26	55	46
	grazed (C1)	44	100	35
	grazed (C3)	32	63	
F	ungrazed	23	83	78
	grazed (F1)	35	77	39
	grazed (F3)	41	69	
A	ungrazed	9	81	92
	grazed (A1)	33	62	20
	grazed (A3)	34	23	
D	ungrazed	36	50	39
	grazed (D2)	32	68	50
	grazed (D3)	71	44	
H	ungrazed	9	80	94
	grazed (H1)	52	82	51
	grazed (H3)	43	76	
G	ungrazed	18	80	92
	grazed (G1)	25	87	92
	grazed (G2)	10	81	
I	ungrazed	11	88	96
	grazed (I1)	18	60	95
	grazed (I2)	8	74	

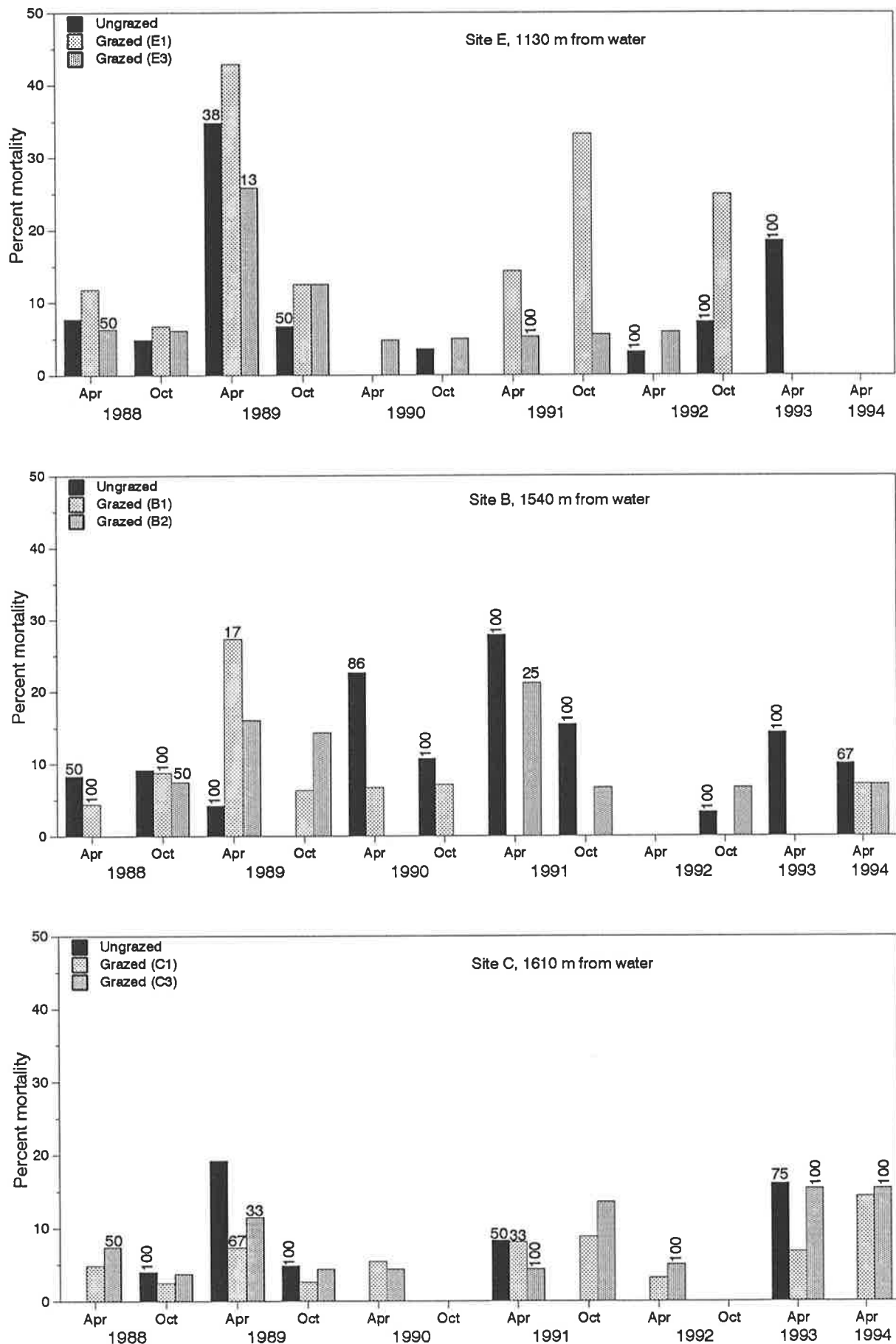


Fig. 5.5. Mortality on a single enclosed and two grazed plots at nine sites in Yanaby. The numbers indicate the percentage of total mortality due to seedlings and juveniles. For bars without numbers all mortality was due to adults and sub-adults. Note that the data for April 1994 is for a 12 month census period, not the usual 6 months. Continued over the page.

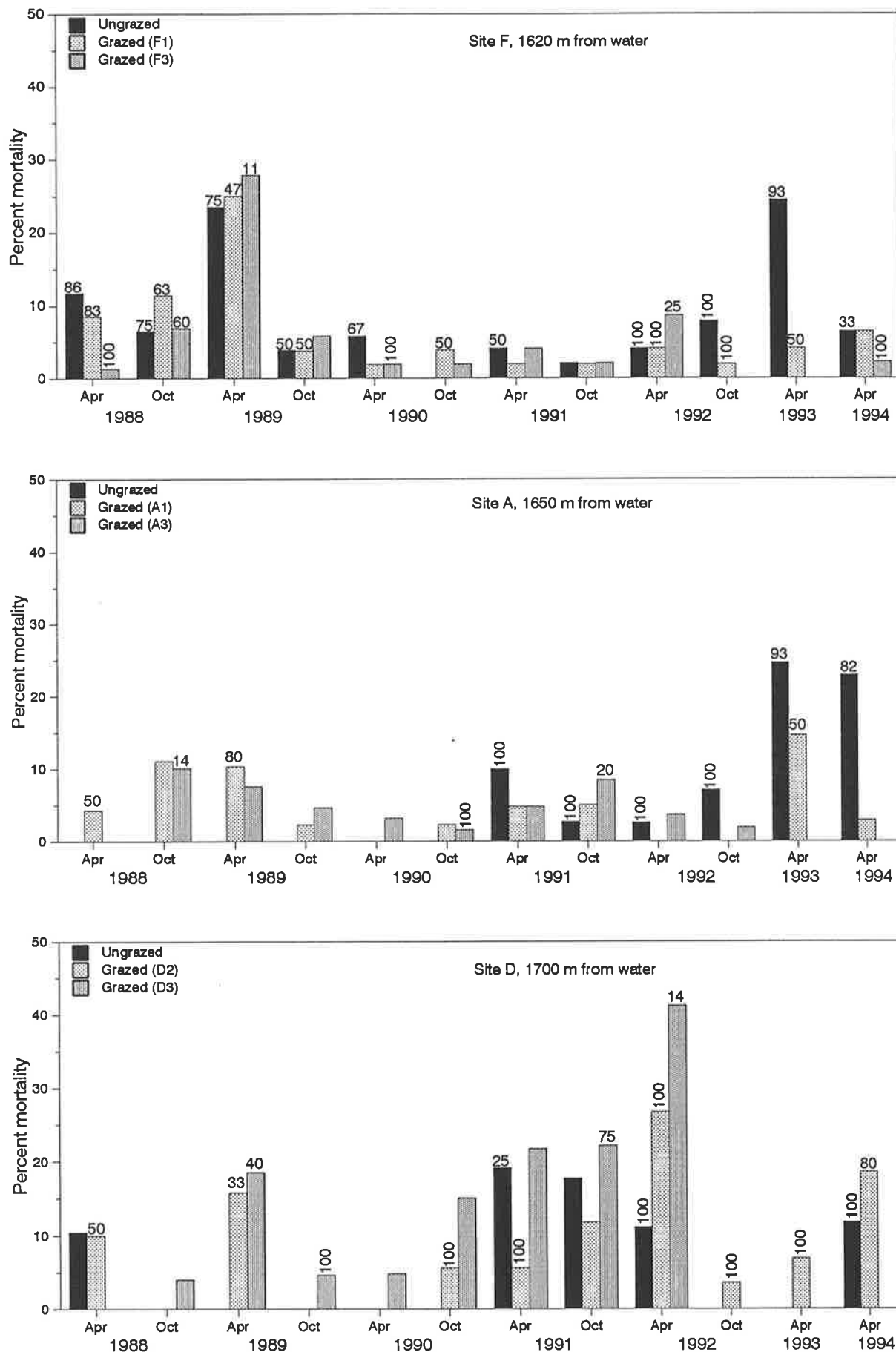


Fig. 5.5. (continued). Mortality on a single exclosed and two grazed plots at nine sites in Yanaby. The numbers indicate the percentage of total mortality due to seedlings and juveniles. For bars without numbers all mortality was due to adults and sub-adults. Note that the data for April 1994 is for a 12 month census interval, not the usual 6 months. Continued over the page.

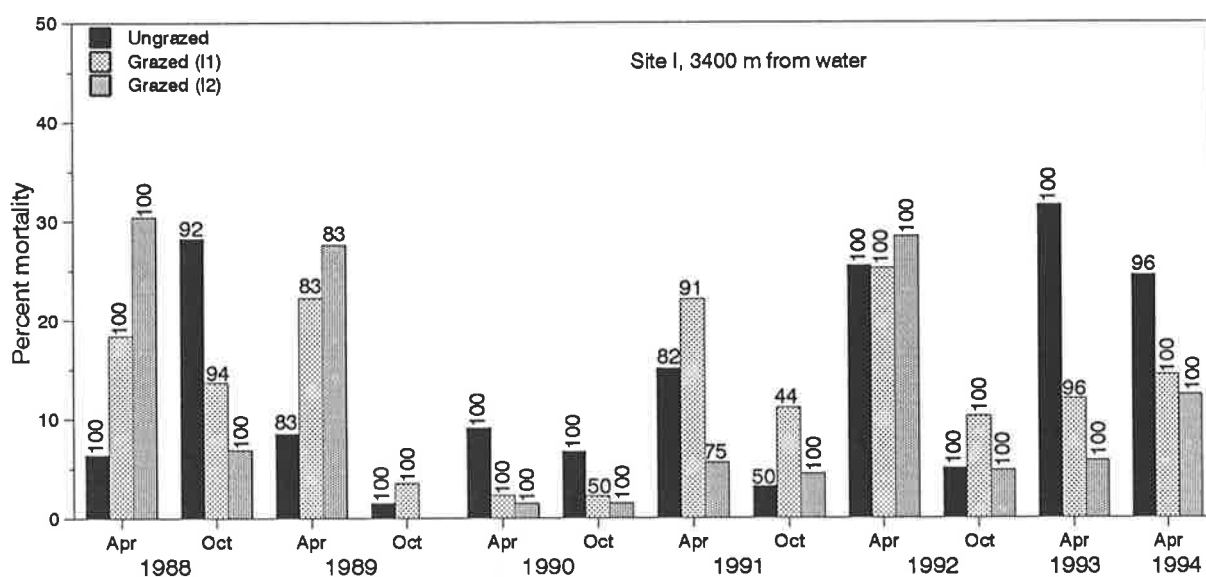
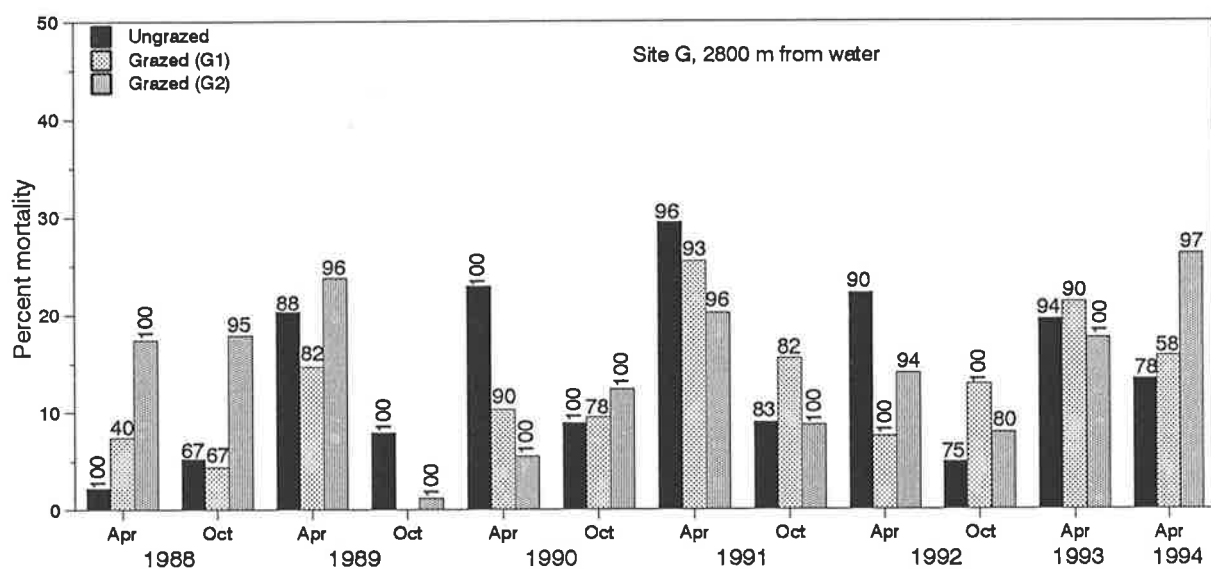
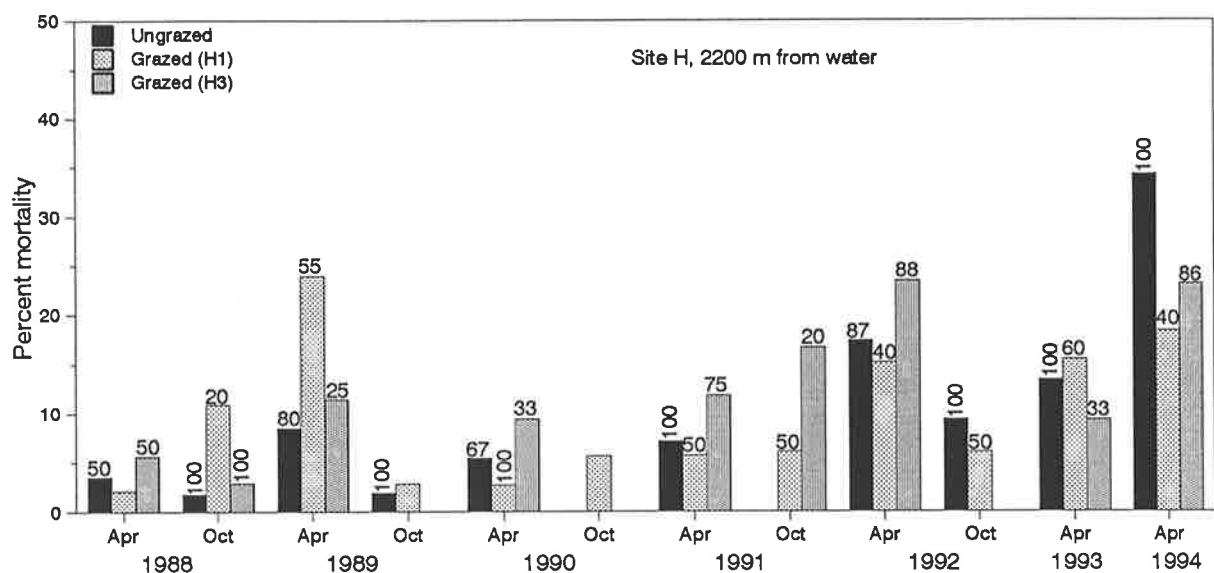


Fig. 5.5. (continued). Mortality on a single exclosed and two grazed plots at nine sites in Yanaby. The numbers indicate the percentage of total mortality due to seedlings and juveniles. For bars without numbers all mortality was due to adults and sub-adults. Note that the data for April 1994 is for a 12 month census interval, not the usual 6 months.

early in the study but moderate amounts on the grazed plots, while later the situation was reversed. In comparison, site E had considerable mortality on both treatments early in the study, but later the exclosed plot registered much less mortality. Mortality was usually higher in summer than in winter.

The differences in patterns of mortality between large and small plants helps to explain the temporal trends in overall mortality described above and the lack of a treatment effect in the overall data set. In the first part of the study, when high rates of mortality were observed on most plots due to the dry conditions up until April 1989, mortality at sites close to the water (e.g. sites B and E) was mainly of the largest size-class, and often occurred on both grazing treatments (Figure 5.5). This was because all plants, including those on the exclosures, had a history of heavy grazing prior to the study. Later, the exclosed plot at some of these sites (e.g. sites A, B and E), having begun to recover from the effects of earlier grazing, supported a greater number of seedlings. This increased the overall mortality rate despite protection from grazing because of the naturally low survival of saltbush seedlings. At other times, both grazed and exclosed plots at these sites recorded lower mortality because of higher rainfall. At sites further away from the water where grazing pressure was light, mortality on both grazing treatments throughout the study was mainly of seedlings rather than adults, and was similar on both grazing treatments.

Population Growth Rates and Stable Stage Distributions

As expected from the log-linear analyses, population growth rates differed between sites and between grazing treatments at many sites (Table 5.7). On most grazed plots $\lambda < 1.0$, indicating that the saltbush population was in decline on these plots over the 6.5 years of the study, but there was a trend of increasing λ at greater distances from water (regression: $\lambda = 0.767^{***} + 0.00009^{***} \cdot \text{distance(m)}$, $R^2 = 0.63$). The site closest to water (site E at 1130 m) had the lowest population growth rate ($\lambda \approx 0.8$). Only at sites G and I, the two sites furthest from water (> 2200 m), was $\lambda \approx 1$, indicating these populations were stable. Populations on exclosed plots at many sites also declined, mainly at those

Table 5.7. Population growth rates (λ) for saltbush, estimated from the time-invariant population models, for grazed and ungrazed plots at nine sites in Yanaby. Growth rates are also expressed as $\ln\lambda$. Sites are arranged in order of increasing distance from water.

Site	Plot	λ	$\ln\lambda$
E	ungrazed	0.981	-0.0192
	grazed (E1)	0.722	-0.3258
	grazed (E3)	0.887	-0.1195
B	ungrazed	1.008	0.0075
	grazed (B1)	0.917	-0.0868
	grazed (B2)	0.894	-0.1116
C	ungrazed	0.984	-0.0158
	grazed (C1)	0.915	-0.0889
	grazed (C3)	0.953	-0.0487
F	ungrazed	0.976	-0.0246
	grazed (F1)	0.944	-0.0574
	grazed (F3)	0.893	-0.1135
A	ungrazed	1.007	0.0072
	grazed (A1)	0.942	-0.0602
	grazed (A3)	0.949	-0.0529
D	ungrazed	0.976	-0.0245
	grazed (D2)	0.942	-0.0594
	grazed (D3)	0.911	-0.0935
H	ungrazed	1.026	0.0256
	grazed (H1)	0.904	-0.1008
	grazed (H3)	0.933	-0.0690
G	ungrazed	1.030	0.0299
	grazed (G1)	0.986	-0.0141
	grazed (G2)	1.034	0.0335
I	ungrazed	0.999	-0.0007
	grazed (I1)	1.088	0.0844
	grazed (I2)	1.017	0.0164

sites close to water (sites C, D, E, and F), but at a slower rate than the respective grazed plots. The remaining exclosed populations were stable.

Stable size distributions (SSD) were mostly dominated by adults and were of three main forms (Figure 5.6). Exclosures and grazed plots at sites well away from the water (sites G and I) were those most likely to have U-shaped distributions, with adults making up the largest fraction of the population, the smallest size-class the second largest fraction and the intermediate classes the smallest fraction. Grazed plots at sites closer to water had J-shaped SSDs, being dominated by the adult size-class and the fraction in the remaining size-classes diminishing with a decline in size-class. Bimodal distributions, in which the highest proportion of individuals occurred in the adult size-class and the next highest fraction was in the second size-class (juveniles), were less common although there was no trend in their occurrence in the paddock. One grazed plot at site E was an exception to the domination of the SSD by the adult size-class. On this plot the third size-class (sub-adults) was the largest, with 50% of individuals.

Initial stage-class distributions (ISD) are also presented in Figure 5.6. Normally these could be compared with the SSD using log-linear analysis, but in this case low frequencies in many size-classes for numerous plots, resulting in >20% of cells having expected frequencies less than one, meant these tests would be unreliable.¹ Instead a graphical comparison was made. Comparison of these distributions can indicate whether the populations on each plot were in equilibrium with the rates of growth, survival and fecundity measured during the study. If the distributions are different it may suggest temporal variations in these rates prior to and during the study, or alternatively errors in the estimation of the demographic rates (Enright and Watson 1991). The last point is particularly relevant for models of long-lived species which are based on rates measured over a short period of time.

¹Low expected frequencies in cells of contingency tables analysed with log-linear models tend to cause the rejection of too many models (Sokal and Rohlf 1981).

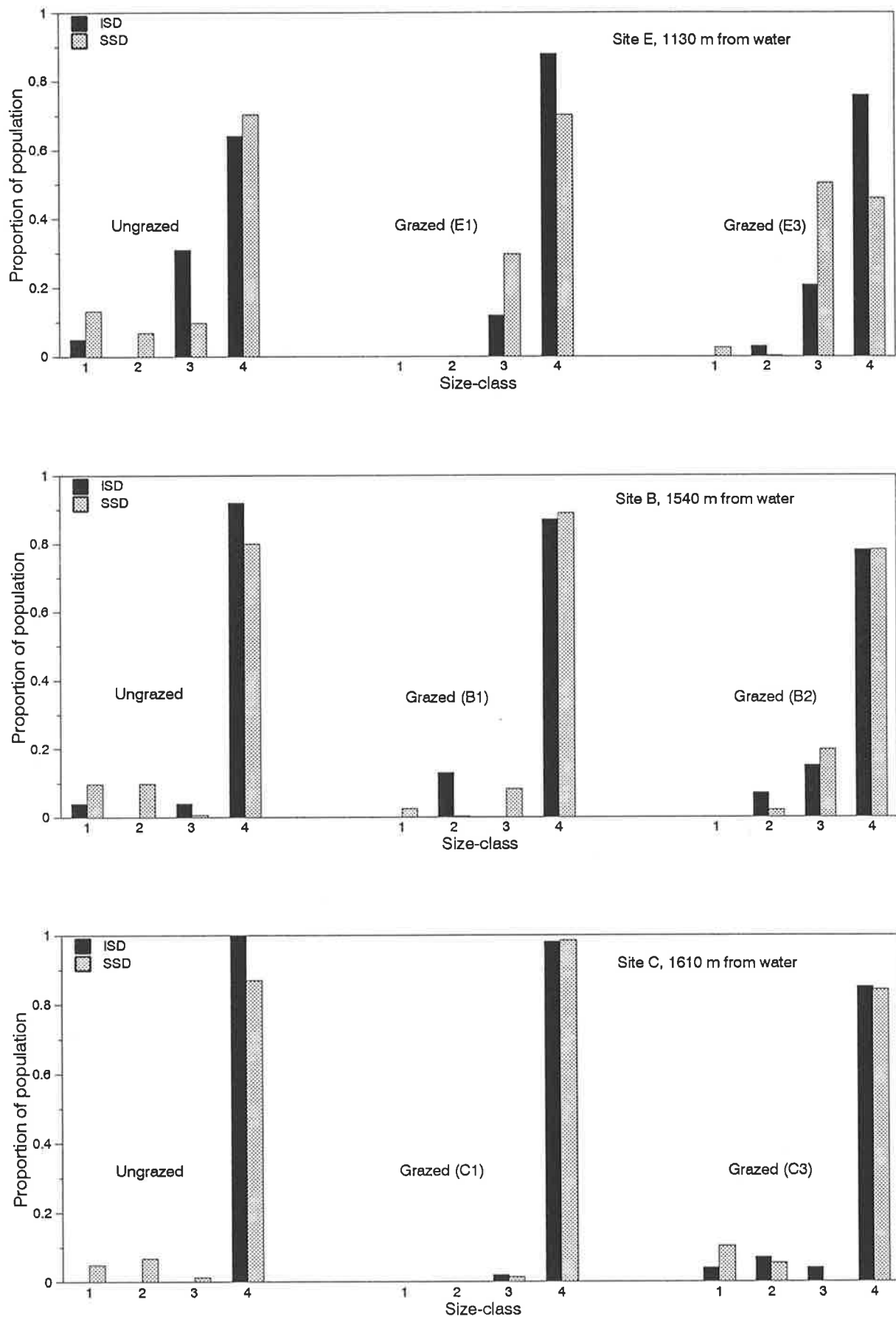


Fig. 5.6. Initial (ISD) and stable (SSD) size-class distributions for a single exclosed and two grazed plots at nine sites in Yanaby. Graphs are arranged in order of increasing distance from water. The figure is continued on the following pages.

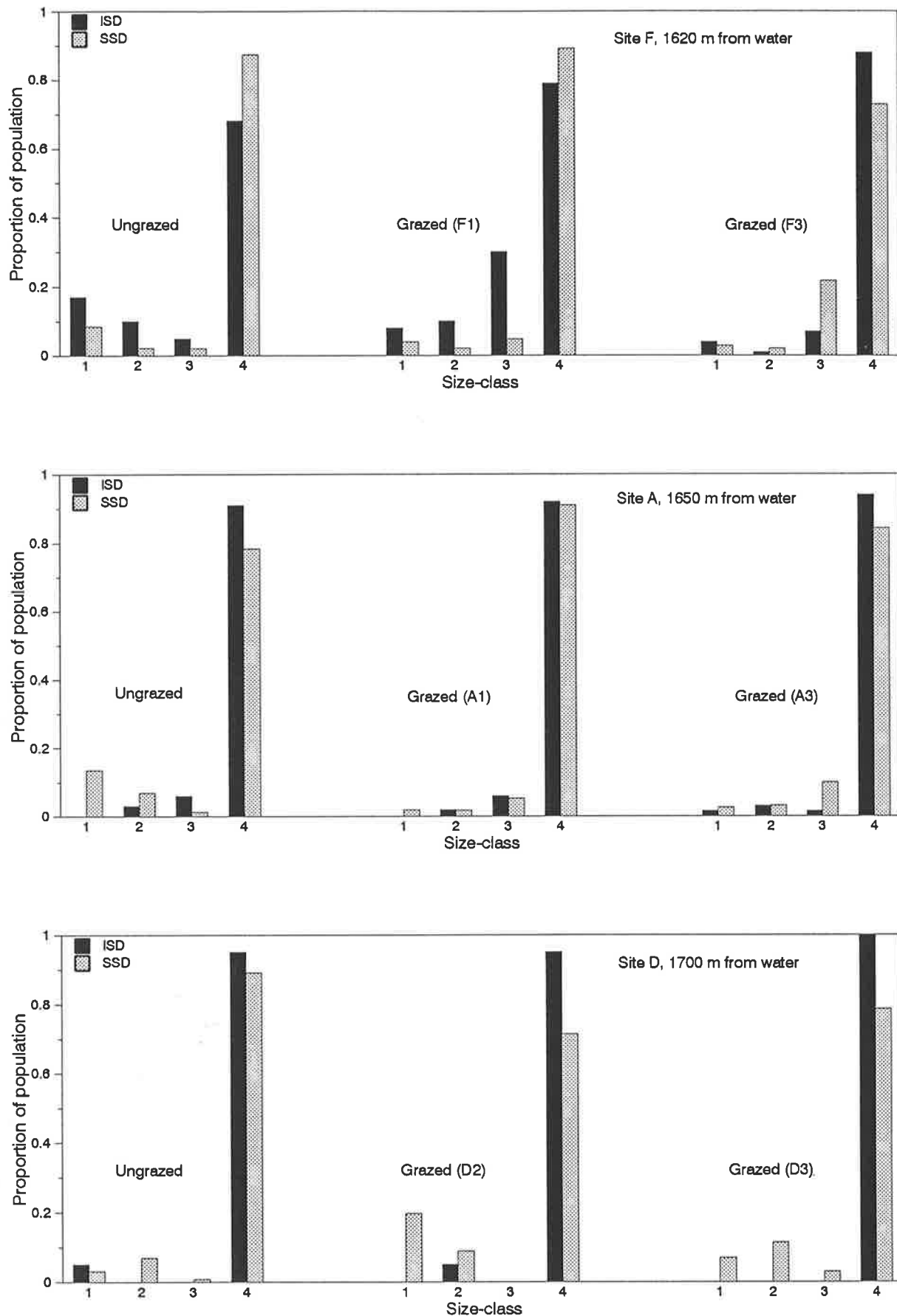


Fig. 5.6. (continued). Initial (ISD) and stable (SSD) size-class distributions for a single exclosed and two grazed plots at nine sites in Yanaby. Graphs are arranged in order of increasing distance from water. The figure is continued on the following page.

