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# Dynamics of Arid-Land, Perennial Plant Populations with an Examination of Potential Causal Agents

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# DYNAMICS OF ARID-LAND, PERENNIAL PLANT POPULATIONS WITH AN EXAMINATION OF POTENTIAL CAUSAL AGENTS

by

Henry George Gardiner

A dissertation submitted in partial fulfillment
of the requirements of the degree

of

DOCTOR OF PHILOSOPHY

in

Range Science

Approved:

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H. George Gardiner.

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# ABSTRACT

## Dynamics of Arid-land, Perennial Plant Populations with an Examination of Potential Causal Agents

by

H. George Gardiner, Doctor of Philosophy
Utah State University, 1984

Major Professor. Dr. Brien E. Norton
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Rigorous statistical examination of the population dynamics of a number of long-lived perennial plant species permitted an interpretation of changes in those populations and the establishment of potentially important causal agents. Survival and recruitment of six species from the mulga-zone rangelands of Western Australia varied across three climatically different periods following the removal of domestic livestock.

Two species' populations (Eragrostis xerophila and Maireana glomerifolia) had their rates of increase reduced by kangaroo and euro grazing. Both survival and recruitment of Eragrostis xerophila were reduced by this grazing while Maireana glomerifolia suffered reduced recruitment during all periods. These negative effects were most pronounced during the post-drought period of more "normal" rainfall. Three other species populations responded positively to grazing. Recruitment and survival of Eremophila spectabilis, were affected by grazing, particularly on a poor condition site, while differences in recruitment were more important for Eremophila leucophylla. Frankenia pauciflora had increased recruitment and survival during the post-drought period. The sixth species (Ptilotus obovatus) suffered increased mortality and reduced recruitment during the post-drought period.

Relative rates of change in management related groups of 18 species, including the six examined in more detail, were presented as a viable addition to the analysis of trend in rangeland vegetation. Grazing by kangaroos significantly reduced the rate of recovery of destocked rangeland pastures.

Site and seasonal factors affected all species populations examined. Site induced differences affected survival of all six species examined, highlighting the difficulty of replicating large scale experiments in rangeland vegetation. Different seasonal sequences (very wet, very dry, and more "normal") produced different species population responses. Populations of most species increased during the very wet, and more "normal", post-drought period, but declined, or remained static, during the drought. Potentially competitive relationships were examined at one site where the complexity of juvenile plant survival responses to seasonal conditions, treatment and to neighbor-free-space suggest potential competition, but more importantly reflect a need for more detailed study.

A re-examination of Danthonia caespitosa population data collected by O.B. Williams in rangeland areas of New South Wales indicates the importance of grazing by merino sheep, seasonal conditions, and the cohort within which a plant is recruited. The extreme variability of the data highlights the need for experimental designs that take account of the frequency and importance of causal agent impact, and are related to the dynamism of the population.

(240 pages)

# CHAPTER I

# STATEMENT OF THE PROBLEM

# Introduction

The effects of man on his environment have, for years, dominated the research interests of applied biological and natural scientists. Documentation of these effects in rangelands has been widespread; however, attempts to identify causal agents have not generally led to widespread management changes. This lack of adoption is due to a number of complex sociological factors as well as a lack of concensus on the meaning of the detected responses. Range scientists, as members of the biological research fraternity, are directly concerned with the complex and varied (both spatially and temporally) ecosystems of arid and semi-arid lands. Their overall goal is to understand these fragile systems so that by wise management they can optimize production while ensuring the preservation of these lands.

Pivotal to the concept of developing wise management strategies is the need to reliably detect changes in the vegetation and/or soil resource, and to accurately relate those changes to causal factors. Controlled experiments may enable the identification of factors which, in isolation, may produce significant changes. Mathematical modelling and complex multivariate analysis can suggest particular hypotheses that should be tested. Ultimately, however, for the establishment of management procedures, the whole interacting system must be examined and relationships between key parameters described unambiguously. From this base of information realistic interpretation of the dynamics of the vegetation resource and sound inference for management purposes can be derived.

Traditional methods of measuring change in rangeland vegetation have included estimates of plant density, cover, biomass, and frequency, as means of detecting changes in species composition through time (Gardiner and Norton 1983). These changes have been interpreted in terms of seral status and viewed from within the framework of succession theory. The establishment of causal relationships depends on the ability to link possible causal agents with some immediate effect or response. By its very nature the successional approach prohibits the establishment of such links in many arid ecosystems because of the extreme spatial and temporal variability, the complexity of impinging environmental factors, and the long-term nature of successional changes. In addition, parameters chosen to express this kind of change are not directly attributable to physiological plant processes; they are generally averages both spatially and temporally (for example, plant density), or are simply indices (often unverified) of some more basic underlying parameter or parameters (for example, plant cover or frequency).

In 1978 Klemmedson et al. issued a plea for concentration of research on the characteristics and dynamics of rangeland plant populations. Austin (1981) suggested the need for a pause, a rethinking of the direction of research, again pointing to the need for more detailed information about the dynamics of populations of individual plants. He suggested that detailed studies correctly constructed and executed, based on individual plant records, provided a "perhaps unachievable" ideal approach to this research. Austin (1980) emphasized that only after establishing the underlying mechanisms operating within ecosystems can changes in those ecosystems be interpreted with confidence.

## Objectives

The research reported here applies new analytical technology to individual plant records and uses the probability of survival of those individuals as a parameter for testing specific hypotheses related to change in semi-arid rangelands in Australia. Survival of individuals of five perennial shrubs and a perennial grass in Western Australian rangelands are estimated three times in nine years and used to examine a number of possible change agents, in particular, seasonal conditions, site, and grazing by large native herbivores. Recruitment data, coupled with survival estimates and incorporated into rate of change analysis permits the autecological responses of these plant populations to be quantified. Rates of change in plant populations are also examined as a means of comparing differences in net changes on areas protected from and open to grazing by kangaroos and euros. Rigorous hypothesis testing based on individual plant responses is used to examine the role and use of plant population studies in clarifying basic tenets in range science, in particular issues of trend and the effects of management practice on plant populations. The analysis approach was tested by using the methods to examine the effects of grazing by sheep, and of precipitation events, on populations of a perennial grass in rangeland areas of New South Wales.

## Definition of Terms

Change -- The difference between the value of any parameter at time t and its value at a previous time t-n (n=1,2,....). There is no attempt to separate long-term, permanent change from short-term fluctuation.

Range Condition -- The present status of a particular area of range vegetation. By implication there is reference to some perceived optimum in terms of natural condition (climax) or a production optimum for a particular use or combination of uses.

Climax -- That theoretically stable state of the vegetation of a particular area that would be achieved, given its geographical location and climatic characteristics, if sufficient time elapsed without perturbation. This state is said to be achieved if species composition is not changing significantly through time.

Trend -- The long-term, permanent change in range condition of a particular area of range vegetation. Usually defined as upward or downward in relation to a perceived optimum.

Survival -- The persistence of a living individual from time t to time t+1.

Survival Rate -- The estimated probability that an individual present at time t will be present at time t+1. For a population of individuals this is expressed as the proportion of those present at time t that are still present at time t+1, i.e. $S = N_{t+1}/N_t$ where S is the survival rate and has values between 0 and 1, and N is the number in the defined cohort of the population.

Recruits -- The numbers of new individuals that entered the population between two sampling dates and are still alive at the second date. The number of these recruits present at the second recording date represents the net input to the population during the period defined by the two recording dates. This number will be the net of seed production minus all deaths in this new group up to the time of recording. It is considered that much of the density dependent control in arid-land plant populations will have occurred before plants are recorded as recruits.

Recruitment -- Absolute numbers of recruits, rather than relative rates, were used in this study. The rationale for this approach is based on the overriding influence of environmental factors in determining the number of individuals being recruited. Coupled with the presence of soil seed reserves, and the small number of individuals on the plots relative to the total plant population of the site (a factor of the relatively small plot size) this suggests that recruitment on a plot during any period is independent of initial population size for any particular population.

Neighbor-free space-- The two dimensional area around an individual within which all points are closer to that individual than to any other. This area is defined by Theissen Polygons drawn about each individual (Vincent et al. 1976) and is calculated using program SPACE (Bayn 1982) with the following assumptions:-- The two dimensional area of the study site is allocated to individuals on the basis of equal weighting regardless of size, age or species.

Population -- a group of individuals of a particular species. The term may be used in reference to different spatial scales. In this study it generally refers to individuals contained within the defined boundaries of recording sites and should not be confused with the statistical population which is defined as the set of all possible individuals and from which the sample (those individuals within the plot boundary) is selected.

Community -- a group of populations connected by effects of one population on the demography or genetic constitution of the other.

Ecosystem -- the plexus composed of both abiotic entities and at least one organism, which are related by the exchange of energy and matter. The definitions of population, community and ecosystem are those expressed by MacMahon et al. 1978.

Grazed/ungrazed -- plants growing on areas open to or protected from grazing by large native herbivores. Use of these terms does not imply that all plants were physically grazed on the grazed areas, but rather that the potential for grazing by large herbivores existed (grazed) or did not exist (ungrazed) in the particular plant populations.

Kangaroos -- a term used to include all large native herbivores grazing at Yeelirrie station including red kangaroos (*Megaleia rufa* Desmarest) and euros (*Macropus robustus* Gould).

Rate of Population Change -- The absolute change in numbers in a population from time t to time t+1. Not to be confused with the relative rate of change in which the change is expressed as a ratio of the initial population size. It is considered that for examining potential causal agents it is appropriate to examine absolute change rather than relative rates.

# CHAPTER II

# REVIEW OF LITERATURE

## The Changing Rangelands

Changes in the vegetation that make up the rangelands of the world are often taken for granted: any level of use by domestic stock is bound to change the nature of the vegetation.

> Activities of man and his livestock, such as grazing, . . . . ., have qualitatively or quantitatively changed almost all of the World's vegetation.
>
> Stoddart et al. (1975), p. 25.

That change has occurred in most rangeland regions of the world is generally unchallenged and evidence has been cited in terms of reduced carrying capacity, reduced stability, soil erosion, depauperate species compliments compared with relic sites, increased frequency of famine, and desertification. Inevitable though they are, changes in rangeland ecosystems may occur at such a slow rate that they go unnoticed until some dramatic event, such as a severe drought, draws attention to the loss of large portions of the vegetation.

Australian rangelands are no exception and changes were perceived as early as 1892 (Dixon 1892), less than half a century after settlement. While there is little recorded vegetational evidence of this deterioration, other biotic indications are present. Perry (1967) points to the inability of pastoral regions in western New South Wales to carry the numbers of livestock run prior to the major droughts in the early twentieth century. Newsome and Corbett (1977) formalized this and provided more evidence in the form of the extinction of some small marsupial species, and the dramatic reduction in the range of many others. The degradation is explained by Newsome and Corbett (1977) in terms of a reduction in the accumulated, presettlement phytomass store, (i.e. reduction in the number of long-lived palatable plants) and the reduced productive capacity of the changed rangeland.

Piosphere effects (Lange 1969) provide stark visual evidence of changes in the vegetation; however, these changes are not necessarily always towards reduced production. Williams (1955) describes a disclimax grassland that may be more productive than the pristine saltbush. Perry (1974) expressed concern that the rangelands of Australia as a whole were continuing to deteriorate, an opinion supported by rerecorded transects in the pastoral regions of South Australia (Lay 1979).

Very little objective evidence is available to verify the dynamics of the degradation of Australian range grazed by livestock but Noble (1979) outlined a number of approaches that have been used to examine and describe changes in rangeland vegetation in Australia. Most research has concentrated on following changes after the removal of livestock and comparing these to changes on grazed plots; this has been done at only a few places in the vast pastoral regions of the continent. Classic studies have been initiated at the Koonamore (T.G.B. Osborn) reserve in South Australia (Wood 1936, Hall et al. 1964, and Noble 1977), Kunoth paddock near Alice Springs (Low 1978), Falkiner Memorial Field Station near Deniliquin (Williams 1955), and near Cunnamulla in Queensland (Roe 1962). Response rates of the vegetation to destocking have generally been slow, leading to predictions of eradication of some species from grazed, shrub-dominated rangelands of southern Australia (Crisp 1978, Crisp and Lange 1976, Barker and Lange 1969, and Lange and Willcocks 1980). The invasion by the European rabbit is cited as a factor contributing to the prevention of recovery.

Western Australian rangelands, while generally developed later than much of the rangeland in eastern Australia, have also been subject to overgrazing and degradation. A royal commission in 1940 (Fyfe 1940) cited degradation of rangeland pastures as the major cause of economic difficulties being experienced by pastoralists. A similar government report (Anon 1979) reiterated this cause of pastoralists' economic difficulty. This extensive report provided stock number declines similar to those referred to by Perry (1967) as evidence for the decline in the pastures, particularly in the shrublands of the mulga zone, and in the marginal areas of the Pilbara region. An earlier report (Wilcox 1963) described degradation of drainage areas and mulga (*Acacia aneura* F.Muell) in rangelands of the Wiluna-Meekatharra area as "severe".

The extensive nature and low productivity of rangelands in Western Australia pose serious barriers to any rehabilitation effort. A large scale Government financed revegetation project in the Kimberley region has met with considerable success (Fitzgerald 1975). Research on the effects of different management strategies, potential rehabilitation methods, or improved pasture species is noticeably absent except for in the wetter tropical margin.

Any attempt to rehabilitate the rangelands will have to be associated with careful measurement of the effects of the various recommended management strategies. The recording of changes and the establishment of possible causal factors will be necessary to evaluate potential approaches to the improvement of rangelands in Western Australia.

## A Plant Population Approach

Understanding plant communities, their responses to climatic conditions, grazing by livestock and wildlife, and perturbation of any kind, man-made or natural, is the goal of plant and range ecologists. Of particular interest to the range scientist is the ability to test specific hypotheses about the responses of arid and semi-arid vegetation to perturbation, in particular grazing by livestock; to provide information that can be applied to the wise management of this resource. Traditional concepts based on the theories of succession (Dyksterhuis 1949,1958, and Sampson 1917,1919) as outlined in basic range science texts (Heady 1975, and Stoddart et al. 1975) have come under increasing scrutiny as the knowledge of the ecology of arid and semi-arid vegetation has developed. More importantly the original theory has failed to explain an increasing number of detected vegetation responses (Westoby 1979/1980, Norton 1978, Foran et al. 1978, and Wilson and Tupper 1982).

Appreciation of the diversity of structure in rangeland ecosystems has led to the development of a more functional theory by Westoby (1979/1980). He postulates a simplified classification of range ecosystems into two basic types. Type I (author's name) ecosystems are those in which the phytomass produced is largely removed by a single agent, such as fire, on a regular basis. Dense grasslands (short and tall grass prairie, tropical savanna grassland) would typically fall into this class. The available vegetation is so dense that the removing agent acts with equal impact on all components of that vegetation, hence all plant species are subject to the same pressures.

Traditional analysis of trend in range condition based on the theories of succession are likely to hold under these conditions. The relative importance of large grazers as removers of biomass, however, may be overrated by Westoby in the light of estimates as low as 15 per cent of above-ground phytomass removed by primary consumers on the tall grass prairie (French 1979).

Type II (author's name) ecosystems would include many of the semi-arid and arid systems in which the vegetation is sufficiently sparse to permit selective phytomass removal, and in which only a small proportion of the phytomass produced is removed by a single agent. The majority of phytomass is either converted to unpalatable woody material or directly re-enters the system in the decomposition cycle. These ecosystems would include many of the shrublands of the world, including those of the Mulga Zone of Western Australia. Application of the traditional theory to these ecosystems is unsupported, or at least there are many "special cases" or exceptions to its application.

Measurement of change in these two ecosystem types, and association with causal agents, is likely to follow different paths. In Type I systems the amount of phytomass produced and the effects of different treatments on that production are likely to be of greatest interest to the land manager. Traditional methods of trend detection have concentrated on the application of succession theory and change in seral stage. This change is manifest in different species composition based on phytomass estimates (or indices such as cover) and may provide an adequate measurement of change useful to a manager of Type I ecosystems. Additionally, because of the uniformity of impact of change-inducing agents on Type I ecosystems, spatial and temporal averages are less likely to obscure the essential dynamics of the system than in more selectively impacted systems.

To be able to separate change due to environmental fluctuation from longer term changes due to either successsion or perturbation requires that recordings be taken of appropriate parameters (Gardiner and Norton 1983, West 1983) at the level of the essential dynamics of the system. In sparse (Type II) ecosystems the greater opportunity for selective impact will increase the variability of that impact on individuals, increase the range of effects, provide a variety of potential change-inducing agents impacting each individual, and will increase the likelihood of unique responses from different individuals and reduce the usefulness of spatially and/or temporally averaged parameters. Harper (1980) presents a case for studying populations of plant parts, and plant population responses as the most logical means of establishing causal relationships, an approach in keeping with the individualistic responses expected in Type II ecosystems.

It is acknowledged that the simplification presented here should not exclude possibilities such as ecosystems that have spatial or temporal variation sufficient to permit the expression of the two types of ecosystem at different locations or at different points in time, or of ecosystems intermediate to these two extremes. Selection of the important parameters to be measured in a particular investigation should be based on the known nature of the ecosystem and the specific objectives of the study. Consideration of the above points may permit the selection of more appropriate parameters for the detection of change in range ecosystems.

Application of traditional trend concepts to semi-arid rangelands has often led to recommended management strategies such as the removal of livestock or a specific rotational grazing system as means of rehabilitating degraded range (Anon 1979, Heady 1975, Stoddart et al.1975). There is an increasing body of evidence that suggests this approach is unproductive in the long term (Biswell 1956, Heady 1958, Tueller 1973, Norton 1978, West et al. in press). Failure has been due to the application of theory not applicable to that particular ecosystem type.

An examination of population processes (survival and recruitment) provides an appropriate level of recording for testing hypotheses related to change in ecosystems, particularly Type II systems (Peet and Christensen 1980 and Harper 1980). This approach will permit the development of specific models of range ecosystems and the application of appropriate statistical methods that will generate rigorous inferences about plant population dynamics and potential change agents (Silvertown 1982, Crawley 1983, and Likens 1983).

While these approaches may be time consuming and tedious (Austin 1981) they may well provide the only viable avenue to increased understanding.

The question remains: should research be restricted to easily observed parameters and indices that have dubious potential for the development of a working understanding of the system just because they are simple to record, quick and repeatable. If the objective is to develop an understanding of the dynamics of arid ecosystems then it seems reasonable to examine parameters that reflect those dynamics.

Methods involving recordings of large numbers of individual plants through time may permit a more meaningful examination of the dynamics of the ecosystems. To some extent a plant population approach may overcome problems such as the difficulty of replicating experiments because of the spatial and temporal heterogeneity of arid-zone vegetation. An examination of recruitment and survival, parameters that can be appropriately modeled by mathematical expressions, reduces information wastage common to currently used spatially or temporally averaged parameters, and also avoids some of the problems associated with the use of indices such as frequency.

Analysis of population data has been widespread in animal studies, but has received scant consideration by plant population biologists. While animal scientists, in particular wildlife biologists, have continued to develop population models of increasing complexity (Brownie et al. 1978, Bart and Robson 1982, White et al. 1982, White 1983), plant ecologists have tended to rely on simplistic, descriptive comparisons of life table data (Harper and White 1974, Williams 1968, 1969, 1970, Williams and Roe 1975), an approach shown by Anderson et al. (1981) to be of limited value for valid inference. Harper (1977) established a foundation for the application of plant population analyses but did not address the problems of making rigorous, statistically sound inference from that data. This lack has become manifest in the literature as researchers have applied commonly accepted statistical tests without due consideration of the underlying assumptions of their particular experimental situations and data sets ( West et al. 1979, West 1979, Law 1981). By comparison with the complexity of analyses applied to animal studies, plant population analyses can best be described as descriptive.

Plant population models are intrinsically simpler than those used in wildlife analyses, primarily because plants are sessile and consequently sampling is easier. Plant population models do not include assumptions related to recapture probabilities, and migration components can be more easily established. Generalized models devised for animal populations (White 1983) can thus be applied to plant populations with little more than a reduction of the number and complexity of assumptions.

## Analysis of Plant Survival

Pearl (1928) and later Deevey (1947) described population behavior using generalized survivorship curves (Fig 1) that have been popularized in general ecology texts. These curves are visual representations of the survivorship information in life tables, in particular, age specific survivorship (Begon and Mortimer 1981). Survivorship curves were used to describe the population dynamics of particular species in a general manner, thus permitting descriptive comparisons between populations. These early approaches were made by animal biologists but had obvious application to populations in general, be they plant or animal.