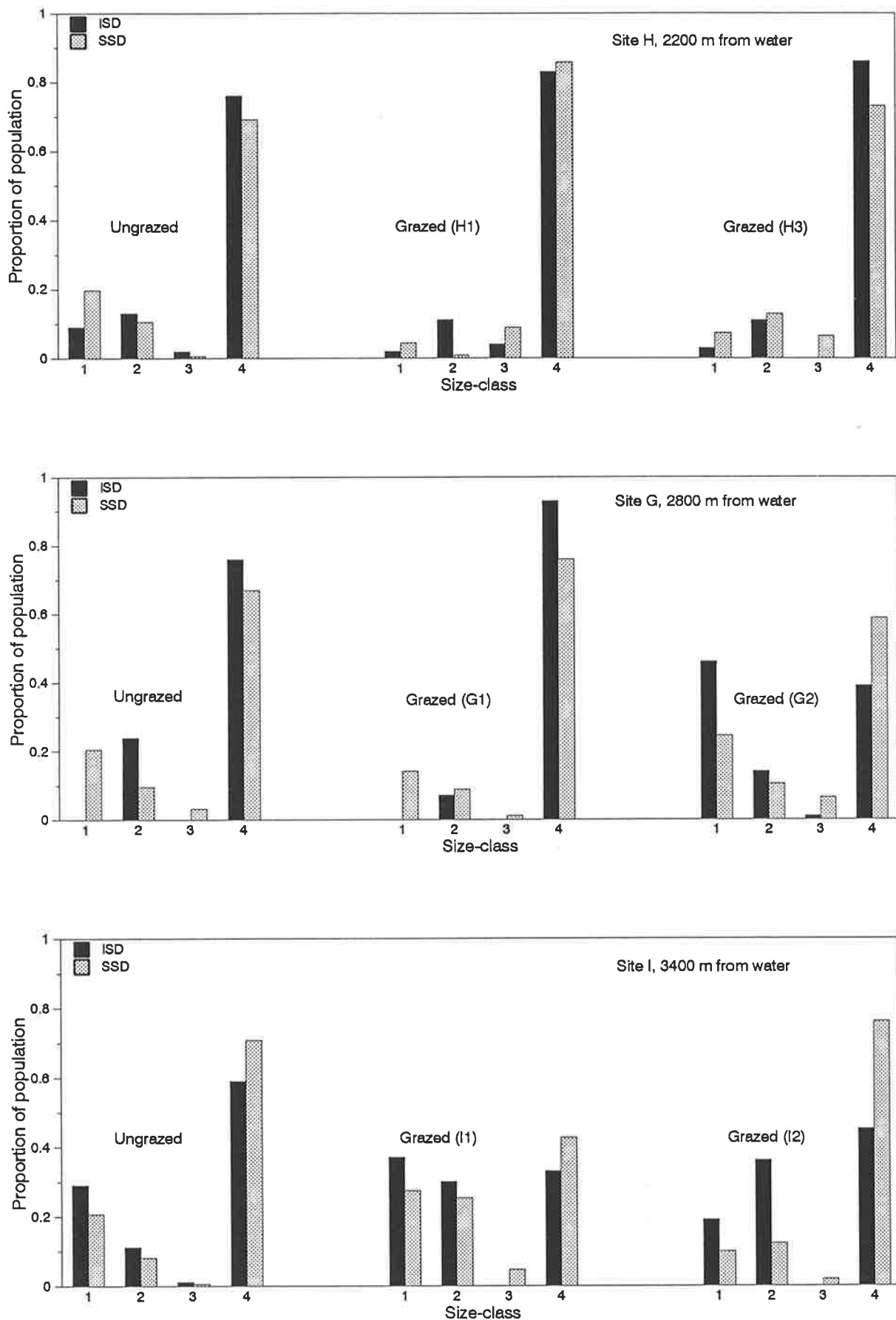


Fig. 5.6. Initial (ISD) and stable (SSD) size-class distributions for a single excluded and two grazed plots at nine sites in Yanaby. Graphs are arranged in order of increasing distance from water.

The majority of plots showed some differences between the SSD and ISD, although the grazed plots nearer the water tended to have distributions which appeared similar. Differences were most obvious for the exclosures, where seedlings made up a larger proportion of the population in the SSD than that observed in the field at the start of the study. This suggests the protection of the exclosed populations from grazing during this study altered demographic rates compared to before the study (in particular an increase in recruitment). In contrast, because of continued grazing, demographic rates on the grazed plots during the study were not different to those prior to the study which resulted in the observed ISD. The differences in distributions for the plots furthest from water were inconsistent, with some plots showing more seedlings, juveniles and sub-adults and fewer adults in the SSD, and other plots showing the reverse trend. Because of the lack of proper statistical comparison, however, these observations should be viewed with caution.

Elasticity and LTRE Analyses

In a very recent paper, Caswell and Trevisan (1994) advised that caution be exercised in the use of conventional methods, as described earlier, for calculating elasticities of product matrices, because periodic variation amongst the individual matrices may sometimes lead to errors in the elasticities in the product matrix. They gave an example where the largest elasticities occurred in different locations in summer and winter matrices, but in the product matrix an entirely different pattern of elasticities occurred because the contributions of the important seasonal elements were spread over the whole matrix. I calculated elasticities for the individual seasonal matrices for a number of plots in this study and found they were not substantially different to those of the product matrices reported here.

A consistent feature of the elasticity matrices (Table 5.8) was the large contribution to the population growth rate from the survival (i.e. stasis) of adult shrubs (size-class 4). In all matrices but one this was the major component (generally 70 to 90%) of the population growth rate, regardless of whether the population had a negative ($\lambda < 1$) or positive ($\lambda > 1$) rate of growth and regardless of the site or grazing treatment. The contributions

Table 5.8. Transition matrix elasticities (as percentages) for saltbush on ungrazed (U) and grazed (G) plots at nine sites in Yanaby, for transition matrices pooled over all transition periods from October 1987 to April 1994 (see Table 5.3). Sites are arranged in order of increasing distance from water. Continued on the following pages.

	Size-class	1	2	3	4		1	2	3	4
Site E	1	1	0	0	3	Site B	0	0	0	2
U	2	2	1	0	1	U	1	1	0	1
	3	1	2	2	4		0	0	0	0
	4	0	2	7	73		0	2	1	91
G (E1)	1	0	0	0	0	G (B1)	0	0	0	0
	2	0	0	0	0		0	0	0	0
	3	0	0	11	11		0	0	4	2
	4	0	0	11	67		0	0	2	91
G (E3)	1	0	0	0	0	G (B2)	0	0	0	0
	2	0	0	0	0		0	1	0	1
	3	1	0	38	16		0	0	9	10
	4	0	0	16	29		0	0	10	70
Site C	1	0	0	0	1	Site F	0	0	0	1
U	2	1	3	0	1	U	1	0	0	1
	3	0	0	0	0		0	0	0	1
	4	0	2	1	90		0	1	1	94
G (C1)	1	0	0	0	0	G (F1)	0	0	0	1
	2	0	0	0	0		0	0	0	0
	3	0	0	0	1		0	0	1	3
	4	0	0	1	98		0	0	4	89
G (C3)	1	1	0	0	1	G (F3)	0	0	0	1
	2	1	2	0	1		0	0	0	0
	3	0	0	0	0		0	0	5	12
	4	0	2	0	92		0	1	12	67

Table 5.8. (continued). Transition matrix elasticities (as percentages) for saltbush on ungrazed (U) and grazed (G) plots at nine sites in Yanaby, for transition matrices pooled over all transition periods from October 1987 to April 1994 (see Table 5.3). Sites are arranged in order of increasing distance from water. Continued on the following page.

	Size-class	1	2	3	4		1	2	3	4
Site A	1	0	0	0	1	Site D	0	0	0	2
U	2	1	2	0	1	U	1	2	0	2
	3	0	0	0	0		0	0	0	0
	4	0	1	1	93		1	3	0	87
G (A1)	1	0	0	0	1	G (D2)	0	0	0	0
	2	0	0	0	1		0	0	0	0
	3	0	0	1	2		0	0	0	0
	4	0	1	3	90		0	0	0	100
G(A3)	1	0	0	0	1	G (D3)	0	0	0	2
	2	1	1	0	0		2	4	0	5
	3	0	0	4	3		0	1	0	1
	4	0	1	3	85		1	6	2	77
Site H	1	1	0	0	2	Site G	1	0	0	3
U	2	2	3	0	1	U	2	3	0	2
	3	0	0	0	0		0	2	1	1
	4	0	3	1	86		1	2	3	80
G (H1)	1	0	0	0	0	G (G1)	0	0	0	1
	2	0	0	0	0		1	1	0	1
	3	0	0	2	2		0	0	0	0
	4	0	0	2	93		0	2	1	91
G (H3)	1	0	0	0	0	G (G2)	1	0	0	2
	2	0	6	0	2		2	4	0	1
	3	0	0	2	2		1	1	3	2
	4	0	2	3	81		0	2	4	77

Table 5.8. (continued). Transition matrix elasticities (as percentages) for saltbush on ungrazed (U) and grazed (G) plots at nine sites in Yanaby, for transition matrices pooled over all transition periods from October 1987 to April 1994 (see Table 5.3).

	Size- class	1	2	3	4
Site I	1	0	0	0	1
U	2	1	1	0	1
	3	0	0	0	0
	4	0	1	0	94
G (I1)	1	2	0	0	4
	2	3	10	0	4
	3	0	3	2	1
	4	0	5	4	63
G (I2)	1	0	0	0	1
	2	1	1	0	1
	3	0	1	0	1
	4	0	1	1	91

from the three other size-classes were generally minor. The exception to this trend was on a grazed plot close to the water point (plot E3) where stasis of sub-adult shrubs (size-class 3) made the major contribution (38%). Reproduction and growth generally contributed little to the population growth rate (consistent with the minor contribution of the smallest size-classes), even at sites where considerable recruitment was observed during the study. Maximum reproductive contribution was approximately 8% (plot I1), although the contribution of reproduction and growth varied between matrices, including between grazed plots within a site. While the contributions to the population growth rate from the three smallest size-classes were minor, within these size-classes growth generally appeared to be more important than stasis.

The contributions of the differences in the various demographic rates to differences in population growth rates on grazed plots at different distances from water are indicated by the results of the LTRE analysis. To simplify the analysis I grouped sites based on λ (the average for grazed plots at each site) and used the mean of the matrices from the sites in each group. This was possible because of the trend of higher λ at increasing distances from water and because plots with similar population growth rates also had similar structures in their elasticity matrices. Three groups were defined: those where $\lambda > 1$ ('distant' group, mean of sites G and I, mean $\lambda = 1.03$, mean distance from water of 3100 m), those where $\lambda \approx 0.93$ ('intermediate' group, mean of sites A,C,D,F and H, mean $\lambda = 0.93$, mean distance from water of 1750 m) and those where $\lambda < 0.91$ ('close' group, mean of sites B and E, mean $\lambda = 0.86$, mean distance from water of 1340 m). Pairwise comparisons were made between these mean matrices. Plots of the differences between groups in stage-specific fertility, survival and growth probability, measured relative to the mean of the two groups being compared, and the corresponding contributions to the differences in population growth rates, are presented in Figure 5.7. This produced a slightly different picture to the analysis of demographic fate presented earlier because the differences in demographic rates detected in the LTRE analysis are not necessarily significant in a statistical sense.

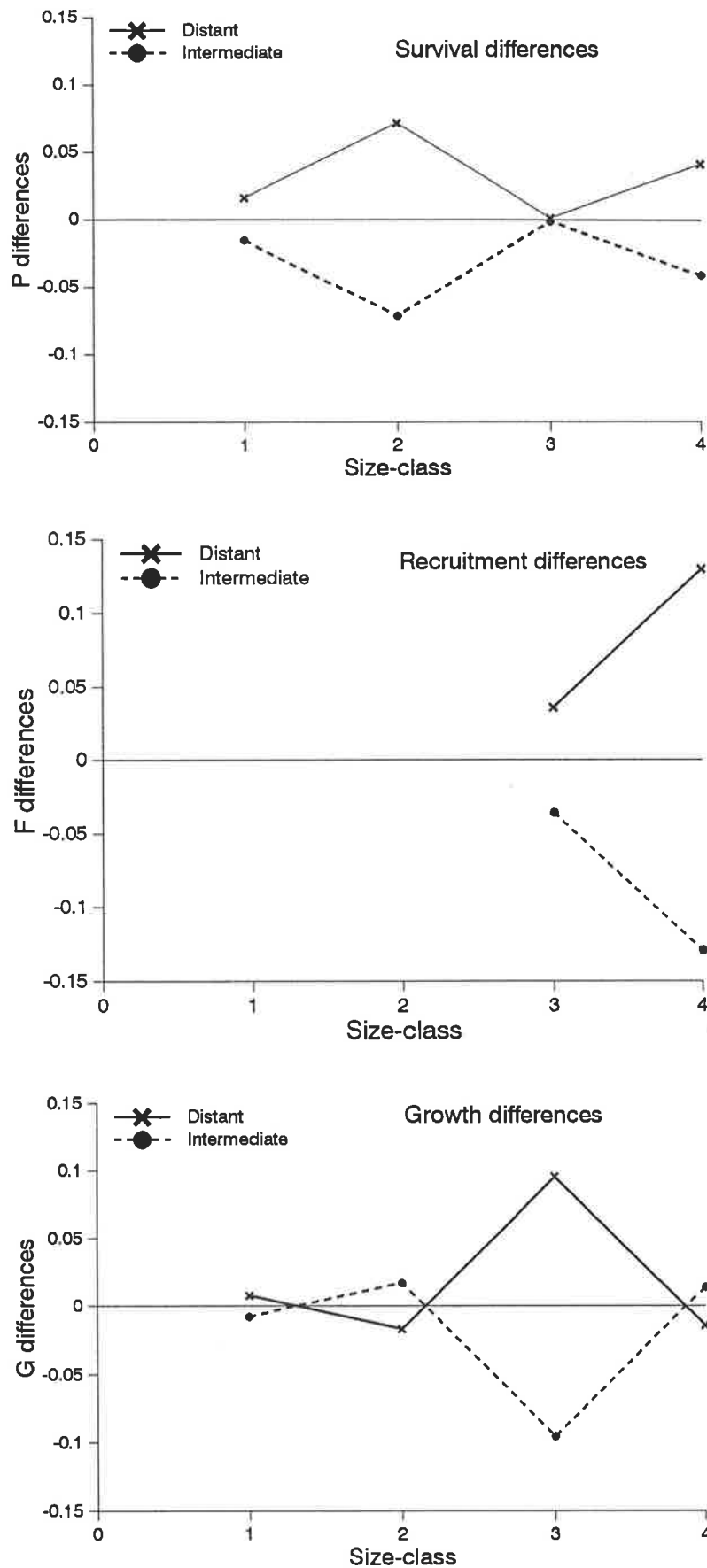


Fig. 5.7(a). Differences between distant and intermediate sites in the probability of survival (P), recruitment (or fertility, F) and growth (G) of four size-classes of saltbush on grazed plots. See text for explanation of site groupings. The figure is continued on the following pages.

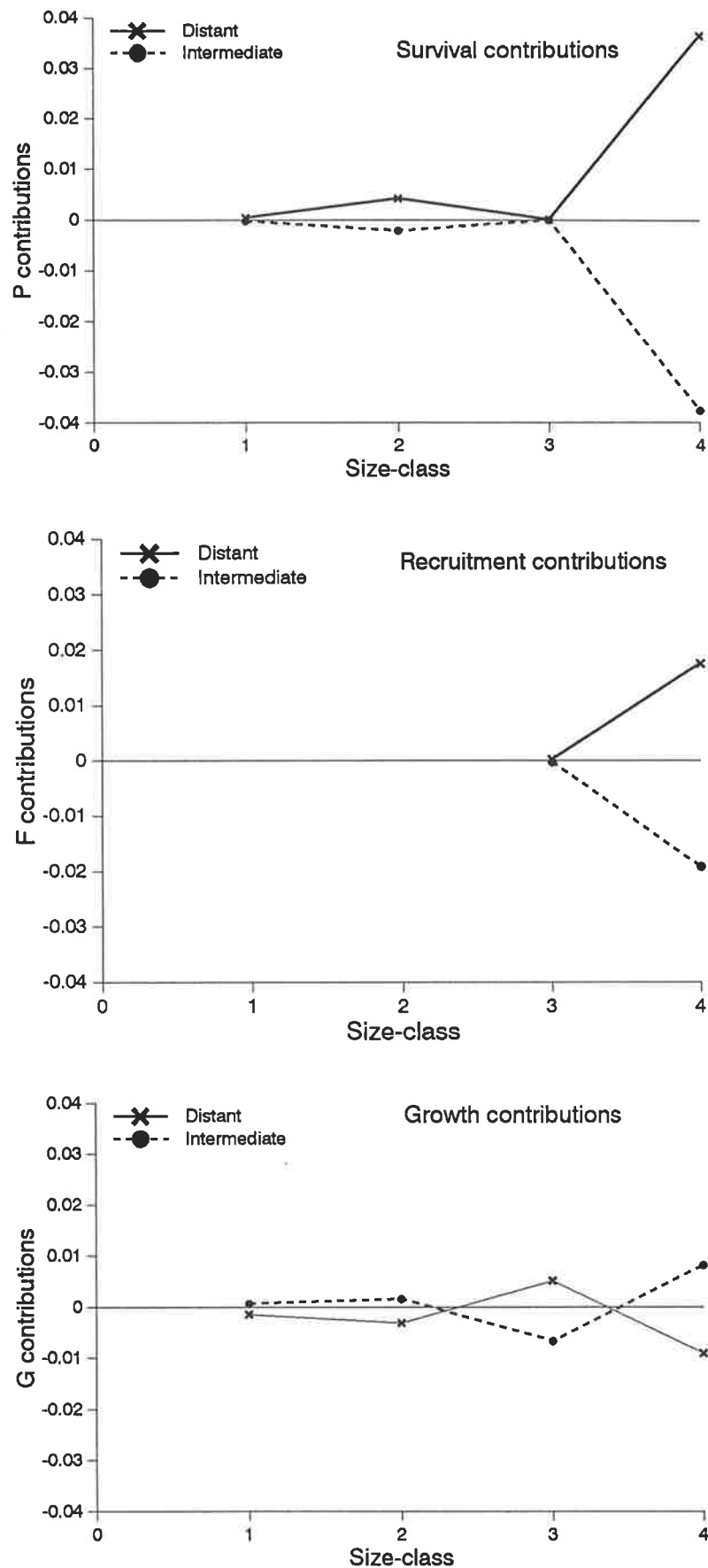


Fig. 5.7(b). The contributions of differences in survival (P), recruitment (or fertility, F) and growth (G) of four size-classes of saltbush to the differences in population growth rate (λ) between grazed plots at distant and intermediate sites. Continued on the following pages.

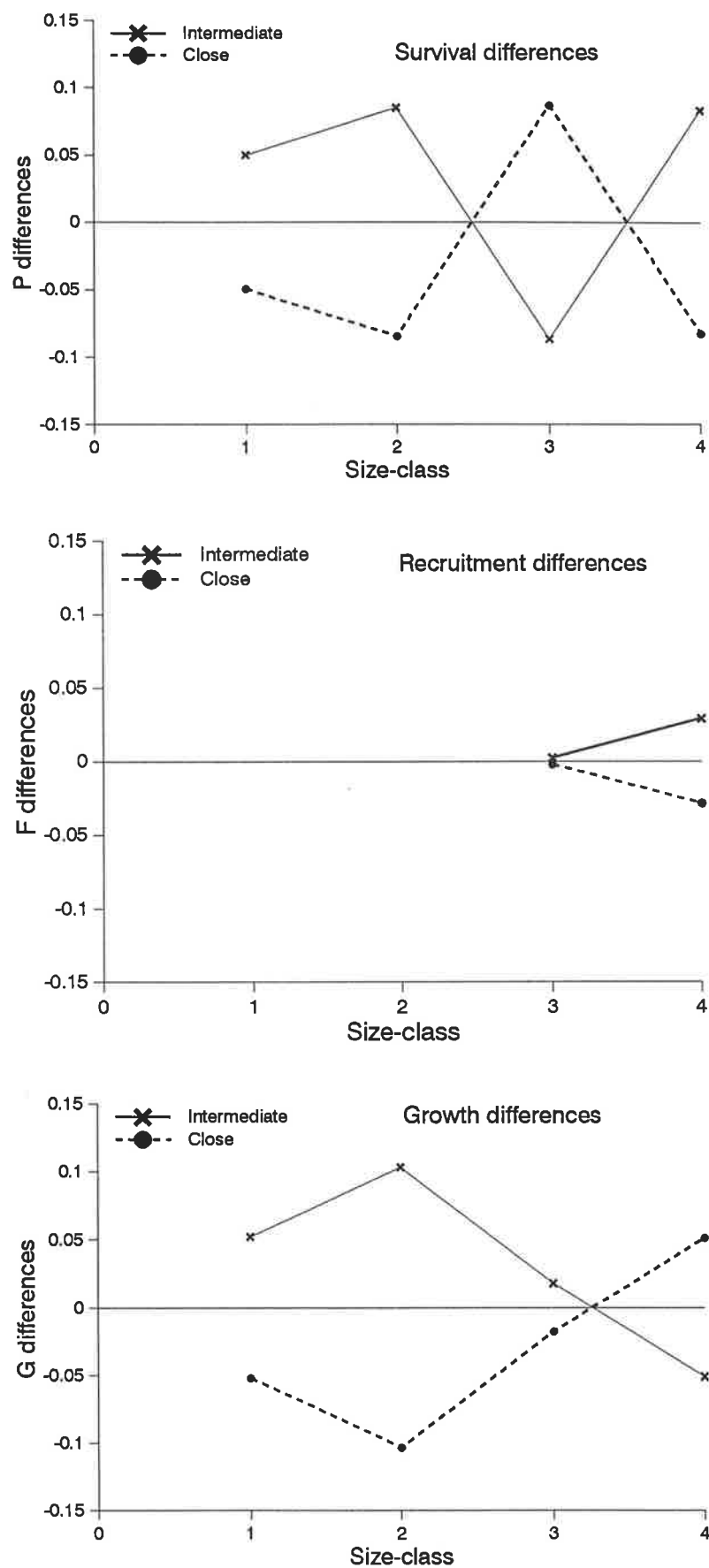


Fig. 5.7(c). Differences between intermediate and close sites in the probability of survival (P), recruitment (or fertility, F) and growth (G) of four size-classes of saltbush on grazed plots. See text for explanation of site groupings. The figure is continued on the following page.

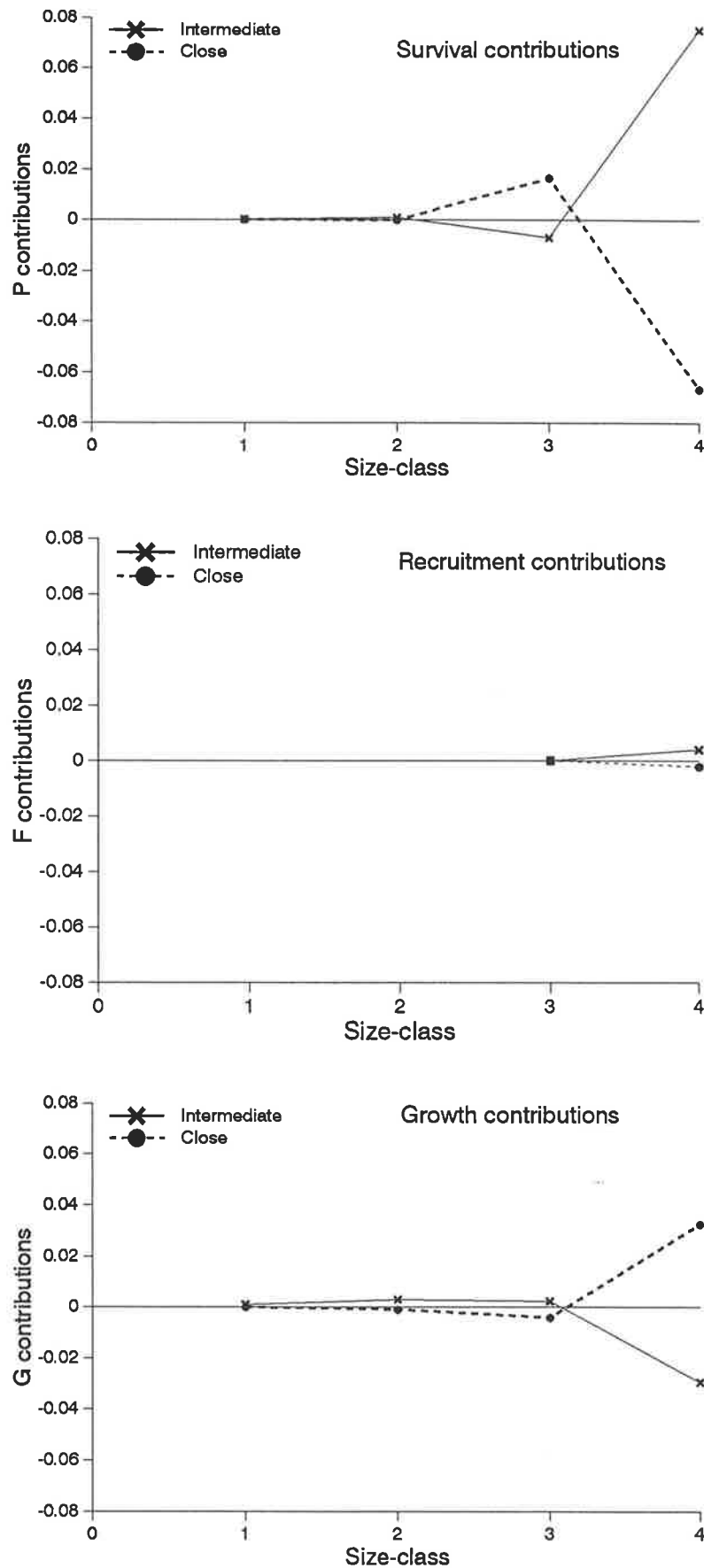


Fig. 5.7(d). The contributions of differences in survival (P), recruitment (or fertility, F) and growth (G) of four size-classes of saltbush to the differences in population growth rate (λ) between grazed plots at intermediate distance and close sites.

Comparing the distant and intermediate groups it can be seen that although the distant group has a large fertility advantage, a survival advantage for size-class two (juveniles) and four (adults) and a large growth advantage for size-class three (sub-adults), it is the greater reproduction and survival of adults at distant sites that mostly contribute to the difference in λ . Of these two processes, higher adult survival is most important with a contribution to the difference between the distant group and the mean of 0.0364, compared to 0.0175 for reproduction (Figure 5.7). While the distant group had a fertility advantage over the intermediate group, the latter group had a fertility advantage over the close group (Figure 5.7). In addition, the intermediate group had a survival advantage for adults compared to the close group, but a survival disadvantage for sub-adults. Although the intermediate group is also shown to have a survival and growth advantage over the close group for seedlings and juveniles, this should be treated with caution because of the limited numbers of individuals in these size-classes on close plots. The apparent growth advantage for adults in the close group (Figure 5.7) actually represents shrubs becoming smaller and reverting from size-class four to size-class three (since both positive and negative growth are included in the analysis), and the survival (i.e. stasis) advantage of size-class three in the close group reflects the higher progression of these plants to the adult size-class in the intermediate group. The major contribution to the difference in λ , however, arises from the greater survival of adults in the intermediate group (contribution to difference of 0.0748). Differences in recruitment contributed little. The greater number of adults reverting back to sub-adults at close sites effectively reduces the difference in λ between the two groups (contribution of 0.0323) but may have longer-term consequences in increasing the difference in λ through the reduction in the proportion of reproductive adults in the population.