Analysis of populations of annual and short-lived plant species has been extensive (for example, Antonovics 1972, Harper 1977, Law 1981, Bazzaz and Harper 1976, Cavers and Harper 1967, Smith 1983, Harper and Gajic 1961, Leverich and Levine 1979, Schaal and Leverich

1982, Sharitz and McCormack 1973, Loria and Noy-Meir 1979/80), but fewer long-term studies of perennial species have been conducted (Tamm 1948, 1956, 1972a, 1972b, Williams 1955, 1968, 1970, West 1979, West et al. 1979, Norton 1978, Wright and Van Dyne 1981). Notable in terms of the length of continuous data sets and consistent recordings are the studies of Tamm (loc. cit.) and Williams (loc. cit.). Tamm concentrated on graphical presentations and compared the estimated slopes of various portions of the survivorship curves. Williams' studies on perennial grasses involved much larger numbers of individuals and he also compared the form and slope of the survivorship curves (Williams 1968). Detection of perennial grass response to grazing was attempted (Williams 1969) using a response index derived from a ratio of density changes in grazed and ungrazed plots, while half life was used to make inferences about the effects of year, cohort and grazing on Danthonia caespitosa and Enteropogon acicularis populations. Austin et al. (1981) have treated the same data to multivariate analysis and have ranked succession, seasons, soils and grazing (in that order) as factors affecting the survival of these two grasses.

Sarukhan and Harper (1973) examined populations of three species of Ranunculus over a period of 2.5 years. Comparisons of the depletion curves, cohort survivorship and death risks revealed basic differences in the responses of these species to their environment. These data were used to establish the life history characteristics of each species, however, rather than to make sound inferences about responses to environmental variables. In this sense the majority of plant population studies have been deterministic in nature.

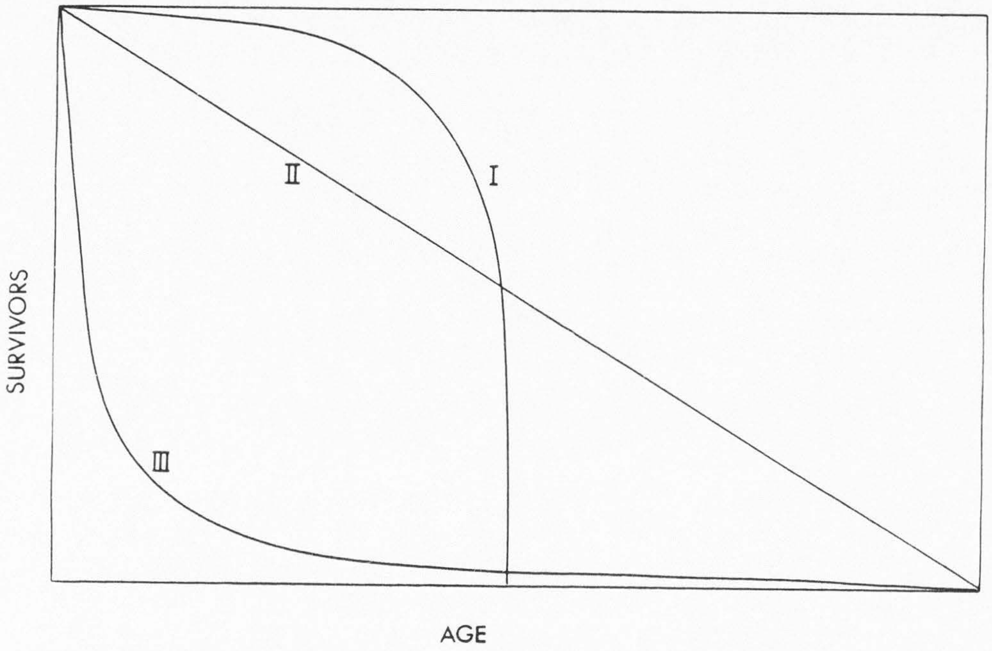

Figure 1. Idealized survivorship curves used to explain different types of population response, Deevey (1947).

Woody perennial species have generally been examined using age-class derived, static life tables. Ageing of individuals has been by growth ring analysis (Auclair and Cottam 1971), bud scar patterns (Hett and Loucks 1968) and historically known invasion events (Tueller and Blackburn 1974). Inference about changes in these populations and possible causal events is thus difficult if not impossible.

> It is seldom possible to age the trees in a forest so accurately (or in sufficient numbers) that discrete year classes can be separated and, in most such data, groups of years are taken together to make an age class. This hides annual variations in mortality and recruitment;...
>
> Harper 1977, p 623.

Harper points out many shortcomings of using age structure for making inferences about population behaviour in tree and shrub species, in particular problems of clonal growth, the lack of a demonstrable, consistent relationship between age and size, and the apparent lack of stability in populations regarded as "virgin" and therefore, by assumption, stable.

Harper (1977), Harper and White (1974) and more recently Austin (1981), Beeftink (1979/80), and Likens (1983), reaffirm the need for plant population studies using recordings on individual plants in permanent plots as the most profitable research avenue to "expand understanding of structure and function in ecological relationships" (Beeftink 1979/80). A number of perennial plant investigations (Williams 1968, 1969, 1970, Crisp 1978, Austin et al. 1981, West 1979, West et al. 1979, Norton 1978, Wright and Van Dyne 1981) have been conducted in arid zone pastures using permanent quadrat recordings of individual plants. Chart quadrat or photopoint data have been used for these studies. Several (Crisp 1978, West et al. 1979) suffer from the lack of sufficiently large numbers of quadrats or cover too few individuals to provide sound evidence on which to base inferences. Others have been content to restrict analyses to descriptive or deterministic comparisons (Williams 1968, 1969, 1970, Wright and Van Dyne 1981) while a few have attempted to draw sound statistical inferences from their data (West et al. 1979, Austin et al. 1981). This dearth of studies attempting statistical analysis can be attributed, at least in part, to the relatively recent evolution of Plant Ecology from a descriptive to a quantitative science.

The West et al. (1979) analysis of sagebrush-grass data from south eastern Idaho attempted to compare and contrast the slopes and shapes of survivorship curves using a regression approach and the non-parametric, Kolmogorov Smirnov test. Austin et al. (1981) employed multivariate (PCA) methods in an attempt to sort long-term changes from short-term fluctuations in data collected earlier by Williams (1970), and to assign possible causality to succession, seasonal effects, soil and grazing in explaining the variation in demographic responses of *Danthonia caespitosa* and *Enteropogon acicularis*.

While they offer alternatives to the interpretation of population data these approaches utilize modifications of the original parameters into indices such as density and curve slope, and do not attempt to model the basic process of plant survival, nor do they permit rigorous mathematical testing of specific process-related hypotheses. Their modifications of the original data appear to be related more to the historic use of parameters than to a careful analysis of the specific processes that are occurring at the individual plant level. Norton

(1978) highlights the inadequacy of traditional interpretation of permanent quadrat data in terms of density and cover changes on salt desert shrubs in southwestern Utah.

Modelling of the basic population processes, particularly survival, has become common in the wildlife literature (Brownie et al. 1978, White et al. 1982, White 1983). This approach allows the assumptions of various models to be tested for their appropriateness to particular data sets using classical statistical methods of Maximum Likelihood (Mood et al. 1974, Miller 1981, Edwards 1972), and for the specific testing of hypotheses related to the process of surviving.

Chiang (1960a, 1960b) developed the stochastic basis and original probability density functions for survival processes within cohorts of individuals. His formulation of the binomial approximation of the survival process within populations was based on the Bernoulli nature of the act of surviving over a particular period. This permitted the derivation of a multinomial probability distribution function useful for making inferences about the survival of individuals in cohorts.

Knowledge of the mathematical nature of the survival process and the application of the classical procedures of Maximum Likelihood permitted the analytical solution to a number of models for bird survival based on banding data, given a range of assumptions (Brownie et al. 1978). This provided the stimulus for the application of numerical methods and the derivation of a general approach for the use of survival data in specific hypothesis testing (White 1983). White's computer program (SURVIV) can be used for testing any mathematical model of survival based on the multinomial probability density function. The program tests for goodness-of-fit of each model to the data set in hand and then tests specific hypotheses about the survival process by constructing Likelihood Ratio Tests between models of varying complexity. Although developed for the analysis of animal populations the program (SURVIV) is applicable to all forms of survival data and can be applied without modification to the analysis of plant survival.

## The Importance of Kangaroos and Euros

The concept of rangelands as the supplier of raw materials for multiple uses (livestock industries, wildlife habitat, recreation, watershed, mineral and energy supply, and defense) has long been accepted in the United States. This is not the case in many other parts of the world where pastoralism still lays claim to single use of the land. Often compared with United States rangelands in terms of livestock industries, Australian rangelands have not been considered a multiple use resource, particularly where wildlife is concerned, by other than a relatively small group of arid zone researchers. Low human population densities, the contiguous nature of rangeland areas, the lack of intermingled farm land and the apparent ubiquity of major wildlife species have contributed to the lack of awareness by the general populace to the potential of the Australian areas, and has permitted the maintenance of a largely single-use management philosophy.

Increased sensitivity of city dwellers subject to the popular media and international pressure during the 1970s did stimulate research on kangaroos and euros. Conflicts with pastoralists and adjacent agricultural land users have, however, provided the greatest impetus to wildlife research. It is not research derived from any concept of multiple use or species conservation, but rather from a common belief that wildlife (particularly kangaroos and euros) should be regarded as vermin, in direct competition with livestock industries.

Specific examples of apparently excessive numbers of these large herbivores and their potential to compete with domestic stock are detailed by Ealey and Suijdendorp (1959) and Griffiths and Barker (1966). Ealey and Suijdendorp's study in the northwest of Western Australia indicated high numbers of euros, considerably above presettlement levels, were a possible cause of the decline of the sheep industry in the region. Griffiths and Barker (1966) refer to the pest status conferred on red kangaroos in Queensland.

Newsome (1975) provides a lengthy explanation of the reasons for what appears to be an historically supportable contention that kangaroo and euro numbers are considerably above presettlement levels. He attributes the increases to changes in the nature of the forage and the habitat induced by grazing livestock, the "marsupial lawns" produced by grazing cattle removing the dry grass and inducing fresh, green regrowth so essential to the diet of the kangaroo. Euro numbers reported by Ealey and Suijdendorp are thought to have increased because of the changes in plant communities toward a preponderance of unpalatable spinifex in the northwest following overgrazing by sheep. Additionally, the provision of permanent, artificial water supplies for livestock has removed the natural population-limiting factor of lack of water during droughts. These apparent benefits for the large macropods have been accompanied by dramatic declines and even extinctions of smaller marsupial species, attributed by Newsome (1971) to removal of cover so necessary for avoidance of predators, and to increases in the activity of those predators.

Determining the absolute numbers of kangaroos utilizing an area of rangeland is difficult. Aerial survey techniques developed and used extensively by Graeme Caughley and his coworkers (Caughley, Sinclair and Wilson 1977, Caughley and Grigg 1982, and Caughley et al. 1983) indicate kangaroo numbers of between two and five per square kilometer are not uncommon in pastoral areas. These translate to considerably fewer animal units, on average, than attributable to livestock inhabiting the same areas. This should not be taken to imply that higher local densities are not found. Low and others (1981) recorded average densities of from 3.6 to 0.06 per square kilometer, but during periods of high kangaroo densities up to 75 percent of those present were found in only one plant community. Work in central Australia (Newsome 1965, Low and Low 1975, Low et al. 1973, and Low et al. 1981) documented changes in the utilization of plant communities with weather changes, seasonal fluctuations and the availability of green forage.

Insistence by livestock producers that the numbers of Kangaroos are unnaturally high and claims of high forage consumption, shown to be overstated (Griffiths et al. 1974), stimulated a number of studies to determine the nature and extent of the dietary overlap between kangaroos and sheep and cattle (Griffiths and Barker 1966, Ellis et al. 1977, and Storr 1968). Others have examined the spatial and temporal interactions between kangaroos and livestock (Newsome 1965, Low and Low 1975, Low et al. 1973, Low et al. 1981, and Johnson and Bayliss 1981).

Cattle and kangaroo diets appear to overlap considerably, both being predominantly grass eaters; however, the central Australian work indicates a spatial and temporal separation in all but very dry seasons, when competition becomes severe (Low et al. 1981).

Sheep and kangaroo diet overlap is less pronounced during good seasons, sheep being predominantly forb and browse eaters compared with grass-eating kangaroos. Under very lush conditions, Ellis et al. (1977) found greater overlap than during intermediate conditions. Griffiths et al. (1974), on the other hand, found overlap increasing with the increase in drought stress. Squires (1982) suggests that any utilization of the same forage resource constitutes competition despite temporal separation. Most of the evidence indicates the effects of kangaroos on livestock production may be minimal during good seasons, but during droughts there is likely to be considerable conflict of interest between the livestock producer and the wildlife.

None of the studies have addressed the question of the effects of the increased grazing pressures exerted on the vegetation by kangaroo populations considerably larger than were present presettlement. Degradation of the pastures has been attributed solely to the action of the livestock, despite evidence of increased populations of kangaroos.

# CHAPTER III

# SOUND INFERENCE FROM PLANT POPULATION DATA

## Introduction

Beeftink (1979/80), in his introductory speech to the second symposium of the working group of succession research on permanent plots, emphasized the need for research that would enable mechanisms and causal agents to be identified. That permanent plots should be used for these studies was implicit from the group's title. Klemmedsen et al. (1978) offered a similar plea for research in rangelands as did Likens (1983) in his presidential speech to the Ecological Society of America. Austin (1981) saw recordings on individual plants as the ultimate but perhaps unachievable form of recording plant information for ecological inference. These studies can take two forms: first a detailed examination of each of the demographic processes: seed set, germination, recruitment, growth, and mortality. Detailed studies should be considered in the same light as autecological studies of individual species, and can be used to establish possible links to causal agents. A second form of demographic study needs to account for changes in the populations and communities of plants as they occur through time. Studies of this nature will be attempting to quantify net changes of populations and the compound vegetation responses referred to as succession or, in range science, as trend.

### Data Collection

The specific methodolgy for recording population data in a form suitable for survival analysis will vary with the particular study objectives, species of interest, its growth form and physical attributes. The aim of all methods is to provide unambiguous data in a form that can be converted to specific cohort survival rates through time. Common to most studies is the need to record individual plants, to be able to relocate and positively identify a particular individual on sequential recording dates. Two general methods have been widely used: mapping individuals within a defined plot, or clearly tagging individuals to permit their re-examination.

### Mapping

The scale and technique of mapping will vary with the nature of the population being studied. Each map should be of an area large enough to include as many individuals as possible and yet sufficiently small that all individuals can be accurately recorded. These maps, called chart quadrats, have been made of areas as small as 1 $dm^2$ for some annual species and up to 5 $m^2$ for sparse perennial shrubs (Norton 1978). Maps have been created using transparent mapping tables (Burdon et al. 1983), gridded quadrats (Norton 1978, and West 1979), and pantographic methods (Canfield 1957). Most studies have attempted to record additional parameters such as foliar cover from these quadrats.

A modification of the chart quadrat method that has been used in sparse vegetation is the photoplot method. Photographs have varied in scale from complex stereo photographs of meter square plots (Wimbush et al. 1967) to small scale (1:250) aerial photographs of 20 x 30 meter plots (Hacker 1978). Intermediate scale photographs have been acquired using boom devices to photograph from up to seven meters above the ground (Goodwin and Walker 1972; Owens et al., in press, see Appendix 3). Useful information for population studies has been extracted only after mapping from the photographs and extensive ground truthing.

## Tagging

An alternative to mapping is to tag a number of individuals in each successive cohort and to follow these individuals through time. This is a particularly useful approach when individuals are small or are part of a closely packed population. For example; aerial stems of rhizomatous species, such as Juncea (Tamm 1956) and Carex (Noble et al. 1979), individuals of a dense annual/biennial weed population (Lee and Hamrick 1983), or tillers of caespitose grasses, such as Agropyron desertorum and Agropyron spicatum (Caldwell et al. 1981).

## Sampling Intensity

Sufficient individuals should be recorded to permit estimation of the parameters of interest to within predetermined levels of precision. This necessitates pilot sampling over at least one time interval. Program SURVIV (White 1983) has a subroutine that can be used to calculate the number of individuals that need to be recorded to obtain a particular level of precision. As more of these types of studies are conducted the number of individuals required for sound inference will become more obvious. All cohorts should have sufficient numbers for reliable inference, implying that a variable plot size or tagging approach will have advantages over a fixed plot approach, particularly for species that have variable survival rates and variable cohort densities.

Ideally the interval between sampling dates should be equal, preferrably related to some biological time scale or developmental stage (Robotnov 1978). The time interval used will differ according to the objectives of the study. Weekly intervals during the growing seasons would be more likely to be meaningful for annual plants while intervals of a year or longer may be preferrable for hypotheses about the behavior of perennial shrubs. Sampling related to climatic sequences may be appropriate for longer-lived perennials. Models are easier to formulate and data easier to interpret if the intervals are based on some biologically important time frame.

## Survival Analysis

Analysis of the survival of individuals within populations is one aspect of the detailed studies that can be achieved using new technology. Survival, is one of the three basic parameters that can be used to define the dynamics of a population, fecundity and growth being the other two (Silvertown 1982). Survival can be used as a parameter for testing specific hypotheses about forces impacting a particular plant population or community (group of populations). Data collected on the survival of individuals within specifically defined cohorts (dynamic life tables, Silvertown 1982) will permit the use of the probability of an individual surviving from time t to time t+1 as the parameter for rigorous testing of these hypotheses.

Recent developments in the studies of wildlife populations (White 1983) can be applied directly to the analysis of the survival of plants. The following is a guide to the form of the data, mathematical models and hypothesis testing procedures used for making these inferences. The methods are based on the use of a FORTRAN computer program (SURVIV) written by G.C. White (1983).

Assumptions

Individual plant records permit the identification of mortality events during a given time interval. Each of these mortality events is a Bernoulli random variable, it is a success/failure event; the plant either lives or dies. Assuming these events are independent of each other then a number of them (a random sample) will be a Binomial random variable. The probability density function of a binomial random variable can be written as:--

$$\frac{N!}{x!\,(N-x)!} \cdot P^{x}\,(1-P)^{N-x}$$

where $x$ = the number of deaths
$P$ = the probability of dying
$N$ = the number of individuals present at the beginning of the period.

If each binomial random variable is used to estimate a single probability of survival then a number of these random variables can be combined to estimate a number of survival rates. This combined distribution is called the multinomial distribution of k-1 random variables and is written:--

$$\frac{N!}{x_1!\ldots x_{k-1}!\,x_k!} \cdot P_1^{x_1} \ldots P_{k-1}^{x_{k-1}} \cdot P_k^{x_k} \quad .$$

This relationship was demonstrated for cohort data by Chiang (1960a, 1960b) and has been applied to radio-collared elk populations (White 1983). Given this distribution, the likelihood function (Mood et al. 1974) is defined as the product of all possible probabilities given the data matrix.

$$L(P|x) = C \cdot P_i^{x_i} \quad \text{for } i=1,2,\ldots,k-1$$

$$\text{where } C = \frac{N!}{\prod x_i!} .$$

Other assumptions are primarily associated with this multinomial model. All individuals once assigned to a cohort must be identifiable as belonging to that cohort at future sampling times. Death of an individual must be identifiable and movements of individuals must be accounted for. The unit defined as an individual for the purpose of the study must be identifiable.

## Analytical Estimation

Estimates of each of the survival rates can then be obtained by the method of maximum likelihood, which estimates the value of each parameter so as to maximize the value of the likelihood function. These can be calculated for simple data sets by taking the first partial derivative of the likelihood function with respect to the parameter of interest, setting it equal to zero and solving.

The estimate of $P_1$ is found by setting $\frac{\partial L(P|x)}{\partial P_1}$, equal to zero and solving for $P_1$.

## Numerical Estimation

For more complex data sets the analytical solution for the estimates may be difficult and in many cases impossible to derive, in which case the estimator is said to be not of a closed form. In these situations a numerical or iterative solution using successive approximations can be used (Miller 1981). In general terms this involves inserting an initial value for the parameter, calculating the value of the likelihood function, changing the parameter value and recalculating the function. This process is repeated iteratively for all parameters and their maximum likelihood estimators are those values that maximize the likelihood function value. White (1983) used this approach in program SURVIV, thus providing the benefit that the program can be applied to all forms of survival model. It has a measure of procedural generality not afforded by analytical methods.

## Model Formulation

Testing hypotheses using this approach depends on the correct formulation of the sub-models (mathematical representation of the assumptions underlying each hypothesis) and their representation in algebraic form. Sequential recording of cohort data permit the construction of a triangular data matrix, for example: data collected as part of the Yeelirrie study (Chapter 4) for the species Maireana glomerifolia are presented in Table 1 (total species data are presented in Appendix 2). The data matrix has the general form shown in Table 2.

To formulate this data matrix into a multinomial model it is necessary to consider the individuals that die during each period. Thus $D_{i,j,g} = N_{i,g} - R_{i,j,g}$ is the number of grazed individuals from cohort i dying during the jth period. Using this transformation on all cohorts results in the transformed data matrix in Table 3.