DISCUSSION

Population Changes - The Role of Grazing, Climate and Time

Population growth rates determined in this study indicated that the saltbush population was in decline over much of Yanaby. The rate of decline of the saltbush population was high at many sites, being greatest on grazed plots at sites near water where population

growth rates (λ) as low as 0.7 were obtained. Meanwhile, populations on both grazed and exclosed plots were stable or slowly increasing ($\lambda \geq 1$) at the sites the greatest distance from water. The results of the study suggest that grazing by sheep was a primary factor contributing to the decline in the size of the saltbush population, but because of spatial variation in grazing the decline was not universal or of equal magnitude throughout the paddock. Of course the phenomenon of grazing being concentrated around water points, resulting in reduced densities of palatable plants, is widely accepted and has been demonstrated by studies of the spatial patterns in population structure around water points (Lange 1969, Graetz and Ludwig 1978, Barker 1979) and of the early development of piospheres (Andrew and Lange 1986b). However, this study has shown that under continuous grazing, declines in saltbush population size may continue to occur in paddocks even after many years of grazing. In addition, this study has identified the mechanisms involved in this change and in particular the impact of grazing on the various demographic processes. The magnitude of the declines in population size on the grazed plots at different distances from water were due to demographic processes being differentially affected at different sites together with the contribution of these rates to population growth.

Grazing by sheep is implicated as the main cause of population decline because of the differences in population change and demographic processes between grazed and ungrazed plots within sites and by contrasting population responses on grazed plots located at different distances from water, and which therefore were subjected to different levels of grazing. These comparisons are complicated by the grazing history of the paddock prior to the study, including the existence of an established piosphere, and the interaction of climatic effects with grazing effects in influencing population processes. Also, the length of time of exclosure was important in determining the degree of difference between grazed and exclosed treatments at a site. Thus, there appeared to be little difference in the dynamics of the populations between the grazing treatments at sites closer to the water point for the first 2-4 years of the study. Mortality of adults at these sites was similar on both treatments early in the study (but higher than at more distant

sites), as was recruitment, which was low compared to the distant sites. This suggests a residual effect on these shrubs from grazing experienced prior to the exclosures being erected at the commencement of the study. Similar persistent effects of grazing have been reported for yield and seed stalk production in arid zone forage shrubs in North America (Cook and Child 1971). The effects of livestock activity in compacting the soil and reducing the infiltration of moisture (Thurrow 1991) are also likely to be long-term, and may have affected the dynamics of saltbush on the exclosures. In addition, there is the possibility that other unknown factors with persistent effects may have influenced the population in the period just prior to the study, although this seems unlikely.

After a long period of no grazing, which included both dry and wet periods, demographic rates (particularly recruitment and growth) in the exclosed populations increased, suggesting a recovery of vigour and an increase in seed production (see Chapter 7), while on grazed plots the vigour of the plants continued to appear poor. Consequently, the population changes presented here are the result of both earlier and contemporary grazing pressure. However, the similarity of the ISD and SSD for many plots (apart from the exclosures) suggests there have been no recent major changes in the demographic rates.

There was no evidence to suggest that kangaroos and rabbits, or any other herbivores, had any effect on the saltbush population. This is supported by the defoliation data for the exclosed plots, which rabbits and kangaroos frequently entered (see Chapter 4), and other studies which have reported that these herbivores rarely graze saltbush (Ratcliffe 1936, Hall *et al.* 1964).

Apart from grazing by sheep, fluctuations in climate were important in determining saltbush population size in Yanaby. However, because of spatial variation in grazing the relative importance of these two factors varied across the paddock, resulting in different patterns of fluctuation in the population at different sites. Thus climate was most important at sites where grazing was light, with fluctuations in numbers tracking variations in climate, particularly rainfall. Recruitment and subsequent death of seedlings

and/or juveniles were mainly responsible for fluctuations in numbers. The number of seedlings increased following rainfall events of at least 50 mm and then decreased during dry periods or in summer. These findings are consistent with earlier studies that found 50 mm of rainfall spread over several days was necessary for germination of saltbush (Williams 1979) and that the survival of seedlings is poor (Crisp 1978).

Elsewhere in the paddock, at locations where grazing was heavy, grazing was the dominant factor controlling population size, although interactions with climate were important in determining mortality rates of established plants. Grazing inhibited recruitment at these sites and because of this, temporal variation in the number of individuals was much less than at the lightly grazed sites. At a number of sites, reductions in the number of established shrubs due to grazing were the only population changes to occur. Mortality of heavily grazed adults tended to be higher during extended dry periods, but it is difficult to determine whether this was due simply to the increased defoliation of shrubs during this period (see Chapter 4) or an interaction between defoliation and moisture stress. Little is known about the simultaneous effects of defoliation and moisture stress on plants and it is an interaction which requires further study (Ludlow 1986, Hart and Norton 1988). While some plants are reported to benefit in the short term from grazing during water stress, because the smaller leaf area reduces moisture loss (Trumble and Woodroffe 1954, Chambers and Norton 1993), increased mortality of grazed saltbush shrubs during moisture stress is probably a consequence of the reduced root growth which occurs following defoliation (Hodgkinson and Baas Beeking 1977). This would limit a plant's access to moisture deeper in the soil profile. This is consistent with the findings of Leigh and Mulham (1971), who reported that fewer saltbush shrubs died when heavily grazed if they were watered, although completely defoliated shrubs died regardless of soil moisture availability. My results differ from those of Eldridge *et al.* (1990) who concluded that the mortality rate of adults increases in dry periods irrespective of whether the plants are grazed or not, but generally support those of Crisp (1978), who reported a constant low rate of mortality for ungrazed adult shrubs. The exacerbation of grazing related plant mortality by moisture stress has also

been reported for several other arid zone species (Scholes 1985, Chambers and Norton 1993).

It is frequently reported that the dynamics of rangeland plants are dominated by climatic fluctuations and the effects of grazing are secondary (e.g. Turner 1971, Norton 1978, O'Connor 1994). Eldridge *et al.* (1990) also noted this in the dynamics of saltbush. My results highlight the importance of the level of grazing pressure in determining the relative strength of these factors in controlling population dynamics, at least for perennial species, and indicate the need to interpret population changes in the context of the grazing pressure imposed. At higher levels of grazing the relative influence of climate decreases, although it can still have a synergistic effect on the population with grazing or other disturbances. Appreciation of this frequently overlooked point is necessary for the proper understanding of potential grazing impacts.

Spatial Patterns in Demographic Processes

The detection of spatial patterns in the rates of certain demographic processes suggests that grazing is having an impact, either direct or indirect, on these rates at certain locations because of the spatial trends in grazing pressure. In Yanaby, the rates of several demographic processes and the demographic fates of individuals in certain size-classes varied across the paddock in response to variations in grazing pressure, but because of variations in the sensitivity of these processes to grazing, they were differentially affected across the paddock. Higher levels of grazing are likely to affect processes more severely, and the more insensitive processes will only be affected at higher grazing pressures.

Recruitment

Grazing created spatial patterns in the recruitment of saltbush, which increased linearly with distance from water. Recruitment was prevented or markedly reduced on plots at distances up to 2200 m from water where grazing pressure was high to moderate, suggesting the capacity for saltbush to recruit under these levels of grazing is low. My

results contrast with those of Eldridge *et al.* (1990) who reported that the appearance of saltbush recruits was unaffected by grazing at a distance of 1200-1500 m from water on the Mundi Mundi plain in western New South Wales, and those of Graetz (1980) on the Riverine plain in NSW, who observed that grazing actually stimulated the recruitment of seedlings compared to ungrazed exclosures. However, in the study by Eldridge *et al.* (1990) it is possible that the shrubs were only lightly grazed, since it was not clear what level of grazing the shrubs actually experienced. In Graetz's (1980) study it seems that the saltbush population was in good condition prior to his study (judging from shrub densities) so that in the short term, the decline in the density of mature adults under grazing which he observed, would have created gaps for the establishment of new seedlings from seed. Reduced recruitment under grazing may result from lower seed availability due to the effects of defoliation on seed production (Bastrenta 1991, Hodgkinson 1991) or because of soil surface conditions inimical to seed germination and establishment, perhaps due to trampling of the soil cryptogamic crust by livestock and the consequent accelerated loss of nutrients and moisture (Graetz and Tongway 1986, Harper and Marble 1988). The question of reduced recruitment in this study will be considered in Chapter 7.

Adult Mortality

Significant effects of site and grazing treatment in the log-linear analysis of demographic fate (Table 5.4) suggests there were spatial patterns in many demographic processes as well as differences between grazed and exclosed plots because of sheep grazing. However, for the grazed treatment, increased adult mortality close to water and a greater reduction in shrub size were the only significant differences. The highest recorded adult mortality over the 6.5 years of the study was 82% at 1130 metres from water, which was the site closest to water. This compares with 16% adult saltbush mortality at a distance of 50 m from a water point during the first eight years following establishment of the water point, a period which included a severe drought (Andrew and Lange 1986b). The latter study was carried out in similar vegetation to the present one (the study sites are approximately 20 km apart), with similar stocking rates and under the same management.

The high mortality of adult shrubs on grazed plots close to water is consistent with earlier reports concerning the inability of saltbush to tolerate defoliation (Wilson *et al.* 1969, Leigh and Mulham 1971, Graetz 1986).

The trend towards greater reversion of size-class four shrubs to size-class three near water reflects the direct action of grazing in reducing the dimensions of the shrubs. Although this was balanced in some cases by progression to size-class four, stasis of these sub-adult shrubs was greater at these sites than at more distant sites. In contrast, at the sites where grazing was less severe shrubs in size-class three generally progressed to the next class and remained there. The increase in the proportion of the population in a non-reproductive growth stage at the heavily grazed sites may contribute to the reduced recruitment recorded at these sites.

Survival and Growth of Seedlings and Juveniles

Many studies have reported that the mortality of seedlings of woody species is increased by grazing (Eckert *et al.* 1986, Gardiner 1986, Lange and Graham 1983, Owens and Norton 1992). Consequently, a stipulation of many grazing management practices for arid zone perennial species is that grazing pressure should be relaxed when seedlings are present or during periods when germination and establishment are likely to ensure that young plants are able to establish (Crisp 1978, Silander 1983, Hacker 1987, Westoby *et al.* 1989). Seedlings are considered to be less tolerant of grazing than mature plants because they have fewer carbohydrate reserves and their small size suggests that a much larger proportion of an individual's biomass will be removed in a defoliation event than for a larger adult plant (Archer and Pyke 1991). Indeed, Crawley (1983) suggested that if plant mortality is an important effect of herbivores in altering plant abundance, then it is most likely to result from increased mortality of seedlings rather than of mature individuals.

In my study there was no significant effect of site on the demographic fate of seedlings and juveniles on grazed plots. This implies grazing was having no effect on the survival

and growth of saltbush seedlings and juveniles (Table 5.4), although my sample sizes on the two plots closest to water were particularly small (note that the LTRE analysis however suggests that there was an effect, although this is not statistically significant). Similar findings concerning the lack of effect of grazing on saltbush seedlings and juveniles were reported by Eldridge *et al.* (1990), and earlier Graetz (1980), who suggested that rainfall has a greater influence on seedling fate than grazing. In a later study, however, Graetz (1986) reported that the proportion of juveniles in the population was increased by heavy grazing because adult shrubs were eliminated, therefore reducing competitive pressure on seedlings.

There are a number of possible reasons for the absence of a grazing effect on seedlings and juveniles. It may be related to the low biomass of seedlings which makes them of insufficient feed value for sheep to graze (insufficient return for the energy expended in seeking them out and grazing them), their small size may make them difficult to find or graze, especially since approximately 80% of seedlings are found under the canopy of adult shrubs (Williams 1979), or they may contain some compound or metabolite not found in adults which makes them unpalatable. In small-plot graze-down experiments it has been noted that saltbush seedlings are shunned by grazing sheep even though there may be little other forage available (Lange *et al.* 1992). The sheep in these experiments actually ceased grazing at low levels of available biomass, rather than graze the seedlings. This behaviour was attributed to the seedlings being too small an amount of forage for sheep to be bothered with. However, this is difficult to imagine in small experimental plots where the energy cost of grazing these seedlings would be small. A possible alternative explanation is that the seedlings are unpalatable to sheep. Since seedlings of many woody species are more susceptible to defoliation than the adults, seedlings can have greater chemical defences against grazing than adults (Bryant *et al.* 1992). This question has not been examined for saltbush and while it is a possibility, it also seems unlikely to be the reason for the lack of grazing effect given the general lack of herbivore defences typical of Australian vegetation (Anderson 1982). Another study has shown that the size of the seedling is important in determining whether herbivory influences seedling

survival and growth. Parker (1982) found that small seedlings of arid zone shrubs were not affected by grazing but were killed by desiccation, while large seedlings were killed by herbivory. While these findings lend support to the hypothesis that sheep do not graze saltbush seedlings because of their small size, the most likely reason for saltbush seedlings to be unaffected by grazing in full-size paddocks is the protection from grazing and trampling afforded them by being located under adult shrubs, as has been reported for other woody shrubs (Owens and Norton 1992). A similar lack of a grazing effect on the fate of seedlings of preferred forage shrubs has also been reported in the arid Karoo region of South Africa. Milton (1994) observed that sheep grazing and trampling had no effect on the survivorship of seedlings of *Osteospermum sinuatum*, but in this case the lack of grazing effect was attributed to the tolerance of individuals to grazing, something which seems unlikely in saltbush.

In contrast to the grazed plots, a significant effect of site on the fate of seedlings and juveniles was detected for the exclosed plots. (Note that sample sizes were higher for this analysis than that for the grazed plots, because of higher recruitment, so this analysis is more powerful.) Survival and growth were higher on exclosed plots in the vicinity of the water point than further away. Studies have shown that reduced adult densities can lead to improved seedling survival and growth because of reduced competition for moisture and nutrients (Parker and Salzman 1985, Milton 1994). Also, seedling survival can be greater in disturbed environments because of nutrient-enrichment or greater moisture accumulation (Hall *et al.* 1964, Dean and Milton 1991). Soils around water points are highly disturbed (Andrew and Lange 1986a) and may therefore provide a more favourable environment for seedlings. Both the reduced density of adults, with the effect of lower competition for moisture and nutrients, and the disturbed soil surface may explain the improved survival and growth of saltbush seedlings on exclosed plots near the water point. If this is so, and grazing was having no effect on seedling establishment and growth, a similar response would have been expected on the grazed treatments. That this was not detected is most likely explained by the small numbers of seedlings on the grazed plots near the water point during the study, rather than a negative impact of grazing on

the survival and growth of seedlings.

Importance of Demographic Processes to Population Growth

The importance of changes in demographic rates to alterations in population growth need to be considered in terms of the contributions each rate makes to the population growth rate (λ), which reflects the life-history strategy of the species (Silvertown *et al.* 1992). Elasticity analysis quantifies these contributions, or in another sense, the sensitivity of λ to changes in these rates. In saltbush, the largest elasticity was associated with survival of adults, with a much smaller contribution from reproduction. Survival and growth of the smaller size-classes were least important to population growth, with negligible contribution to λ in many cases. This pattern of contributions to λ is common amongst woody and long-lived species (Caswell 1986, Silvertown *et al.* 1993, O'Connor 1993), which generally have stable populations ($\lambda \approx 1$) when undisturbed, and indicates that survival of established adults is very important in maintaining the population growth rate in these species (i.e. λ is highly sensitive to changes in the survival of these individuals). Small contributions to population growth from recruitment and the survival and growth of the smaller size-classes are not surprising for long-lived species. Recruitment and growth of seedlings in most long-lived species is often of little importance in maintaining the population because of the longevity of established plants (Harper 1977), which may occupy a site for many years. Consequently, it has been suggested that the successful establishment of new individuals often occurs only when a safe site becomes available following the death of an established plant (Briese 1982, Andersen 1989). Also, being long-lived species, there are many opportunities for plants to reproduce and recruits to establish during the life-span of an individual.

In saltbush, the large contribution of adult survival to λ reflects the species' life history strategy for coping with the unreliable rainfall regime, and in particular the unpredictability of drought. This strategy is the tolerance of drought by the established adult plants (Westoby 1980). Silvertown *et al.* (1992, 1993) suggested this pattern of contributions to λ was common amongst species classified as possessing a 'stress-tolerant'

life-history strategy (Grime 1977) and although they were unable to demonstrate this conclusively, for saltbush, this link between the two approaches to life history strategies seems plausible. As would be expected, the stress-tolerant strategy is common amongst many long-lived arid zone perennials (Grime 1977, Stafford Smith and Morton 1990), but there have been no other studies which have attempted to determine the population growth rate or examine the elasticities for species of this type.

Although stasis and growth of saltbush seedlings and juveniles were common transitions in this study (at least at lightly grazed sites or in exclosures), the contributions to λ from recruitment and the survival and growth of recruits were small, partly because seedling mortality was high. On most plots mortality in this size-class accounted for most of the mortality recorded. High levels of seedling mortality are usual for saltbush (Crisp 1978, Eldridge and Westoby 1991), most likely due to moisture stress, which is the main cause of the poor seedling survival common in many arid zone species (Beatley 1974, Hennessy *et al.* 1984, Auld 1990, Harrington 1991). The location of the majority of saltbush seedlings close to adults or under their canopy, both observed in this study and reported by Williams *et al.* (1978), is likely to mean they suffer intense competition with adjacent adults for moisture and/or nutrients, where they are at a disadvantage because of their shallow roots (Williams *et al.* 1978, Young 1988, Reichenberger and Pyke 1990, Eldridge *et al.* 1991). It has also been suggested that the shading of seedlings by adults may cause light stress, which in turn reduces seedling root growth and limits the ability of desert shrub seedlings to tolerate moisture stress (Mauchamp *et al.* 1993). I recorded high levels of seedling mortality but once individuals had advanced to stage class 2 the probability of mortality diminished, which is consistent with the Deevey Type III survivorship of saltbush seedlings reported by Crisp (1978).

Despite the low contributions of stasis and growth of seedlings and juveniles to λ , these size-classes may have an important role in ensuring that gaps which occur are rapidly occupied by saltbush and not other species. Noble (1986a) noted that it is not uncommon for "advanced-growth seedlings" of saltbush to survive indefinitely in close proximity to

established shrubs. He suggested that although these seedlings were suppressed by their neighbours, their ability to persist meant that they could rapidly exploit any gaps which occurred through the death or weakening of their neighbours. This certainly may have been occurring at my lightly grazed sites, particularly with plants in size-class two, but because of the scarcity of these smaller plants compared with the number of adults, and the low mortality of adults at these sites there is little contribution of these size-classes to λ . The existence of suppressed seedlings which grow and rapidly occupy gaps that form in the vegetation is also widely recognised to occur in dominant tree species in rainforests, where gaps in the canopy often form following severe windstorms (Hubbell and Foster 1986).

Spatial Patterns in λ - Mechanism of Population Change

The effect of grazing in reducing the rate of population growth was not a result of all population processes being equally affected by grazing but was limited to changes in the rates of a few stage-specific demographic processes. Shifts in the rates of these processes across the paddock in accordance with variation in grazing pressure, together with the sensitivity of λ to these processes, determined the spatial pattern in population growth.

Overall, the most important effects of grazing in reducing the population growth rate of saltbush were the lowering of both adult survival and the recruitment of seedlings (fertility contribution). However, the pairwise comparisons in the LTRE analysis showed there were spatial patterns in the degree to which these were important in reducing λ . Changes in recruitment were shown to be important in reducing λ on grazed plots at intermediate sites compared with the more lightly grazed distant sites, but were not important in the difference between intermediate and close sites. In comparison, changes in adult survival contributed to differences between both pairs of groups. Thus, the difference in λ between the intermediate and close groups was almost entirely due to differences in adult survival; despite recruitment at close sites being very low, this was not important to the differences in the population growth rate between these sites.

The spatial patterns in the importance of recruitment and adult survival to differences in λ suggest these processes vary in their sensitivity to grazing. Examining the magnitude of the differences in these processes between the two pairs of groups (Figure 5.7) shows that the largest difference in recruitment occurred between the distant and intermediate groups, while for adult survival the largest difference was between the intermediate and close groups. This suggests recruitment is more sensitive to grazing than the survival of adults since it is more severely affected at greater distances from water (and hence lighter grazing pressure). In addition, adult survival contributed the most to the population growth rate at heavily grazed sites, which also suggests it is the process most tolerant of grazing.

For many species the production of seed is the demographic process which is most sensitive to grazing (Crawley 1983, Hodgkinson 1991), and this is one possible explanation for recruitment in saltbush apparently being more sensitive to grazing than the survival of adult shrubs (the effect of grazing in reducing saltbush recruitment is examined in Chapter 7). This relative sensitivity of the different demographic processes can be explained in terms of the priorities for resource allocation within the plant. There are usually trade-offs in the resources allocated to reproduction, growth and survival in plants (Charlesworth 1980), and allocation of resources to reproduction can result in reduced survival (Harper 1977, Law 1979). For many species, particularly long-lived arid zone species with a large investment in structural tissues such as roots and stems, the priority is for the survival of established plants, particularly since the chance of seedlings establishing and surviving to maturity is low (Beatley 1974, Westoby 1980, Stafford Smith and Morton 1990). Consequently, when a plant is defoliated most resources are diverted to growth functions and the replacement of the leaf tissue removed by herbivores, and flowering is delayed. It is only when carbohydrate levels are restored that energy is allocated to reproduction (Crawley 1983).

It has long been recognised that mature saltbush shrubs are persistent when not grazed (Crisp 1978) but they are considered to be readily killed by grazing (Leigh and Mulham

1971). However, Milchunas and Lauenroth (1993) proposed that adaptations which facilitate the survival of arid zone shrubs during drought can assist a species in the tolerance of grazing, an hypothesis which seems to be consistent with my results. The population strategy of coping with drought by having stress-tolerant adults appears to limit the negative effects of grazing on the saltbush population, since this stage is the part of the saltbush life-cycle most tolerant of grazing. Despite this, differences in adult mortality were the major cause of changes in the population growth rate at different distances from water. However, this tolerance means that reductions in λ due to grazing are much smaller than would otherwise be the case, in view of the high sensitivity of λ to changes in adult survival. This is not to say, however, that saltbush could be considered tolerant of grazing in comparison with other species; mature saltbush shrubs do appear to have poor tolerance of grazing compared to many other species.

Small-Scale Spatial Variation

The dynamics of plant populations can vary considerably over small spatial scales (Sarukhán and Harper 1973) in response to small-scale variation in the environment (Louda 1982, Fowler 1984). Moloney (1988) found that population growth rates of *Danthonia sericea* in a mown field in North Carolina varied over a small spatial scale (within a 28 x 12 m area) due to differences in the rates of growth and mortality of seedlings and small individuals over a soil and vegetation gradient. In addition to the large-scale spatial variation in λ associated with grazing, I observed variation in the population dynamics of saltbush between grazed plots within sites which was not readily explained. It was for this reason that the results of each grazed plot were presented separately rather than as a mean. These differences included variation in λ , differences in patterns of elasticities in the transition matrices and differences in number of individuals, particularly the number of recruits. In chenopod shrublands, edaphic conditions and water distribution patterns vary over scales from metres to hundreds of metres (Tongway 1994) and Malik *et al.* (1976) have shown that patterns in the structure of saltbush populations occur at scales from 1-60 metres, and are related to variations in microtopography and soil nutrient, moisture and salinity status. Although such spatial

patterns in soil salinity have been shown to create small-scale heterogeneity in grazing pressure, with plants in more saline patches being grazed less (Hacker 1987), I believe that in Yanaby demographic rates of saltbush varied at a small scale mainly in response to the effect of local edaphic conditions on the shrubs, since my observations suggested that defoliation of saltbush was fairly uniform amongst plots within a site. It is also possible that this variation was contributed to by local conditions of nutrient and moisture availability on a plot affecting the tolerance of a population to grazing (Maschinski and Whitham 1989). It should be noted that this small-scale variation had only a minor effect on λ compared to the changes in λ due to the differences in grazing pressure between sites at different distances from water. Larger sample sizes would have overcome much of this variation between plots at a site but were not practical in this study.

CONCLUSIONS

- Spatial variation in sheep grazing pressure in Yanaby resulted in marked declines in the size of the saltbush population over much of the paddock during this study, with the rate of decline being highest at sites nearer the water point.
- This decline was a result of negative impacts of grazing on certain size-specific demographic rates, specifically the survival of adult shrubs and recruitment. The survival and growth of seedlings and juveniles were not affected by grazing.
- The rate of population decline was determined at a site by the grazing pressure, the sensitivity of the various demographic processes to grazing and the sensitivity of the population growth rate to the affected demographic processes.
- Because recruitment was more sensitive to grazing impact than adult survival there were spatial patterns focussed on the water point which reflected differences in the importance of these vital rates to changes in the population growth rate with distance from water. Recruitment was therefore more severely reduced by grazing at greater

distances from water than adult mortality, and so was more important in differences in population growth rate at these distances.

- Saltbush is characterised as having a stable population when ungrazed, and the survival of adults is the process most important to maintaining the population growth rate.

Recruitment is of little importance in maintaining ungrazed populations. This life history strategy is influential in determining the response of the population to grazing. This strategy of drought tolerance via adult survival results in this process being the most tolerant of grazing, so that at heavily grazed sites this contributes most to the population growth rate. Despite this, increases in adult mortality due to grazing were the major cause of changes in the population growth rate at different distances from water.

- Interactions of grazing with climate were important in determining population changes; in particular, the mortality of heavily grazed adult shrubs was increased by drought.

CHAPTER 6

TIME-VARYING POPULATION MODELS FOR SALT BUSH

INTRODUCTION

Background

It is widely recognised that demographic rates in most populations are not constant but vary with time, mostly in response to environmental fluctuations. Several studies have recorded such variations for populations of certain species and have shown that the population growth rate can exhibit substantial temporal variation as a consequence (Bierzychudek 1982, Moloney 1988, O'Connor 1993). In arid environments the rates of plant demographic processes, including germination, seedling establishment, growth, flowering, seed production and mortality, vary in many species chiefly in response to rainfall fluctuations (Beatley 1974, Mott 1979, Westoby 1980). However, because of the seasonal and yearly unpredictability of rainfall in these areas (Anderson 1982), particularly in Australian rangelands (Stafford Smith and Morton 1990), these rates are likely to vary not in a regular seasonal fashion but in a stochastic manner.

This temporal variation immediately invalidates one of the assumptions behind the time-invariant matrix models used in the previous chapter, that of the environment and hence the demographic rates being constant (Cohen 1979, Caswell 1989). Therefore, time-invariant models do not provide any insights into the future size or behaviour of the population, but rather provide a summary of population performance under the conditions experienced during the observation interval. Projecting time-invariant matrices into the future is meaningless since an estimate of $\lambda < 1$ for the matrix implies certain extinction while $\lambda > 1$ would represent continued exponential growth. Estimates of $\lambda = 1.0$, which indicate a stable population would be extremely rare. Clearly, for a full understanding of the long-term trends in a population, models need to incorporate temporal variation in demographic rates.

In recent years advances have been made in the theory of demographic analysis in variable environments which incorporate temporal variation in demographic rates (Cohen 1979, Tuljapurkar 1989, Caswell 1989). In particular, Cohen (1979) described the use of randomly varying deterministic transition matrices to estimate long-term population growth rates in stochastic environments. Extinction of the population is a possibility in stochastic environments, even when λ is positive and rapid population growth occurs under certain conditions (Tuljapurkar and Orzack 1980, Caswell 1989). These models can be used to provide estimates of the probability of extinction and the time to extinction (Tuljapurkar and Orzack 1980, Lande and Orzack 1988). A few empirical studies of terrestrial plants have utilised this approach, including those of Bierzychudek (1982), Menges (1990) and Kalisz and McPeck (1993).

The form of time-varying matrix population models is:

$$\mathbf{n}(t+1) = \mathbf{A}(t)\mathbf{n}(t) \quad (6.1)$$

where $\mathbf{A}(t)$ is the transition matrix for the time interval t to $t+1$ and $\mathbf{n}(t)$ is a column vector whose elements, $n_i(t)$, represent the size-class distribution of the population at time (t) . This is similar to the time-invariant model where the population vector is repeatedly multiplied by the transition matrix, but in this case there is a pool of deterministic transition matrices to choose from for each iteration of the model. These may be chosen in a regular pattern (appropriate for a reliable seasonal environment) but in a stochastic model the transition matrix $\mathbf{A}(t)$ is randomly selected from the set of matrices which describe the transitions in the population. In this way environmental stochasticity is incorporated. These models do not include demographic stochasticity (i.e. the chance application of demographic rates to individuals), which is much more difficult to model, although it can be approximated by using a binomial distribution to sample the number of survivors after application of the transition probabilities (Akçakaya 1991).

Aims

The results presented in the previous chapter clearly indicated that the density of the

saltbush population over much of Yanaby declined markedly during the period of the study. The time-invariant matrix models used to analyse population changes identified those population processes which were affected by grazing and those that were important in causing reductions in the population growth rate at various distances from water. Recruitment and adult survival were both shown to be reduced by grazing and were important in reducing λ , although to different degrees depending on the location in the paddock.

However, the rates of most demographic processes varied temporally and often the changes brought about by grazing were related to particular seasonal conditions. A high level of adult mortality was associated with a particularly dry period and while recruitment was generally decreased by grazing, there was an improvement in recruitment levels on many grazed plots in the years of better rainfall in the later part of the study. Thus the long-term consequences of grazing for the population are difficult to assess from a 'short-term' study such as this. The future of the plant population could well depend on the nature, frequency and sequence of seasonal conditions experienced, and the consequent impact on rates of recruitment, growth and mortality and the level of grazing. In the long term a trend in the population may result which differs from that recorded during the data collection period. For example, the increase in recruitment recorded later in the study on some plots could potentially result in the replacement of all the shrubs that died during the dry period if conditions remained favourable for sufficient time (although for a number of the heavily grazed sites local extinction of the saltbush population seems inevitable). Therefore, the long-term implications of grazing for the saltbush population will depend on the balance of the demographic rates over time. To assess this, models are needed which take into account temporal variation in demographic rates in response to climatic fluctuations and grazing.

The main aim of this study was to investigate the likely long-term future of the saltbush population under continuous grazing for each of the study sites in Yanaby, using

stochastic matrix population models. Specific aims were:

- 1) to assess long-term population stability under grazing for a range of 'climate' scenarios by estimating long-term population growth rates under fluctuating conditions, particularly for 'intermediate' sites.
- 2) to estimate the probability of extinction and length of time to extinction for declining populations.
- 3) to examine the potential for recovery of the population at the sites where a decline in population size was observed during the years of poor rainfall in my study.

METHODS

The time-varying models utilised the data on transition rates collected during the study as the basis for the models, with temporal variation in these rates being chiefly attributed to fluctuations in rainfall and the consequent effects of grazing pressure on the shrubs. Two main model specifications were examined. The first was a stochastic model with a projection interval of one year and with temporal variation in transition rates arising from fluctuations in rainfall being simulated by the random selection of matrices. This model assumed that the sequence of matrices was unimportant. The second was a stochastic model with a six month projection interval but which attempted to include the effects of a sequence of bad seasons on transition probabilities. In addition to running the models using a random number sequence, actual rainfall records were also used to determine the sequence of the transition matrices in the simulations. Neither of the models incorporated demographic stochasticity.

In the yearly model four types of year were defined, namely: 1) good summer with a poor winter; 2) good summer/good winter; 3) poor summer/good winter; and 4) poor summer/poor winter. These classifications were based on the amount of rain received in summer and winter, since this would be the most important factor influencing

demographic rates. The yearly transition matrices for these models were based on the data collected over 5.5 years from October 1987 to March 1993, which gave 11 matrices each representing a period of approximately six months for each plot. Because of the small number of matrices available, only two types of seasons were defined, either good or poor. Good seasons were those which received rainfall greater than decile 5 while rainfall in poor seasons was equivalent to decile 5 or lower. Summer (October to March) and winter (April to September) matrices were classified as good or poor seasons according to the amount of rainfall received during September to February for summer matrices and March to August for winter matrices. Rainfall data for Iron Knob (approximately 20 km from Yanaby), supplied by the Bureau of Meteorology, Adelaide, was used for these determinations. After classifying the seasons an average matrix was calculated for each of the four possible combinations of type of season and time of year. The appropriate average matrices were then multiplied to create the four yearly matrices.

As indicated above, two different simulations were run, one (the stochastic model) using random numbers to select a type of year, each type having an equal probability of occurring, while the other simulation was based on actual rainfall records for Iron Knob dating from 1911 until 1993. The initial population size and structure observed in the field was utilised as the starting point for the simulations. The stochastic model was run for 100 years (100 iterations), which is much longer than the time required for the deterministic models (Chapter 5) to reach stability.¹ Twenty-five replicate runs were performed using different random number sequences. The population growth rate was calculated for each run (as described later) and the mean of these is presented here.

In the second model the projections were made on a seasonal (six monthly) basis rather than a yearly projection interval and incorporated a transition matrix representing a 'very poor summer'. This model was an attempt to simulate infrequent extraordinary conditions, particularly those associated with the temporal sequence of climatic

¹Maximum number of iterations required for stability in the deterministic models was 24.



conditions, which can be important in the dynamics of arid zone plant populations (Griffin and Friedel 1985). During the study, high rates of adult mortality were recorded over the 1988-89 summer, a period which received poor rainfall (decile 3) and also followed two seasons of poor rainfall (deciles 2 and 4). Consequently herbage levels were low and grazing of saltbush was high, both of which contributed to the high adult mortality (and poor seedling survival). Mortality rates during a period of similarly low rainfall later in the study were not substantially increased, suggesting the sequence of dry seasons was important in causing high adult mortality. The yearly stochastic model would therefore tend to overestimate the mortality of adults in dry summers which did not follow a series of dry seasons, so the transition matrix for summer in 1988-89 was used to represent a 'very poor summer' matrix. The remaining seasonal matrices were calculated as for the yearly model. Again the model was run using both a random number series and actual rainfall records to specify the sequence of seasons, but when a poor summer was specified by the model, if the two previous seasons were also poor the 'very poor summer' matrix was selected. Otherwise the normal poor summer matrix was used in the simulations. Twenty-five replicate runs each of 200 iterations (equivalent to 100 years) of the random number simulation were completed.

The population growth rate for each model was estimated from the projected population size according to the maximum likelihood estimator suggested by Heyde and Cohen (1985), i.e.,

$$\ln \lambda = \frac{\ln N(T) - \ln N(1)}{T-1} \quad (6.2)$$

where $N(T)$ is the sum of the individuals in all size-classes at time (T), after the final iteration. Since the natural log of λ is being used here, $\ln \lambda = 0$ for stable populations, for growing populations $\ln \lambda > 0$ and for shrinking populations $\ln \lambda < 0$. It should be noted that in this case λ is not the eigenvalue of a projection matrix or an average projection matrix but is used here to conveniently represent the population growth rate. The probability of

extinction of the population on each plot was determined as the percentage of the 25 replicate runs that became extinct within the 100 years of simulation. Extinction is difficult to define for models such as these because if there are positive elements in the initial population vector $\mathbf{n}(t)$ then the vector $\mathbf{n}(t+1)$ will also be positive, although these elements may be very small (Tuljapurkar and Orzack 1980). In this case extinction was said to have occurred when the number of individuals in all four size-classes fell below one. The mean time to extinction for those runs that became extinct was also determined. For the simulations based on the actual rainfall records an approximate 95 % confidence interval for the estimate of $\ln\lambda$ for each plot was calculated from the population track according to Heyde and Cohen (1985), i.e.

$$\ln\lambda \pm z_{0.05/2} \hat{\sigma}(T-1)^{-1/2} \quad (6.3)$$

where T is the number of projection periods in the time series on which the estimate is based, and the standard deviation σ of $\ln\lambda$ is estimated by

$$\hat{\sigma} = \left(\frac{1}{2} \left(\frac{\pi}{2} \right)^{1/2} \left(\frac{1}{\ln(T-1)} \sum_{j=1}^{T-1} j^{-3/2} |\ln N(1+j) - \ln N(1) - j \ln \lambda| \right. \right. \\ \left. \left. + \frac{1}{\ln(T-2)} \sum_{j=1}^{T-2} j^{-3/2} |\ln N(2+j) - \ln N(2) - j \ln \lambda| \right) \right) \quad (6.4)$$

where j is the j th time step. If the confidence interval for each estimate of $\ln\lambda$ encompasses 0.0 then $\ln\lambda$ is not significantly different from zero.

Since stochastic models exhibit weak ergodicity, i.e. the initial population structure has a major influence on the outcome of stochastic models in the early stages of simulation (Tuljapurkar and Orzack 1980), estimates of population growth rate from these periods may not be true long-term rates. It is not until the transient effects of the initial stage distribution are eliminated that true growth rates obtained. However, the main interest here was on the likely future of the field populations so the extinction probability simulations were run using the initial stage distribution as the starting point. To obtain

true long-term population growth rates, transient effects are eliminated by using an arbitrary initial population with many iterations of the model (usually > 1000 iterations).

RESULTS

The results of all models were similar in terms of the general direction and magnitude of changes in the size of the saltbush population. I will therefore concentrate on the results from the yearly stochastic model (Table 6.1). There was a trend of declining saltbush populations on grazed plots ($\ln\lambda < 0$) near the water point (e.g. sites A, B, D, E, F and H, with the lowest annual $\ln\lambda$ being -0.23 on plot E1) but at more distant sites the populations were either stable ($\ln\lambda = 0$) or slowly growing ($\ln\lambda > 0$; highest $\ln\lambda$ was 0.06 on plot I1). Most of the grazed populations within 2200 m of water which declined over the 100 years of simulations had a high probability (normally 100%) of becoming extinct in this time (Table 6.1). As expected, for grazed plots close to the water extinction was rapid, occurring in as little as 11-15 years, but at certain plots at intermediate distances from water time to extinction was as long as 90 years, depending on the model. No populations on plots greater than 2200 m from water became extinct.

The trends on the exclosed plots varied spatially, depending on distance from water, in much the same manner as the grazed plots. Many of those closer to water recorded negative growth rates and although they were declining at a slower rate than the matching grazed plots, they still were certain (i.e. they had a 100% probability) of becoming extinct within the projection period of 100 years. Several others had some chance (28-92%) of surviving the 100 years, despite negative population growth rates. However, the length of time to extinction for the exclosed plots was generally greater than for the corresponding grazed plots, consistent with the slower rate of decline. Other exclosed plots at intermediate distances from water (e.g. sites A, F and H) and those further away from water (sites G and I) had 100% chance of surviving for 100 years, since they had positive growth rates, growth rates close to zero or had very slow rates of decline.

Table 6.1. Results from the yearly stochastic model. Estimated population growth rate (expressed as $\ln\lambda$), extinction probability and the number of years to extinction for saltbush on ungrazed and grazed plots at nine sites in Yanaby. The values are means of 25 runs of the model, which used four types of good and poor years and was run for 100 years. S.D. of $\ln\lambda$ estimates is shown. The percentage of runs going to extinction gives the extinction probability. Sites are arranged in order of increasing distance from water.

Site	Plot	$\ln\lambda$	S.D.	extinction probability (%)	years to extinction
E	ungrazed	-0.0532	0.0078	100	64
	grazed (E1)	-0.2350	0.0498	100	12
	grazed (E3)	-0.1023	0.0049	100	29
B	ungrazed	-0.0364	0.0076	72	79
	grazed (B1)	-0.0935	0.0085	100	34
	grazed (B2)	-0.1049	0.0117	100	30
C	ungrazed	-0.0249	0.0032	8	97
	grazed (C1)	-0.0805	0.0013	100	47
	grazed (C3)	0.0045	0.0096	0	
F	ungrazed	-0.0256	0.0013	0	
	grazed (F1)	-0.0627	0.0063	100	66
	grazed (F3)	-0.0895	0.0072	100	43
A	ungrazed	0.0138	0.0031	0	
	grazed (A1)	-0.1071	0.0092	100	36
	grazed (A3)	-0.0966	0.0092	100	43
D	ungrazed	-0.0458	0.0045	100	64
	grazed (D2)	-0.0352	0.0028	100	81
	grazed (D3)	-0.1992	0.0049	100	15
H	ungrazed	0.0402	0.0052	0	
	grazed (H1)	-0.1342	0.0093	100	27
	grazed (H3)	-0.0800	0.0090	100	42
G	ungrazed	0.0390	0.0029	0	
	grazed (G1)	-0.0009	0.0043	0	
	grazed (G2)	0.0553	0.0006	0	
I	ungrazed	-0.0082	0.0045	0	
	grazed (I1)	0.0602	0.0054	0	
	grazed (I2)	0.0169	0.0032	0	

The results of these time-varying models suggest that the increases in recruitment and survival which were recorded during the study, were insufficient to compensate in the long term for the high levels of adult mortality which occurred on many of the heavily grazed plots. Interestingly, this also applies to many of the exclosures at sites which were closer to water and reflects the long-term effects grazing can have on the population dynamics of perennial arid zone species.

Surprisingly there were only minor differences in the results from the various model specifications. Although the population growth rates calculated from models with a projection interval of one year are not directly comparable with those from the model of the very poor summer (since the population growth rates in this model represent periods of six months), it is possible to compare extinction probabilities and extinction times between these models. As expected, allowing for the run of poor seasons in the model (Table 6.2) generally resulted in reduced probabilities of extinction and greater extinction times than the yearly stochastic model. This was because the frequency of high adult mortality was reduced due to the requirement for a run of poor seasons before the transition matrix representing a very poor summer was selected in the model. Both exclosed and grazed plots exhibited this response but the grazed plots still generally went to extinction. There were a few exceptions to this pattern, including where extinction time was shorter on the 'run of season' model or not substantially different between the models. These exceptions did not appear to be related to distance from water or grazing treatment and simply reflect the fact that some plots suffered greater adult mortality at times other than during the very poor summer in 1988-89.

There also were differences, although not consistent ones, between the rainfall models and the stochastic models. Generally the rainfall models (Table 6.3) resulted in a marginally lower $\ln\lambda$ for most plots and consequently extinction times were shorter than for the stochastic models, although the reasons for this are not clear. In most cases population growth rates in the rainfall models were significantly different from zero at the

Table 6.2. Results from the seasonal stochastic model. Estimated population growth rate (expressed as $\ln\lambda$), extinction probability and the number of years to extinction for saltbush on ungrazed and grazed plots at nine sites in Yanaby. The values are means of 25 runs of the model, which used a 'very poor summer' transition matrix when the three previous seasons were poor. The model was run for 100 years (200 iterations). S.D. of $\ln\lambda$ estimates is shown. The percentage of runs going to extinction gives the extinction probability. Sites are arranged in order of increasing distance from water.

Site	Plot	$\ln\lambda$	S.D.	Extinction probability (%)	Years to extinction
E	Ungrazed	-0.0219	0.0056	92	75
	Grazed (E1)	-0.1071	0.0262	100	13
	Grazed (E3)	-0.0427	0.0032	100	35
B	Ungrazed	-0.0185	0.0031	92	82
	Grazed (B1)	-0.0434	0.0104	100	37
	Grazed (B2)	-0.0535	0.0069	100	30
C	Ungrazed	-0.0079	0.0024	0	
	Grazed (C1)	-0.0392	0.0006	100	48
	Grazed (C3)	0.0055	0.0045	0	
F	Ungrazed	-0.0107	0.0009	0	
	Grazed (F1)	-0.0271	0.0036	100	76
	Grazed (F3)	-0.0386	0.0062	100	50
A	Ungrazed	0.0071	0.0016	0	
	Grazed (A1)	-0.0510	0.0058	100	36
	Grazed (A3)	-0.0480	0.0051	100	43
D	Ungrazed	-0.0346	0.0048	100	42
	Grazed (D2)	-0.0151	0.0020	80	90
	Grazed (D3)	-0.1002	0.0039	100	15
H	Ungrazed	0.0190	0.0017	0	
	Grazed (H1)	-0.0652	0.0061	100	27
	Grazed (H3)	-0.0394	0.0039	100	42
G	Ungrazed	0.0216	0.0012	0	
	Grazed (G1)	-0.0006	0.0016	0	
	Grazed (G2)	0.0279	0.0003	0	
I	Ungrazed	-0.0057	0.0017	0	
	Grazed (I1)	0.0319	0.0020	0	
	Grazed (I2)	0.0103	0.0012	0	

Table 6.3. Rate of population increase ($\ln \lambda$), 95 % confidence intervals for $\ln \lambda$ and years to extinction for the yearly and seasonal (incorporating a transition matrix for a very poor summer) time-varying models based on the Iron Knob rainfall sequence. Sites are arranged in order of increasing distance from water. Plots without a time to extinction did not become extinct within the projection period of 83 years. See text for further explanation. * indicates $\ln \lambda$ is significantly different from zero.

Site	Plot	Yearly			Seasonal (with v. poor summer)		
		$\ln \lambda$	95 % C.I.	years	$\ln \lambda$	95 %	years
E	Ungrazed	-0.0642*	± 0.0284	52	-0.0324*	± 0.0215	52.5
	Grazed (E3)	-0.2287*	± 0.0943	11	-0.1055*	± 0.0398	11.5
	Grazed (E3)	-0.0941*	± 0.0155	31	-0.0408*	± 0.0068	35.5
B	Ungrazed	-0.0462*	± 0.0182	64	-0.0240*	± 0.0196	64
	Grazed (B1)	-0.1065*	± 0.0286	30	-0.0527*	± 0.0168	29
	Grazed (B2)	-0.1140*	± 0.0312	27	-0.0563*	± 0.0131	27.5
C	Ungrazed	-0.0247*	± 0.0118		-0.0100*	± 0.0086	
	Grazed (C1)	-0.0794*	± 0.0029	48	-0.0392*	± 0.0024	48
	Grazed (C3)	0.0087	± 0.0272		0.0058	± 0.0127	
F	Ungrazed	-0.0243*	± 0.0176		-0.0107*	± 0.0086	
	Grazed (F1)	-0.0710*	± 0.0082	58	-0.0321*	± 0.0055	63
	Grazed (F3)	-0.1068*	± 0.0144	35	-0.0536*	± 0.0154	35
A	Ungrazed	0.0104	± 0.0181		0.0058	± 0.0101	
	Grazed (A1)	-0.1303*	± 0.0271	29	-0.0604*	± 0.0161	29
	Grazed (A3)	-0.1247*	± 0.0343	32	-0.0639*	± 0.0211	31
D	Ungrazed	-0.0419*	± 0.0085	71	-0.0293*	± 0.0077	49.5
	Grazed (D2)	-0.0338*	± 0.0172		-0.0162	± 0.0178	
	Grazed (D3)	-0.2061*	± 0.0377	15	-0.1040*	± 0.0365	14.5
H	Ungrazed	0.0429*	± 0.0245		0.0215*	± 0.0164	
	Grazed (H1)	-0.1418*	± 0.0104	25	-0.0716*	± 0.0126	24.5
	Grazed (H3)	-0.0994*	± 0.0339	33	-0.0509*	± 0.0288	31.5
G	Ungrazed	0.0411*	± 0.0141		0.0233*	± 0.0172	
	Grazed (G1)	-0.0021	± 0.0203		-0.0011	± 0.0154	
	Grazed (G2)	0.0548*	± 0.0173		0.0272*	± 0.0117	
I	Ungrazed	-0.0097	± 0.0186		-0.0072	± 0.0147	
	Grazed (I1)	0.0587*	± 0.0286		0.0305*	± 0.0185	
	Grazed (I2)	0.0157	± 0.0282		0.0091	± 0.0141	

5% level (Table 6.3), including a number of the lightly grazed plots which had positive population growth rates (e.g. plots at site G).

The population growth rates generated by the time-varying models were not substantially different to those from the time-invariant models in Chapter 5 (compare Tables 5.7 and 6.1). Growth rates tended to be slightly lower in the stochastic model than the time-invariant model, but for only two plots were there differences between the two models in the direction of population changes. The exclosed population at site B was declining according to the stochastic model but was growing slowly judging from the time-invariant model. In contrast, plot C3 (a grazed plot) returned a slightly positive growth rate in the yearly stochastic model but a negative rate in the time-invariant model.

DISCUSSION

General Discussion of Results

It should be recognised from the outset that the models presented here utilised, in some cases, transition matrices derived from observations of as few as twenty individual plants, over only a few seasons. This problem of small sample sizes was overcome in the time-invariant matrices presented in Chapter 5 by pooling transition frequencies over the entire study period. However, in order to have an adequate number of matrices for the time-varying models pooling was necessarily restricted so that sample sizes were lower than what would normally be considered desirable for accuracy and minimal error.

Nonetheless, in view of the difficulty of collecting large amounts of detailed demographic data for long-lived species, it was considered worthwhile examining the data in greater detail by these simulations, until more extensive data are available.

The time-varying projections confirm the conclusions from the deterministic models. The results suggest that in the long-term saltbush populations will continue to decline under constant stocking pressure over large areas of the paddock and that fluctuations in

demographic rates, particularly recruitment and mortality, do not prevent this decline. Indeed the models indicate that grazing will lead to local extinction of the saltbush population in much of the paddock over the long term. This would occur most rapidly near water and more slowly further away, but still with certainty at sites up to approximately 2000-2500 metres away from the water point. As we have seen in Chapter 5, this decline will result from reduced recruitment and increased adult mortality.

Clearly the use of stochastic models provides valuable insights into the likely future behaviour of a population growing in a stochastic environment where the transition probabilities vary over time. This makes them useful tools for studies such as population viability analysis in fluctuating environments (e.g. Menges 1990). Obviously the accuracy and realism of these models will depend on the range demographic rates used as the basis for a model, and these are affected by the conditions prevailing during field studies. Therefore these models essentially reflect past conditions, so using them to examine future behaviour assumes that the transition matrices include the full range of possible conditions and year/season types. The period during which my field observations were carried out encompassed a good range of seasons, including some when rainfall was poor (below decile 5) and others when rainfall was excellent (equal to decile 10). Increased mortality, particularly of grazed adults, was generally associated with a poor summer while during good seasons mortality rates declined and on many plots recruitment increased. However, the higher levels of recruitment were not sufficient to compensate for the high levels of mortality on many grazed plots, as indicated by the continued population decline suggested by the models. Therefore, despite having a wide range of seasonal conditions in my study the populations were projected to decline further and become locally extinct.

On the assumption that these trends are real, how do grazing and climate contribute to such temporal trends? We have seen in Chapter 5 that recruitment and adult survival are affected by grazing, but to understand the behaviour of a population in a fluctuating

environment an appreciation of both the nature and scale of environmental variability and the population biology of the species involved is needed. These factors are important in determining the future behaviour of a population and the likelihood of extinction (Kalisz and McPeck 1993), and aspects of these factors will be discussed below.

Role of Recruitment in a Stochastic Environment

Although the elasticity analysis presented in the previous chapter showed that recruitment makes only a small contribution to the population growth rate of saltbush, recruitment may have an important role in stabilising population growth in a stochastic environment. Stochastic fluctuations in demographic rates can have a destabilising effect on population growth and reduce $\ln \lambda$ (Boyce 1977, Tuljapurkar and Orzack 1980, Smith and Trout 1994), as well as increase the probability of random extinction (Tuljapurkar and Orzack 1980, Gotelli 1991). Stochastic conditions can lead to extinction even when the expected growth of the population is high (Tuljapurkar and Orzack 1980, Caswell 1989).

However, constant recruitment in populations growing in unpredictable conditions can stabilise population growth and reduce the probability of extinction. Even though many seedlings might die naturally, if there is always a probability of some individuals surviving through to the final stage or size-class in all environments then continual recruitment can reduce the likelihood of chance extinction (Tuljapurkar and Orzack 1980, Gotelli 1991).

Recruitment of saltbush during my study was essentially continual on plots well away from water despite a wide range of climatic conditions, although the number of recruits appearing at each census did fluctuate considerably.¹ This is supported by a number of other studies which have reported that recruitment in saltbush is constant but the size of cohorts can vary, mainly in response to rainfall (Crisp 1978, Eldridge and Westoby 1991). Therefore it is possible that recruitment has an important role in the long-term by contributing to the stability of population growth at sites furthest from water where there

¹See Chapter 5.

is little grazing. This suggests the ability to maintain some recruitment in most years may be another adaptation to the unpredictability of rainfall, in addition to the high tolerance of adults to moisture stress. It is consistent with Noble's (1986a) assertion that the ready availability of young plants as a regenerative bank is important in the maintenance of the population in the long term.

In contrast to the lightly grazed sites, recruitment was much more infrequent and more episodic on moderately grazed sites, and virtually non-existent on the most heavily grazed sites. Through this episodic recruitment grazing will destabilise population growth and make the population more sensitive to environmental fluctuations that normally might have few long-term consequences, even if high levels of recruitment were occasionally achieved at these sites. Thus the population will be more prone to extinction under fluctuating conditions. This may also partly explain the projected extinction of the population on the exclosures at sites B and E despite these plots recording moderate increases in the number of shrubs at times during the study. Therefore the ability to maintain some level of recruitment at most times would seem a useful strategy for certain perennial plant species in a stochastic environment.

Importance of the Sequence of Seasons

Obviously the frequency of good and poor seasons will be important in determining the behaviour of a population, but autocorrelation between year/season types can also have long-term ramifications for a population. Kalisz and McPeck (1993) reported that higher levels of positive autocorrelation between the conditions in consecutive years can result in more rapid extinction in populations of annuals because of the negative effects of a string of poor seasons. My field observations showed that the sequence of season types was important in determining the level of adult mortality in saltbush at heavily grazed sites. Increased mortality was associated with a poor summer which was preceded by two poor seasons, a poor winter and a poor summer. In other poor summers, increased rates of adult mortality were not recorded, which suggests that mortality was only increased under

grazing following a sequence of poor seasons. The models which selected the transition matrix for a poor summer based on the conditions in the previous seasons attempted to simulate these patterns.

The sequence of seasons may also be important to achieve high levels of recruitment under grazing. Increased recruitment was recorded later in the study after a few seasons with good rainfall, although by comparing recruitment between plots which had never been heavily grazed and plots that had, it is clear that grazed plots never achieved the higher levels of recruitment possible on many ungrazed plots. This suggests that a run of good years will be necessary for further improvement in numbers through recruitment and the replacement of the shrubs which died during the dry period because of grazing. However, there is no data to indicate whether this would occur, particularly if grazing of the shrubs continues, or what effect there would be on the population. This suggests a potential limitation in my projections, since such recruitment might reverse the trend of declining populations. Nevertheless, as I have already pointed out, irregular recruitment is likely to increase the probability of local extinction.

In the short term, the inability of the populations to respond rapidly during good seasons may be a consequence of reduced plant vigour following heavy grazing and poor seasonal conditions, as was discussed in the previous chapter, so that a run of good seasons is needed for plant vigour to recover sufficiently for reproduction to occur. This will limit the benefits to the population of a solitary good season. However, in the longer term recovery of plant density might be limited by a low intrinsic rate of increase ($r_{\max}$) for the species, which would be consistent with the normal long-term stability of saltbush populations (i.e. $\lambda=1$ or $r=0$). Since saltbush possesses a stress-tolerant life-history strategy¹ it is mainly adapted to coping with fluctuations in moisture availability through the ability of established shrubs to survive moisture stress, with only a small contribution to the population growth rate from recruitment. The intrinsic rate of increase of the

¹As discussed in Chapter 5.

species is likely to be inherently low since, when the population is undisturbed and stable, high rates of increase are unnecessary so reproductive effort is restricted (Grime 1977). Thus when there is increased mortality under grazing the ability of saltbush to rapidly regenerate is limited, so recovery is slow. Therefore grazing increases the importance and influence of the run of season types for saltbush populations. This can have important implications for the management of these shrublands, which will be discussed in Chapter 8.

Although there was no evidence of significant autocorrelation¹ in the six monthly rainfall data, the generally greater rates of decline indicated in the rainfall models compared to the stochastic models may be due to a more frequent occurrence of runs of poor seasons by chance than in the stochastic models. Of course a lack of autocorrelation in rainfall does not necessarily mean that there is no autocorrelation in demographic rates between successive periods, as indicated by the residual effects of grazing on behaviour of the population at some sites.