Table 1. The number of individuals surviving in three grazed and three ungrazed cohorts of *Maireana glomerifolia*.

| | | Number Surviving Until | | |
|---|---|---|---|---|
| | $N_i$ | 1976 | 1979 | 1982 |
| GRAZED | 121 | 119 | 116 | 113 |
| | 27 | | 14 | 12 |
| | 6 | | | 3 |
| UNGRAZED | 127 | 125 | 124 | 113 |
| | 152 | | 61 | 55 |
| | 113 | | | 86 |

Table 2. The general form of the data matrix for *Maireana glomerifolia*.

| 1973 | 1976 | 1979 | 1982 |
|---|---|---|---|
| $N_{1,g}$ | $R_{1,1,g}$ | $R_{1,2,g}$ | $R_{1,3,g}$ |
| | $N_{2,g}$ | $R_{2,2,g}$ | $R_{2,3,g}$ |
| | | $N_{3,g}$ | $R_{3,3,g}$ |
| $N_{1,u}$ | $R_{1,1,u}$ | $R_{1,2,u}$ | $R_{1,3,u}$ |
| | $N_{2,u}$ | $R_{2,2,u}$ | $R_{2,3,u}$ |
| | | $N_{3,u}$ | $R_{3,3,u}$ |

where $N_{i,g}$ = the total number of the grazed cohort i present at its initial recording, and $N_{i,u}$ = the total number of the ungrazed cohort i present at its initial recording. $R_{i,j,g}$ = the number of individuals in the grazed cohort i present at recording time j, and $R_{i,j,u}$ = the number of individuals in the ungrazed cohort i present at recording time j.

Note: each half of the data matrix is triangular so that only the first cohort is present at all recording times. Cohort two is made up of the individuals that were recruited between the first and second recording time, hence it has survival rates from only the second recording time to the third and from the third to the fourth. Similarly, cohort three has only one estimable survival rate, from time three to four.

Table 3. The general form of the transformed data matrix for the Maireana glomerifolia example with the components that make up the cells of a multinomial model.

| 1973 | 1976 | 1979 | 1982 | Surviving 1982 |
|---|---|---|---|---|
| $N_{1,g}$ | $D_{1,1,g}$ | $D_{1,2,g}$ | $D_{1,3,g}$ | $N_{1,g}-D_{1,1,g}-D_{1,2,g}-d_{1,3,g}$ |
|  | $N_{2,g}$ | $D_{2,2,g}$ | $D_{2,3,g}$ | $N_{2,g}-D_{2,2,g}-D_{2,3,g}$ |
|  |  | $N_{3,g}$ | $D_{3,3,g}$ | $N_{3,g}-D_{3,3,g}$ |

The matrix is repeated for the ungrazed half of the data set with the subscript g changed to u.

The $D_{ij}$'s are the numbers of individuals in cohort i dying during period j for i = 1,2,3 and j = 1,2,3 and algebraic expressions for each of them are used to estimate the rate of survival for each cohort in each period (for example:-- $D_{1,1,g}= N_{1,g} \times (1-S_{1,1,g})$,

$D_{1,2,g}= N_{1,g} \times S_{1,1,g} \times (1-S_{1,2,g})$,

$D_{1,3,g}= N_{1,g} \times S_{1,1,g} \times S_{1,2,g} \times (1-S_{1,3,g})$,

etc.). These algebraic expressions can be completed for the other cohorts for both grazed and ungrazed circumstances and are entered in the PROC MODEL phase of program SURVIV (Appendix 1). This will form the model on which all estimation and testing procedures are based. A sub-model of this in which all survival rates are permitted to vary has the fewest assumptions and is referred to as the general or unconstrained model. (It should be noted that input during all phases of program SURVIV must be in FORTRAN code).

## Hypothesis Testing

Constructing hypothesis tests requires comparison of a reduced or simplified sub-model that embodies the assumption that is to be tested with a general sub-model that does not include the constraints associated with the assumption being tested. For the present example we will examine the assumption that grazing by kangaroos has no effect on the survival of individuals. An appropriate reduced model for testing this assumption is one in which the grazed cohort's survival rates are set equal to the corresponding ungrazed cohort's rates. A general sub-model would be one in which all the survival rates were permitted to vary. Estimates of each survival rate under the general and reduced sub-models are substituted into the appropriate likelihood functions resulting in two numerical values which are used to construct a likelihood ratio test of the hypothesis. It should be noted that this test is valid only if the reduced sub-model forms a more constrained model within the general sub-model.

The likelihood ratio test is constructed by taking the natural logarithm of the ratio of the numerical value of the likelihood function of the reduced model to that of the general model. Multiplied by minus two this ratio is approximately Chi square with degrees of freedom equal to the number of constraints by which the general and reduced models differ. The test can be written as;

$$-2 \log \frac{L_{(red)}}{L_{(gen)}} = -2(\log L_{(red)} - \log L_{(gen)}),$$

where $L_{(red)}$ is the numerical value of the reduced sub-model likelihood function and $L_{(gen)}$ is the numerical value of the general sub-model likelihood function.

For the Maireana glomerifolia example the test statistic is:

-2 (-24.37 - (-19.85)), or a Chi square value of 9.04 with six degrees of freedom; probability level for alpha is 0.1838. Thus we fail to reject the hypothesis that grazing by kangaroos does not affect survival of Maireana glomerifolia. With larger data sets it would be possible to test a variety of hypotheses using different reduced submodels. The end result would be a series of hypotheses that would identify acceptable simplifications of the original model and an indication of factors that affect plant survival.

## Power of the Tests

Personal intuition should be used when setting the alpha levels for these tests and should be based on the relative importance of type I and type II errors. Program SURVIV has simulation capabilities that can be used to establish the power of a particular test. When setting alpha levels it is necessary to consider that for a given sample size, the power of the test will decline as the alpha level is reduced (Cohen 1977).

## Pinpointing the Significance

In much the same way as multiple range tests (Steel and Torrie 1980) can be applied following a significant F test, z tests can be used to test for differences between pairs of estimates of survival rates. Confidence intervals (95 percent) output from program SURVIV can be used in a similar way to identify significant pair-wise comparisons thus permitting interpretation of responses to potential causal agents. It is not recommended that this additional step be taken unless the likelihood ratio test rejects the null hypothesis under consideration and the results should only be used as a guide to interpreting differences and not as a stand-alone test of those differences.

## Establishing Functional Relationships

One advantage of the maximum likelihood approach is that parameter estimates are not restricted to a simple, one factor, form. They can be expressed as functions of other variables such as precipitation, grazing intensity, soil moisture etc., provided there are sufficient data points, bearing in mind that for each new variable to be estimated two of the general model parameters must be amalgamated, i.e., one degree of freedom is lost for each extra parameter estimated. The *Maireana glomerifolia* data set is not large enough to permit testing of functional relationships of any consequence.

## Limitations

The maximum likelihood approach to survival analysis is extremely flexible and can be used to test hypotheses about weekly survival rates of annual plants, daily survival of small seedlings, or longer term survival of perennial species recorded annually. There are, however, some limitations to the approach. Mostly these are imposed by computer capability. Maximizing the likelihood function for large parameter models is difficult because of the need to maximize functions in a large multi-dimensional space. Very complex models may be difficult to formulate and the results difficult to interpret. Because the process of solution is iterative it is possible to have situations in which convergence does not occur and parameter estimates will be incorrect. Complex functional relationships will reduce the number of survival rates that can be estimated. Tests of hypotheses using likelihood ratio tests are only approximations to the Chi square distribution and caution should be exercised when small sample sizes are involved.

## Rates of Population Change

### Introduction

Survival is but one of two processes that determine the fitness of a population. Crawley (1983) emphasizes the need to consider both survival and recruitment if the total impact of management, site, biotic, or climatic factors is to be clarified. The success of a population under a particular set of conditions can then be defined as its absolute increase during any defined period. In many populations both the survival and recruitment processes are strongly density dependent (Silvertown 1982, Crawley 1983). This control mechanism has been invoked to explain stable states, such as climax, and to explain why plants do not completely dominate larger areas of the globe. In arid lands the impact of density dependence is likely to be greatest at the seed and seedling level and any stabilizing influence of purely density dependent control is likely to take a subordinate role to the vagaries and stresses of the weather and the impact of grazing livestock (Crawley 1983, Chambers 1979).

An examination of rates of change in populations under various treatments, on different sites, during different seasons, with different neighbors at different densities, may permit some clarification of the observed variability of population responses in natural plant communities. To this end it is necessary to examine both recruitment and mortality. These processes are often viewed deterministically (Silvertown 1982, Crawley 1983, and Varley et al. 1973) when used to consider theoretical rates of population change. However, the inadequacy of knowledge about the driving mechanisms and impinging forces limits the usefulness of this approach for examining natural plant populations. The models developed by animal population biologists and applied to survival analysis utilize a stochastic approach. Bhat (1971 p.3) suggests both the processes of survival and birth (recruitment) should be treated stochastically.

## The Models

The binomial nature of the survival/death process was explored earlier but the recruitment process in arid-land plant populations may be more appropriately modeled as a Poisson process. It seems reasonable to assume that the number of individuals actually recruited onto a plot will be very small relative to the potential number; very few of the seeds produced germinate at any one time, and only a few of these establish to become recruits into the population defined within the plot boundaries. Establishment of individuals on the plot is essentially independent of the original population within the plot boundary, being more influenced by the individuals in the surrounding populations. This is particularly so when the plot size is small relative to the surrounding population and when the seeds are relatively mobile. Feller (1968; p 153-56) described processes with these characteristics as being well approximated by the Poisson probability density function, he described this as a Poisson process.

Thus is seems reasonable to examine the process of change in arid-land plant populations during any defined time interval as a combination of Poisson input (recruitment) and Binomial output (death). Details of this model were explored by Hoel et al. (1972 p.53-56) who used a different example of the same model we have assumed to represent the process of change in arid-land plant populations. Their model has a combined probability density function (p.d.f) derived by taking the product of the binomial and poisson p.d.f.

$$f(B,S) = \frac{e^{-B}B^{b}}{b!}\binom{N}{d}(1-S)^{d}(S)^{N-d}. \; . \; . \; . \; . \; . \; . \; . \; . \; . \; . \; . \; . \; . \; . \; . \; 1.$$

where B is the expected number of births, S is the expected survival rate, b is the actual number of births and d is the actual number of deaths recorded from an original population size N. It is thus possible to test the hypothesis of zero change in the numbers of a population from time t to t+1 by constructing a likelihood ratio test using the constrained model where $B-(N(1-S))=0$.

While this hypothesis is of some interest to plant demographers, it is of greater management interest to compare rates of change between two populations (e.g., between grazed and ungrazed populations of the same species). To explore this hypothesis it is necessary to use the joint p.d.f. involving the product of two p.d.f.s of the same form as in equation 1 above.

$$f(B_i,S_i) = \prod_{i=1}^{2} \frac{e^{B_i}\, B_i^{\,b_i}}{b_i!}\binom{N_i}{d_i}(1-S_i)^{d_i}(S_i)^{N_i-d_i}. \; . \; . \; . \; . \; . \; . \; . \; 2.$$

To develop maximum likelihood estimators of each of the parameters ($B_i$, and $S_i$ for i = 1,2.) it is easier to apply numerical methods (page 33) and thus establish the values of the log likelihood function for constrained and unconstrained models necessary to test hypotheses about rates of change.

## Hypothesis Tests

Three types of hypothesis were tested, the first involved each of the populations separately, and the other two tested differences between two poulations. The hypotheses tested included:--

1. Change in the numbers of both populations 1 and 2 is not different from zero, i.e., $B_1 = N_1(1-S_1)$ and, in a separate test, $B_2=N_2(1-S_2)$.

2. The change in numbers of population 1 is not different from population 2, i.e. $B_1 - N_1(1-S_1) = B_2 - N_2(1-S_2)$. Estimators needed to derive the value of the constrained model necessary for this test were solved numerically using a model in which each of the net change in numbers was set equal to a variable Z.

3. The ratio of the expected number of recruits ($B_i$) to the expected death rate ($1-S_i$) was not different between the populations,

i.e., $$\frac{B_1}{(1-S_1)} = \frac{B_2}{(1-S_2)} = Y,$$

where Y is the estimated ratio under the constrained model.

The Hoel et al. (1972) model can be used to consider the long-term implications of particular recruitment and death rate values. They demonstrated that, providing rates of input and output did not change, their joint model was distributed Poisson with:

parameter lambda = $B/(1-S)$, where $B$ = the number of inputs (recruits) and $(1-S)$ is the rate of output (death rate). Therefore two populations for which the ratio $B/(1-S)$ were equal would, given no change in recruitment or death rate, eventually equilibrate at the same number of individuals. This ratio can be considered as a measure of the internal behavior of the populations under examination, it provides information similar to examining relative rates of change.

Interpretation of relative rates of change to demonstrate competition and/or compensatory interactions between different populations is dependent on several assumptions. First, any single estimate of relative rates of change is but one estimate of what is going on in those populations, it is necessary to first test whether one rate is significantly different from another that is supposedly responding to it. Second, any attempt to demonstrate competitive or compensatory interactions should necessarily involve all the potentially interacting populations. Determining which these might be for a plant community is beyond current methodology and would require a level of recording seldom approached in arid-land plant studies. Thus, while relative rates of population change offer an alternative means of describing population behavior, they are difficult to use in any attempt to relate changes to potential causal agents.

Observations of plant populations are only possible at discrete sampling times, and given the assumptions of Poisson recruits, and Binomial deaths, the ratio $B/(1-S)$ provides information consistent with making valid inferences about the responses of those populations to external impacts (potential change inducing agents). The use of absolute rates of change (Hypothesis 2 p 43) and the $B/(1-S)$ ratio (Hypothesis 3 p 43) enable the testing of hypotheses about absolute responses to potential causal agents as well as about the method by which those agents effect that absolute change.

The results from the application of the first hypothesis to both populations provides estimates of their rates of change important for interpreting the second and third hypotheses. Sequential application of the second and third hypotheses tests for differences in rates of change and permits inferences about the nature of the population response. It can be determined whether the survival and/or recruitment responses are different in the two populations. There are four possible outcomes from the sequential examination of these latter hypotheses:--

1. Both hypotheses can be rejected, in which case the inference is the populations are behaving differently due to differences between the ratios of recruits to death rate. Net change can also be affected by the size of the initial populations, a factor which when operating alone can be separated by hypothesis combination 3 below.
2. Both hypotheses fail to be rejected, in which case the populations are behaving in the same manner, both in terms of net result and in terms of the survival and recruitment responses.
3. The first hypothesis (rate of change the same for both populations) could be rejected and the second ($B/(1-S)$ the same) fail to be rejected, in which case the populations are behaving differently due to an initial population size difference.
4. The first hypothesis may fail to be rejected and the second rejected, in which case the net behavior of the two populations is the same but the recruitment and death processes are responding differently. The net effect is due to a fortuitous balancing of

differences between the recruitment and death response.

The effects of treatment, biological differences or environment on population responses can thus be attributed to effects on recruitment or mortality, or to differences in the initial population sizes.

A BASIC computer program was developed[a] to calculate test statistics for a number of hypotheses about pairs of populations. The program utilized Newton/Raphson methods (Miller 1981) to numerically derive the maximum likelihood estimates of the parameters of interest.

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[a] Mathematical formulae were clarified and the BASIC program written by Dr M.D. Brennan, Mathematics Dept., Utah State University, Logan UT.

# CHAPTER IV

# SURVIVAL OF PERENNIAL SHRUBS AND GRASSES AFTER DESTOCKING YEELIRRIE STATION, IN THE MULGA ZONE RANGELANDS OF WESTERN AUSTRALIA.

# Introduction

Detecting change in the perennial component of arid-zone pastures in Australia has concentrated on traditional cover, density and biomass measures (Hall et al. 1964, Hacker 1979, Graetz 1980, and Wilson et al. 1982). Few studies have addressed the population dynamics of these pastures (Williams 1968, Crisp 1978, Crisp and Lange 1976). Most have emphasized the detection of change and some have speculated as to possible causes of the change (Hall et al. 1964, Crisp and Lange 1976, Lange and Willcocks 1980, and Crisp 1978); however, few have attempted to experimentally detect the causal agents (Williams 1968, Crisp 1978, and Lange and Willcocks 1980).

The detection of change per se has little value in terms of improving management; it is attribution to causal factors that is important (Crawley 1983). Experimentation using the dynamics of populations offers considerable promise for understanding changes in rangeland ecosystems and their possible causal factors (Silvertown 1982, Harper 1980, and Crawley 1983). The development of this autecological understanding is essential to the development of wise management strategies that will permit utilization without downward trend in rangeland pastures.

Grazing of semi-arid rangelands in Western Australia by sheep and cattle for the past century or more has been associated with changes in the vegetation regarded by many as detrimental (Fyfe 1940, Carder 1978). Recent reports (Wilcox and McKinnon 1972, and Anon. 1979) have highlighted this apparent downward trend in the condition of the rangeland, and have cited grazing livestock as the major factor contributing to the deterioration. Reducing stock numbers and, in some instances, complete destocking have been recommended as remedial management strategies. In the absence of concrete research evidence on the effects of destocking on the vegetation, optimistic recommendations were made along the lines of "reduce stock numbers and see what happens." Reliable detection of the effects of destocking and separating them from site features, climatic fluctuation, the effects of grazing by large native herbivores (kangaroos, euros and emus), past grazing history differences, or other physical and environmental factors, requires a rigorous experimental approach to the measurement and interpretation of changes in the vegetation resource.

Of particular importance to station (ranch) owners have been the effects of populations of kangaroos thought to be significantly above pre-settlement levels in these arid areas (Davies 1973, Newsome 1975). Information on this topic in Western Australian rangelands is sparse (Ealey and Suijdendorp 1959). Research in other areas has attempted to discover the competitive relationship between these herbivores and their livestock competitors, with particular emphasis on dietary overlap (Caughley 1964, Frith 1964, Newsome 1971, Low et al. 1981, and Low 1979), but no studies of the effect of these increased populations on the vegetation could be found. This latter question is especially poignant in the light of government recommendations to destock large areas of Western Australian rangeland. Of particular relevance is the question of the recovery rates of the vegetation in destocked areas, the detection of changes in the vegetation in areas grazed by or protected from grazing by kangaroos and the assignment of possible causal factors to those changes.

In 1972 Western Mining Corporation located extensive uranium deposites on Yeelirrie station, purchased the property and removed all the sheep. This provided an opportunity to examine the effects of large scale destocking on the recovery of the vegetation. Previous research had been conducted at Yeelirrie on kangaroo movements (Oliver unpublished) and it was known that relatively large populations of kangaroos were present. Testing hypotheses about the recovery of rangeland vegetation and the effects of kangaroo grazing on that recovery was thus possible on a whole property scale.

The specific objective of this portion of the research was to:-- Identify factors influencing perennial plant survival in destocked arid zone pastures at Yeelirrie station, in the Goldfields region of Western Australia. Factors examined were to include, climatic patterns, site variables, and large native herbivore activity. Particular emphasis was placed on the effects of grazing by kangaroos.

# Materials and Methods

## Study Site

### Location

The study area is located on Yeelirrie station, (27 deg. 17 min. south, 120 deg. 05 min. east) a 275 000 hectare pastoral property in the Mulga (*Acacia aneura* F. Muell.) zone rangeland areas of Western Australia (Fig 2). Altitude at the station homestead is 496 m and the maximum relief is less than 100 m.

### Climate

The climate is arid (Meigs 1953), continental, with a bimodal (summer/winter) precipitation pattern. All the precipitation falls as rain and averages 225 mm annually with a coefficient of variation of 50 per cent (Mabbutt et al. 1963). Winter rainfall is from the passage of westerly frontal systems while tropical cyclones and thunderstorms account for the majority of the summer rainfall. Evapotranspiration exceeds 250 cm per year with summer monthly rates exceeding 70 cm. The combination of erratic rainfall and high evaporation rates results in periodic, short growing seasons and frequent droughts. Winter months provide the most reliable growing periods.

Summer maximum temperatures are high (on average 20 days above 40°C) winter minima are mild and the incidence of frost rare -- approx 10 days per year (Western Mining Corporation 1978). Growth periods are restricted by lack of soil moisture, not low temperatures.