Large Events and Co-occurrence of Events

Many recent reports have discussed the importance of large events in bringing about major changes in vegetation composition in rangelands, with unusually high rainfall or extremely long dry periods being most mentioned (Griffin and Friedel 1985, Neilson 1986, Westoby 1988), while Noble (1986b) stressed the importance of the fortuitous co-occurrence of several events. Noble (1986b) used the example of western myall trees (*Acacia papyrocarpa*), which require good initial rains, follow-up rains, freedom from herbivory and reduced competition to successfully establish. Large events of this nature could result in alterations to the saltbush populations which are independent of grazing or would over-ride the effects of grazing. I found no evidence in my field study to suggest that large infrequent events are important in saltbush dynamics, particularly for ungrazed

¹Examined with the autocorrelation procedure in Statistix 3.1. (Analytical Software 1991), and using 95% confidence limits.

populations. On their own, both heavy rains and a drought year of moderate severity had little lasting effect on the saltbush populations. Heavy rains resulted in higher recruitment but subsequent mortality of many seedlings negated the effects of the large recruitment, as has been reported by Eldridge and Westoby (1991). However, the co-occurrence of drought and severe grazing was instrumental in bringing about reductions in saltbush density. The possibility remains however, that by itself, a more severe drought than the one during this study could be important to saltbush dynamics. Crisp (1975) and Westoby *et al.* (1989) suggested that high saltbush mortality can occur in droughts of severity of the order of 1-4 events per century. If such events are important it will be necessary to incorporate their effects into population models.

Overall it seems that large events on their own are not particularly important to ungrazed stable populations of saltbush and are not consistent with the species' continual recruitment strategy. In comparison, however, successful recruitment and establishment of bluebush (*Maireana sedifolia*) seedlings, a species which often is co-dominant with saltbush but has a longevity up to five times greater than saltbush, is episodic and requires a run of years of heavy rainfall to initiate flowering, seed production, germination and establishment and the availability of safe sites irrespective of grazing (Wotton 1993). This demonstrates the diversity of life-history strategies that occurs within the perennial growth-form of arid zone plants (Westoby 1980).

Validity of Models

Validation of the models presented here is not possible in the normal sense, partly because of the limited data available and also because the aim was not to predict actual population size but to examine trends in the populations. However, the projected decline and local extinction of the saltbush population at many sites in the paddock is of serious concern and has important implications for management of shrublands, so it is important that the validity of the results be considered.

As already mentioned, the details of the results from the models discussed here may be limited by the restricted sample size on a number of heavily grazed plots, the use of only two replicates at each site for the grazed treatment and no proper replication of the exclosed treatment. However, the predictions for heavily grazed plots with higher sample numbers indicated a similar long-term decline in the population, supporting the general trends at more heavily grazed sites.

Another limitation may be the short time that data was collected; while 6.5 years is long in comparison to many demographic studies and my study did include a wide range of seasons, there remains a lack of knowledge on the distribution of demographic year types. Further long-term studies will be needed to address this problem. In particular the effects on demographic rates, especially recruitment, of excellent seasons or very high rainfall following average or good seasons, rather than following poor seasons as in this study, is lacking. However, the likelihood that this would occur could be limited because very high rainfalls are often associated with the end of a cycle in the El Niño-Southern Oscillation (Nicholls 1991). This phenomenon is important in causing drought in much of Australia, so these rains may invariably follow dry periods (although the influence of the Southern Oscillation on climatic patterns is not as strong in South Australia as in the eastern parts of Australia).

A number of other limitations were apparent in the matrix models. They assumed linearity between demographic processes, i.e. transition rates within a matrix were all affected to the same degree by changes in environmental conditions. This is clearly a simplification, since many processes would respond in a curvilinear manner. Often there were not discrete boundaries between season types in the transition matrices and fluctuations in rainfall and transitions did not always correspond because of lagged effects, although this would be of no significance in the stochastic models because each matrix had an equal probability of occurring.

Despite these limitations I believe the models provide an accurate assessment and an improved understanding of the long-term consequences for saltbush populations of continuous grazing by sheep.

Further Work

Apart from addressing the limitations specified above, further work is required to more accurately predict the actual changes in saltbush population size under grazing. The incorporation of the effects of density dependence on recruitment, survival and growth of seedlings into population models will be an important aspect of this, since my models predicted unrealistically high plant abundances at many sites where recruitment was high. For example, maximum population sizes for the plots that did not become extinct in the yearly model ranged from realistic figures of 52-110 plants to an extreme of 62,266. However, to date there has been no work to examine the issue of density dependence in saltbush. In addition, the theory for incorporating density dependence into matrix population models is only poorly developed (Caswell 1989). A further limitation is the effect of spatial heterogeneity on the strength of density dependence, due to local variation in density and other environmental factors (Bierzychudek 1982). If density dependence does operate then greater rates of population increase at lower densities may also be expected once plant vigour has recovered and flowering and seed production occurs. Some evidence that density dependence operates in saltbush was apparent in the increased survival of seedlings on exclosures near the water point where adult density was reduced.

Demographic stochasticity is also likely to be important for populations where density has been markedly reduced, since the chance application of vital rates to a few individuals will have a large effect. This will be particularly important if the population is approaching extinction, so this factor should also be included in future models. Demographic stochasticity will have little impact on healthy populations though, because of the greater abundance of individuals.

The probability of local extinction and the ability of the population to recover from high mortality of established plants may depend on the size and longevity of the seed bank. An abundant supply of seed may protect against local extinction because dead plants are more likely to be quickly replaced by seedlings once favourable conditions return. The role and dynamics of the seed bank should be considered in the development of future matrix models and these models should include a seed stage in the population vector. Previously there has been little information on saltbush seed banks and the effects of grazing, but these issues are examined in the next chapter.

CONCLUSIONS

- Population growth rates derived from a simulation of fluctuating conditions confirmed that saltbush populations at many sites in the study paddock were declining due to the effects of sheep grazing.
- The simulations suggested temporal variation in demographic rates due to fluctuations in rainfall are not likely to result in long-term stability of these populations. Reductions in plant density due to heavy grazing in extended dry periods are unlikely to be fully offset by recruitment during better periods. Extremely good seasons, however, may lead to some recovery.
- There is a strong possibility that the decline in the saltbush population at sites up to 2200 m from the water point in Yanaby will result in local extinction of the populations. The models suggest this may occur in as little as 10 years at sites closer to water and up to 90 years for the more distant sites.
- This long-term decline under grazing is in part due to the limited ability of saltbush populations to recover from the loss of large numbers of established shrubs by the recruitment of new plants. A run of years with good rainfall appears to be necessary for

substantial recruitment to occur under grazing.

- Because a few seedlings appear in most years on ungrazed sites recruitment has an important role in stabilising population growth in these populations, although the contribution it makes to the population growth rate is small.

CHAPTER 7

FLOWERING AND ASPECTS OF SEED BANK DYNAMICS UNDER GRAZING

INTRODUCTION

Background

Flowering and Seed Production

Flowering in arid zone plants is chiefly controlled by soil moisture availability (Beatley 1974, Mott 1979, Evans *et al.* 1991). Thus flowering of perennial species occurs mostly in response to rainfall, although some deep-rooted tree and shrub species which have access to moisture deep in the soil profile can flower in periods of no rain (Maconochie and Lange 1970, Davies 1976). Because rainfall is unpredictable in these areas, flowering in many species is opportunistic, occurring at any time of the year following sufficient rainfall (Mott 1979, Wotton 1993). Unlike in many species from mesic environments, temperature and photoperiod generally are unimportant or have a secondary role in controlling flowering times and events in arid zone perennial, and also many annual, species (Mott 1979).

The size of flowering event (i.e. number of flowers produced per plant) and resulting seed production are often directly related to the amount of rainfall received (Mott 1979, Marshall *et al.* 1986, Dye and Walker 1987, O'Connor 1991). Reduced moisture availability will decrease flower and seed production and in extremely dry years flowering may be completely inhibited (Davies 1976, Beatley 1974, Mott 1979). In addition to fewer seeds being produced, seed size may be reduced under conditions of moisture stress (Marshall *et al.* 1986). Seeds developed under such conditions have been found to have significantly lower germination percentages (Mott 1979, Hendrix and Trapp 1992) and smaller seeds are likely to have a reduced ability to successfully establish seedlings because emergence is delayed and the seedlings are less competitive (Hendrix and Trapp 1992). The consequences of these changes could be expected to be most

severe in an adverse environment such as the arid zone, where the period of favourable moisture conditions is normally short.

Seed Banks

Since the availability of seed when conditions are favourable for germination and establishment (e.g. the availability of a vacant space with appropriate seed bed conditions, suitable conditions of moisture temperature and freedom from predators) is important for population persistence (O'Connor 1991), some species develop seed banks to mitigate the effects of fluctuations in seed production (Cohen 1966, 1967). Seed banks can also have an important regenerative role, acting as protection against adverse environmental perturbations which may threaten the survival of established plants. Therefore the existence of a seed bank can enhance the long-term survival of a species. For example, using matrix population models Kalisz and McPeck (1993) have demonstrated how a persistent seed bank can reduce the probability of local extinction of an annual species in a variable environment.

Annual and ephemeral species are particularly reliant on seed banks so they normally have large soil seed pools (Parker *et al.* 1989). Perennial plants, on the other hand, generally do not form large persistent seed banks because of the longevity of established plants and their ability to withstand environmental fluctuations (Harper 1977, Kemp 1989, O'Connor 1991), although this is not always the case (Parker *et al.* 1989). An example of this is where catastrophic disturbance, such as fire, is a feature of the environment. The seed banks of perennial species tend to be more transient and often seed will germinate or die soon after release from the parent (O'Connor 1991).

Seed longevity varies considerably between species. It is primarily under genetic control (Begon *et al.* 1990) but it can be reduced by numerous environmental factors once the seed enters the seed bank. Loss of seeds from the seed bank occurs through germination, death (senescence), decay, predation, deep burial and dispersal to another site (Parker *et*

al. 1989, O'Connor 1991). Germination is usually initiated immediately upon imbibition of the seed but many species possess some form of dormancy mechanism to regulate germination. Dormancy acts to delay germination until conditions are favourable for the establishment of seedlings, and to spread the risk associated with fluctuations in the environment. Three main types of dormancy are commonly recognised (Harper 1977):

- 1) Innate dormancy, where the seed has an absolute requirement for a specific stimulus, often involving seasonal stimuli such as moisture, temperature and photoperiod for dormancy to be broken;
- 2) Enforced dormancy, imposed by an external stimulus such as a lack of adequate moisture, darkness or low temperature, and persisting only while the seed is exposed to those conditions;
- 3) Induced dormancy, produced by an external stimulus, but persisting after the stimulus has been removed, by causing a physiological change in the seed.

A gradual attrition of viable seed occurs through natural death or senescence of seeds. This can be caused by changes in the genetic material of seeds, including lesions and fragmentation of DNA, chemical changes related to enzyme action and excessive seed desiccation (Mayer and Poljakoff-Mayber 1989). Decay of seeds occurs through pathogenic infection (Janzen 1977), a process that can be accelerated by moist, warm conditions that favour fungal activity. Predation by mammals, birds and insects can cause significant losses of the seed of some species in certain ecosystems. Large seeds tend to suffer more severe predation than smaller ones, so that changes in the species composition of the seed bank results (Louda 1989). This can often favour annual species which tend to have smaller seed than perennial trees and shrubs. Ants are a common and important predator of seeds (Kemp 1989, Gordon 1993), particularly in Australian ecosystems (Morton 1985). However, seed predators can also facilitate seed dispersal since a fraction of the seeds collected by granivores may escape destruction (Buckley 1982). Many seeds possess eliasomes, specialised food appendages rich in energy, to encourage collection, and therefore dispersal, by ants since the seed itself is usually

discarded intact once the eliasome has been removed (Buckley 1982). Alternatively, ingestion and subsequent defecation of seed by large herbivores can distribute seed widely (Molinillo and Farji Brener 1993). Dispersal also may occur through the action of wind, water and the attachment of seeds with prickly or adhesive surfaces to animals. Deep burial by the digging activities of mammals or the caching of seed below ground by ants, may prevent germination or establishment (Drake 1981).

Herbivory Effects on Flower and Seed Production

Grazing may affect the flowering performance of plants through the consumption or damage of flowers by herbivores (Bergstrom and Danell 1987, Roundy and Ruyle 1989, O'Connor 1991), although the flowers of some plants are shunned by herbivores, or by altering allocation patterns in the plants by the removal of leaf tissue (Bilbrough and Richards 1993, Obeso 1993). This response involves a trade-off in resource allocation patterns between survival, reproduction and growth, where survival and recovery of leaf tissue after defoliation is of higher priority than reproduction (Marshall *et al.* 1986, Obeso 1993). Because of these priorities in the allocation of resources, reproduction is one of the demographic processes most sensitive to grazing, and is the first to suffer following the onset of grazing (Crawley 1983, Hodgkinson 1991). The response of the plant can be complete cessation of flowering, the delaying of flowering, the production of fewer flowers or the production of fewer or smaller seeds (Jameson 1963, Bosch and Dudzinski 1984, Crawley 1985, Maschinski and Whitham 1989, Milton 1994). As discussed above, smaller seeds have lower viability and are likely to have a reduced ability to successfully establish seedlings. Some plants are apparently able to compensate for tissue lost to herbivory by increasing rates of growth and/or flowering and seed production (Islam and Crawley 1983, Paige and Whitham 1987). These increases have been attributed to changes in plant architecture resulting in increased inflorescence production (Paige and Whitham 1987, Orr and Evenson 1991a). However, the issue of such over-compensation is the centre of much debate. Obeso (1993) suggested that when considered over the long term there is less evidence to support the case for over-

compensation in fecundity because of the delayed cost of reproduction.

Changes in flower production will alter input to the seed bank. Sustained heavy grazing can reduce or eliminate the seed bank of palatable species by reducing input to the seed bank (Kinucan and Smeins 1992, O'Connor and Pickett 1992). The implications of such changes for a population will depend greatly on the life history of the species, since this will determine the stages of the life cycle which are limiting in a species. For example, changes in reproductive performance may ultimately have little impact on recruitment and population size because the rates of processes later in the life-cycle may outweigh fluctuations in seed production levels. The seed bank is a part of the life cycle where the loss of genets is commonly high, so different levels of input or seed storage may be unimportant (Andersen 1989). However, reduced seed bank size can reduce the ability of perennial grass populations to tolerate severe environmental fluctuations and to regenerate after disturbance (O'Connor 1991, Coffin and Lauenroth 1992, Kinucan and Smeins 1992).

Flowering and Seed Banks in Saltbush

Little is known about the flowering behaviour of saltbush, and the information reported in the literature is mainly anecdotal. Flowering in saltbush can occur at any time of the year and is normally initiated by rainfall of 25-50 mm (Williams 1979, Briese 1982). Winter and spring rainfalls are reported to produce the best seed crop (Beadle 1952). Because of the opportunistic nature of flowering, it may occur once or several times a year or it may not occur for several years (Hall *et al.* 1964, Williams 1979, Briese 1982). The number of fruits/seeds produced appears to be related to the amount of rainfall, with more fruit being produced after heavier falls of rain, but actual seed production is unknown.¹ Once dry, the mature fruit are gradually shed from the parent plant; my observations suggest this normally begins about 6-8 weeks after flowering. The seed is

¹However, from several *ad hoc* estimates I suggest that a typical female bush 40 cm high, 45 cm long and 40 cm wide can produce approximately 2000-2500 fruits following good rains.

round and flattened, approximately 1.5-2.5 mm in diameter, and is normally retained in the papery bladder (false fruit) after being shed from the plant (Williams 1979).

Dispersal of the fruits is only over short distances of 1-2 m in 'healthy' stands of saltbush where plant density is high, and most collect under the canopy of the parent plant (Malik *et al.* 1976, Williams 1979). Occasional dispersal over distances of several kilometres may be effected by whirlwinds (Williams 1979).

Little also is known concerning the size or dynamics of the seed bank of saltbush although several studies have examined the role of ants in dispersal and predation of saltbush seed. Ants have been observed to consume up to 83% of the saltbush seed on the ground (Williams 1972, Briese 1982). Studies of the longevity of saltbush seed stored under laboratory conditions have found that it could survive up to 5-7 years (Burbidge 1945, Beadle 1952). The longevity of seed in the field has not been investigated but several anecdotal reports suggest saltbush seed can survive for 3-6 years (Knowles and Condon 1951, Hall *et al.* 1964). Williams (1979) suggested that saltbush produces both hard and soft seed but earlier Beadle (1952) reported that saltbush does not produce hard seed.

Aims

Grazing by sheep produced a spatial pattern in recruitment in Yanaby, with many sites recording negligible recruitment over the 6.5 years of the study. The population models presented in Chapter 6 suggested that the saltbush population at many of these sites was destined for local extinction. This was despite several periods with good rainfall.

Obviously some recruitment will be necessary to maintain the population in the long term so it is important to identify the specific reasons for poor recruitment under grazing, i.e. what population process or processes are being affected by grazing to bring about this lack of recruitment.

There are number of possible reasons for an absence of recruitment on many of the grazed plots including a lack of viable seed, a seed bed not suitable for germination and establishment of seedlings (i.e. availability of 'safe-sites' [Harper 1977]) or the destruction of seedlings after germination. The examination of the fate of seedlings in Chapter 5 provided some evidence that grazing was not significantly affecting the survival of seedlings, although seedling numbers at two heavily grazed sites were too low to be certain. Consequently, one aim of this study was to investigate whether a lack of seed due to the effects of grazing on flowering was the main cause of low recruitment.

Andrew and Lange (1986b) reported that the consumption of saltbush flowers by sheep had reduced the proportion of shrubs with flowers within 400-600 m of a new water point after 2.5 years of stocking, suggesting that a lack of seed may be an important factor limiting recruitment.

Related to the possibility that seed is lacking is the question of the longevity of seeds in the field. The persistence of seed for some time after a flowering event will be important in determining the ability of a population to withstand fluctuations in climate and the ability to regenerate after severe grazing, particularly if grazing reduces the frequency of flowering. The longevity of seed in the field is likely to differ from that stored in a laboratory because of factors such as fluctuations in rainfall and temperature, pathogens and seed predation, so it is important that longevity be assessed under field conditions.

Specific aims of work presented in this chapter therefore were:

- 1) to examine the effect of grazing on flowering of saltbush by quantifying spatial patterns in flowering over the paddock;
- 2) to quantify the size of the saltbush seed bank at various sites across the paddock and examine variation in seed bank size between years;
- 3) to examine the retention of viability by saltbush seed in the field.

METHODS

Experimental Methods

Flowering

During the first three years of the study the incidence of flowering was quantified by simply noting the presence of new or recent flowers (on both male and female plants) or fruits on the shrubs which were being used for the estimates of defoliation intensity (Chapter 4). This was done for both the grazed and exclosed treatments at each site on most occasions that the leaf tags were counted for the defoliation estimates. Flowering data was first collected in June 1988, although some minor flowering occurred prior to this date. Thus there were twenty shrubs per treatment per site for each of the nine sites, and shrubs were inspected at intervals of approximately six weeks. However, when flowering of shrubs was slight, data was not collected. Following the cessation of defoliation estimates in 1990 the incidence of flowering was noted during the collection of the demographic data (Chapter 5) for all adult shrubs that were measured and charted on each plot for the demographic studies. These records were taken at six monthly intervals, normally in April and October of each year, but again flowering data was only collected when a major flowering event occurred.

Estimation of the Seed Bank

Soil samples were collected from grazed areas in the vicinity of the experimental plots at five sites in Yanaby (sites A, C, E, F and G), chosen to represent a range of long-term grazing pressure (sites varied from 1130 to 2800 m from the water point). Because the majority of saltbush seeds remain clustered around the parent plant (Williams 1979) I sampled the seed bank in 1 m² quadrats centred on adult female saltbush shrubs. At sites E and F it was occasionally impossible to determine the sex of the shrubs, so it is not known whether some of the shrubs sampled were male or female. The shrubs were randomly selected from vegetation typical of the particular part of the paddock, with 3-5 shrubs being sampled at each site. After placing the quadrat around a shrub the soil surface was swept with a dustpan and broom and this litter and loose soil was collected

into paper bags. Approximately the top 10 mm of soil was then scraped from the surface with a trowel, keeping the soil from under the canopy of the shrub separate from the remainder of the quadrat. The second 10 mm depth of soil was also collected from the area under the canopy and bagged separately. Since saltbush does not possess a burial mechanism for its seed, and cracking of the soil surface is not common, sampling at a greater depth was not considered necessary. Care was needed to ensure that samples from one shrub were not contaminated with seed from another through seed and fruits remaining on the broom between samples. Samples were collected in late March or early April for three consecutive years, 1990-92, from a different set of shrubs each year. Thus the seed bank available for germination and establishment of seedlings in the following winter, the most favourable time for recruitment (Williams 1979), was assessed. On returning to the laboratory samples not processed immediately were spread out to ensure they were air-dry, since although samples were not collected when the soil surface was moist, a number of samples were slightly damp.

The accurate determination of the size of the soil seed banks is a difficult and time-consuming task, so in many demographic studies the seed bank stage of the life cycle is often ignored. The most common methods for the enumeration of the seed bank involve flotation, germination or elutriation techniques and numerous variations of these procedures have been tested. Flotation techniques involve the use of high density solutions to separate the lighter seed from heavier soil particles to facilitate counting of the seeds. Solutions of various salts such as K_2CO_3 are commonly used. Recent improvements to this method to improve the handling of small seeds include the use of centrifugation of the soil/seed suspension together with image analysis to rapidly count the seeds (Buhler and Maxwell 1993). Germination methods involve maintaining the soil samples under conditions of moisture, light and temperature known to be favourable to the germination of the seeds. However, this method can be slow and often requires a large amount of space in glasshouses or germination chambers. In addition it does not allow the identification of the dormant portion of the seed bank and requires prior

knowledge on the conditions necessary for germination of the species involved (Thompson and Grime 1979). Elutriation methods involve washing and sieving the soil sample through a series of sieves and manual counting of the seeds.

Because I was interested in the seed of only one species I initially attempted the flotation method for separating saltbush seed from the soil samples. I used a chlorinated hydrocarbon solvent, tetrachloroethylene, as the suspension agent, following the method of Carter *et al.* (1977). This has the advantage that solutions do not need to be prepared (it is readily available as dry cleaning fluid) and the high specific gravity (1.62) improves the separation of soiled seed and naked seed of large-seeded species (Carter *et al.* 1977). It was thought this would make it suitable for the large seed of saltbush. This solvent has also been shown not to affect the viability, nor establishment and early growth of several temperate pasture species (Carter *et al.* 1977). However, I found this method to be unreliable and slow, with a proportion of the organic matter, including some seeds, settling to the bottom of the solution rather than floating. Increased standing time did not increase the amount of material floating to the surface. Similar problems with this method have been reported for other suspension liquids, including lengthy standing times, the need for samples to be washed many times and unreliable results because of variation in the density of seeds (Gross 1990, Buhler and Maxwell 1993).

Because of the problems with the flotation method I settled on a form of elutriation. This method can also be laborious but it is particularly suited to species with large and easily identifiable seed (Gross 1990). My samples were dry sieved through a 2 mm mesh screen and then both the coarse and fine portions of the sample were wet sieved through a 600 μm mesh screen. Samples were then oven-dried at 60°C and were examined under an illuminated magnifying lens to manually separate the saltbush seed and fruits from the remaining soil and organic matter.

The accuracy of this method was tested by preparing six soil samples containing known

numbers of seeds and fruit and recovering them from the samples with the method described (the time-consuming and laborious nature of this method precluded more extensive testing). These test samples were prepared using soil from a long-established domestic garden in the arid zone with a soil type similar to that at the study site. It seemed a reasonable assumption that these soil samples were free of naturally occurring saltbush seed and fruit. Litter and twigs collected from around saltbush shrubs and hand sorted to ensure there were no seeds or fruits present was added to the soil samples to simulate a true sample. A quantity of seeds/fruits, known only to someone not involved in processing and sorting the samples, was then added to the samples and mixed. The seeds used in these samples were collected from under shrubs in the field and so were contained in fruiting bladders at various stages of weathering. These test samples showed that 80-93 % of seeds were being recovered with this method. No seeds were found in a sample to which no seeds had been added. As an additional check some of the actual field samples were sorted twice to locate any seeds or fruits missed on the first occasion. This confirmed the estimates of seed recovery from the test samples. For samples which were found to contain large amounts of seed in the first counting of seeds, no additional seed was recovered from 55 % of the re-examined samples. For the remaining 45 %, seed numbers increased by 4-15 % after re-checking the samples.

The seed bank data presented is the sum of the number of seeds recovered from the litter and the top 10 mm of soil, both from under the shrub and the surrounds within the 1 m² quadrat. The samples for the second 10 mm layer of soil were not included because in most cases they contained few seeds and the area of the quadrat over which these samples were collected varied depending on the spread of the canopy of the shrub.

Seed Longevity

The longevity of saltbush seed in two micro-environments in the field was investigated by placing parcels of seed in the field and recovering samples at regular intervals and testing the viability of the seeds. Fifty saltbush fruits were placed in each of 36 bags (9 cm × 9

cm) made from beige-coloured knitted shade-cloth (30% light transmission), and the bags were sown up. Shade-cloth was used instead of the usual 'nylon stocking' because the latter material has been shown to deteriorate considerably in less than two years of exposure in the field (Silcock and Smith 1990). In addition, light is reported to have no effect on the germination of saltbush seed (Burbidge 1945). Care was taken to ensure that the fruits were spread evenly inside the bags and were not clumped together. The bags were numbered and placed in the field at a lightly grazed site in Yanaby on April 2, 1991, with half being allocated to a 'canopy' treatment and the other half an exposed treatment. For the canopy treatment three bags were placed amongst the litter under the canopy of each of six established shrubs. The bags were secured to the ground with a single wire pin. The remaining 18 bags were spread out in a rectangular grid (3 m $\times$ 1 m) in an open, flat area and secured to the ground by covering them with wire netting which was then pinned to the ground. The fruit/seed samples used in this experiment were collected from this location the previous August. At that time the fruits had recently matured and were harvested directly from the shrubs. They were stored in air-tight jars in a darkened cupboard in an air-conditioned building, maintained mostly at 20-25°C, until the experiment began. The germination percentage of samples of the seed was determined when the bags were placed in the field. The excess seed not needed for the field treatments was stored in paper bags in the air-conditioned building during the experiment to act as a 'control' treatment.

Three bags from each treatment were randomly selected and retrieved from the field on each sampling occasion at 3, 6, 9, 12, 18 and 24 months after placement in the field. At collection any sign of germination and the general condition of the bags were noted. Upon returning to the laboratory the fruits were carefully removed from the bags, broken open to remove the seed and the fate of the seeds determined. Possible fates were germinated, ungerminated, decayed/dead or empty (i.e. the fruit never contained a seed). Seeds were classified as having germinated if they either showed some signs of radicle or cotyledon activity or an empty testa was all that remained, and shrunken black seeds were

considered dead. The ungerminated seed was divided into two portions and tested for viability. At these times samples from the laboratory stored seed were also taken (six replicates of 25 seeds), the seed excised from the bladder and the percentage fill recorded. These seeds were also tested for viability. As I did not have access to suitable germination facilities the germination tests were performed by the Seed Testing Laboratory of the South Australian Department of Primary Industries. Seeds were germinated on moist filter paper at 15°C with a 12 hours light:12 hours dark photoperiod (cool white fluorescent light) for 21 days, with counts being made each day and germinated seed being removed at counting. After 21 days seeds which had not germinated were classified as dead/decayed or dormant by dissecting the seed; those which remained plump and with a normal appearance to the embryo and endosperm were considered dormant. Thus, with this experimental procedure I was able to determine field germination, remaining germinable seed, dormant seed and dead seed on each sampling occasion, as well as estimate percentage fill.

Data Analysis

Flowering

Log-linear analysis was used to examine the effect of site (S) and grazing treatment (T) on the proportion of plants with and without flowers (F) at each sampling date. The first model fitted ST, SF, TF tested whether the three-way interaction between site, treatment and proportion with flowers was significant. If this model was rejected then the interaction was significant and no further analysis was performed for that sampling date. If the interaction was not significant the model ST, TF was fitted to test for the effect of site on the proportion of shrubs with flowers and the model ST, SF was fitted to test the effect of treatment on flowering. Simple linear regressions were calculated between the proportion of plants with flowers and distance from water.

Seed Bank

Because of the laborious nature of the method for processing each sample, the seed bank

could be quantified for only a limited number of sites. For this reason and because the number of seeds recovered from the seed bank was negligible at most sites, and at other sites the number was often many times greater, meaningful statistical analysis was not possible nor necessary. Consequently, only the mean seed number and standard error for each site for each year of sampling are presented.

Seed Longevity

The effect of treatment (i.e. canopy or exposed) on the fate of seed (i.e. germinated, germinable, dormant, dead) was examined with log-linear analysis. The control treatment was excluded from this analysis since it was clearly different from the two field treatments. As for the flowering data, the three-way interaction between treatment, time and fate was tested first (after adding 0.5 to each cell of the contingency table) and then separate models were fitted for each sampling date to test for an effect of treatment on fate. The percentage of viable seed (germinable plus dormant seed) remaining was further analysed to test whether it was affected by the treatment and the length of time in the field. An analysis of variance was performed on the percentage of viable seed after arc-sine transformation. Individual means were compared using a least significant difference test.

All analyses in this chapter were carried out using the Statistix 3.1 computer program (Analytical Software 1991).

RESULTS

Flowering

Flowering of lightly grazed or ungrazed saltbush occurred frequently in Yanaby during the course of the study (Figure 7.1), normally in response to rainfall of at least 30 mm. However, since there were long periods between data collection, especially in the last 3.5 years of the study, it is probable that some flowering events occurred which were not recorded. Also, given that minor flowering was not recorded, it is impossible to define

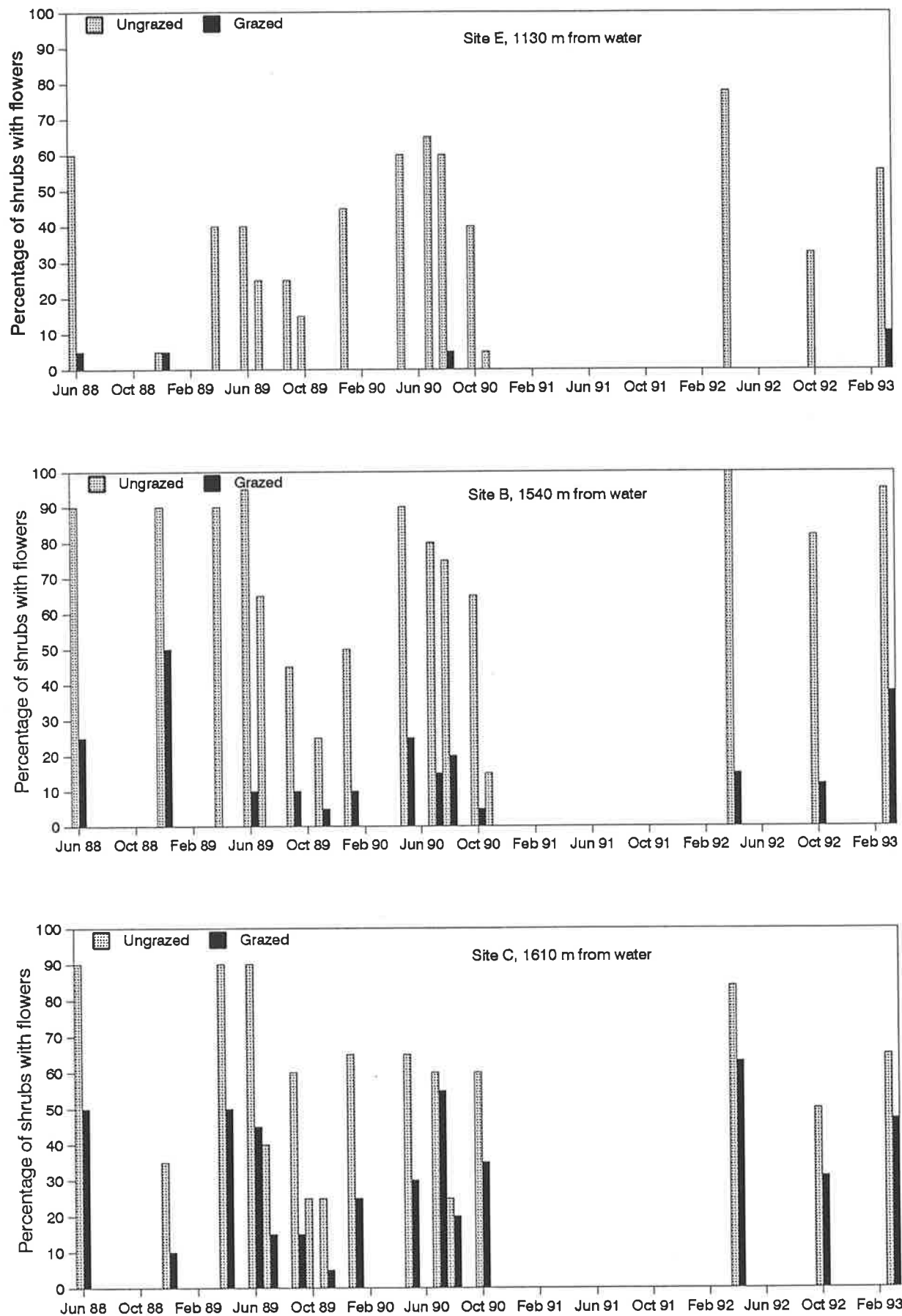


Fig. 7.1. The proportion of shrubs with flowers for grazed and exclosed plots at nine sites in Yanaby, on various sampling occasions. Graphs are arranged in order of increasing distance from water. The figure is continued on the following pages.

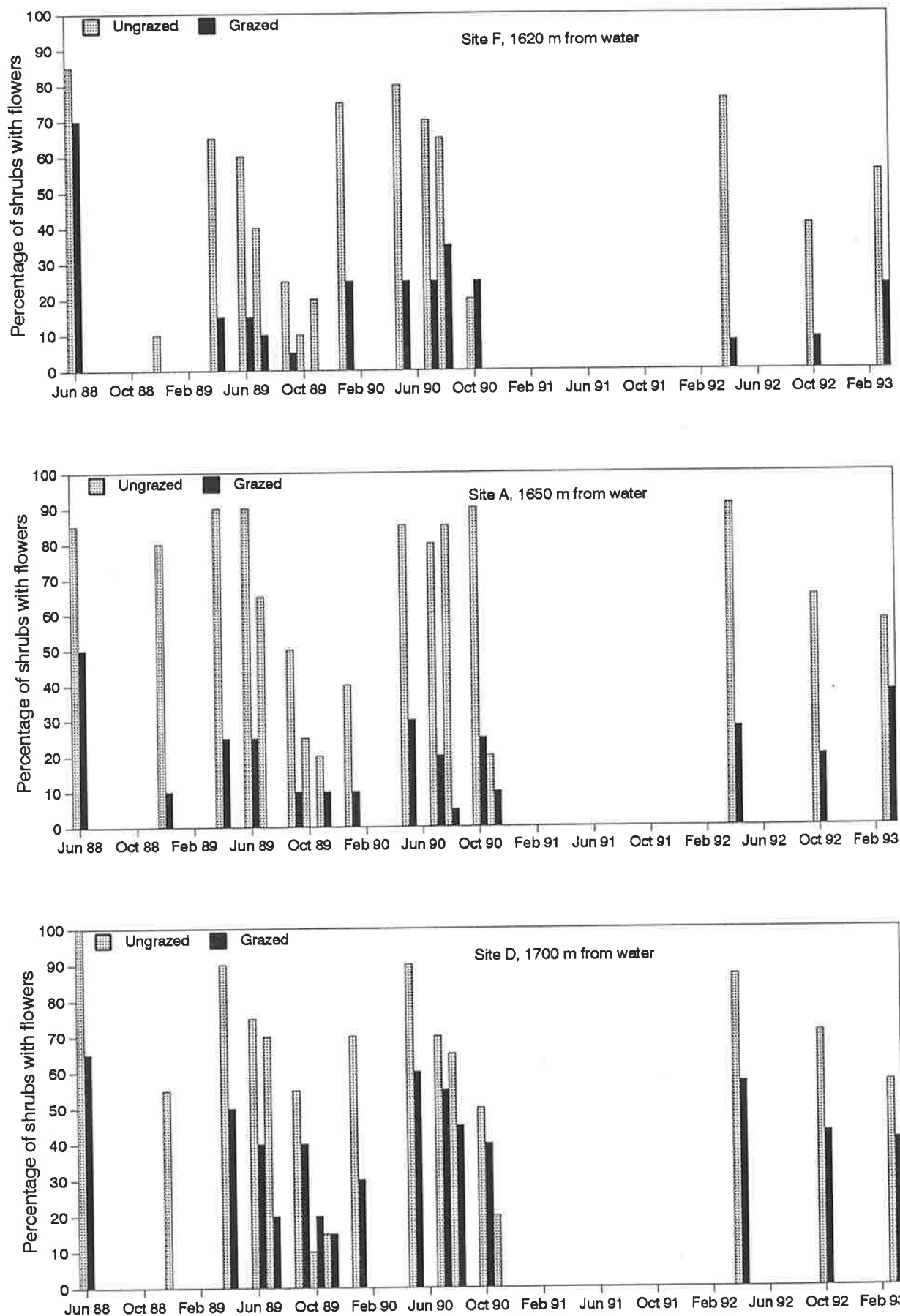


Fig. 7.1. (continued) The proportion of shrubs with flowers for grazed and exclosed plots at nine sites in Yanaby, on various sampling occasions. Graphs are arranged in order of increasing distance from water. The figure is continued on the following page.

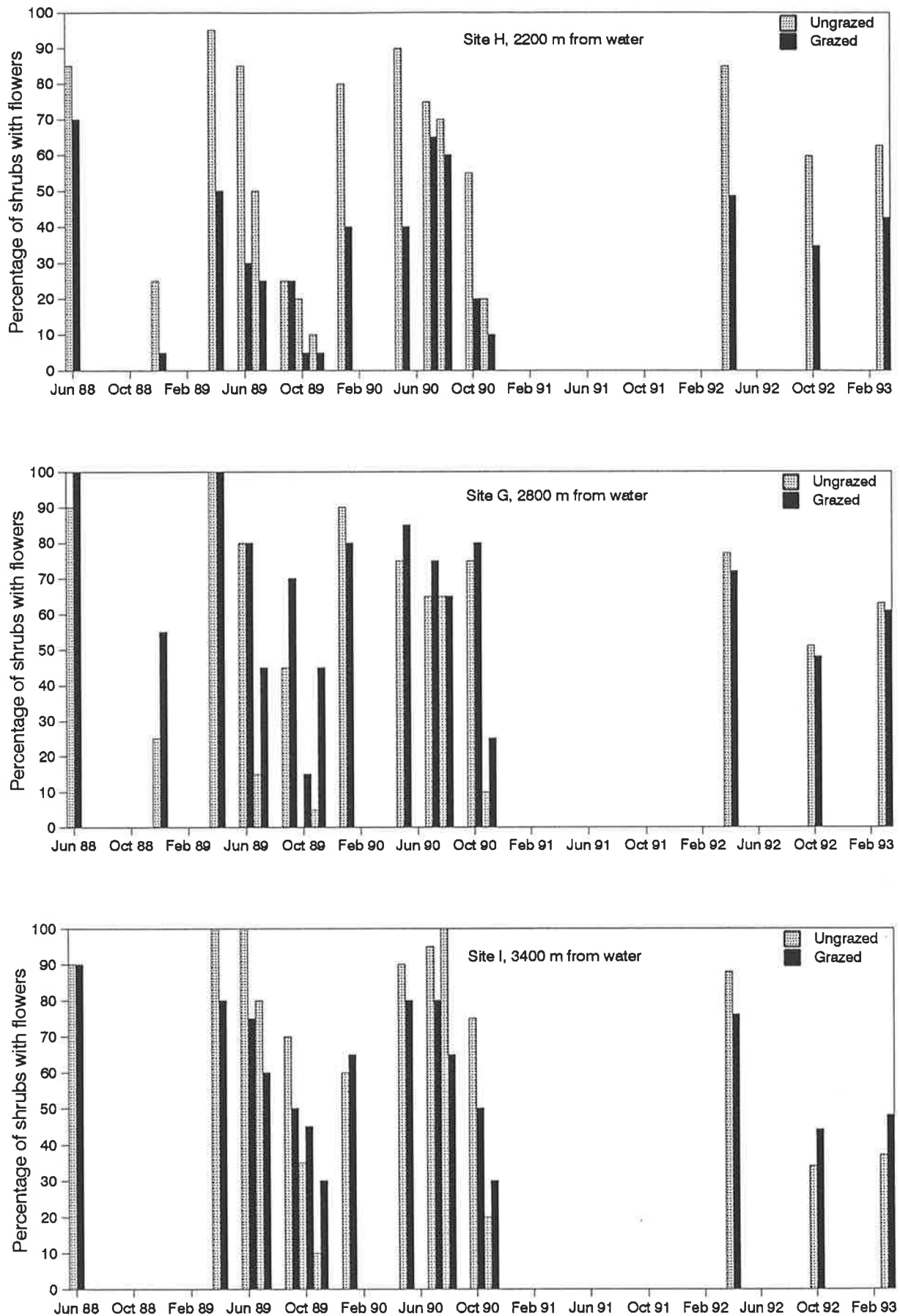


Fig. 7.1. (continued). The proportion of shrubs with flowers for grazed and exclosed plots at nine sites in Yanaby, on various sampling occasions. Graphs are arranged in order of increasing distance from water.

the true frequency and duration of flowering events. The data presented in Figure 7.1 therefore is not an entire record of the frequency of flowering. The fact that data is presented for a particular time reflects when shrubs were scored for flowering rather than the actual frequency of flowering. Nonetheless, from the data it would seem that saltbush flowered on a regular basis during the first three years of the study but the magnitude of the flowering events was variable over time.

Log-linear analysis of flowering showed that on most occasions the interaction between site, grazing treatment and the proportion of shrubs with flowers was significant (Table 7.1). By examining the raw data (Figure 7.1) it can be seen that the proportion of shrubs with flowers was consistently higher on both grazed and ungrazed plots at greater distances from water (with peak rates of 100% of shrubs with flowers) and at sites closer to water, exclosed plots recorded higher levels of flowering than grazed plots. At these sites there were occasions when no shrubs on grazed plots flowered, while 50-95% of shrubs on the corresponding exclosed plots did flower at these times (e.g. sites A, B, D and E during 1989 and site E during 1990). Therefore the frequency of flowering on grazed plots near water was much lower than at more lightly grazed sites. In particular, grazed plots at site E (the site closest to water) failed to flower to a substantial extent for the duration of the study. On most occasions the percentage of shrubs with flowers increased linearly with distance from water for the grazed plots but not the exclosed plots (Table 7.1). However, on the exclosed plot at site E, a smaller fraction of shrubs flowered than exclosed plots elsewhere on most occasions.

Seed Bank

Saltbush seeds found in the samples were of two types; plump brown seeds which were still contained in the papery bladder (in various states of decay) and 'free' seeds,¹ which were black and shrunken and contained little embryo tissue or endosperm. The black

¹The identity of these seeds could not be confirmed but it was assumed they were dead saltbush seeds, since a number of similar seeds were found in the samples from the field treatments in the seed longevity experiment, but none was found in the laboratory samples.

Table 7.1. Analysis of the proportion of saltbush shrubs with flowers on grazed and ungrazed plots at nine sites in Yanaby, on various sampling occasions. The log-linear analysis tests the site $\times$ grazing treatment $\times$ flowering interaction. If this was not significant, the site effect and grazing treatment effect were tested separately. $n=20$ for all but the last three sampling occasions, when n ranged from 10-67. The linear regressions describe the relationship between distance from water (in metres) and the percentage of shrubs in flower on the grazed plots at the nine sites (i.e. percentage in flower = $a + b \cdot [\text{distance}]$). On no occasion was a significant regression obtained for the ungrazed plots. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Date	Log-linear analysis		Linear regression		
	d.f.	G ²	a	b	R ²
Jun '88	8	22.01**	-9.27	0.034**	0.68
Dec '88	8	45.99***	-6.46	0.008	0.12
Apr '89	8	12.20	-38.90	0.041**	0.72
Site	16	144.05***			
Grazing treat.	9	118.90***			
Jun '89	8	21.38**	-30.79	0.034**	0.77
Jul '89	8	41.97***	-36.06***	0.028***	0.92
Aug '89	8	21.66**	-28.47	0.027**	0.69
Oct '89	8	26.92***	-25.59*	0.018**	0.70
Nov '89	8	25.81**	-21.27	0.017**	0.67
Jan '90	8	13.05	-34.15*	0.034***	0.83
Site	16	80.03***			
Grazing treat.	9	55.92***			
May '90	8	23.25**	-25.89	0.035**	0.78
Jul '90	8	32.31***	-24.30	0.034**	0.69
Aug '90	8	32.08***	-20.62	0.029**	0.71
Oct '90	8	28.53***	-17.96	0.025*	0.55
Nov '90	8	22.79**	-21.97**	0.015***	0.89
Apr '92	8	51.07***	-19.66	0.031*	0.59
Oct '92	8	37.45***	-9.18	0.018*	0.58
Mar '93	8	25.14**	11.21	0.014*	0.50

seeds were excluded from the results as they appeared to be dead, an observation which was supported by germination tests. The majority of seeds were recovered from the litter component of the samples.

The seed bank was highly variable in size, both spatially (across the paddock and between individual plants at a site) and temporally (across the three years), although the spatial pattern across the paddock was consistent between years (Figure 7.2). The number of seeds in the seed bank was negligible at three of the sites closer to water (sites A, E and F) for all three years. Site C (which was also a 'close' site at 1610 m) recorded a slightly higher number of seeds in the soil, although variation between shrubs was high (mean $\pm$ s.e. was 11.0 ± 8.6 seeds/m² in 1990; in 1991 it was 31.8 ± 29.1 ; and in 1992 it was 23.0 ± 15.2). The situation at site G (2800 m from the water point) was in marked contrast, with the greatest number of seeds in the seed bank in each year being recorded at this site. In 1990 the seed bank at this site was small (37 ± 5.1 seeds/m²) and with little variability between plants but in 1991 and 1992 the seed bank was substantial (626 ± 315.2 seeds/m² in 1991; and 318 ± 169.0 in 1992).

Seed Longevity

The germinability of the seed used in this study was high (*ca.* 99%) at the time samples were placed in the field. This compares with the highest rate reported by Burbidge (1945) of 89% and that by Beadle (1952) of 100%. The proportion of viable ungerminated seeds remaining in the field declined rapidly, with means of 34% and 17% after 12 months for the canopy and exposed treatments respectively. This was mainly due to seed germinating, although seed death was also important during the first three months (Figure 7.3). Large changes in the amount of germinated seed generally (at least for the canopy treatment) followed periods when rainfall exceeded 50 mm for at least one month in the period (Figure 7.3). The fate of seeds differed significantly between the canopy and exposed treatments overall, as indicated by the log-linear analysis ($G^2=81.2$, $DF=20$, $P<0.001$ for fate $\times$ treatment $\times$ time interaction) and for each individual time

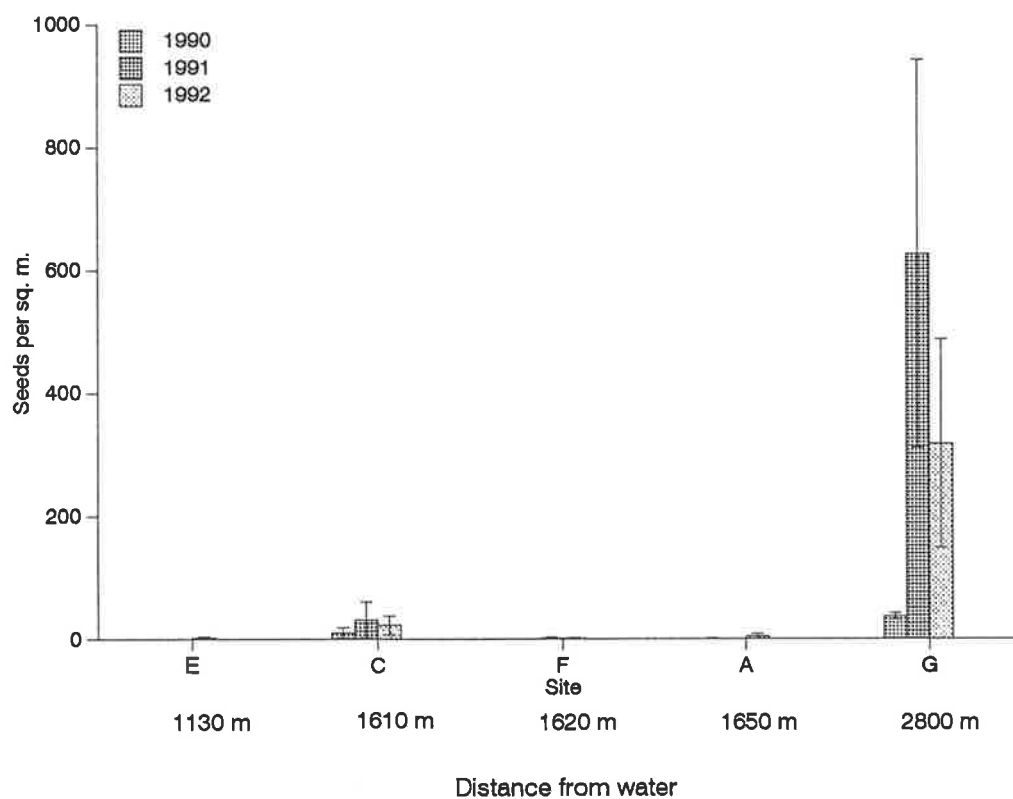
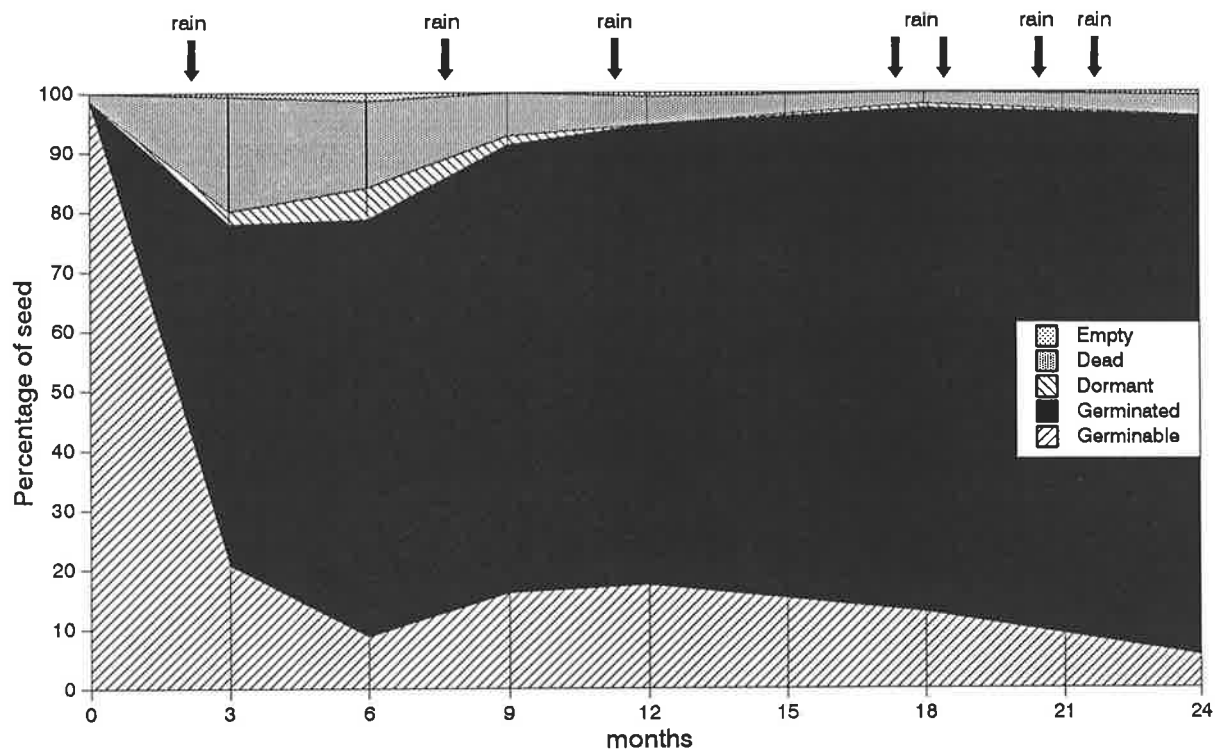
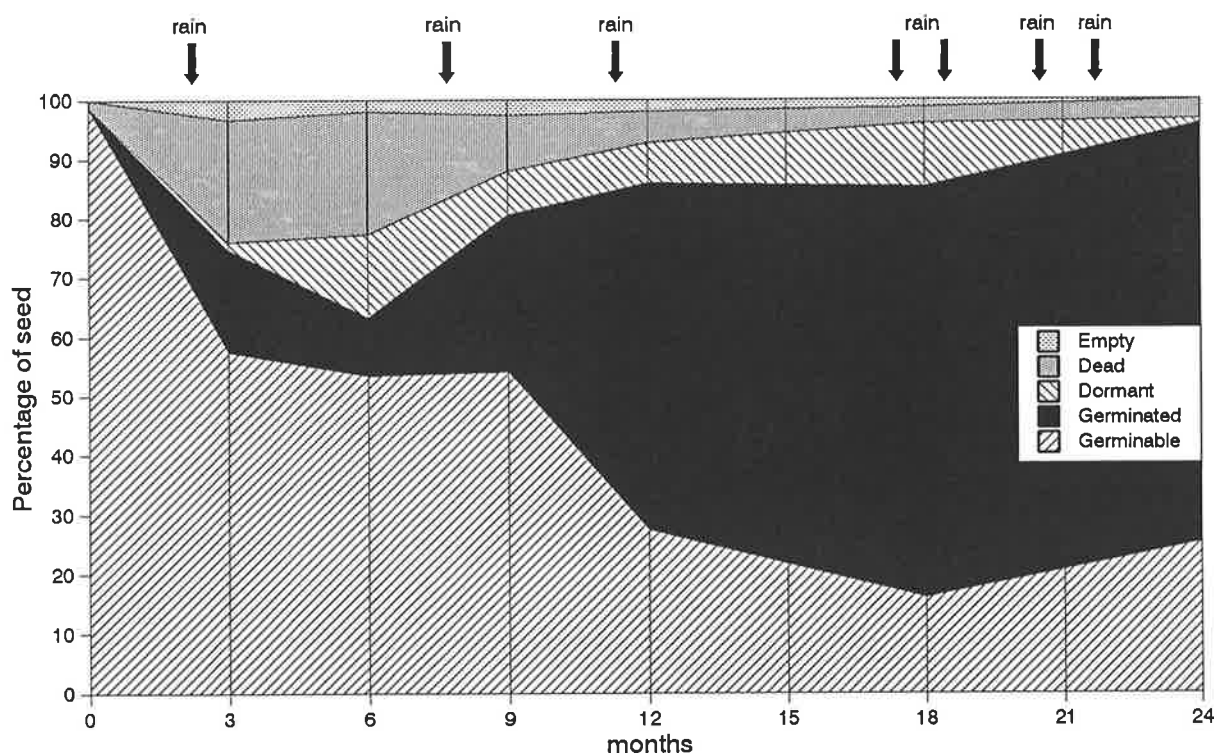


Fig. 7.2. The abundance of saltbush seed in the soil seed bank for three years at five sites in Yanaby. Bars are means ($\pm$ s.e.) of 3-5 samples, each centred on a female bush.