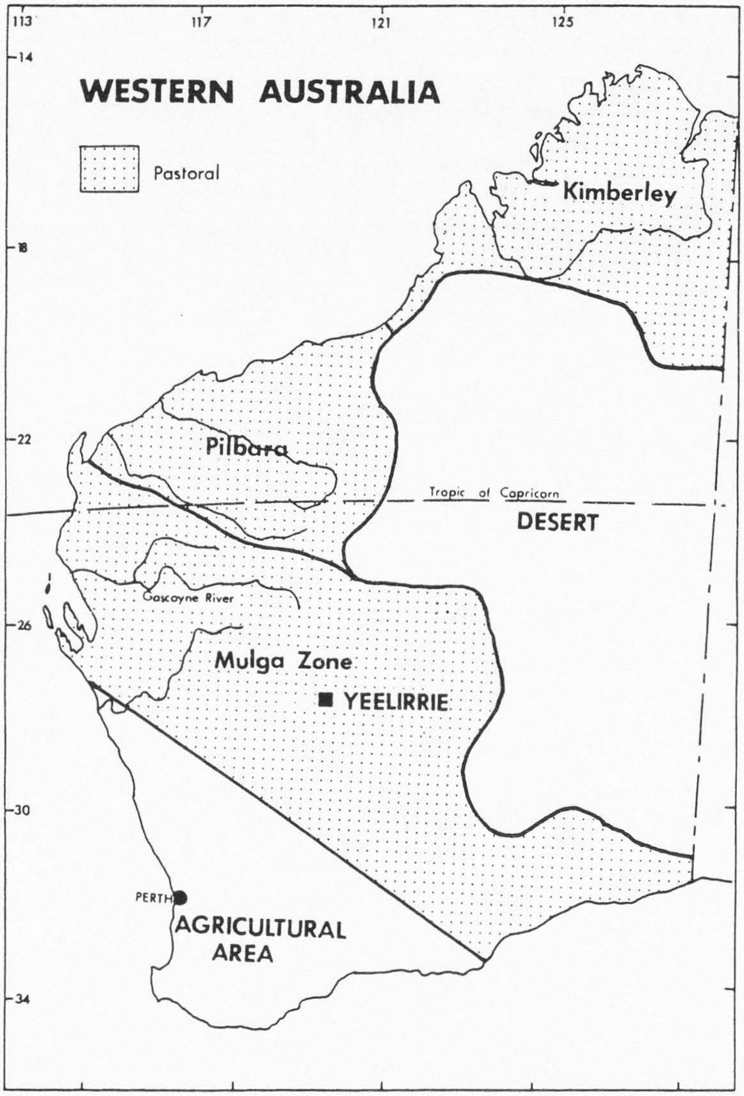

Figure 2. The location of Yeelirrie station and the pastoral regions of Western Australia. (Note: the boundary between the Mulga zone and Agricultural areas is idealized, the actual line follows property boundaries too varied to demonstrate at this scale)

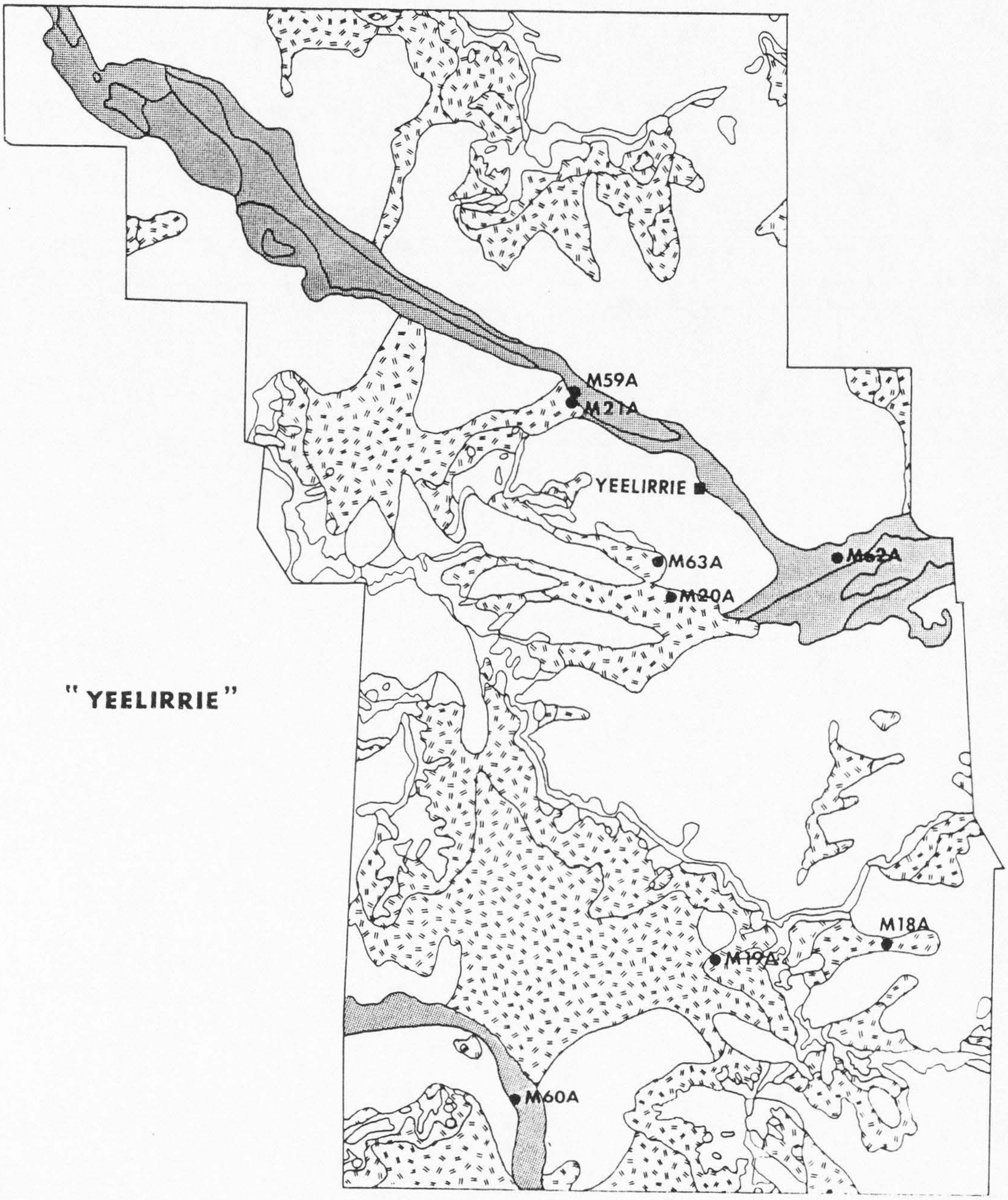

Figure 3. Yeelirrie station showing the major vegetation types and the location of study sites. Key: ▨ mulga woodland, ▩ halophytic shrubland, ☐ unproductive spinifex grassland, and breakaway (erosional remnants of the old Australian plateau) areas.

## Site location

Eight sites were located around the 275 000 hectare property (Fig 3). Of these sites, four contained protected and grazed areas, the remaining four were all grazed. In all cases the major grazers were large native herbivores, red kangaroos (*Megaleia rufa* Desmarest), euros (*Macropus robustus* Gould) and emus (*Dromaius novaehollandiae*), the most important being red kangaroos and euros.

## Vegetation

The vegetation of Yeelirrie station is described by Beard (1976) as four main community types: Mulga-low woodland, shrub steppe, succulent steppe, and salt flats. Churchward's (1977) more specific classification of landforms and regoliths described 13 mapping units based on particular associations of soil, topography and vegetation. To be able to represent these types at a meaningful scale it was necessary to combine these into the four major types shown in Figure 3 where only the productive woodland and shrubland types are highlighted. Within these two types I identified different ecosytems within five of which experimental sites were located. Detailed descriptions of the vegetation and soils associated with each experimental site are presented in Table 4.

## History

Yeelirrie station has a relatively short pastoral history. It was originally leased by the owners of an adjoining property (the Howard family) in 1924 and grazing by sheep commenced soon after. In 1957 an adjoining lease (Altona) was added to the south and the whole became

Table 4. Plant communities and study site characteristics at Yeelirrie station

| COMMUNITY | SITE | VEGETATION | SOILS AND OTHER FEATURES |
|---|---|---|---|
| 1 | M21A<br>M59A | Low halophytic shrubland including *Maireana* spp., *Frankenia pauciflora*, *Ptilotus obovatus* and a variety of annual herbs and grasses in season. | Sandy loams over a limestone hardpan vary in depth from 60 cm to 100 cm. pH varies from 6.5 to 7.5 at the surface, increasing to 8.5 at 60 cm. Slopes are less than 1:500 and sheet flow of surface water is common during high intensity rainfall events. |
| 2 | M62A | Low halophytic shrubland including *Atriplex* spp., *Maireana* spp., *Aizoon quadrifida*, and *Cratystylis subspinescens*, with herbaceous perennials *Ptilotus obovatus* and *Solanum lasiophyllum*. Sparse annual herbs and grasses are present in season. | |
| 3 | M18A<br>M20A<br>M63A | Mulga (*Acacia aneura*) woodland with a low tree layer including mulga and *Acacia linophylla* that may comprise up to 20 percent foliar cover. Below this a sparse shrub layer dominated by *Eremophila* spp., an herbaceous shrub layer including small non-halophytic *Maireana* spp., and a grass layer including *Triodia basedowii*, *Monochather paradoxa* and *Eragrostis xerophila*. Herbaceous annuals are abundant in season. | Sandy red loams of depth greater than 100 cm, pH varies between 5.0 at the surface and 6.5 at 40-60 cm. Localized sheet flow occurs on rare occasions during intense rainfall events. Slope is insiginficant (1:400 - 1:500). |

Table 4 (continued).

| COMMUNITY | SITE | VEGETATION | SOILS AND OTHER FEATURES |
|---|---|---|---|
| 4 | M19A | Low open woodland dominated by *Acacia* spp. with a sparse shrub layer dominated by *Eremophila* spp., and a dense grass layer including *Eragrostis xerophila*, *Monochather paradoxa*, *Neurachne mitchelliana*, *Eriachne helmsii*, and *Triodia basedowii*. Annuals are abundant in season. | Soils are sandier than in community three and have been classified as red loamy sands, pH ranges from 6.0 to 6.5 at the surface with slight increases with increasing depth. Broad areas of water flow are interspersed with large sandy banks. Slopes are between 1:300 and 1:400. |
| 5 | M60A | Crosses an ecotonal region between a localized drainage focus and surrounding woodland areas. The vegetation is dominated by halophytic shrubs including *Maireana pyramidata* with *Eremophila subfloccosa*, while grass areas include *Monochather paradoxa* and *Eragrostis xerophila* with scattered trees (*Acacia aneura* and *Grevillea sarissa*). A variety of annual species are abundant in season. | |

Note: Specific soil information was not collected in communities two or five; however, it can be assumed that pH values will be more alkaline in commnunity 2 as this represents the culmination of a extensive inland drainage system and is only a short distance from existing salt lakes (seasonally flooded). Community 5 would be expected to have variable pH as it crosses an ecotonal region and soils change from a loam to a sandy soil.

known as the present day Yeelirrie lease. Sheep were the major form of livestock grazing although small numbers of cattle and horses have been grazed from time to time. Recorded stocking levels were conservative by local standards and yet range deterioration is evident in some of the more productive ecosystems. The deterioration has been attributed to poor stock distribution and stock concentration for shearing at a central shearing shed.

In 1972 Western Mining Corporation Ltd. purchased the lease as part of a management program to protect and control areas surrounding its Uranium leases located in the central Yeelirrie drainage basin. At this time all remaining livestock were removed from the property and the company provided funds that enabled a vegetation monitoring program to be commenced by the Meekatharra District Office of the Western Australian Department of Agriculture.

## Experimental Procedures

### Site selection

In 1973 1:20 000 scale, black and white, aerial photography was used to select sites which were then established after location by ground survey. Site selection could not be regarded as random over the whole station; however, for practical purposes selection within ecosystems could be considered as random within the constraint that each site had to be between 1 km and 3 km from a functional watering point. A further constraint was that, in order to be worth sampling, the site had to contain a reasonable number of individuals of species important in that ecosystem. Sites were layed out as an extended belt transect

150 meters long and 15 meters wide. This area was divided up into five 30 by 15 meter plots for ease of recording, and the boundaries of these plots marked with white-painted, automobile tire casings.

### Perennial plant data acquisition

Large scale (1:250), color, aerial photographs of each site were acquired using low level (160m) flights in a single engine, fixed-wing aircraft fitted with a 70mm aerial reconnaissance camera, and with a modified navigation and sighting door. The film was developed to color negative and 25cm square color positive prints were obtained in stereo pairs for all portions of the recording plots. Outlines of visible plants were marked in permanent indian ink onto acetate overlay material using a stereo viewer. Overlays and photos were then taken to the field and each plant identified with a coded number, and all additional individuals not initially detected were mapped onto the acetate (Hacker 1978,1979, Carneggie et al. 1971). This mapping procedure was repeated four times during the study (1973,'76,'79,'82). Survival information used in this study was extracted from the sequential maps of each portion of each site.

### Treatments

At each of four sites (M18A through M21A), two similar areas were selected and one of these was fenced to exclude the three types of large native herbivore; all other, smaller native herbivores had access to the protected areas. The fenced areas were controls in the experiment to examine the effect of grazing by kangaroos; adjacent unfenced areas provided the grazed treatment. One 150 by 15 meter belt transect was photographically recorded in each of the control and treatment areas.

### Relative kangaroo grazing intensity

Twenty 5 x 5 meter, permanent plots were located randomly adjacent to each of the treatment sites. For the period 1973 to 1979 all kangaroo dung pellets were removed from these plots at approximately two month intervals. Pellets classified as being fresh, therefore not laterally transported, were oven dried (95°C for 24 hr) and weighed to provide a relative index of grazing by kangaroos and euros at each of the sites.

### Environmental variables

Daily rainfall records from the Yeelirrie homestead were used as representative of the whole station. Spatial variability of rainfall events to some extent invalidates the use of these data for establishing causal relationships and they have been used, therefore, only to classify the seasonal conditions relative to averages.

## Data Analysis

### Plant survival

The survival of individual plants between the sample dates (3 year intervals was taken as the basic demographic parameter of interest. Survival rates were analyzed using the FORTRAN program SURVIV (White 1983) to test a number of hypotheses related to potential factors affecting the survival of perennial plants (see Chapter 3 for details). Gardiner and Norton (1983) presented this approach to testing hypotheses about the survival of an arid zone shrub, Eremophila leucophylla (Appendix 3).

Data sufficient for survival analysis using the SURVIV program were extracted for six species: five shrubs, Maireana glomerifolia, Frankenia pauciflora, Ptilotus obovatus, Eremophila spectabilis, and Eremophila leucophylla, and for the perennial grass, Eragrostis xerophila. All of these species had at least one grazed and one control area with sufficient numbers of individuals for analysis. While they represent only a small proportion of the total number of species on the sites, they do produce more than 75 per cent of the perennial species phytomass accessible to grazing by kangaroos.

### Model details

Details of the models chosen to permit specific hypotheses to be tested vary depending on the structure of the particular data sets. Each species has been treated as a separate entity and any generalizations have been formulated by amalgamating the estimates of meaningful combinations of species. A general model was constructed in which survival rates were permitted to vary by site, period, individual age, and treatment. Progressive simplification of the models by eliminating the effects of one or more of these basic factors permitted the construction of likelihood ratio tests of hypotheses about the effects of these factors on plant survival. Examples of the data sets and models are shown in detail in Appendix 1 and Appendix 2.

### Supporting data

Supporting data on relative kangaroo densities were collected for only the first two periods (1973-1976 & 1976-1979) of the investigation and can be used only to help interpret the findings. Missmatched recording frequencies and insufficient separate data periods prevented the direct use of these data in a regression approach to establish correlative links. Monthly rainfall totals were used to clasify each of the periods into wet, dry, and more "normal."

## Results

### Precipitation

Annual precipitation was extremely variable during the study (mean 276 mm, s.e. 42 mm) and its distribution resulted in three distinctly different precipitation periods (Fig 4). Above-average rainfall was recorded for 1973-1976, well below-average rainfall for 1976-1979, and about normal precipitation for 1979-1982. Despite the variability of the precipitation and one of the worst droughts on record, the numbers of individuals in all three functional species groups (desirable, undesirable and intermediate) used by Wilcox and Morrissey (1979) to describe usefulness for livestock production, increased in density during the course of the investigation (Figs 5 and 6).

### Perennial Plant Survival

Likelihood ratio tests were used to examine a number of hypotheses about possible factors affecting the dynamics of arid zone pastures. First was the proposition that adult survival during any one period was constant (Table 5). There was only one period available for testing this hypothesis and consequently the power of the test was low ( <20%

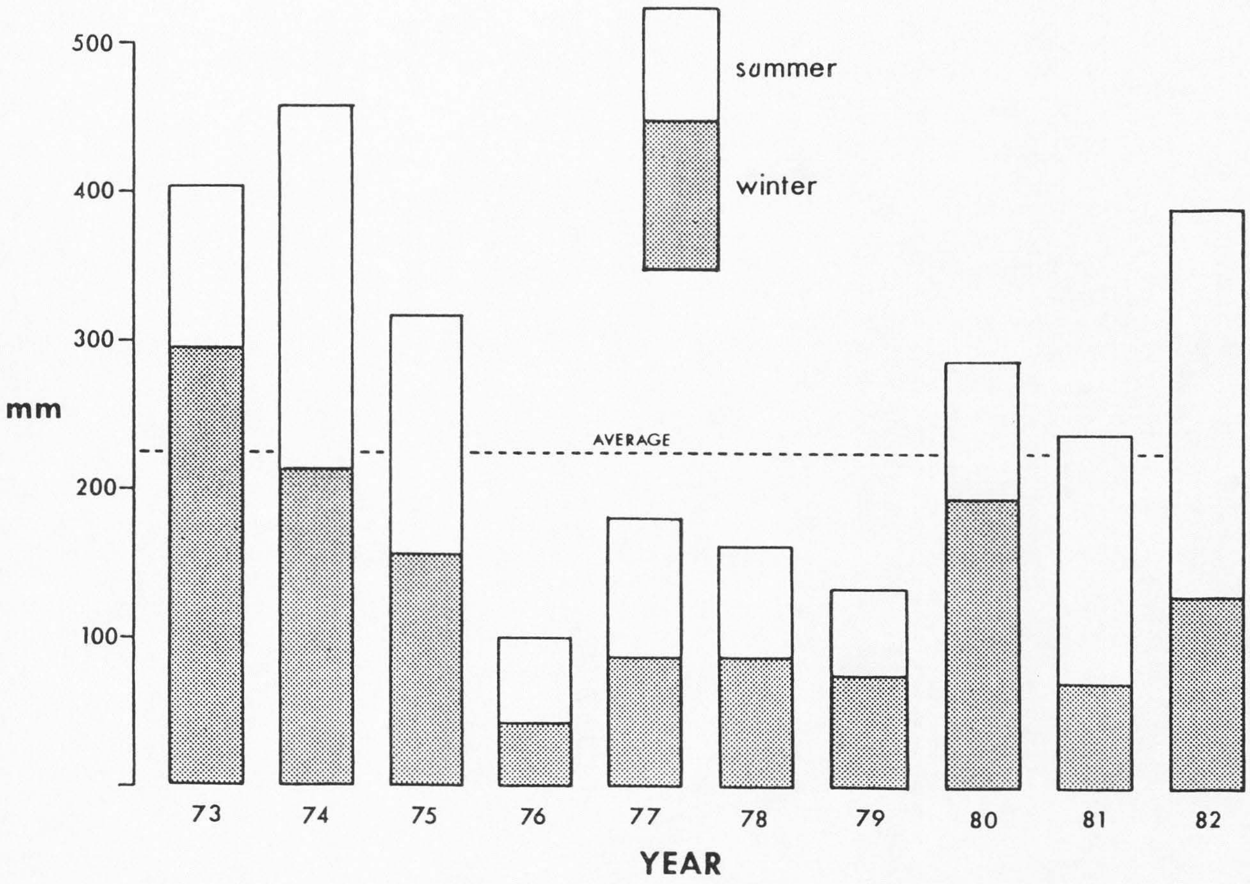

Figure 4. Precipitation recorded at Yeelirrie station homestead, an official weather recording station, for the period 1973-82. (Values are expressed as totals for the water year (April - March). Plant recordings were made in May 1973, 1976,1979,& 1982.

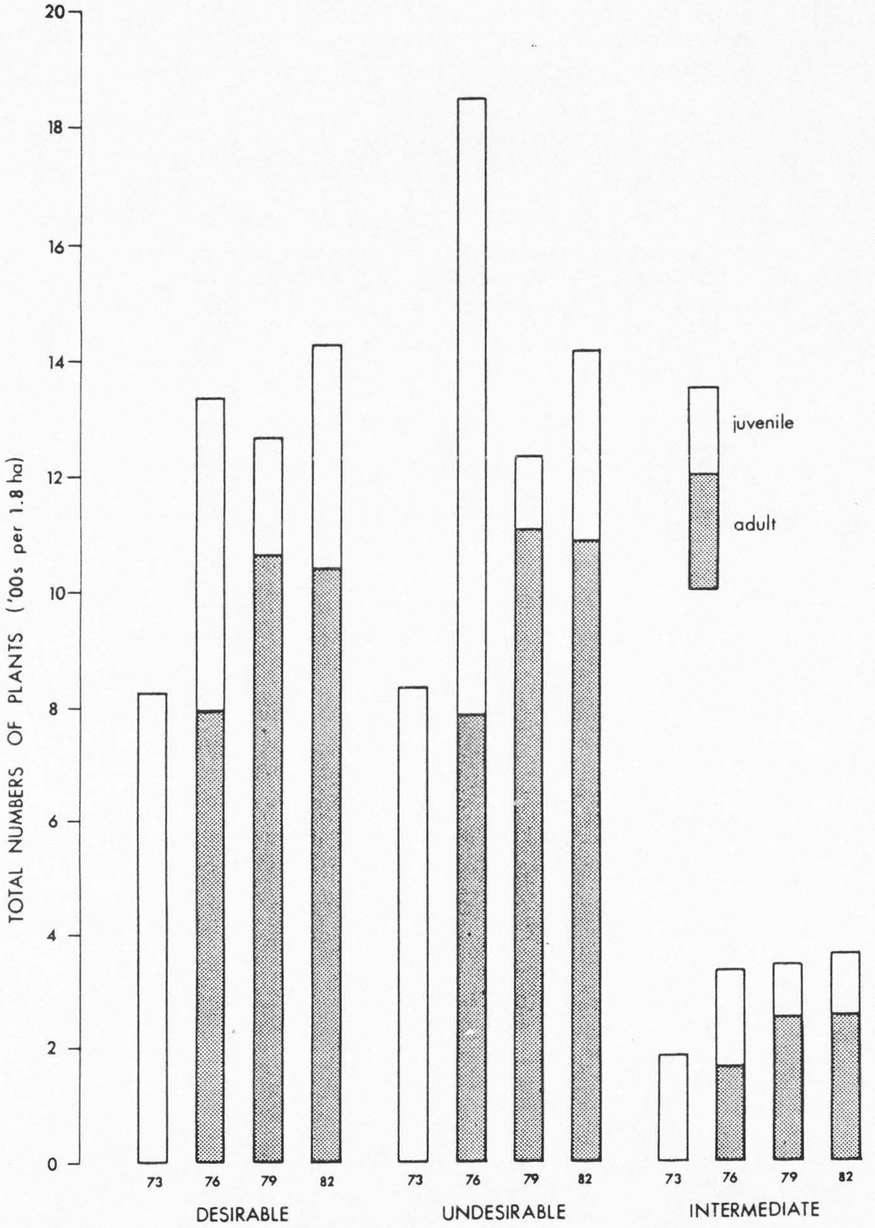

Figure 5. Changes in the numbers of plants in three functional species groups from grazed areas at Yeelirrie 1973-1982.

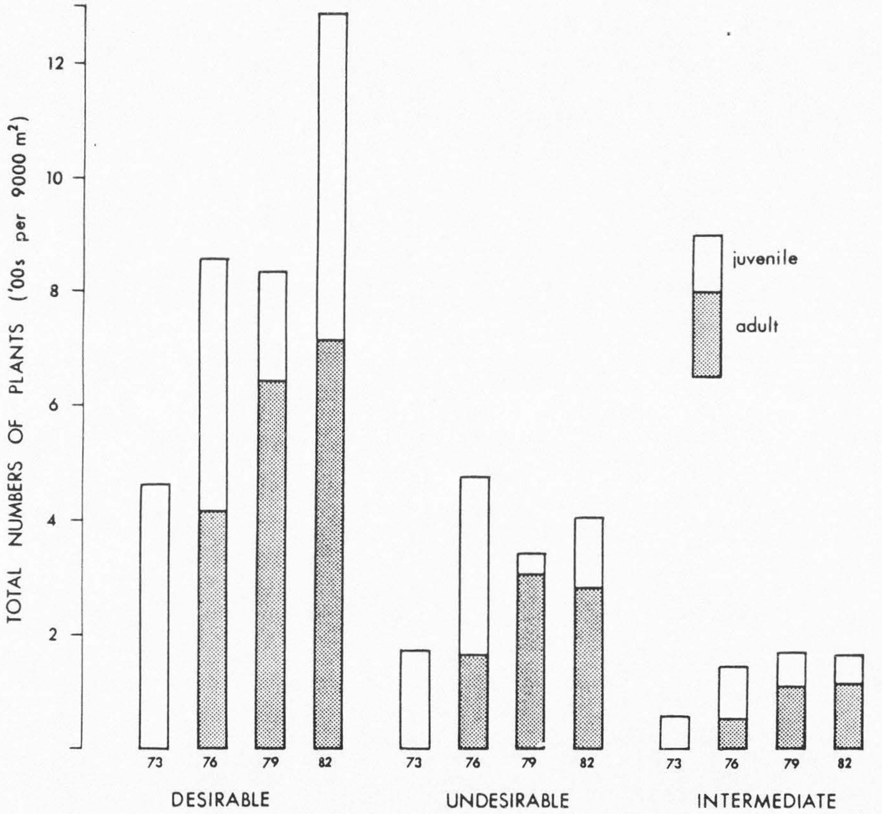

Figure 6. Changes in the numbers of plants in three functional species groups on areas at Yeelirrie protected from grazing by large native herbivores for the period 1973-1982.

for several of the species for which the null was not rejected). Because of the low power of these tests I adjusted the alpha probability level at which I rejected the null hypothesis to 20 per cent. Of the six species examined, three showed significant differences between the reduced and the unconstrained general model. For these three species the unconstrained model was used as the general model for all future tests; otherwise the reduced model, in which $S_{13} = S_{23}$ for all model sub matrices, was used as the general model.

Table 5. Approximate Chi square values for testing the hypothesis that adult survival rates were constant across cohorts during the period 1979 - 1982 ($S_{13} = S_{23}$ for all model sub matrices)

| SPECIES | $X^2$ | df | prob. |
|---|---|---|---|
| Maireana glomerifolia | 3.49 | 2 | 0.191 |
| Frankenia pauciflora | 7.20 | 3 | 0.070 |
| Ptilotus obovatus | .515 | 3 | 0.915 |
| Eremophila leucophylla | 5.61 | 5 | 0.363 |
| Eremophila spectabilis | 7.50 | 6 | 0.284 |
| Eragrostis xerophila | 23.3 | 3 | <.005 |
| TOTAL | 47.6 | 22 | <.005 |

A similar test of the hypothesis that adult survival was equal within the initial mixed-age cohort was rejected for all species at the 20 per cent level. Similar problems were encountered with the low power of these tests.

## Adult Survival

An important assumption of many traditional analyses of plant populations (that adult survival is constant) was tested by comparing a reduced model, in which $S_{11} = S_{12} = S_{13} = S_{23}$ for all model sub-matrices, with previously defined general models. For all species examined, this hypothesis is rejected at the 5 per cent level (Table 6).

Table 6. Approximate Chi Square values for testing the hypothesis that adult survival rates were constant across cohorts and periods. ($S_{11} = S_{12} = S_{13} = S_{23}$ for all model sub matrices).

| SPECIES | $X^2$ | df | prob. |
|---|---|---|---|
| Maireana glomerifolia | 22.4 | 4 | <.005 |
| Frankenia pauciflora | 32.6 | 9 | <.005 |
| Ptilotus obovatus | 17.6 | 6 | 0.008 |
| Eremophila leucophylla | 22.3 | 10 | 0.015 |
| Eremophila spectabilis | 81.7 | 12 | <.005 |
| Eragrostis xerophila | 89.3 | 9 | <.005 |
| TOTAL | 265.9 | 50 | <.005 |

## Site Effects

Sites have different past use histories, perennial species richness and, probably, soil moisture regimes (brought about by spatially variable rainfall events), and may even belong to different ecosystems (Table 7). Likelihood ratio tests of the hypothesis that site has no effect on plant survival indicate all, but one, of the species present on more than one site exhibit significantly different (at the 5 per cent level) survival rates on these different sites (Table 8).

Table 7. Characteristics of experimental sites at Yeelirrie station.

| SITE | ECOSYT'M | CONDITION | PAST USE HISTORY |
|---|---|---|---|
| M18A | 3 | Good | Relatively light grazing past 15 yrs |
| M19A | 4 | Fair | Moderate use prior to destocking |
| M20A | 3 | Poor | Heavy use, concentration paddock for shearing; used to graze horses. |
| M21A | 1 | Fair | Relatively heavy use, more productive areas used heavily during droughts in past years. |
| M59A | 1 | Fair | As for M21A. |
| M60A | 2 | Fair | Moderate use past 15 yrs; heavy use prior to that. |
| M62A | 5 | Fair | Heavy use up to destocking |
| M63A | 3 | Poor | Heavy use, as for M20A. |

Note: I visually estimated condition on the basis of species compliment relative to expected species, based on reference to other areas of a similar type elsewhere in the region.

Grazing by Kangaroos and Euros

The hypothesis that kangaroo and euro grazing has no effect on plant survival was tested by forming likelihood ratio tests of reduced models, in which equivalent grazed and ungrazed survival rates were constrained to be equal, against the general models previously selected. The overall test (Table 9) indicates that grazing by these native herbivores reduces perennial plant survival. Three species

(*Eragrostis xerophila*, *Eremophila spectabilis*, and *Frankenia pauciflora*) showed individually significant responses.

Table 8. Approximate Chi square values for testing the hypothesis that sites do not affect plant survival (equivalent $S_{ij}$'s set equal across site sub-matrices).

| SPECIES | $X^2$ | df | prob. |
|---|---|---|---|
| Frankenia pauciflora | 10.8 | 6 | 0.095 |
| Ptilotus obovatus | 12.5 | 5 | 0.030 |
| Eremophila leucophylla | 33.2 | 14 | <.005 |
| Eremophila spectabilis | 300.4 | 19 | 0.000 |
| Eragrostis xerophila | 14.2 | 6 | 0.028 |
| TOTAL | 371.1 | 50 | <.000 |

*Maireana glomerifolia* was the species with the lowest non-significant probability level and the power of this test indicated a lower bound of 62 percent; therefore, I failed to reject the hypothesis of no grazing effect for this species and for the remaining two that showed non-significant responses to grazing.

### Individual Species Responses

Survival rate estimates and their standard errors for the unconstrained general models are presented for all species in Table 11. These estimates have been used to assist in the interpretation of differences detected in the more powerful likelihood ratio tests used previously.

All six species responses to several potential causal agents are summarized in Table 10.

Table 9. Approximate Chi square values for testing the hypothesis that grazing by kangaroos and euros has no effect on perennial plant survival (equivalent $S_{ij}$'s were set equal across grazed and ungrazed populations).

| SPECIES | $X^2$ | df | prob. |
|---|---|---|---|
| Maireana glomerifolia | 9.06 | 5 | 0.110 |
| Frankenia pauciflora | 21.0 | 5 | <.005 |
| Ptilotus obovatus | 8.02 | 5 | 0.170 |
| Eremophila leucophylla | 10.5 | 10 | 0.408 |
| Eremophila spectabilis | 36.4 | 10 | <.005 |
| Eragrostis xerophila | 64.9 | 6 | <.005 |
| TOTAL | 149.9 | 41 | <.005 |

Table 10. Summary of the responses of six perennial species to several potential causal agents.

| | Potential Causal Agent | | | |
|---|---|---|---|---|
| Species | Grazing | Site | Age | Cohort (1979-82) |
| Maireana glomerifolia | no | N/A | yes | yes |
| Eremophila leucophylla | no | yes | yes | no |
| Ptilotus obovatus | no | yes | yes | no |
| Eremophila spectabilis | yes | yes | yes | no |
| Eragrostis xerophila | yes | yes | yes | yes |
| Frankenia pauciflora | yes | no | yes | yes |

### Maireana glomerifolia

*Maireana glomerifolia* was only present on one site. It showed no significant survival response to grazing. Adult survival, which varied between 86% and 99%, was higher than juvenile survival (40% to 76%). Ungrazed juveniles survived better during the more normal years following the drought than during the drought (76% vs 40%).

### Eremophila leucophylla

Adult survival, with a range between 100% and 86% was higher than juvenile survival (86% and 50%) when compared over all treatments and sites.

### Ptilotus obovatus

Grazed adults had significantly lower survival on M59A than on M21A during very wet years (88% vs 97%), while grazed juveniles survived better on site M21A during the drought and during more normal years following the drought.

### Eremophila spectabilis

Grazing during drought years improved adult survival by 8 percent (90% vs 98%) on site M18A, while on site M20A, a poorer site in the same ecosystem, the improvement was 30 percent (52% vs 82%). Grazing during more normal years following the drought had the effect of reducing adult survival by 11.5 percent (96.5% vs 85%). Juvenile survival was reduced by grazing, by from 8 percent (77% vs 69%) during drought years, to 47 percent (69% vs 22%) during more normal years following the drought on site M18A. Grazing during drought reduced juvenile survival on site M20A by 14 per cent (20% vs 34%).

### Eragrostis xerophila

Adult plants had significantly higher survival rates in all periods when not grazed. This advantage for ungrazed plants varied from 11 percent (85% vs 96%) during the wet period, to 44 percent (40% vs 84%) during more normal years (1979-82), when the two adult cohorts were averaged. The advantage was 14 percent (84% vs 98%) during drought years. Juvenile survival was depressed by 22 percent (56% vs 34%) when grazed during more normal years following drought, but showed a positive 13 percent response to grazing (44% vs 57%) during drought years.

### Frankenia pauciflora

Adult survival was 22 percent (98% vs 76%) higher on grazed than on ungrazed areas during the more normal period following the drought. Juvenile survival was lower (75% and 34%) than adult survival (100% and 76%) when compared across treatments. This species showed no significant response to site.

## Herbivore Responses

Dung weights deposited at each site were used to provide an index of relative grazing pressure (Fig 7). By far the most used site was M21A; however, M18A and M19A received relatively heavy grazing at different times during the study. Only on site M20A was grazing consistently low relative to other sites.

Table 11. Survival rates for six plant species in areas grazed by kangaroos and euros and in control areas for all sites on which the species were present. Standard errors are in parentheses.

| | | | | ADULT | | JUVENILE | |
|---|---|---|---|---|---|---|---|
| SPP | SITE | PERIOD | COH'T | GRAZED | UNGRAZED | GRAZED | UNGRAZED |
| | M21A | 73-76 | 1 | .98 (.012) | .98 (.011) | | |
| | | 76-79 | 1 | .97 (.014) | .99 (.008) | | |
| Maireana glomerifolia | | | | | | .52 (.096) | .40 (.040) |
| | | 79-82 | 1 | .97 (.015) | .91 (.026) | | |
| | | | 2 | .86 (.094) | .90 (.038) | | |
| | | | 3 | | | .50 (.204) | .76 (.040) |
| | M18A | 73-76 | 1 | .96 (.020) | .95 (.023) | | |
| | | 76-79 | 1 | 1.0 (.105) | 1.0 (.112) | | |
| | | | 2 | | | .67 (.051) | .72 (.048) |
| remophila leucophylla | | 79-82 | 1 | .99 (.011) | .93 (.028) | | |
| | | | 2 | .93 (.034) | .97 (.022) | | |
| | | | 3 | | | .69 (.128) | .78 (.098) |
| | M19A | 73-76 | 1 | .96 (.014) | .91 (.034) | | |
| | | 76-79 | 1 | .98 (.011) | .97 (.021) | | |
| | | | 2 | | | .79 (.055) | .86 (.073) |
| | | 79-82 | 1 | .96 (.015) | .95 (.026) | | |
| | | | 2 | .98 (.023) | .95 (.051) | | |
| | | | | | | .76 (.103) | 1.0 (.302) |
| | M60A | 73-76 | 1 | .95 (.028) | | | |
| | | 76-79 | 1 | .86 (.045) | | | |
| | | | 2 | | | .75 (.217) | |
| | | 79-82 | 1 | .96 (.028) | | | |
| | | | 2 | 1.0 (.000) | | | |
| | | | 3 | | | .50 (.354) | |
| | M21A | 73-76 | 1 | .97 (.028) | .86 (.066) | | |
| | | 76-79 | 1 | .79 (.069) | .88 (.068) | | |
| Ptilotus obovatus | | | 2 | | | .76 (.050) | .85 (.043) |
| | | 79-82 | 1 | .85 (.068) | .67 (.103) | | |
| | | | 2 | .80 (.054) | .72 (.059) | | |
| | | | 3 | | | .74 (.062) | .81 (.048) |
| | M59A | 73-76 | 1 | .88 (.031) | | | |
| | | 76-79 | 1 | .86 (.034) | | | |
| | | | 2 | | | .62 (.061) | |
| | | 79-82 | 1 | .77 (.045) | | | |
| | | | 2 | .77 (.068) | | | |
| | | | 3 | | | .52 (.087) | |

Table 11 (continued).

| | | | | ADULT | | JUVENILE | |
|---|---|---|---|---|---|---|---|
| SPP | SITE | PERIOD | COH'T | GRAZED | UNGRAZED | GRAZED | UNGRAZED |
| remophila spectabilis | M18A | 73-76 | 1 | .96 (.028) | .95 (.026) | | |
| | | 76-79 | 1 | .98 (.021) | .90 (.037) | | |
| | | | 2 | | | .69 (.036) | .77 (.038) |
| | | 79-82 | 1 | .85 (.053) | .96 (.024) | | |
| | | | 2 | .79 (.038) | .84 (.037) | | |
| | | | 3 | | | .22 (.098) | .69 (.121) |
| | M20A | 73-76 | 1 | .96 (.016) | 1.0 (.000) | | |
| | | 76-79 | 1 | .82 (.028) | .52 (.104) | | |
| | | | 2 | | | .20 (.018) | .34 (.063) |
| | | 79-82 | 1 | .88 (.027) | .83 (.108) | | |
| | | | 2 | .90 (.031) | .79 (.094) | | |
| | | | 3 | | | .62 (.075) | .43 (.187) |
| | M63A | 73-76 | 1 | .79 (.047) | | | |
| | | 76-79 | 1 | .37 (.063) | | | |
| | | | 2 | | | .09 (.042) | |
| | | 79-82 | 1 | .82 (.082) | | | |
| | | | 2 | .75 (.217) | | | |
| | M19A | 73-76 | 1 | .92 (.074) | | | |
| | | 76-79 | 1 | .92 (.080) | | | |
| | | | 2 | | | .52 (.093) | |
| | | 79-82 | 1 | .91 (.087) | | | |
| | | | 2 | .93 (.064) | | | |
| | | | 3 | | | .67 (.272) | |
| agrostis xerophila | M18A | 73-76 | 1 | .85 (.045) | .96 (.031) | | |
| | | 76-79 | 1 | .84 (.048) | .98 (.023) | | |
| | | | 2 | | | .57 (.049) | .44 (.050) |
| | | 79-82 | 1 | .48 (.072) | 1.0 (.000) | | |
| | | | 2 | .37 (.063) | .68 (.070) | | |
| | | | 3 | | | .34 (.088) | .56 (.085) |
| | M20A | 73-76 | 1 | .59 (.092) | | | |
| | | 76-79 | 1 | .82 (.093) | | | |
| | | | 2 | | | .33 (.082) | |
| | | 79-82 | 1 | .43 (.132) | | | |
| | | | 2 | .27 (.134) | | | |
| | | | 3 | | | .43 (.059) | |

Table 11 (continued).

| | | | | ADULT | | JUVENILE | |
|---|---|---|---|---|---|---|---|
| SPP | SITE | PERIOD | COH'T | GRAZED | UNGRAZED | GRAZED | UNGRAZED |
| Frankenia pauciflora | M21A | 73-76 | 1 | .97 (.022) | .97 (.018) | | |
| | | 76-79 | 1 | .97 (.022) | .91 (.033) | | |
| | | | 2 | | | .44 (.047) | .34 (.043) |
| | | 79-82 | 1 | .98 (.017) | .76 (.051) | | |
| | | | 2 | .90 (.044) | .88 (.033) | | |
| | | | 3 | | | | .58 (.142) |
| | M62A | 73-76 | 1 | .97 (.017) | | | |
| | | 76-79 | 1 | .89 (.033) | | | |
| | | | 2 | | | .50 (.167) | |
| | | 79-82 | 1 | .98 (.016) | | | |
| | | | 2 | 1.0 (.471) | | | |
| | | | 3 | | | .75 (.153) | |

Total kangaroo and euro populations are difficult to estimate, although important to making inferences about the response of herbivores to changes in the vegetation and vice versa. An attempt to follow grazing pressure was made by using the weight of dung collected at each site as an index of total grazing pressure at the four sites where paired treatment and control areas were recorded (Fig 8). These estimates are extremely variable but do suggest that grazing pressure increased during the early part of the drought (1976-77) but stabilized at about pre-drought levels by the end of 1977.