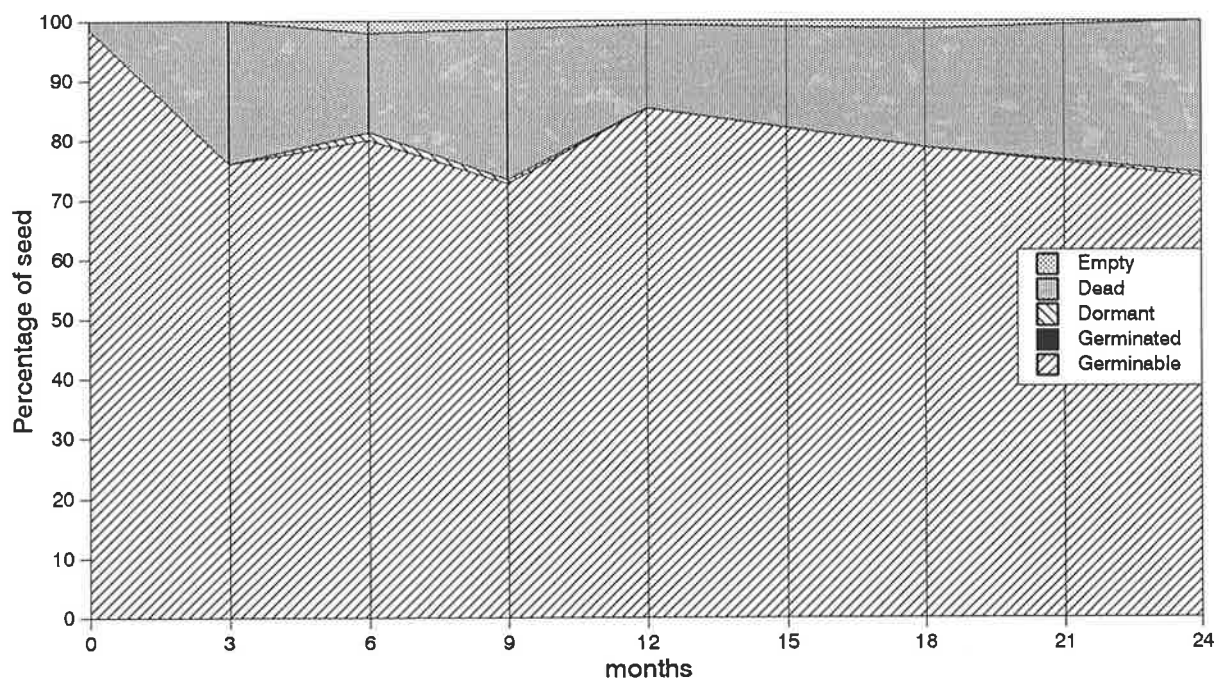


(a) Exposed seed.



(b) Seed under canopy.

Fig. 7.3. The fate of saltbush seed in two micro-environments in the field over two years and for seed stored in the laboratory over the same period. Rainfall events greater than 50 mm are indicated for the field treatments. The figure is continued on the following page.



(c) Control seed (stored in the laboratory).

Fig. 7.3. (continued). The fate of saltbush seed in two micro-environments in the field over two years and for seed stored in the laboratory over the same period. Rainfall events greater than 50 mm are indicated for the field treatments.

($P < 0.001$ for each time). The analysis of variance on the percentage of seeds still viable also indicated that treatment (controls excluded), time and the interaction were significant (Table 7.2). Controls were excluded because they were clearly different from the field treatments. The mean percentage of viable seed (i.e. germinable and dormant seed) remaining was significantly different between the canopy and exposed treatments on each sampling occasion (shown by LSD test, $P < 0.05$; see Table 7.3 for means). Significant differences in means between sampling occasions within a treatment are also indicated in Table 7.3.

The difference in the amount of seed to germinate was the main distinction between the canopy and exposed treatments. The rate of germination in the field treatments initially was greatest for the exposed seed; 70% of the seed had germinated within six months of placement in the field, while for the canopy treatment this level of germination was not achieved until 18 months in the field (Figure 7.4). Consequently, in the final samples, collected from the field 2 years after placement, 26% of the canopy seed was ungerminated viable seed compared to 5% for the exposed seed (Table 7.3). In contrast, the proportion of seeds remaining viable in the samples stored in the laboratory fell to approximately 75-80% within the first three months and then remained around this level for the rest of the study (Figure 7.3). The field treatments also developed a degree of dormancy, which was first apparent after three months in the field but was lost by the end of the study. The incidence of dormancy was higher on the canopy treatment than for the exposed, relative to the original number of seeds in each sample, but was generally similar on the two field treatments relative to the number of ungerminated viable seeds present at the time, although it varied considerably between samples and dates (range from 0-40%). Approximately 1-2% of the control seed exhibited dormancy between 3 and 9 months.

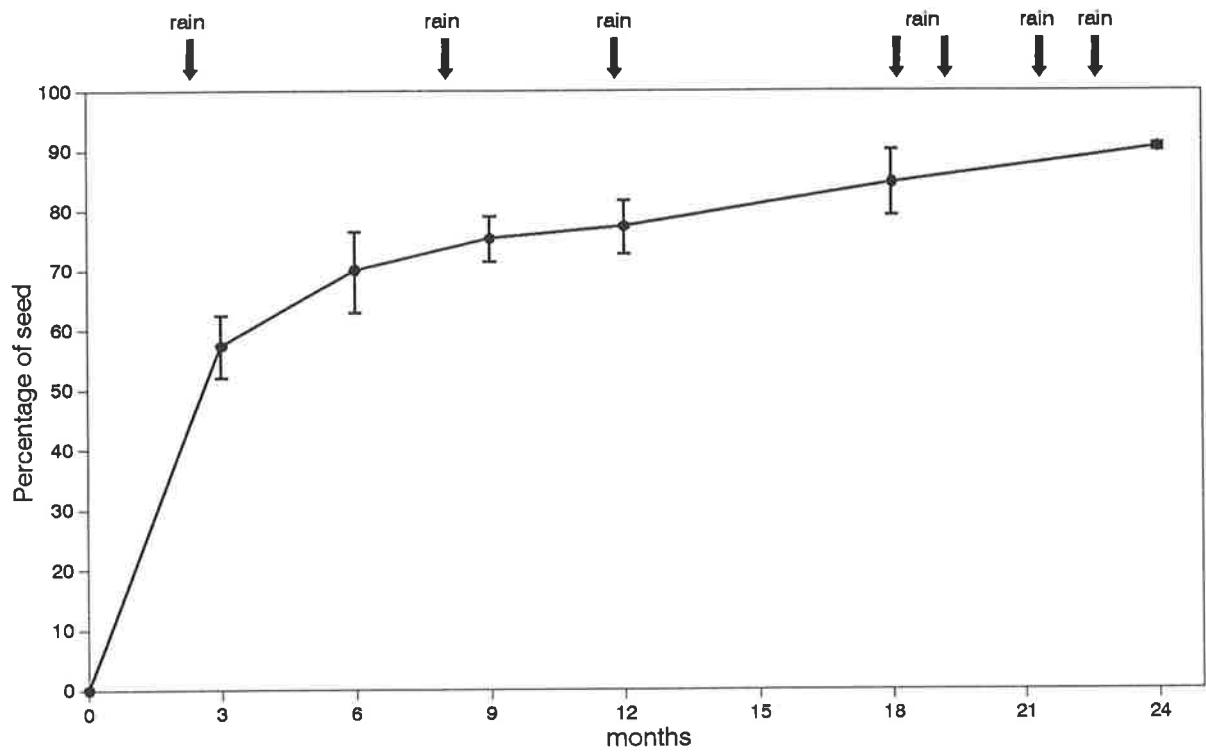
An unexpected result was the decline in the number of dead seeds after three months for both field treatments. The most likely explanation for this is that, later in the study, dead

Table 7.2. Analysis of variance of the percentage of saltbush seeds remaining viable for two field treatments (under canopy and exposed) on six occasions over two years. The data was arc-sine transformed for analysis.

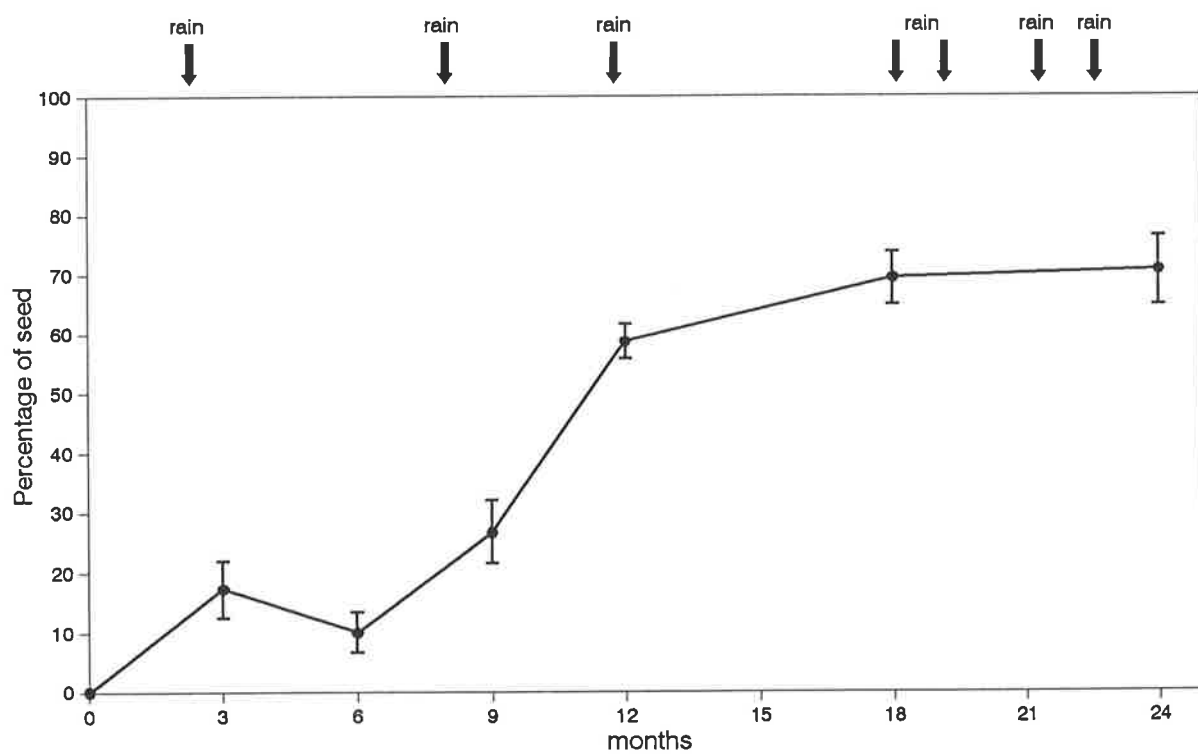
Source	DF	SS	MS	F	P
Treatment (A)	1	3929.0	3929.0	107.02	0.0000
Time (B)	5	1816.2	363.25	9.89	0.0000
A*B	5	657.30	131.46	3.58	0.0147
Rep (C)					
A*B*C	24	881.08	36.71		
Total	35	7283.6			
Grand Average	1	3.8124E+04			

Table 7.3. The mean percentage of saltbush seeds remaining viable over two years, for seed located under the canopy of established shrubs and for exposed seed. Values are back-transformed means calculated from the analysis of variance. Means followed by the same letter within treatments are not significantly different, $P < 0.05$. All means are significantly different between treatments for each length of time in the field. See Figure 7.3 for the results for the seeds stored in the laboratory.

Time in field (months)	3	6	9	12	18	24
Canopy seed	60.8 ^a	69.5 ^a	63.3 ^a	34.4 ^b	26.9 ^b	25.5 ^b
Exposed seed	22.8 ^a	14.2 ^{a,b}	16.8 ^a	17.0 ^a	11.6 ^{a,b}	5.4 ^b



(a) Exposed seed.



(b) Seed under canopy.

Fig. 7.4. Cumulative germination of saltbush seed in two micro-environments over two years. Values are means ($\pm$ s.e.) of three samples. Rainfall events greater than 50 mm are indicated.

seeds were being wrongly classified as having germinated. This is supported by the levels of dead seed in the laboratory samples which were similar to those from the field after 3 months. Towards the end of the study the bladders surrounding the seed had decayed considerably and often several bladders had become clumped together, occasionally making it difficult to ascertain whether a seed had died and decayed or germinated. The reduced amount of germinated seed in the six month samples in the canopy treatment was also surprising, and although this was associated with a higher proportion of dormant seed, it is not clear why this occurred.

DISCUSSION

Spatial Patterns in Flowering and the Seed Bank

Grazing reduced the proportion of saltbush shrubs in flower, with heavier grazing near water having a more severe effect on flowering. As a result the proportion of shrubs with flowers increased linearly as distance from water increased. However, although it was not quantified, observations suggested that the number of flowers on those shrubs that did flower at the heavily grazed sites was markedly lower than at more lightly grazed sites. (Note that in the scoring method I employed, which was a fairly insensitive method, a shrub needed to have only one recently developed flower or fruit to be regarded as flowering.) This pattern also applied to the exclosures near the water point for much of the study, becoming less apparent later, suggesting that the main mechanism by which sheep grazing was reducing the incidence of flowering was by preventing the initiation of flowers by the shrubs. This does not exclude the possibility that sheep were also consuming flowers, as reported by Andrew and Lange (1986b) in their study of grazing in a new piosphere, but it has previously been reported that sheep generally avoid grazing male shrubs when in flower (Graetz 1978, Williams *et al.* 1978).

The spatial patterns in flowering on grazed plots at the paddock scale were paralleled by

spatial patterns in the seed bank. Flowering on grazed plots close to the water (e.g. sites A, E and F) rarely exceeded 30% so it is not surprising to find that the seed bank at these sites was negligible. Flowering at site C (1610 m from water) was often in the order of 50% and this was reflected in a higher number of seeds in the seed bank. Similarly, at site G (2800 m) flowering was consistently 60% or higher resulting in a substantial seed bank. This trend between sites, associated with the sheep grazing gradient focussed on the water point, clearly suggests that grazing by sheep was severely reducing the seed bank at sites closer to water by reducing flowering of the shrubs and consequently input to the seed bank.

The effect of grazing in reducing seed production and thus seed bank size has frequently been observed (Bosch and Dudzinski 1984, Bastrenta 1991, O'Connor and Pickett 1992, Kinucan and Smeins 1992). However, few studies have considered the potential for spatial variation in this effect. An exception is the study by Coffin and Lauenroth (1992). They found that overall, grazing by cattle reduced flower and seed production by *Bouteloua gracilis*, a perennial bunchgrass in semi-arid USA, but enhanced the differences in seed production caused by spatial variation in soil texture. They concluded that spatial patterns in the ability of the population to recover after disturbance (either by cattle or other agents) would result.

A number of studies have revealed a non-linear relationship between herbivore feeding and seed production (Islam and Crawley 1983, Hodgkinson 1991). While I detected a linear relationship between the incidence of flowering and distance from water, it was not the purpose of my study to determine the form of such a relationship in saltbush between seed production and grazing pressure, and the design of my study precludes any firm conclusions being drawn on this pattern. Thus the true nature of the spatial pattern across the paddock of flowering, seed production and seed bank size may involve non-linear rather than linear trends, including the possibility of thresholds of change. This could have important implications for management of saltbush populations under grazing and

suggests that establishing the true nature of the relationship is an area requiring further work.

I assessed the size of the saltbush seed bank by sampling in the immediate vicinity of adult female shrubs. However, spatial patterning of seed banks in arid areas occurs naturally at various scales because of the spatial distribution patterns of plant communities, populations and individuals and the dispersal of seed by herbivores or granivores and the action of wind and water (Kemp 1989). Therefore, the possibility exists that my results do not give an accurate picture of the size of saltbush seed bank. This seems unlikely though, since limited dispersal of seed resulting in the concentration of seed around the parent shrub, as suggested for saltbush (Williams 1979), is common amongst desert shrubs (Reichman 1984). Furthermore, the rapid germination of the exposed seed in the longevity experiment implies that seed deposited between the shrubs will have a short life and therefore be more unlikely to result in large accumulations of seed. If these assumptions are valid, the overall size of the seed bank in an area will depend on the abundance of female shrubs.

Seed Longevity

The longevity of saltbush seed under the field conditions during this study was considerably shorter than both that found in earlier studies for saltbush seed stored in a laboratory and the expected field longevity based on these studies. Burbidge (1945) and Beadle (1952) reported longevity of 5-7 years for laboratory seed, with 71% still germinable after two years in the latter study, while Beadle (1952) and Hall *et al.* (1964) speculated that longevity in the field would be 3-5 years. Of course, the disparity between longevity in the laboratory and the field is not unexpected. Nevertheless, some seed (5% for the exposed treatment and 26% for the canopy seeds) remained viable after two years in the field.

Climatic conditions were an important influence on seed longevity in this study, although

the rapid decline in seed numbers made it difficult to detect consistent patterns. Reductions in the availability of viable ungerminated seed occurred mainly as a result of seed germination, which was influenced by the patterns of rainfall and temperature, particularly for the canopy seed. The study years received five rainfall events exceeding 50 mm during autumn, winter or spring when temperatures and evaporation rates would have been low to moderate, conditions which are favourable for the germination of saltbush seed (Burbidge 1945, Williams 1979). Had rainfall been much lower during the study it is likely more viable seed would have remained after the two years.

Rainfall and temperature also are important influences on seed decay and death rates. In particular, the study by Burbidge (1945) indicated that high temperatures at times when moisture is present can cause damage to saltbush seed resulting in a marked reduction in the number of viable seeds. This prompted her to suggest that summer rains may be detrimental to soil seed reserves. Because of the chance that dead seeds were being wrongly classified as having germinated it is not possible to determine the influence of rainfall and temperature on seed death and decay in this study. Nevertheless, based on Burbidge's findings it could be expected that the heavy summer rain in December 1992 and January 1993 would have killed many seeds, so it is surprising that there was not a substantial decline in the number of viable seeds during this period. The sudden increase in the proportion of dead seed in the laboratory samples over the first three months is also surprising and cannot be explained.

The micro-environment in which seed was located influenced the longevity of seed, with longevity being greater for seed positioned amongst the litter under the canopy of established shrubs than for seed on open ground. This was due to an overall lower rate of seed germination for the canopy treatment. Being located under the canopy appeared to affect seed longevity in two ways, initially by decreasing the rate of germination over the first three months, which subsequently resulted in a greater proportion of the original seed samples apparently developing induced dormancy compared to the exposed seed.

The initial reduced rate of germination under the canopy is probably related to the effect of a high concentration of chloride ions in the litter under the canopy. Beadle (1952) proposed that germination of saltbush seed is inhibited by concentrations of chloride ions in the papery bracteoles and bladder appendages in which the seed is encased. Since saltbush leaves accumulate large amounts of salts on the surface of their leaves during growth, the litter of dead saltbush leaves under saltbush shrubs has a high concentration of chloride ions, resulting in the germination of many of the seeds falling amongst the litter being inhibited (Beadle 1952). Consequently there appears to be a degree of enforced dormancy which reduces the rate of germination in the field but has no lasting effect on germination, as the seeds germinate readily when removed from their bladders for testing in the laboratory. Beadle suggested this mechanism protected the seed from germination following small rainfalls when successful establishment is unlikely, because in such cases the rainfall received would be insufficient to leach the salts from the litter and bladders to permit germination to proceed. A further explanation for the increased rate of germination in the exposed seed compared to the canopy seed is simply that exposed seed were more thoroughly moistened during rain, especially lighter falls, than the seed protected under the canopy of established shrubs.

The development of induced dormancy in saltbush seed has not previously been reported but it appeared to be affecting the germination and longevity of seed in the field, since some viable seed recovered from the field remained ungerminated in the laboratory tests after 21 days. This dormancy was apparently acquired after placement of the seed in the field since only a negligible amount of seed in the control treatment exhibited dormancy. Also, the seed tested after three months in the field showed little dormancy but after six months in the field an increase in the proportion of dormant seed was apparent. It is difficult to determine what factor was responsible for inducing this dormancy. Canopy-induced dormancy has been reported to occur in other species because of a shift in the ratio of red to far-red light under the canopy of established adults, which induces a physiological change in the seed (Leopold and Kriedemann 1975, Begon *et al.* 1990).

Thus when seed is tested for germinability the seed remains dormant. However, this does not explain the apparent induced dormancy in the exposed seed (which affected 0-36% of exposed viable seed at different times), unless the shade-cloth seed bags also altered the ratio of red to far-red light in a manner similar to what a shrub canopy might. Low winter temperatures are another possibility as the stimulus for inducing dormancy since the number of dormant seeds was highest during or following winter. It is interesting to note that the 'control' seed from the laboratory also exhibited a minor amount of dormancy between three and nine months. As these seeds were stored under reasonably constant conditions this suggests that the seed were either predisposed to develop dormancy or perhaps the conditions during the germination tests were affecting the results. However, this effect was small compared to the level of dormancy in the field treatments and is probably of no consequence.

Despite the apparent detection of some dormancy in this study the significance of it to the population appears minor because both the induced and the enforced dormancy are short-lived effects (most seed germinates within 1-2 years), and often only a small number of seeds were dormant. Induced dormancy may have a small benefit since the production of some dormant seed in arid zone plants may be important in spreading the risk of germination in an unpredictable climate over a longer period (Jurado and Westoby 1992). Enforced dormancy associated with the canopy of established shrubs potentially might act to reduce the chances of seed germinating under the adult shrub where competition is high and the likelihood of seedling survival is low (Reichenberger and Pyke 1990). Also, seeds remaining under a shrub have a greater chance of a seedling successfully establishing if they germinate after the adult has died (Parker and Salzman 1985), so a supply of dormant seed under a shrub would facilitate the rapid occupation of the site following the demise of the adult. However, given the relatively short period of dormancy it seems unlikely that there would be much benefit to the population for these reasons. Rather, as Beadle (1952) suggested, the most likely benefit of the dormancy associated with the canopy of established shrubs is to prevent germination after small

rains, when the chances of seedling survival are low. In contrast, seeds dispersed away from an established shrub are more likely to germinate following small rains, but they may be favoured by being dispersed into depressions (Malik *et al.* 1976) and may have a greater chance of successful seedling establishment because of reduced competition¹. Thus while there is a greater likelihood that germination would proceed following light rains that are insufficient for establishment to occur, there may still be a chance of seedling establishment in many cases. These two alternative approaches may be beneficial to the population because they would appear to maximise the chances of successful recruitment in an unpredictable environment.

As mentioned above, the longevity of seed in the field is liable to vary in time depending on climatic conditions, with drought, for example, likely to extend the retention of viability by the seed. Thus, my results are an indication of potential seed longevity under the conditions of this study, which were favourable for seed germination, and actual seed longevity in the field may differ from my results for several reasons. Firstly, there is the possibility that the seed bags increased germination or decay by retaining moisture for longer than would naturally occur. However, in the field seed is normally found either amongst the litter under shrubs or in nearby shallow depressions amongst other litter (Malik *et al.* 1976). Loss of moisture from bladders in both of these situations is likely to be slower than for loose exposed seed on the ground, so that germination rates under similar conditions to those in this study may not be substantially different from those recorded here.

Secondly, my method also ignored the potentially large effects of ant predation on seed longevity. For example, Williams (1972) found that ants removed up to 83% of the saltbush seed on the ground. From this it is reasonable to infer that the longevity of

¹A study which examined the effects of different microsites, including the proximity to adult shrubs, on the survival of saltbush seedlings (Eldridge *et al.* 1991) found the effects of microsites were inconsistent between cohorts, with seedlings sometimes faring worse near established shrubs than seedlings in the open, but not always.

much of the seed in the field is likely to be somewhat lower than my results indicate.

Seed Bank Dynamics

Seed bank size at site G, a very lightly grazed area of the paddock, varied between years partly in response to fluctuations in flowering and germination, which in turn fluctuated with rainfall. Flowering in saltbush generally occurs in response to rainfalls of 25-50 mm and germination is initiated by rainfall of approximately 50 mm (Williams 1979). My results are consistent with these patterns. Large increases in the seed bank in autumn 1991 followed good flowering in 1990, but good rains of approximately 60 mm during both winter and spring in 1991 resulted in the germination of many seeds (see graph of recruitment, Figure 5.3), so that mean seed bank size in the following year had been reduced by approximately half. However, the good rains would also have been expected to increase flowering and input to the seed bank and so counteract this decline. The study paddock was visited on only a few occasions in 1991 so the flowering behaviour for the year is not known, but no flowering was observed during the few visits to the paddock. Possible explanations for the lack of balance between seed loss and gain include the possibility the shrubs did not flower to any great degree because the plants need time to recover resource levels following previous flowering efforts, or that ants consumed much of the seed, or that much of the seed produced during the year germinated soon after being shed from the parent.

Although my study was not a definitive examination of the seed bank dynamics of saltbush, taken together, the results presented here on flowering, seed bank levels and seed longevity imply that saltbush seed banks in ungrazed situations are highly dynamic. Flowering and seed production occur frequently but longevity of seed in the seed bank is low, with the seed bank becoming rapidly depleted mainly through the effects of seed germination and predation by ants. I recorded a 17-fold increase in the seed bank between the first two years at the lightly grazed site, from 37 seeds/m² in 1990 to 626 seeds in 1991, followed by a halving of the number of seeds in 1992. This temporal

variability in the number of stored saltbush seeds suggests the seed bank is transient. Therefore frequent replenishment of the seed bank through flowering appears crucial to maintaining regular recruitment.

Seed banks of other arid zone perennial species also have been reported to be highly variable, both temporally and spatially (Hodgkinson *et al.* 1980, Coffin and Lauenroth 1989, Kemp 1989). For example, the seed bank of the perennial shrub *Chrysothamnus viscidiflorus* in north-western Nevada, fluctuated from 10-370 seeds/m² over a year (Kemp 1989), levels similar to those for saltbush. These relatively small transient seed banks for perennial shrubs are in strong contrast to the very large persistent seed pools reported for short-lived species. Westoby *et al.* (1982) reported mean seed densities for three species of short-lived grasses in western New South Wales of 7,700 seeds, 26,000 seeds and 50,000 seeds/m², with annual seed survivorship of 81 % or greater. It would be expected that selection pressures would have favoured the development of persistent seed banks in arid zone species because of the erratic nature of rainfall and frequency of drought, and this is generally true for annual and ephemeral species (Kemp 1989). However, in the case of long-lived perennials, the persistence of the adult rather than a seed bank protects against adverse climatic fluctuations. Many of these species therefore rely on a strategy of producing a small amount of short-lived seed on a frequent basis, with frequent germination, so the seed banks of these species tend to be transient and are composed of seed produced during the last good rains (Kemp 1989, O'Connor 1991). From my studies it would appear that saltbush utilises this strategy.

The seed bank dynamics of other perennial chenopods have not been quantified so comparisons are difficult, but the findings of a recent autecological study suggest bluebush (*Maireana sedifolia*) utilises a slightly different strategy. Wotton (1993) reported that maximum longevity of bluebush seed in the field is approximately six months, but in contrast to saltbush flowering of bluebush is a rare event (she recorded five sparse and patchy flowering events in four years in response to several periods of

above-average rainfall). Consequently, Wotton suggested that for most of the time germination is limited by a lack of viable seed, and successful reproduction will depend on the co-occurrence of rare episodic rainfall events to initiate flowering and seed production and then permit germination to proceed while viable seed is present. The differences in these strategies are likely to be related to the longer life-span of bluebush (150+ years) compared to saltbush (11+ years) (Crisp 1978), since bluebush would not need to reproduce as frequently as saltbush to maintain the population.

Importance of Low Seed Availability Under Grazing

Although recruitment was shown to be of little importance in maintaining the population growth rate (see demographic analysis in Chapter 5), the importance of recruitment to the maintenance of population size increases if the rate of adult mortality increases under grazing. Recruitment of new individuals through the establishment of seedlings from seed is the only mechanism whereby replacement of the dead adults can occur and plant density can approach normal levels. Low seed availability due to poor or infrequent flowering is likely to limit the ability of the population to recover from increased mortality of adult shrubs, whether grazing-induced or natural. However, a number of studies have shown that the availability of safe-sites for germination and establishment is often more important in controlling recruitment than seed number (Andersen 1989, Eriksson and Ehrlén 1992, Wotton 1993). While the elimination of established saltbush shrubs by heavy grazing would create gaps for recruits to occupy, grazing and trampling activity at such sites will alter soil surface conditions, including rates of infiltration and nutrient and litter levels, which have been variously reported to either discourage the establishment of recruits (Graetz and Tongway 1986) or favour recruitment (Dean and Milton 1991). Therefore, an increase in seed availability may or may not result in higher levels of recruitment depending on seed bed conditions. It is not possible to ascertain from this study the relative importance of these two factors in reducing the recruitment of saltbush at sites nearer to the water point, although it is reasonable to conclude that low

seed availability at many sites in Yanaby due to grazing would be a major contributing factor.