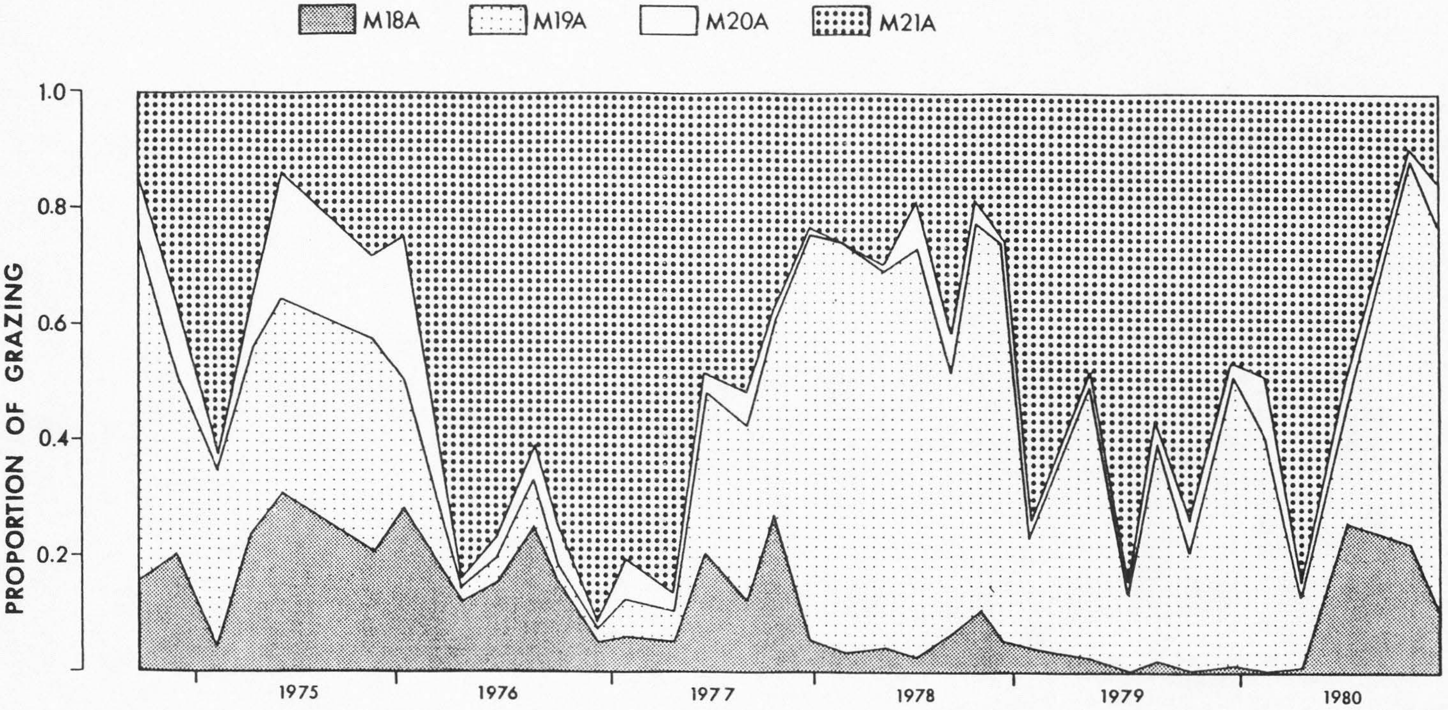

Figure 7. Relative grazing intensity at four paired sites as determined by the proportion of dung(by dry weight) collected from each site

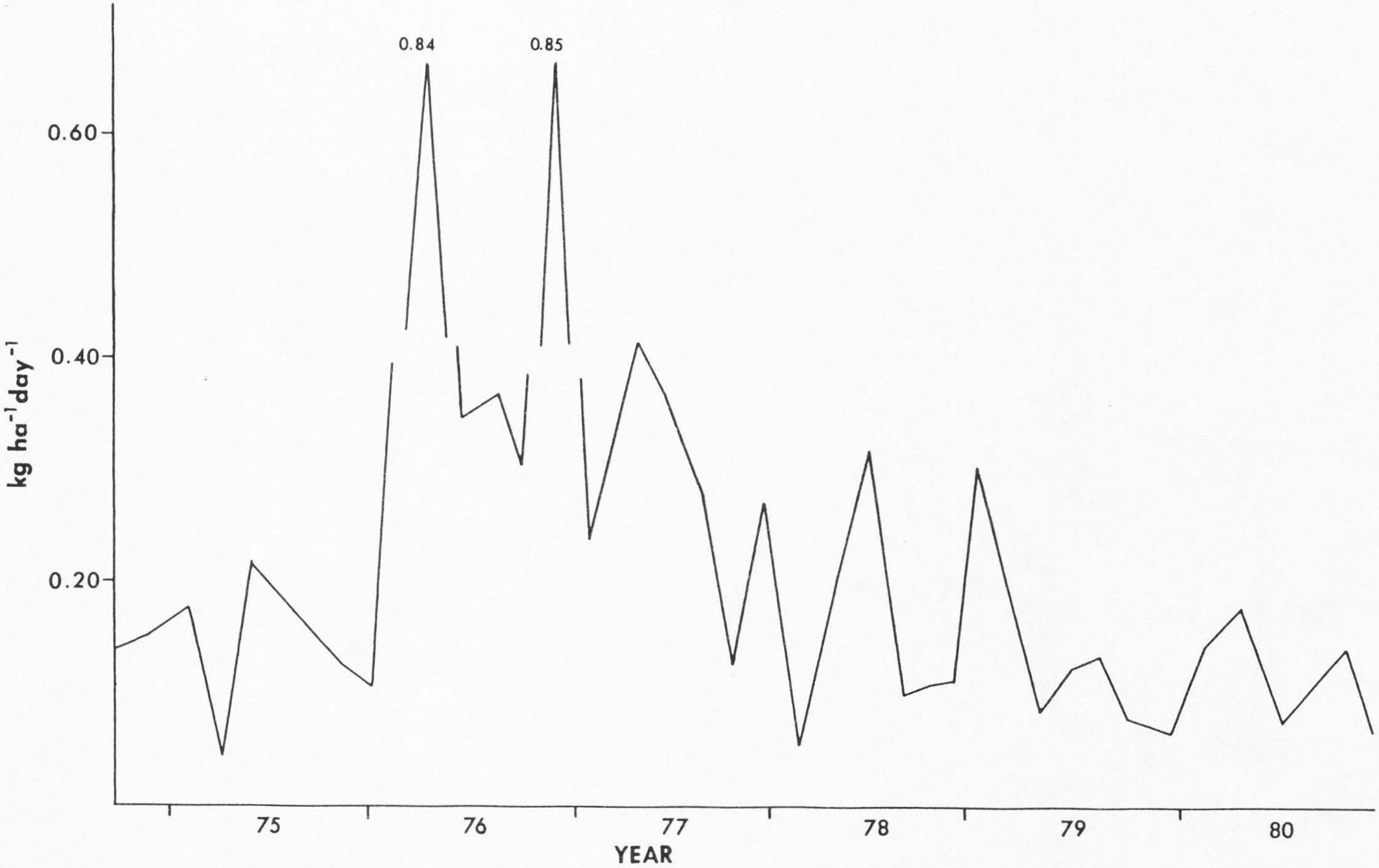

Figure 8. An index of total grazing pressure as indicated by the total dry weight of kangaroo dung collected from all sites

## Discussion

Most studies involving arid zone plants point to some climatic factor (seasons, Austin et al. 1981, rainfall, Wilson et al. 1982, and precipitation, Chambers 1979) as having the dominant role in determining the dynamics of the vegetal component of arid ecosystems. That precipitation provides the major driving force in arid ecosystems (Westoby 1979/80) was not under question in this study. Results from Yeelirrie confirmed that seasonal conditions play a major role in the plant survival process. This effect was more pronounced on juvenile individuals than on adults and did significantly affect the rate of recovery following the removal of livestock.

Other factors over which management has little or no control are the spatial heterogeneity and historical differences associated with different sites within management units. Rainfall events are spatially very variable in arid lands (MacMahon and Schimf 1981) as are the soils and biotic components of the ecosystem. These elements render traditional, replicated plot techniques less viable for testing hypotheses in arid-zone vegetation, particularly when low plant density and clumped vegetation necessitate the use of rather large plots. All species except Frankenia peuciflora, exhibited significant differences as a result of this plexus of physical and historical factors lumped together as site effects.

No attempt was made to experimentally separate these factors in this investigation, although this would seem to be a potentially profitable line for future research as promoted by Austin (1981). The implication of the effect of site on both survival and recruitment is that averages, or combinations of recordings taken across sites, are unlikely to enable identification of causal agents for responses in these autecological examinations of species. The importance of establishing causal agents for any changes that are detected cannot be overemphasized (Crawley 1983); the detection of change simply for the knowledge that change has occurred would appear to be problematical (Beeftink 1979/80). Any sampling system that fails to account for the essential differences between sites, or attempts to identify causes of change by association with indices averaged over a number of different sites, will succeed merely by chance.

The dominance of climatic and site factors on the dynamics of plant populations does not; however, prevent the identification of possible change inducing agents over which the manager has some control. In particular the manager of the range can control the number of animals using the range, when, and for how long they use it. Control over wildlife will be less stringent than for livestock and may be subject to legal controls by management agencies. This control will vary for different countries and for states within those countries; for example, in the United States wildlife are subject to state and federal regulations and nation-wide conservation pressures while in Australia each state has sole responsibility for wildlife control and much more onus is placed on the land-holder. There have been examples of extensive control, such as the poisoning and shooting program to control euro numbers in the northwest of Western Australia (Ealey & Richardson 1960), but most control of wildlife populations is by regulated harvest such as hunting in the United States, and by licensing procedures for members of the kangaroo pet meat industry in Australia where strict quotas are set on the annual harvest.

To enable sound decisions concerning the three aspects of animal control (stocking density, grazing season and grazing period) the effects of each on range ecosystems needs to be determined reliably and with reasonable accuracy. Traditional methods of measuring change in rangelands (Gardiner and Norton 1983) may, by their very nature and dependence upon replicated plot designs, prevent the detection of the more subtle effects of grazing because of the dominance of stochastic climatic and variable spatial factors. Application of rigorous statistical procedures to survival within a number of plant populations in this study enabled the detection of significant effects of grazing by kangaroos, and provides a tool for testing specific hypotheses related to the dynamics, and possible causal agents thereof, in arid-zone plant populations.

Kangaroo and euro populations, while present at relatively low densities when compared to livestock on similar rangelands (Caughley et al. 1983), are likely to be considerably above presettlement densities on these previously waterless plains (Newsome and Corbett 1977). There is no evidence that numbers of kangaroos on Yeelirrie increased as a result of the removal of livestock; however, despite the lower levels of use, grazing by kangaroos and euros significantly affected the survival of three of six species at some time during this ten year investigation.

Eragrostis xerophila, a desirable forage species that is extremely resistant to grazing by livestock (Wilcox and Morrissey 1979), was the most important forage species affected by kangaroo grazing. Adult plant survival was reduced by as much as 44 per cent when grazed during a period of "normal" rainfall years following the drought, and survival was significantly reduced by grazing during all other periods. Juveniles suffered a reduced survival of 22 percent on grazed areas during more "normal" years following drought, but actually had a 13 per cent advantage over plants on protected areas during the drought. This apparently anomolous result suggests different controlling factors are acting on populations on protected and grazed areas during the drought. Further explanation is not possible without more detailed studies of likely controlling factors.

Eremophila spectabilis, an undesirable increaser, unpalatable to livestock and not evident in kangaroo diets, responded positively to grazing. Survival response was variable, with greater benefits for grazed adults in drought years on the poor site (M20A). This response is typical of an undesirable increaser, as described by Dyksterhuis (1958). The potential exists for a dramatic increase in the population of this species on areas grazed by kangaroos. Its increaser status was enhanced by kangaroo grazing, particularly on the poor condition site. Initial differences in the density of this species between the grazed and ungrazed areas were great (853/ha on the grazed and 102/ha on the ungrazed area) and it is likely these differences contributed to the responses detected. A moderating influence on the potential population explosion of this species is that survival of juveniles on both sites is reduced on grazed areas. While evidence from diet information collected in conjunction with this study (Oliver unpublished) suggests this species is not grazed by kangaroos, the small amount of phytomass contained in each juvenile plant may not have been detected by diet sampling procedures.

Grazing Frankenia pauciflora during the more "normal" seasons following the drought favored the survival of adults, but no other effects of kangaroo grazing on survival were detected.

The pronounced effects of kangaroo grazing on plants at Yeelirrie is in direct contrast to the less defined effects of grazing by sheep reported by Williams (1968), and by Williams and Roe (1975) for a number of arid zone grasses. They were; however, as dramatic as the inablility, in the opinion of Williams and Roe, of Enteropogon acicularis to survive under heavy grazing by sheep. Williams' (1968 and 1969) failure to detect any effects of different intensities of sheep grazing on Danthonia caespitosa populations, and his conclusions that the grassland forms a stable disclimax, may be a result of his analytical methods. Austin et al. (1981) examining the same data discounted grazing as a significant factor in the dynamics of the grassland, but their conclusion may have been due to the overwhelming contribution to the population variance made by seasons, succession and soil factors.

Crisp (1978), Crisp and Lange (1976), and Lange and Willcocks (1980) concluded that grazing by livestock and the effect of rabbits combine to threaten the persistence of shrub and tree populations in the southern semi-arid shrub zone of Australia. These conclusions were supported by the Yeelirrie results where grazing by native herbivores slowed recovery rates of desirable and favored undesirable species.

The effect of grazing by kangaroos paralleled the effects of livestock grazing, strengthening the concept of competition between kangaroos and livestock reported by Newsome (1971) and Low et al. (1981) in central Australia. Indications are that the grass component of the pastures at Yeelirrie will decline and Eremophila species will tend to increase their dominance of the shrub component of the pasture. Grazing by kangaroos is facilitating this change to less productive pastures.

The practical management implications of the Yeelirrie results represent only a portion of their significance. Demonstration of the fallacy of the assumption that survival of different groups of adults is similar in any given period adds strength to Harper's (1977) case against the use of age class data to estimate survival rates of long-lived perennial species. The widely applied static life table approach (Silvertown 1982) of deducing dynamics from age structure should not be used for the analysis of arid zone plant populations because the basic assumption of constant rates of adult mortality has been shown to be untenable for the six arid land species examined at Yeelirrie. I concur with Harper (1977) that the assumptions of this type of analysis are too restrictive to permit valid identification of causal relationships.

## Conclusions

Rigorous analysis of survival in populations of five shrubs and a perennial grass leads to conclusions that physical, biological and/or historical site differences, and grazing by kangaroos, affected plant population dynamics at Yeelirrie station in the mulga zone rangelands of Western Australia.

Grazing by kangaroos and euros reduced the survival rate of Eragrostis xerophila by as much as 44 per cent. This effect was more pronounced during a more "normal" rainfall period following a severe drought. Opposite effects were detected in two undesirable species, for which survival was favored on grazed sites by up to 30 per cent for Eremophila spectabilis, and by 22 per cent for Frankenia pauciflora.

While plant numbers have increased since the removal of domestic stock, grazing by kangaroos and euros is favoring undesirable species and therefore leading to a continued decline in the quality of these rangelands. Management strategies based on the reduction or removal of livestock would seem to be insufficient to guarantee improving range condition, particularly if the populations of kangaroos and euros are not similarly controlled. More research should be encouraged to examine the effects of management innovations on the dynamics of rangeland plant populations.

Constant adult mortality across cohorts, a crucial assumption employed when using age structure (static life-table) data to infer population responses, was violated by species examined at Yeelirrie. This suggests this approach to the interpretation of population dynamics is inappropriate for these species and casts doubt on its usefulness for other long-lived species.

The use of statistically powerful likelihood ratio tests included in program SURVIV will enable a more rigorous examination of the effects of many management, physical and historical factors on plant survival. Experiments can now be designed to establish causal relationships with the knowledge that a more powerful tool is available to aid in analyzing and interpreting the results.

# CHAPTER V

# RATES OF POPULATION CHANGE: THE NET EFFECT OF RECRUITMENT AND DEATH PROCESSES

## Introduction

Decisions based on the effects of management on rangeland plant communities are often based on information about one, or a few, species. This concept of the key species (Stoddart et al. 1975, and Standing 1938) has been applied extensively by management agencies in North American rangelands (Smith 1965) and implicitly by similar managers in Australia (Wilcox and Morrissey 1979). Characterizing the behavior of populations of these key species in response to management and to environmental variables via demographic methods is one avenue by which change can be examined and related to potential causal agents.

The analysis of plant survival information covered in detail in Chapter 4 represents only one aspect of the examination of the process of change in plant populations. Recruitment of individuals into the defined population is occurring concurrently with the loss of individuals from that population. The net effect of these two processes determines the absolute rate at which the number of individuals in a particular population is changing. Crawley (1983) refers to this net effect as the "fitness" of the population.

Recruitment into desert plant populations is thought to be episodic, although little evidence supporting this contention has been presented in range literature. West et al. (1979) postulated episodic recruitment but were unable to support this hypothesis with their data. Williams' (1968) perennial grass data suggest some species maintain a low level of recruitment most of the time but they depend on occasional massive recruitment events to maintain the population over long perids during which there is a net loss to the population. Crisp (1978) and

Crisp and Lange (1979) presented evidence that indicates recruitment is prevented by herbivory on young plants of some populations of southern Australian shrubs. Lange and Willcocks (1980) experimentally demonstrated the ability of grazing sheep to selectively remove a species from arid zone shrublands. By its very nature recruitment is more difficult to study than survival; cohort data provide multiple survival events for each cohort but only one recruitment event. Long-term observations on repeatedly recorded populations are thus necessary to build up enough information to permit rigorous testing of recruitment as a separate process in plant populations.

A population can, however, be regarded as an entity within which the two processes are occurring simultaneously. Each recording interval can be used to define a rate of change in the population that can be examined either relative to time or to the initial population size. The binomial approximation to the death process during single recording periods was established in Chapter 3, adequately demonstrated by Chiang (1960a and 1960b) and utilized by White (1983) in the development of program SURVIV. The Poisson approximation of the birth (recruitment) process was demonstrated by Bhat (1971) and Chiang (1968) and its application to arid zone plant populations discussed in Chapter 3. Both approximations were combined by Hoel et al. (1972) to form a joint density function appropriate for testing differences between rates of change in populations.

Traditional population studies have concentrated on rates of change in populations relative to the original number of females (Varley et al. 1973, Silvertown 1982, and Crawley 1983); however, I contend that a more reasonable parameter to examine in plant populations is the number of individuals added to or lost from the population, i.e., the net change in number of individuals during a particular time interval. The large number of offspring (seeds) generated by each adult plant coupled with the low probability that any one of these offspring will survive to become a reproducing adult suggests that the Poisson approximation is appropriate. The dominance of environmental factors in the dynamics of arid-land plant populations, coupled with the low probability that a seed will become a viable recruit, indicates it may be relevant to consider the number of recruits per unit time as the birth process.

This chapter considers absolute rates of change in the number of individuals in populations of the six species for which detailed survival analyses were presented in Chapter 4. This rate parameter is used to test specific hypotheses about the effect of grazing by kangaroos and to examine the mode by which the change is effected.

## Methods

Recruitment information was collected as an integral component of the plant survival study (Chapter 4) and was recorded for each interval by determining new individuals added to site maps during each recording period. Information from the six species for which unambiguous location data could be extracted from the maps was used in this analysis, matching the survival information used in Chapter 4. Data from the four sites with paired grazed and ungrazed areas were analyzed using maximum likelihood methods (Mood et al. 1974). Likelihood ratio tests were used to compare rates of change in eight grazed and eight ungrazed populations (two species occurred on two sites). Development of the tests was based on a joint density function derived from the assumed Poisson recruitment and Binomial death processes. Numerical solution was necessary and Newton/Raphson methods outlined by Miller (1981) were used to compute maximum likelihood estimates for the number of recruits and the survival rate under constrained models. These methods are outlined in Chapter 3 and a BASIC program was used to calculate the test statistics.

Three basic hypotheses were tested, the first being: the rate of change in the numbers of a particular population was not different from zero. This test essentially permits inference about the magnitude and direction of change in all populations. Tests of the second hypothesis, vis., two populations (grazed and ungrazed) changed at the same rate over a particular time interval, permitted inference about the effect of grazing by kangaroos on rates of change of populations of each of the six species. This second hypothesis was used in conjunction with the third, the ratio of the number of recruits divided by the death rate (B/(1-S)) was the same for the two populations examined in the second test, to explore the types of response exhibited by each species during each recording period. Effects of grazing and/or precipitation can be manifest via either the recruitment or the death process (Crawley 1983), and numerical differences in population changes can be due to effects on either or both of these processes as well as being a result of different initial population size.

The last two hypotheses,

1) rates of change in two populations are the same, and

2) recruitment and death responses as measured by the ratio (numbers of recruits/death rate) are the same in both populations,

when applied to the same pair of populations generate four possible outcomes, each with a unique interpretation (Chapter 3, page 43).

a. Both hypotheses can be rejected, in which case the conclusion is that the two populations are behaving differently in terms of both net change and the processes that are impacted.

b. Both hypotheses are not rejected, in which case the populations are behaving in the same manner as a result of similarly impacted processes.

c. The first hypothesis may be rejected and the second not rejected, suggesting the populations are behaving differently despite similar impacts on the recruitment and death processes, leading to the conclusion that differences in rates of change are due to initial population size differences.

d. The first hypothesis can fail to be rejected and the second rejected, leading to the conclusion that the net population changes are the same but the processes impacted are different, the similarity of net result being due to a balancing of responses to the impacts.

Each of the recording intervals was categorized as wet (1973-76), dry (1976-79), or more "normal" (1979-82) based on rainfall data presented in Chapter 4 (Fig 4). Responses to treatment were interpreted in the light of this information.

All significance levels are set at alpha = 0.05 unless otherwise stated.

## Results

### Recruitment

The number of individuals recruited into each population varied among the recording periods (Fig 9). Higher recruitment was observed during the wet period (1973-76) than during the drought (1976-79), or post drought, more "normal" period (1979-82). Grazing reduced recruitment of *Eragrostis xerophila* during the more "normal" period (Fig 9a), of *Maireana glomerifolia* during all three periods (Fig 9b), and of *Ptilotus obovatus* during the more "normal", post-drought period (Fig 9d). *Eremophila leucophylla* recruitment was stimulated by grazing at one site (M19A) during the wet (1973-76) and post-drought periods (Fig 9c), while recruitment of *Eremophila spectabilis* was greater on grazed areas at site M18A during the 1973-76 (wet) period and at site M20A during all periods (Fig 9e). *Frankenia pauciflora* had a small, but significant, recruitment advantage on protected areas during the wet (1973-76) and dry (1976-79) periods, but was more strongly favored on grazed areas during the post-drought (1979-82) period (Fig 9f).

### Rates of Population Change

#### *Individual species* (Table 12)

All six species populations increased significantly during the wet period whether grazed or ungrazed. *Ptilotus obovatus* increased significantly during the dry period, while all others either decreased or

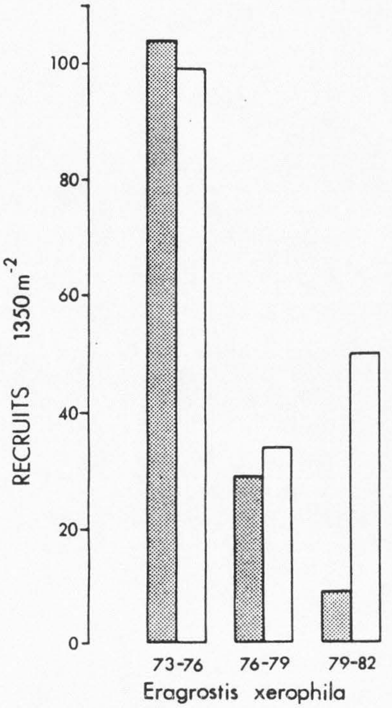

Fig 9a

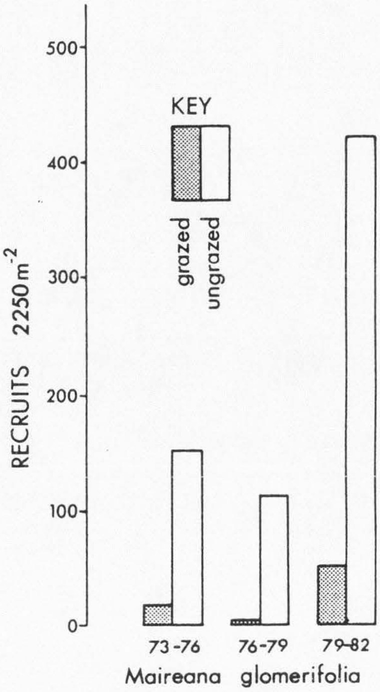

Fig 9b

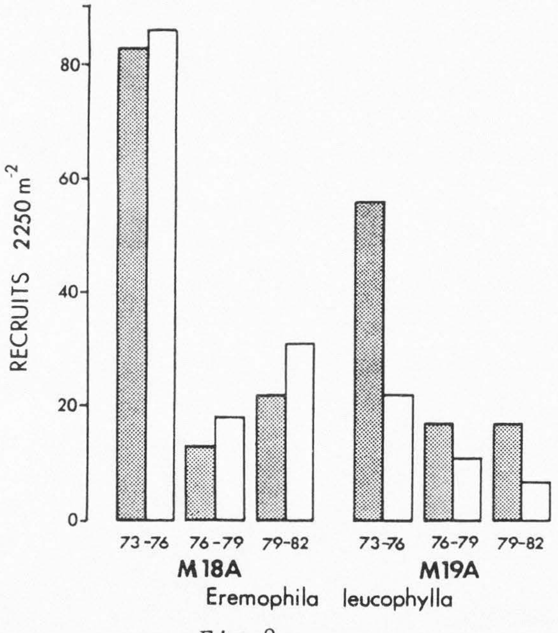

Fig 9c

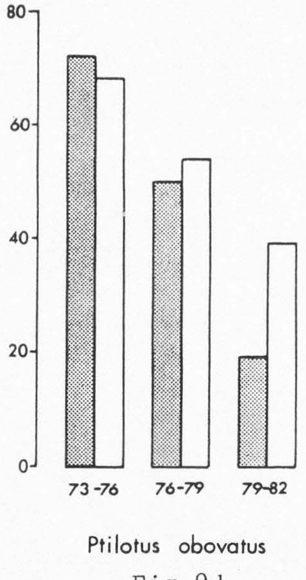

Fig 9d

Figure 9. The numbers of six species recruited during three three year periods on grazed and ungrazed areas at Yeelirrie station.

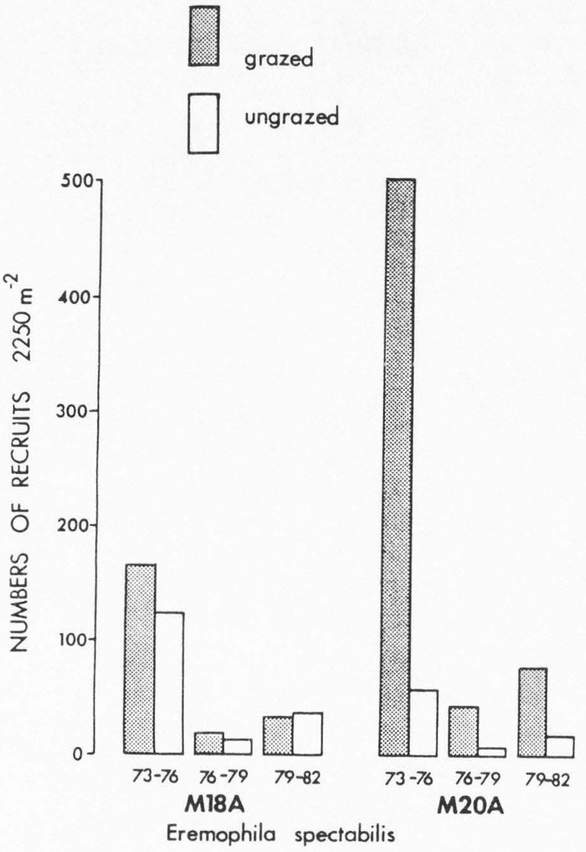

Fig 9e

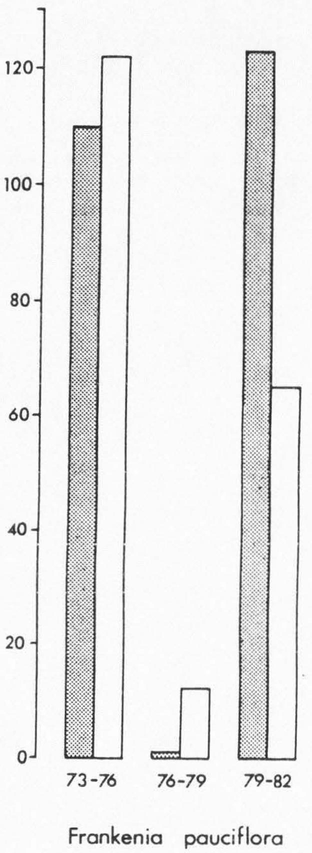

Fig 9f

Figure 9. (Continued)

Table 12. Changes in the numbers of individuals in eight grazed and eight ungrazed populations of six perennial plant species during three different climatic periods. N.B. Each Chi square value has one degree of freedom.

Grazed Populations

| | Erxe | Magl | Erle M18A | Erle M19A | Ersp M18A | Ersp M20A | Frpa | Ptob |
|---|---|---|---|---|---|---|---|---|
| Initial/ha | 496 | 533 | 440 | 756 | 218 | 853 | 284 | 156 |
| WET (1973-76) | | | | | | | | |
| Response/ha/yr | 232 | 24 | 117 | 74 | 244 | 729 | 160 | 105 |
| Chisq | 127.7 | 15.27 | 105.1 | 50.35 | 359.7 | 953.2 | 184.7 | 129.7 |
| Prob | <.000 | <.001 | <.000 | <.000 | <.000 | <.000 | <.000 | <.000 |
| DRY (1976-79) | | | | | | | | |
| Response/ha/yr | -62 | 0 | -9 | 0 | -52 | -584 | -93 | 39 |
| Chisq | 8.803 | | 5.301 | .1297 | 19.64 | | 86.68 | 11.16 |
| Prob | <.005 | | 0.022 | 0.270 | <.001 | | <.000 | <.005 |
| "NORMAL" (1979-82) | | | | | | | | |
| Response/ha/yr | -178 | 67 | 19 | 0 | 0 | 47 | 173 | 0 |
| Chisq | 79.50 | 42.88 | 5.890 | 1.337 | 1.993 | 9.600 | 164.4 | 1.905 |
| Prob | <.000 | <.000 | 0.017 | 0.497 | 0.177 | <.005 | <.000 | 0.187 |

Ungrazed Populations

| | Erxe | Magl | Erle M18A | Erle M19A | Ersp M18A | Ersp M20A | Frpa | Ptob |
|---|---|---|---|---|---|---|---|---|
| Initial/ha | 333 | 698 | 391 | 329 | 293 | 102 | 342 | 124 |
| WET (1973-76) | | | | | | | | |
| Response/ha/yr | 240 | 222 | 121 | 22 | 179 | 83 | 178 | 95 |
| Chisq | 177.3 | 230.3 | 112.6 | 8.958 | 208.2 | 107.3 | 202.1 | 110.0 |
| Prob | <.000 | <.000 | <.000 | <.005 | <.000 | <.000 | <.000 | <.000 |
| DRY (1976-79) | | | | | | | | |
| Response/ha/yr | -54 | 31 | 0 | 0 | -31 | -61 | -111 | 61 |
| Chisq | 6.485 | | .9169 | 2.411 | 10.56 | | 73.06 | 32.01 |
| Prob | 0.011 | | 0.467 | 0.032 | <.005 | | <.000 | <.001 |
| "NORMAL" (1979-82) | | | | | | | | |
| Response/ha/yr | 299 | 560 | 28 | 0 | 22 | 0 | 62 | 0 |
| Chisq | 125.6 | 477.4 | 9.269 | .8527 | 4.481 | 2.211 | 19.57 | .1396 |
| Prob | <.000 | <.000 | <.005 | 0.385 | 0.036 | 0.154 | <.001 | 0.723 |

did not change. More "normal" years (1979-82) resulted in all species populations either not changing or increasing, with one exception, (*Eragrostis xerophila*, which declined significantly on grazed areas).

*Treatment effects* (Table 13)

Grazing by kangaroos significantly reduced rates of population increase for *Maireana glomerifolia* during all periods, *Eragrostis xerophila* during the post drought years, and *Eremophila spectabilis* on a good condition site (M18A) during this same period. Rates of population change were significantly increased for *Eremophila leucophylla*, and for *Eremophila spectabilis* (on two sites) during the wet years. On site M20A *Eremophila spectabilis* benefited from protection during the drought but grazing stimulated the rate of population growth in post drought years, a response similar to that displayed by *Frankenia pauciflora* during this same period. The magnitude of population responses to grazing varied from an increase of more than 700 individuals in a grazed population of *Eremophila spectabilis* immediately following the removal of livestock (1973-76) from a poor condition site (M20A), to a decrease of 584 individuals per hectare per year for grazed individuals of the same species on the same site during the drought (1979-82). About half the populations did not respond significantly to grazing by kangaroos.

*The nature of the responses* (Table 14)

Responses of each population to grazing are reported here in reference to the four possible responses listed in the methods section. Species for which both hypotheses (1) and (2) were rejected included:

*Eragrostis xerophila* (1979-82), *Maireana glomerifolia* (all periods), *Eremophila leucophylla* (1973-76) on site M19A, *Eremophila spectabilis* (1976-79 & 1979-82) on site M20A, and *Frankenia pauciflora* (1979-82), leading to the conclusion that grazing by kangaroos is affecting either the recruitment or the death process, resulting in different rates of change in the grazed and ungrazed populations of these species. For *Eragrostis xerophila*, recruitment is reduced and mortality increased in the grazed population. *Maireana glomerifolia* responded to grazing by only decreasing recruitment during all periods. *Eremophila leucophylla* increased recruitment on grazed areas, showed no mortality response and had a significantly different initial population size. *Eremophila spectabilis* had both recruitment and mortality significantly impacted by grazing, effects that were coupled with a significantly different initial population size. Both recruitment and mortality of *Frankenia pauciflora* were significantly impacted by grazing during post-drought years.

Initial population size was the major determinant of the different rates of change detected in grazed and ungrazed populations of *Eremophila spectabilis* on sites M18A and M20A during the wet years immediately following the removal of livestock, as indicated by these populations exhibiting response type c, mentioned above. Populations of *Frankenia pauciflora* (1976-79) and *Ptilotus obovatus* (1973-76) exhibited response type d, indicating that the non-significant difference between rates of change in grazed and ungrazed populations is the result of a compensation of response in recruitment by an opposite response in mortality. All other populations behaved in the same manner on both grazed and ungrazed areas

Table 13. Comparison of rates of change in grazed and ungrazed populations of six perennial species. Chi square values all have one degree of freedom.

| | Erxe | | Magl | | Erle M18A | | Erle M19A | | Ersp M18A | | Ersp M20A | | Frpa | | Ptob | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | G | UG | G | UG | G | UG | G | UG | G | UG | G | UG | G | UG | G | UG |
| 1973-76 | | | | | | | | | | | | | | | | |
| Change $\text{ha}^{-1}\text{yr}^{-1}$ | 232 | 240 | 24 | 222 | 117 | 121 | 74 | 22 | 244 | 179 | 729 | 83 | 160 | 178 | 105 | 95 |
| Chi square | .1342 | | 117.3 | | .0510 | | 13.95 | | 6.570 | | 381.1 | | .6107 | | .3393 | |
| Prob | 0.727 | | .000 | | 0.839 | | .005 | | 0.011 | | .000 | | 0.455 | | 0.582 | |
| 1976-79 | | | | | | | | | | | | | | | | |
| Change $\text{ha}^{-1}\text{yr}^{-1}$ | -62 | -54 | 0 | 31 | -21 | -9 | 3 | 9 | -52 | -31 | -584 | -61 | -93 | -111 | 39 | 61 |
| Chi square | .0679 | | | | .8608 | | .3423 | | 2.013 | | | | 1.399 | | 1.679 | |
| Prob | 0.809 | | | | 0.383 | | 0.580 | | 0.146 | | | | 0.241 | | 0.211 | |
| 1979-82 | | | | | | | | | | | | | | | | |
| Change $\text{ha}^{-1}\text{yr}^{-1}$ | -178 | 299 | 67 | 560 | 19 | 28 | 9 | 4 | 0 | 22 | 47 | 0 | 173 | 62 | -13 | -4 |
| Chi square | 195.3 | | 241.7 | | .5653 | | .2357 | | 5.884 | | 4.633 | | 29.42 | | 1.370 | |
| Prob | .000 | | .000 | | 0.468 | | 0.655 | | 0.017 | | 0.033 | | .001 | | 0.245 | |

Note: Erxe = *Eragrostis xerophila*, Magl = *Maireana glomerifolia*, Erle = *Eremophila leucophylla*, Ersp = *Eremophila spectabilis*, Frpa = *Frankenia pauciflora*, Ptob = *Ptilotus obovatus*.

M18A, M19A, and M20A are different sites.

Table 14. The ratio of recruits/death rate compared across grazed and ungrazed populations of six perennial species. Chi square values all have one degree of freedom.

| | Erxe | | Magl | | Erle M18A | | Erle M19A | | Ersp M18A | | Ersp M20A | | Frpa | | Ptob | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1973-76 | G | UG | G | UG | G | UG | G | UG | G | UG | G | UG | G | UG | G | UG |
| B/(1-S) | 697 | 2228 | 1080 | 11932 | 2054 | 1892 | 1587 | 233 | 4092 | 2728 | 9638 | 1311 | 3520 | 4697 | 2520 | 476 |
| Chi sq. | 2.969 | | 4.632 | | .0137 | | 11.44 | | .2070 | | 2.211 | | .0852 | | 4.341 | |
| Prob | 0.089 | | 0.033 | | 0.909 | | .005 | | 0.676 | | 0.154 | | 0.779 | | 0.039 | |
| 1976-79 | | | | | | | | | | | | | | | | |
| B/(1-S) | 86 | 86 | 68 | 377 | 86 | 128 | 249 | 196 | 73 | 57 | 56 | 12 | 3 | 27 | 221 | 382 |
| Chi sq | .0001 | | | | .7968 | | .1434 | | .3719 | | | | 8.801 | | 2.273 | |
| Prob | .990 | | | | 0.401 | | 0.721 | | 0.559 | | | | .005 | | 0.147 | |
| 1979-82 | | | | | | | | | | | | | | | | |
| B/(1-S) | 15 | 621 | 973 | 3146 | 401 | 424 | 343 | 166 | 205 | 218 | 501 | 65 | 2335 | 294 | 90 | 144 |
| Chi sq | 179.9 | | 6.054 | | .0117 | | .9541 | | .0332 | | 19.72 | | 26.59 | | 1.806 | |
| Prob | .000 | | 0.015 | | 0.917 | | 0.356 | | 0.870 | | .001 | | .001 | | 0.198 | |

Note: Erle = *Eremophila leucophylla*, Ersp = *Eremophila spectabilis*, Erxe = *Eragrostis xerophila*, Magl = *Maireana glomerifolia*, Frpa = *Frankenia pauciflora*, Ptob = *Ptilotus obovatus*. M20A, M18A, and M19A are different sites.

as indicated by a failure to reject either hypothesis (1) or hypothesis (2), option b above.

## Discussion

All species examined responded in some way to climatic variation or to combinations of climatic and management factors. Above-average precipitation during the period immediately following the removal of livestock resulted in significant increases in all species populations regardless of treatment. The separation of these two possible causal agents was not possible from the data and it is likely that both are contributing to population increases. Williams (1968) and Williams and Roe (1975) refer to the importance of rare pluvial periods for the germination and establishment of arid zone grass species. On the other hand, traditional trend interpretation (Dyksterhuis 1949 or Humphrey 1949) would predict the recovery of at least the desirable species following the removal of livestock but fails to explain the similar release of undesirable species populations.

Population responses during the drought were variable with some species exhibiting significant declines in number, a response accentuated by grazing for Eremophila spectabilis growing on a poor site (M20A). Declines in other species (Eragrostis xerophila, Eremophila leucophylla (M18A), Eremophila spectabilis (M18A), and Frankenia pauciflora), were not affected by grazing during drought. Thus, although species did decline during the drought, those growing on sites in fair or good condition were not affected by kangaroo grazing. Other species populations remained static during the drought, suggesting an ability to remain essentially dormant, a response similar to that reported by Vorster (1975) for South African veld communities, and by Chambers (1979) for salt desert shrubs in southern Utah. Ptilotus obovatus increased its numbers on both grazed and ungrazed areas during the drought, reflecting an ability to take advantage of rainfall events during the drought by cntinuing to recruit, coupled with an ability to either withstand or avoid grazing by kangaroos. Maireana glomerifolia populations increased significantly on protected areas but were static on grazed areas during the drought.

Following a return to more "normal" rainfall conditions (1979-82) population responses became more predictable using traditional concepts of trend. Both highly palatable, desirable species (Maireana glomerifolia and Eragrostis xerophila) continued to make dramatic gains in number when protected from grazing. The grass (Eragrostis xerophila), however, suffered significant declines on grazed areas, possibly as a result of its preferred status in the kangaroo diet. In a quite different ecosystem Maireana glomerifolia was able to sustain a population increase on grazed areas during this recovery period; however, the rate of increase was reduced by grazing. The responses recorded for these two desirable species leads to the conclusion that grazing by kangaroos following the removal of livestock reduced the rate of recovery of these semi-arid pastures.

During this post-drought period other species exhibited changes of lower magnitude than the two desirable species; the undesirable species, Eremophila spectabilis and Frankenia pauciflora, responded positively to grazing, while the intermediate species, Ptilotus *obovatus*, and the long-lived desirable, *Eremophila leucophylla*, showed no significant change. The greater susceptibility of palatable species to grazing during the more "normal" rainfall period following the drought also concurs with Vorster's (1975) South African and Chambers' (1979) southern Utah results.