Further work is required to establish to what degree low seed availability and altered soil conditions each contribute to poor recruitment at heavily grazed sites and whether recruitment would increase if seed availability was increased. This will have important implications in determining appropriate management practices aimed at improving recruitment levels, especially if there is a difference in the relative rates of recovery of seed numbers and soil conditions (if seed bed conditions are negatively affected by grazing). In Yanaby, protection from grazing for several years resulted in increased recruitment on a number of the exclosed plots which had a history of heavy grazing, but recruitment levels did not match those at lightly grazed sites. Although this recruitment followed a gradual improvement in flowering, it is not known whether seed availability or seed bed conditions were limiting the rate of recruitment.

CONCLUSIONS

- Grazing by sheep reduces the incidence of flowering and input to the seed bank. Gradients in grazing pressure within paddocks, centred on water points, create spatial patterns in flowering and seed bank levels across paddocks.
- A lack of viable seed in the seed bank is at least partly responsible for poor recruitment of saltbush under sheep grazing, which will limit the recovery of saltbush populations following mortality of established shrubs.
- Saltbush seed banks are highly dynamic. Seed input is frequent but longevity of seed in the field is short, partly because saltbush seed exhibits little dormancy and germinates readily. Consequently a large persistent seed bank does not develop.

- Both induced and enforced dormancy appear to reduce the germination of seed located under established shrubs, but these effects are small and short-lived.
- Further work is needed to establish the importance of grazing and trampling effects on the soil surface in limiting the rate of recruitment.

CHAPTER 8

GENERAL DISCUSSION

INTRODUCTION

The chenopod shrublands are a major rangeland type in southern Australia and form the basis of a large livestock grazing industry. In these shrublands bladder saltbush, *Atriplex vesicaria*, is a widespread and dominant perennial shrub which has a crucial role in stabilising the ecosystem, particularly in protecting the soil from erosion during drought, and as feed for domestic livestock (Graetz and Wilson 1984). However, there is concern that livestock grazing is gradually eliminating saltbush over wide areas of the chenopod shrublands (Wilson *et al.* 1988). While this has not been considered to be a problem in the more mesic parts of its distribution, such as the Riverine plain in NSW, where robust and reliable grasslands reportedly emerge upon the decline of the shrub cover (Moore 1952), in the more arid parts of the chenopod shrublands the situation is different. In western NSW, SA and WA, loss of the perennial shrub cover can result in severe soil erosion, complete loss of vegetation or increases in the abundance of weedy species and loss of sustainable carrying capacity (Lange *et al.* 1984).

To understand the potential long-term impact of grazing and effectively manage this impact a detailed knowledge of the population dynamics of the species of interest and the effect of grazing on population processes is needed (Westoby *et al.* 1989, Archer and Smeins 1991). However, an understanding of these interactions must incorporate information concerning the spatial components of herbivory (Coughenour 1991). While there has been a number of studies of grazing impact on aspects of the population dynamics of saltbush, none has considered the spatial patterns in these interactions which result from the uneven use of paddocks by sheep, despite this uneven use being widely recognised. This study has gone some way to improving our understanding of this and provides detailed information on these interactions which should facilitate the development of management practices appropriate for long-term persistence of the

saltbush population under sheep grazing.

In this chapter I will first briefly review this study and the findings of the three main aspects of sheep grazing impact on saltbush that were examined, namely defoliation patterns, the population dynamics of the vegetative part of the life cycle and aspects of the dynamics of the seed bank. I will then assimilate these findings into a description of the circumstances and the process that would lead to the local extinction of saltbush at many sites, as predicted by the stochastic population models presented in Chapter 6. This site-specific population level information will be used to develop a unified understanding of the long-term effects of sheep grazing on saltbush populations under continuous grazing at the water point/paddock level relevant to the broad areas of commercial sheep paddocks. The implications of this for the management of grazing in chenopod shrublands will then be discussed. A state-and-transition model (Westoby *et al.* 1989) which incorporates the spatial element of vegetation change under grazing will also be presented. This should facilitate the presentation of this information to land managers and is a useful way of highlighting important points in the management of grazing of saltbush. Finally, I will suggest a number of areas that warrant further research.

REVIEW OF STUDY

Reliability of Results

This study examined numerous aspects of the effects of sheep grazing on the population dynamics of saltbush at nine locations in a large commercial sheep paddock over a period of 6.5 years. Clearly, in a large scale study of this nature and with limited resources there will be a limit to what can reasonably be achieved and compromises will be necessary in the experimental design. In this study I had to choose between obtaining good estimates of the within site variation and gaining a reasonable understanding of the variation in grazing effects across the paddock. Since characterising the degree and nature of the spatial variation in the population dynamics of saltbush was a major concern

in this study, it was desirable to study the dynamics at as many sites in the paddock as possible, and so get a better idea of the spatial variation in the paddock. Consequently, it was necessary to limit the size and number of plots at each site. This resulted in a small number of individuals in sample populations at certain sites and only limited replication, so analysis of the variation within each site was less than is normally desirable. A further potential limitation was the short duration of the study. Short-term studies of long-lived species in environments where rainfall is erratic and unpredictable and ecological change is at times very slow, may produce results which do not necessarily represent true long-term trends.

Nevertheless, I do not feel these limitations detract from the value of this study, particularly in view of the strength of the trends in population processes which were detected. I believe that the results presented in this thesis are a fair representation of the population dynamics of saltbush and the impact of grazing in the study area during the study period, and provide a strong indication of the likely long-term impact of grazing on the population. The generality of these results to grazing throughout the chenopod shrublands will be discussed below.

Defoliation Patterns

Saltbush in Yanaby was grazed almost exclusively by sheep during the three years of recordings. Generally speaking, the level of defoliation of saltbush was surprisingly high (Chapter 4). The intensity of defoliation increased as the availability of herbage declined and because of a dry period early in the study when herbage levels remained low for around eight months, saltbush defoliation was high for much of this period. Following good rains herbage levels increased so the general level of saltbush grazing declined. However, the level of defoliation pressure varied between sites across the paddock, with the plots closer to the water point experiencing more severe and more frequent grazing. Moderate levels of saltbush grazing occurred at these sites during many periods when other feed was available and, as would be expected, these plots were also the first to be

grazed heavily as feed levels declined. Thus the shrubs here were more chronically grazed and consequently were maintained at a very low level of shrub biomass. Biomass of shrubs at greater distances from water was unaffected by grazing, since these shrubs were only rarely grazed and then only lightly.

Population Dynamics and Grazing Impact

Saltbush possesses a life history strategy which relies heavily on the survival of established shrubs. The adults are persistent and are capable of surviving most droughts, and survival of adults is the major contributor to the population growth rate (Chapter 5). Consequently, ungrazed saltbush populations are quite stable, with recruitment making only a small contribution to the population growth rate. Recruitment appears to be a more or less continual process but the number of recruits is higher with increased rainfall. However, seedling survival is low. Large episodic events do not appear to be important in the dynamics of ungrazed saltbush populations, but drought can interact with grazing to bring about considerable adult mortality.

There were strong spatial patterns in the population dynamics of saltbush under grazing, reflecting the trend of increasing grazing pressure as distance from water decreased. Increasing grazing pressure reduced the population growth rate and at many sites the population growth rate for the duration of the study was negative (Chapter 5). This decline in the population growth rate was primarily a result of both adult mortality increasing and recruitment decreasing nearer the water point. Recruitment is more sensitive to grazing than adult survival so it is more severely affected at greater distances from water. Survival of seedlings does not appear to be directly affected by grazing. The long-term implication of grazing for the saltbush population at many sites closer to water is local extinction and this would appear to happen regardless of the sequence of seasons that occur (Chapter 6).

After several years protection from grazing, which included a period with low rainfall

followed by good rains, saltbush populations which had been grazed until the beginning of the study showed little increase in the numbers of adult shrubs (Chapter 5). Some sites recorded increased recruitment later in the study, but these levels of recruitment did not match those for populations that had not previously been grazed.

Seed Bank Dynamics

The seed bank of saltbush is small and transient since seeds have little dormancy and their longevity in the field is short (Chapter 7). Seeds germinate frequently and ants predate many seeds, so the seed bank is rapidly depleted. Saltbush therefore appears to rely on a strategy of frequent flowering and regular production of seed to ensure that some seed is available for recruitment when favourable rains occur.

Poor recruitment of saltbush in the more heavily grazed parts of the paddock appeared to be strongly influenced by a lack of seed. Grazing of saltbush reduced the production of flowers so that input of seed to the seed bank was low. The reduction of flowering (both numbers of flowers and frequency of flowering) by grazing, together with the normal rapid depletion of the seed bank, quickly leads to a lack of seed for recruitment. Following protection from grazing shrubs do not produce large amounts of seed for several years, even with good rainfall.

CIRCUMSTANCES LEADING TO LOCAL EXTINCTION

By assimilating the information gained in this study concerning the life history attributes of saltbush, the impact of grazing on population processes and the patterns of defoliation it is possible to describe the circumstances that would lead to the local extinction of saltbush (i.e. elimination of the existing population and all seed, at a spatial scale of several hundred metres) at certain sites, as predicted by the stochastic population models. The life history characteristics of saltbush are important in making the species prone to local extinction under a continuous grazing regime similar to that utilised in Yanaby.

Two particularly important attributes are the very high reliance of the population on the survival of adults and the production of only a small amount of short-lived seed (i.e. lack of a persistent seed bank) which is poorly dispersed. The longevity of established shrubs is an important strategy associated with the high tolerance of the species to adverse climatic fluctuations. In the absence of grazing, the ability of adult shrubs to survive droughts of considerable severity and duration means they are able to provide seed for recruitment following drought. However, these attributes are not suited to the long-term survival of the shrubs under grazing.

Sustained heavy grazing over a period of several years leads to a lack of flowering and consequently there is little input of fresh seed into the seed bank for an extended period. The seed bank is rapidly depleted through germination and ant predation and since the survival of seedlings is low, few recruits establish. During subsequent dry periods further severe grazing of the shrubs, which already have reduced vigour due to earlier grazing, results in the death of many adult shrubs. Not all shrubs necessarily die but regeneration following drought is limited, firstly because of low seed availability and secondly because of the frequency of drought. During the short periods of good rain recruitment will depend on the production of seed by the surviving adults. This can take several years as the shrubs have low vigour and resources are probably directed first to putting on new growth and expanding leaf area, and not into flower production. Since dispersal of seed over long distances is limited (most seed remains within a few metres of the parent; Williams 1979) the possibility of natural seed introduction from neighbouring areas is limited. Because of the frequency of intra-seasonal drought in these areas and the high evaporation rates, moisture availability remains high only for a short time so that the probability of substantial seed production by shrubs with reduced vigour is very low. In addition, grazing of shrubs again increases as conditions become drier, which further reduces the prospects for substantial seed production and recruitment. The high frequency of droughts which last several seasons means that further adult mortality may also occur, so that after several such cycles local extinction may result. Of course, the

pattern of climatic fluctuations will also be important in determining the rate of this process, with a sequence of years with unusually good rainfall likely to delay or possibly reverse the process. However, such conditions during the study had little effect and, in practice, the frequency of these conditions is very low.

Interestingly, this process is similar to that proposed for a number of palatable perennial grasses (e.g. *Andropogon scoparius* and *Themeda triandra*) in South Africa (O'Connor 1991). These species have life history attributes similar to those for saltbush (i.e. dependence on adult survival and lack of a persistent seed bank) except the longevity of the grasses is about a third of that of saltbush, at around 10 years. This suggests that many palatable plant species from semi-arid areas with these life-history attributes may be particularly susceptible to local extinction under grazing. An important distinction between the process for saltbush and that for the grasses is that in the latter case the seed bank becomes depleted after the majority of the adults have been eliminated because seed does not persist for long in the seed bank and seedling survival is poor (O'Connor 1991). In contrast, the saltbush seed bank is depleted before the adults are eliminated.

SPATIAL ELEMENT OF GRAZING AND LOCAL EXTINCTION

The spatial patterns in grazing which occur in paddocks and the sensitivity of various population processes to grazing are important in determining both the nature of the process leading to local extinction and the patterns of local extinction across a paddock. Because of their location, plants closer to water suffer sustained grazing pressure, with grazing occurring not just during drought but also over the summer period when other feed is often scarce and sheep water more frequently. Grazing of these shrubs can also occur at other times as sheep travel to and from the water point, even though other feed may be available. Flowering and seed production are more sensitive to grazing than the survival of established plants so in most years the adults survive this grazing but the seed bank becomes depleted. This results in a zone at some distance from the water point

consisting solely of established shrubs; seeds and seedlings are absent. Therefore when adult shrubs die during drought either because of heavy grazing during drought or the effects of sustained grazing pressure, there is no seed available for recruitment and recovery to occur. Consequently, local extinction results. The fact that seed production is markedly reduced and the seed bank becomes depleted before substantial adult mortality occurs (because of the patterns of grazing and the relative sensitivity of these processes) has important implications for the management of saltbush, as will be discussed later.

Local extinction of the shrubs closer to water will obviously result in expansion of the area around the water point which is devoid of saltbush and will be perceived as an expansion of the piosphere (i.e. the zone around the water point in which the composition of the plant community is altered by grazing). It is possible that this process may continue to occur for many years as the stands of saltbush closest to the water point, irrespective of the distance, must experience considerable grazing pressure, and as shrubs are eliminated closer to water those further away begin to experience higher defoliation pressure. Consequently, saltbush can potentially be eliminated from a large proportion of the paddock, although the rate of expansion is likely to decline with time as the length of the 'degradation front' increases as the piosphere expands. The maximum distance that sheep normally graze from water before they need to return to drink will, of course, set an outer limit to this process. In saltbush country, this distance is approximately 3 km (Graetz and Wilson 1984). My study therefore lends support to the hypothesis that even under conservative but continuous stocking saltbush populations continue to be degraded over large areas of sheep paddocks many years after the onset of stocking, so that local extinction of saltbush over much of these paddocks is a strong possibility.

IMPLICATIONS FOR MANAGEMENT

As discussed earlier, maintenance of viable perennial shrub populations is vital in order to maintain the productive potential of the shrublands. In view of the high sensitivity of

bladder saltbush to grazing relative to other chenopod shrubs it commonly occurs with (Graetz and Wilson 1984), management strategies aimed at maintaining saltbush populations will increase the likelihood that the entire plant community is viable and productive.

Priorities for management of the saltbush population can be identified from an assessment of the effects of grazing on the various population processes and the contribution these processes make to the population growth rate. The elasticity analysis presented in Chapter 5 showed that the survival of adult shrubs is the most important part of the life cycle for population maintenance. This study has also shown that continuous grazing can lead to substantial adult mortality. Consequently, the primary aim of management must be to minimise the mortality of established shrubs. The importance of this is further increased because the seed bank becomes depleted before substantial adult mortality occurs, so that once the adults have been eliminated the prospects for natural regeneration in a reasonable time-frame are slight. Reducing or relieving the grazing pressure on shrubs during drought periods may be an important part of minimising shrub mortality. Defoliation of shrubs to the point where they only support about 40 leaves greatly increases mortality (Leigh and Mulham 1971) and should be considered a lower limit for saltbush defoliation.

Although the contribution of recruitment to population growth is small, the establishment of recruits into the population obviously will be necessary to replace shrubs that either die naturally or through the effects of grazing. Because of the sensitivity of reproduction to grazing and the long period required for seed production to occur if the shrubs have been heavily grazed, spelling of shrubs may be needed for lengthy periods when moisture (rainfall) conditions are favourable in order to get significant amounts of seed production. Whether protection of the shrubs from severe grazing during drought times is sufficient for plants to be vigorous enough for flower production is not known. Once seeding has occurred protection from grazing does not appear to be necessary since seedlings seem to

be unaffected by grazing activity.

A State-and-Transition Model For Grazing Management in Saltbush

Westoby *et al.* (1989) proposed a conceptual model of vegetation change in rangelands (the state-and-transition model) which views vegetation as existing in a range of possible alternative *states* with various *transitions* between those states. They suggested this model would be a useful way of organising information about vegetation change for land managers. Because the various states for a vegetation type are alternative positions for the vegetation, certain states may be considered to be more desirable than the others. The aim of research and management, therefore, is to identify the preferred states and the conditions necessary for transitions to occur between states. These transitions can result due to interactions between a range of biotic and abiotic factors including large rainfall events, drought, fire, heavy grazing or resting from grazing. They suggest management should be viewed as a process of taking advantage of opportunities arising because of biotic or abiotic events to force favourable transitions and avoiding hazards that result in unfavourable transitions.

The importance of the spatial element of herbivory and the resulting variability in the impact on the population dynamics of saltbush has been highlighted by this study. Clearly it is necessary for pastoralists and other land managers to recognise this variation when assessing grazing impact and deciding upon management practices, at both the strategic and tactical level (Stafford Smith and Foran 1988). The changes in saltbush under grazing and the circumstances leading to these changes which I described earlier, can be formulated into a state-and-transition model on a paddock/water point scale (i.e. incorporating the spatial elements of grazing impact), which may prove useful to pastoralists and other land managers in assessing whole-paddock grazing impacts and predicting future change. The model demonstrates the dynamic nature of piospheres and emphasises changes in the vegetation that must be avoided because they result in piosphere expansion and they are difficult to reverse (i.e. 'thresholds' such as the

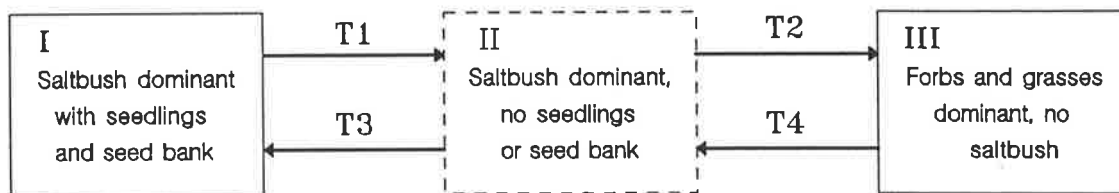
elimination of adults). The model and the states, transitions, opportunities and hazards are described in Box 8.1. How this model relates to a hypothetical water point where the effects of wind and other factors on grazing patterns are ignored, is presented in Figure 8.1. It should be noted that the boundaries between 'adjacent' states will be indistinct in the field, but this should not limit the usefulness of the model.

This formulation of the state-and-transition model for saltbush shrublands differs from that proposed by Westoby *et al.* (1989). In their formulation, the transient state (State II) consisted of seedlings and a seed bank but no adults, which is the opposite of the model I am advancing. The reasons for this discrepancy are not clear but I believe that the fact that the spatial element of herbivory has not been considered in previous studies may be important. Many studies of grazing impact on plant populations are short-term and often involve the introduction of a large number of sheep into relatively small experimental plots consisting of vegetation in good condition, and this has been the case for many saltbush studies (e.g. Wilson *et al.* 1969, Graetz 1986). In small plots short-term heavy grazing quickly leads to the death of adults (within a few months) because of the low tolerance of established saltbush shrubs to almost complete defoliation (Leigh and Mulham 1971). Since these studies are often short-term and the vegetation is initially healthy, seedling and seed abundance are not immediately affected, creating a situation similar to the state II described by Westoby *et al.* (1989). In contrast, my studies have shown that the first change is a depletion of the seed bank and prevention of recruitment. This is because the spatial patterns of grazing in normal size paddocks result in many saltbush shrubs nearer the water point experiencing sustained grazing which is sufficient to prevent reproduction but not to immediately kill the adults.

Extrapolation to other Paddocks

This study was unreplicated so the generality of the results for other paddocks both in the study area and in other parts of the chenopod shrublands is unknown. However, I believe the general findings of the study and the state-and-transition model can be applied

Box 8.1. State-and-transition diagram and catalogues for a bladder saltbush (*Atriplex vesicaria*) piosphere in the chenopod shrublands of SA (after Westoby *et. al.* 1989).



Catalogue of States

State I Saltbush is dominant. Saltbush seedlings and a soil seed bank are present. A small proportion of ephemerals and perennial grasses.

State II Saltbush is dominant but with reduced vigour and with a moderate contribution of biomass by ephemerals and/or perennial grasses depending on seasonal rainfall. There are neither saltbush seedlings nor a soil seed bank. This is a transient state.

State III After adequate rainfall ephemeral forbs and/or perennial grasses are dominant otherwise the ground is bare. All saltbushes are dead and there is no soil seed bank. The soil surface cryptogamic crust is destroyed and erosion is accelerated.

In each of these states perennial chenopods which are more resistant to grazing (e.g. *Maireana sedifolia*) may be present.

Catalogue of Transitions

Transition 1 Continued moderate grazing of saltbush over a number (3-5) of 'average' or dry years without sufficient rest periods, leading to a reduction in plant vigour. This inhibits flowering so there is no input to the seed bank. Seed bank becomes depleted through predation of seeds by ants (Williams 1972), germination and decay. Most germinating seedlings do not survive because of moisture stress. This prevents the recruitment of new seedlings.

Transition 2 Drought together with continued heavy grazing will kill most saltbushes which already have reduced vigour. Actual mortality rate will depend on drought duration. This is a relatively rapid transition which may take as little as one year. It leads to an increase in piosphere size.

Transition 3 Protection from grazing and rainfall to stimulate bush growth, flowering, seed production, germination and establishment. Plants in poor condition need considerable time to increase

their vigour sufficiently to be capable of flowering and setting seed in significant quantities, so several good years or rainfall events in succession are necessary. Consequently this will be a slow transition which may be delayed by the infrequent occurrence of suitable conditions.

Transition 4 For this to occur in a reasonable period of time (5 years), it requires the introduction of saltbush seed by management (saltbush seed is not very mobile [Williams 1979] so it is unlikely to be naturally transported from areas in State I) and protection from grazing, together with rainfall for seedling germination, establishment and growth. It may also require the creation of germination sites by furrowing or pitting of the soil. The probability of success is low and the treatments can be expensive.

This transition can occur naturally over a period of 20-50 years simply by protection from grazing. Areas in State II will respond to protection from grazing and adequate rains so that seeds are produced and seedlings established. Gradually bushes will establish closer to the water as conditions allow, so that the area in State III slowly contracts (c.f. Hall *et. al.* 1964), but this will be too slow to be of practical use to management. This transition leads to a reduction in piosphere size.

Opportunities and Hazards

Because a dense cover of saltbush contributes to the stability of pastoral production and protects the soil from erosion, State I is highly desirable. This state also has conservation value. State III is the most undesirable, so the proportion of a paddock in this state should be kept to a minimum. State II is thus the critical condition because while transition 2 is rapid, transition 4 is slow and difficult to achieve. Transition 2 must be avoided by preventing heavy grazing in drought. The opportunities for flowering and seeding (transition 3) should also be utilised since it is inevitable that transition 1 will occur at some distance from water. Managers however, may be reluctant to utilise these opportunities because they involve the short-term cost of lower stocking rates.

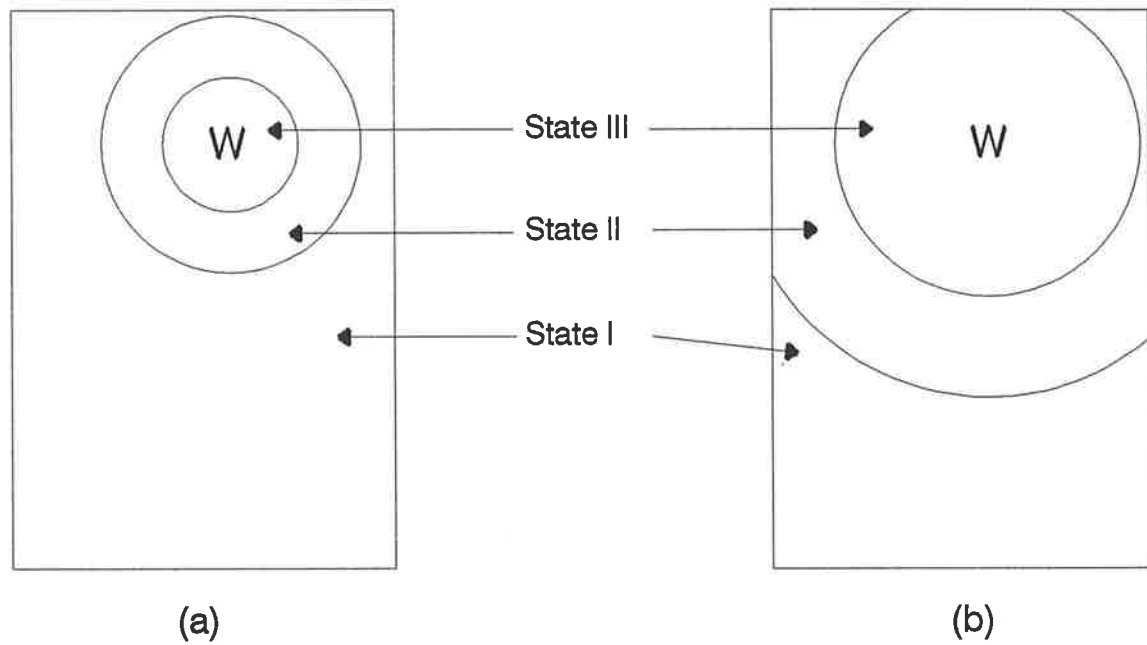


Fig. 8.1. (a) The postulated spatial arrangement around a hypothetical water point (W) of the various vegetation states for saltbush. This ignores the effects of wind, shade and other factors affecting grazing patterns. (b) The vegetation after further degradation. See Box 8.1 for a description of the vegetation states.

to other paddocks. Casual observations in paddocks near the study paddock suggested similar trends to those reported here. Differences between paddocks in the rate of degradation or recovery will arise depending on the amount of saltbush compared to other feed species, the distribution of vegetation types in the paddock, the location of the water point, the climate (more mesic environments will be less likely to suffer degradation because drought is less common and there are more opportunities for recruitment) and, of course, the number of stock. The sub-species of saltbush involved may also have an important bearing on the consequences of grazing. Although there is some overlap, the geographical distribution of the sub-species generally differ in accordance with soil and rainfall patterns (Parr-Smith 1982), which may have resulted in differences arising among sub-species in their life history attributes. Such an effect has been reported for *Artemisia tridentata* sub-species in North America (Bonham *et al.* 1991). Differences in life history attributes may influence the relative ability of the various saltbush sub-species to tolerate grazing.

DIRECTIONS FOR FURTHER RESEARCH

The study of plant-animal interactions in arid rangelands is made difficult by the extensive grazing range of a medium-sized animal species like the sheep and the erratic and unpredictable nature of rainfall, the major driving force of the biological system in these areas (Stafford Smith and Morton 1990). As discussed above, a shortcoming of many studies is the limited time available for the investigation, which means that particular weather sequences which are important for the species in question may be missed. This can be overcome to some extent by population modelling, but the tendency for demographic rates in saltbush in one year/season not to be independent of conditions in the previous year/season limits the model projections. A notable deficiency during my study was a series of good years that were not preceded by poor years. Further research is required to establish the potential of such a series of years to reverse grazing-induced declines in saltbush populations under continuous grazing similar to that reported here.

There are a number of areas that are important in defining specific management practices for saltbush that warrant further investigation. A priority would appear to be improving our understanding of the interaction between drought and grazing and the effects on established shrubs. This would form a basis for refining and then testing specific management practices (such as protection of shrubs from grazing during drought) to examine their impact on shrub mortality and subsequent seed production. Quantifying the minimum level of seed production (or flowering frequency) for population maintenance, and the response of seed production (both seed numbers and viability) to moisture stress and grazing also appear crucial to improved management. As discussed in Chapter 7, studies of the effect of livestock-induced changes in seed bed conditions on seedling establishment would increase our understanding of the factors causing poor recruitment under grazing.

Ultimately, the development of computer-based models which integrate the patterns of grazing impact in paddocks, the population ecology of saltbush and the influence of climate should improve our ability to forecast changes in the state of the vegetation under grazing at any location in a paddock. This would also represent a major advance in our ability to predict the consequences of management decisions and climatic events on the vegetation. These models would enable managers to weigh up alternative practices to minimise the likelihood of undesirable transitions being induced. However, this will require better data sets on the grazing behaviour of sheep and its impact on the population ecology of saltbush under a wide range of climatic conditions than those currently available.

Perhaps the greatest limitation in improving the management of the chenopod shrublands is the difficulty in having information gained from studies such as this adopted by land managers. For new information to be utilised, knowledge concerning plant population biology and grazing impacts will need to be integrated into practical and economically feasible management strategies, with clear benefits for pastoralists. Because there is only

limited information available at present concerning the economic benefits of vigorous and productive shrub communities to pastoral enterprises, this is an important area for future studies.

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