Differences in the types of response evident in each of the populations during each period indicate considerable flexibility:

a) within each species in terms of its response to environmental factors and/or treatments,

and b) in the way different species respond to external factors.

This flexibility is conferred by the variable nature of species responses to different impacts.

*Maireana glomerifolia* exhibited a consistently reduced recruitment on grazed areas during all periods. *Eragrostis xerophila* showed no grazing response until the post-drought period when recruitment was reduced and mortality increased in the grazed population. Drought elicited significant effects on both recruitment and mortality in the grazed *Frankenia pauciflora* population; however, these responses were in opposite directions and balanced each other to produce no significant rate of change response to grazing. The majority of species exhibited no response to grazing during the drought, and the magnitude of population changes detected was generally less than during more favorable climatic periods. The variability of species responses to environmental and management factors, both in terms of the apparent mechanism of that response and the net result, suggests careful interpretation of measurements of change is necessary regardless of what methods are used. Demographic methods have permitted this variability to be detected, a performance yet to be demonstrated by traditional methods.

## Conclusions

Populations of all six species responded positively to the removal of livestock and/or above-average precipitation during the first three years of the study. These two factors could not be separated and it is likely they are interacting in some way to produce the observed increases that ranged from 22 individuals per hectare per year (ungrazed *Eremophila leucophylla* on site M19A) to 729 individuals per hectare per year (grazed *Eremophila spectabilis* on site M20A). Grazing by kangaroos significantly reduced recruitment of the desirable shrub *Maireana glomerifolia* during this period. Other differences in population behavior during the "wet" period were largely due to differences in the initial population size.

Three years of drought caused declines in 10 of the 16 populations but significant grazing responses were evident in only *Maireana glomerifolia* where grazing reduced recruitment and prevented the population increase observed on ungrazed areas, and in *Eremophila spectabilis* where recruitment was reduced and mortality increased, but these impacts were confounded with differences due to different population sizes. The scarcity of grazing responses suggests these species may be less susceptible to grazing during drought, a response detected in North American and South African semi-arid shrub populations.

Responses to grazing were more evident during the three-year period following the drought when more "normal" rainfall patterns were experienced. Eragrostis xerophila grazed during this period had significantly reduced recruitment and increased mortality that led to a decline in the grazed population at the rate of 178 individuals per hectare per year compared with an increase of 299 per hectare per year on the protected areas. Reduced recruitment of Maireana glomerifolia continued to supress the grazed population so that an increase of only 67 per hectare per year was recorded on grazed areas compared with 560 on the protected areas. Reduced mortality and increased recruitment resulted in significant benefits for the grazed population of Frankenia pauciflora (173 $ha^{-1}$ $yr^{-1}$ compared with 62 $ha^{-1}$ $yr^{-1}$) while different initial population size as well as reduced mortality and increased recruitment combined to produce significant benefits for the grazed population of Eremophila spectabilis on site M20A (47 $ha^{-1}$ $yr^{-1}$ vs no change).

# CHAPTER VI

# TREND ON DESTOCKED WESTERN AUSTRALIAN MULGA-ZONE RANGELANDS PROTECTED FROM, OR OPEN TO, GRAZING BY KANGAROOS

## Introduction

The status of a piece of rangeland at one point in time is defined as the condition of that area (Bailey 1945). Changes in this status through time can be separated into two levels, short-term fluctuation produced by the vagaries of weather, and long-term changes of a more permanent nature. This long-term change, trend, has been detected by measuring condition at discrete points in time and the change related to some perceived optimal end-point.

The nature of the perceived end-point of long-term changes has influenced the choice of parameters used to detect trend and affected the interpretation of those changes. Smith (1978) clarified these two paths as: change relative to perceived climax vegetation (Dyksterhuis 1949) called ecological trend, and change relative to a perceived optimum production of some product or collection of products (Humphrey 1949) called production-oriented trend. Wilson and Tupper (1982) to some extent rationalized this divergence but contributed little more than already considered by Bailey (1945) nearly four decades earlier. There has been little or no recent emphasis on predicting future conditions, but rather a concentration on the measurement and interpretation of changes over past years, "retrospective" trend, as characterized by Norton (1981).

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Norton (1981) Unpublished mimeo. Impacts of grazing intensity and specialized grazing systems on vegetation production and composition. Presentation at N.A.S. symposium on impacts of grazing intensity and specialized grazing systems on use and values of rangelands. El Paso, NM. March 16-18, 1981.

Trend has generally been defined as a categorical variable (improvement, retrogression, or no change) and yet the management utility of any measure must be its ability to detect the rate of change. To decide on the optimum strategy for managing rangeland there must be a valid way to compare the effects of a number of strategies on the future production of that land. This can be achieved if the rates of change are reliably measured and if those measures can be used to predict future production potential on a realistic time scale.

Evaluation of even the simplest management strategies, such as the removal of livestock, require some measurement of the rate of change achieved using this strategy compared to alternatives. Responses of vegetation to the removal of livestock have been assumed to result in improvements in range condition, an upward trend (Wilcox and McKinnon 1972, Anon 1979, Stoddart et al. 1975, Dyksterhuis 1949). Management using this assumption has been applied over large areas for many years in Australian rangelands (Wilcox and McKinnon 1972, Mabbutt et al. 1963, and Payne et al. 1974) without an adequate examination of its effects on future production.

A reduction in livestock grazing pressure can result in a recovery of plant numbers, as shown in this study (Chapter 4, Fig 5), greater availability of phytomass, and changes in the frequency of species; however, determining the trend of these pastures requires examination beyond these overt increases. For production-oriented management (Humphrey 1949, and Wilson and Tupper 1982) it is the potential of the area to produce a defined type of product in future years that should be considered. If the removal of livestock does not lead to an increase in potential production, then the practice of stock removal is merely a deferment practice producing results analogous to storing hay for future use. This potential to produce is determined by the mixture of populations of plants (desirable, undesirable and intermediate) that grow on the area in question. Any practice that favors undesirable species while reducing the performance of desirable ones should be regarded as detrimental to the range.

Difficulties in the interpretation of traditional methods, ambiguities caused by characteristics of the variable being measured, inability to separate causal factors, and lack of rate measurement or predictive capability, point to the need for a new approach (Gardiner and Norton 1983, and West 1983).

While it is acknowledged that trend detection methods should consider all elements of the ecosystem relevant to stability, including soil and vegetation information (Bailey 1945), an examination plant population dynamics on a particular site offers an alternative approach to the quantification of the vegetation components of trend (Austin 1981, and Harper 1980). A species with a rapid rate of increase will tend to dominate, while a species that is having an adverse effect on a site will, by corollary, be reducing the rate of increase of desirable species populations. Rigorous comparison of rates of change of important species populations will enable inference about the effects of a particular management strategy on these populations. Detailed examination of the two essential population processes of survival and recruitment will enable changes in population dynamics to be assessed and tested rigorously (Crawley 1983). Potential causal agents can be examined and specific hypotheses tested experimentally using permanent plot records and new computer programs (e.g., White 1983).

## The Influence of Structure

The importance of different structural components in the interactions that occur in plant communities was recognized by Dansereau (1951). Arid zone plant communities are typically composed of at least two strata, an ephemeral low-growing layer and a perennial grass or shrub layer. Communities in the Goldfields region of Western Australia, the area in which the study was conducted, are typically multi-layered (Beard 1976). Methods of detecting change will need to account for the differential effects of one strata on others; for example, particularly long-lived species occupying upper strata for long periods of time (juniper in the Intermountain west, or *Hakea preissii* in chenopod pastures in Western Australian rangelands) will be likely to disproportionately affect lower strata species. Rates of change of species groups should thus be considered within each of the strata present on a site, and their importance related to changes likely to occur in other strata, particularly when species regarded as important for producing the defined product or products are located in the subordinate strata. When examined in each of the strata making up the vegetation at a site, these rates will permit the prediction of change in terms of likely dominants in that stratum.

It will still be up to the individual researcher to ensure that his sampling strategy is adequate to detect the invasion of potential woody weeds or undesirable dominants. However, careful mapping of individual plant locations within permanent plots will reduce the chance of these species being overlooked simply because, at the time of incipient population expansion, they are small or represent only a small proportion of the phytomass present.

This chapter examines the components of recruitment and survival and their effects on the potential population changes in groups of species classified as desirable, undesirable or intermediate for livestock grazing. Rates of population change in these groups, relative to each other, will determine if the future potential of sites at Yeelirrie station to produce forage, suited to livestock production, is improving. Comparison of desirable and undesirable group responses to grazing by kangaroos is also considered as a means of comparing vegetation responses to two management strategies: removing livestock, and removing livestock and kangaroos.

## Methods

Maps of individuals on permanent 150 x 15 meter plots were recorded in 1973, 1976, 1979, and 1982 using aerial photographs (Hacker 1978). Identification of each individual permitted the number of recruits and survivors to be established at each recording time, on four sites at which paired (grazed and protected) areas were maintained. Recordings were taken from plots fenced to exclude kangaroos and from adjacent unprotected recording plots (Chapter 4). Unambigouous location data were collected for a total of 18 species, including the six examined in detail in Chapters 4 and 5. These species were classified as desirable, undesirable, or of intermediate use for livestock production using Wilcox and Morrissey's (1979) classifications (Table 15).

Table 15. Classifications of species recorded on paired grazed and ungrazed areas at four sites on Yeelirrie. (* classified by Wilcox and Morrissey 1979).

| CLASS | SPECIES | |
|---|---|---|
| DESIRABLE | Eremophila leucophylla | * |
| | Rhagodia spinescens | * |
| | Acacia tetragonophylla | * |
| | Maireana pyramidata | * |
| | Maireama glomerifolia | * |
| | Maireana georgei | * |
| | Maireana integra | |
| | Maireana convexa | * |
| | Eragrostis xerophila | * |
| UNDESIRABLE | Eremophila spectabilis | * |
| | Eremophila longifolia | * |
| | Eremophila lachnocalyx | |
| | Cratystylis subspinescens | * |
| | Hakea preissii | * |
| | Frankenia pauciflora | * |
| INTERMEDIATE | Ptilotus obovatus | * |
| | Solanum lasiophyllum | * |
| | Acacia aneura | * |

Rates of change in populations of these groups of species were used to test the hypothesis that the vegetation at Yeelirrie has not responded to kangaroo grazing permitted since destocking. At one site (M21A) the total species compliment was recorded and analyzed to determine the responses detected at that site. Eighteen species from the four paired sites were used to examine responses over a larger range of ecosystems.

Methods of analysis were the same as those used in Chapter 5 and explained in more detail in Chapter 3. Approximate Chi square tests were constructed using likelihood ratio tests of the same hypotheses oulined on pages 43-45 in Chapter 3. Various pairing patterns of the different populations permitted an examination of both the effects of treatment on species group responses, and the relative responses of desirable and undesirable species groups under similar treatment regimes.

## Results

### Responses at Site M21A

#### Changes in population number

Site M21A was subjected to higher levels of grazing than other sites (Chapter 4, Figs 7 & 8) and its low shrub structure permitted complete documentation of all species on the site. During the course of the investigation all species groups increased significantly on both grazed and ungrazed areas (Table 16). Desirable species increased significantly during wet (1973-76) and more "normal" (1979-82) periods on both grazed and ungrazed areas. Drought resulted in a significant population decline on grazed, but no change on ungrazed areas. Undesirable species increased during wet and "normal" periods but declined significantly on both grazed and ungrazed areas during drought. In both species groups the net increases were greater than declines over the nine years of the study. Intermediate species increased significantly on both grazed and ungrazed areas during all periods, except on ungrazed areas where no change was detected during the post-drought period.

Table 16. Expected changes in grazed and ungrazed populations of three species groups at site M21A over three climatically different recording periods.

| | | DESIRABLE | UNDESIRABLE | INTERMEDIATE |
|---|---|---|---|---|
| INITIAL # ha$^{-1}$ | | 671 | 293 | 173 |
| GRAZED | WET (1973-76) | | | |
| | Change/ha/yr | 181 | 161 | 173 |
| | Chi square | 175.2 | 185.4 | 147.3 |
| | Prob | <.000 | <.000 | <.000 |
| | DRY (1976-79) | | | |
| | Change/ha/yr | -89 | -93 | 43 |
| | Chi square | 40.67 | 86.54 | 12.09 |
| | Prob | <.001 | <.000 | <.005 |
| | "NORMAL" (1979-82 | | | |
| | Change/ha/yr | 31 | 99 | 126 |
| | Chi square | 7.695 | 77.76 | 61.41 |
| | Prob | <.005 | <.000 | <.000 |
| Initial # ha$^{-1}$ | | 822 | 360 | 151 |
| UNGRAZED | WET (1973-76) | | | |
| | Change/ha/yr | 307 | 188 | 111 |
| | Chi square | 325.8 | 209.8 | 129.1 |
| | Prob | <.000 | <.000 | <.000 |
| | DRY (1976-79) | | | |
| | Change/ha/yr | 12 | -110 | 64 |
| | Chi square | .3167 | 67.97 | 30.91 |
| | Prob | 0.598 | <.000 | <.001 |
| | "NORMAL" (1979-82) | | | |
| | Change/ha/yr | 619 | 61 | -6 |
| | Chi square | 511.7 | 21.46 | .2052 |
| | Prob | <.000 | <.001 | 0.677 |

## The effects of treatment

Desirable species responded positively to protection during all periods (Table 17 and Fig 10) and intermediate species responded positively to grazing during the more "normal" period (Fig 11). Undesirable species did not respond to grazing during the wet or dry periods, but responded positively to grazing during more "normal", post-drought years (Fig 12). Responses in desirable species populations were due to differences in recruitment (1973-76), and recruitment coupled with differences in population size during dry and more "normal" periods (Table 18). The positive response to grazing in the undesirable species population during "normal" years was due to reduced mortality on grazed areas. Intermediate species populations behaved in the same manner regardless of treatment.

Comparison of population responses of desirable with undesirable species treated similarly (Table 19) reveals a consistent advantage for desirables on protected areas (Fig 13). An advantage due to different population sizes in the wet period, immediately following the removal of livestock (1973-76), was coupled with increased recruitment during 1976-79, and both increased recruitment and reduced mortality during 1979-82 (Table 20). Responses on grazed areas were similar for both species groups except during more "normal", post-drought years, when increased recruitment favored the undesirable species population (Fig 14).

Table 17. Expected changes in populations of three species groups compared across grazed (G) and ungrazed (U) areas at site M21A.

| | DESIRABLE | | UNDESIRABLE | | INTERMEDIATE | |
|---|---|---|---|---|---|---|
| | G | U | G | U | G | U |
| WET (1973-76) | | | | | | |
| Change/ha/yr | 181 | 307 | 161 | 188 | 121 | 111 |
| Chi square | 21.44 | | 1.319 | | .2909 | |
| Probability | <.001 | | 0.250 | | 0.616 | |
| DRY (1976-79) | | | | | | |
| Change/ha/yr | -89 | 12 | -93 | -110 | 43 | 64 |
| Chi square | 16.98 | | 1.126 | | 1.294 | |
| Probability | <.001 | | 0.306 | | 0.258 | |
| "NORMAL" (1979-82) | | | | | | |
| Change/ha/yr | 31 | 619 | 99 | 61 | 126 | -6 |
| Chi square | 333.5 | | 3.967 | | 35.96 | |
| Probability | <.000 | | 0.047 | | <.001 | |

Table 18. The ratio of recruits to death rate (B/(1-S)) for three species groups compared across grazed (G) and ungrazed (U) areas at site M21A.

| | DESIRABLE | | UNDESIRABLE | | INTERMEDIATE | |
|---|---|---|---|---|---|---|
| | G | U | G | U | G | U |
| WET (1973-76) | | | | | | |
| B/(1-S) | 6298 | 12950 | 3663 | 3510 | 1638 | 672 |
| Chi square | .7783 | | .0024 | | 1.190 | |
| Probability | 0.407 | | 0.963 | | 0.288 | |
| DRY (1976-79) | | | | | | |
| B/(1-S) | 73 | 419 | 3 | 33 | 246 | 402 |
| Chi square | 53.27 | | 11.07 | | 2.136 | |
| Probability | <.000 | | <.005 | | 0.162 | |
| "NORMAL" (1979-82) | | | | | | |
| B/(1-S) | 466 | 3744 | 1363 | 330 | 486 | 139 |
| Chi square | 49.06 | | 22.78 | | 24.97 | |
| Probability | <.000 | | <.001 | | <.001 | |

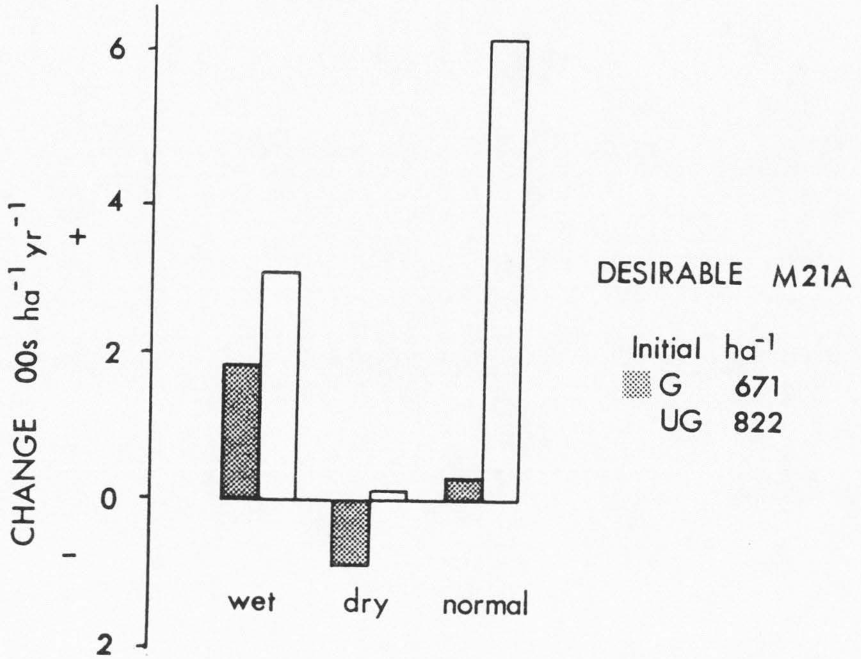

Figure 10. Absolute rate of change of grazed and ungrazed populations of desirable species growing on site M21A.

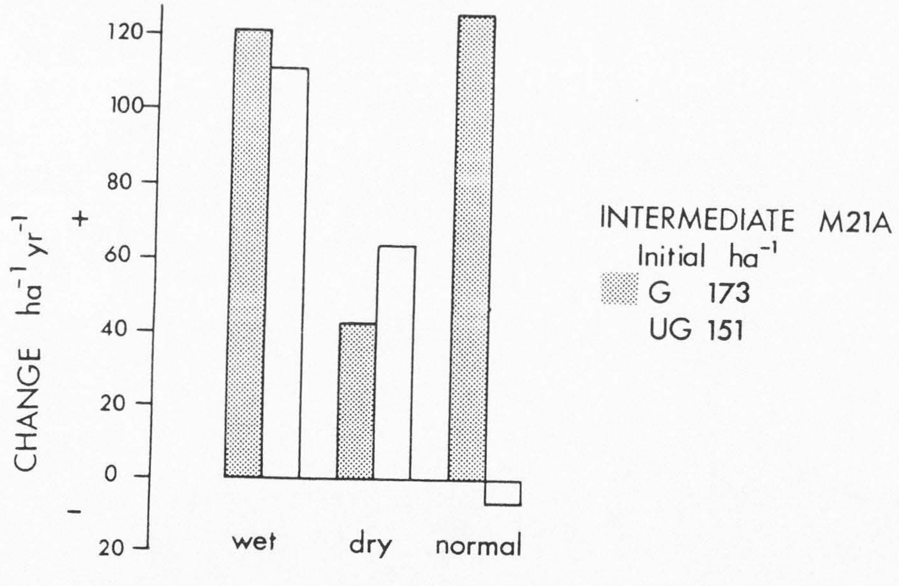

Figure 11. Absolute rate of change of grazed and ungrazed populations of intermediate species growing on site M21A.

Table 19. Expected changes in desirable and undesirable species groups subjected to similar treatment over three climatically different periods at site M21A.

| | GRAZED | | UNGRAZED | |
|---|---|---|---|---|
| | D | U | D | U |
| WET (1973-76) | | | | |
| Change/ha/yr | 181 | 161 | 307 | 188 |
| Chi square | .7201 | | 18.69 | |
| Prob | 0.429 | | <.001 | |
| DRY (1976-79) | | | | |
| Change/ha/yr | -89 | -93 | 12 | -110 |
| Chi square | .0746 | | 26.23 | |
| Prob | 0.798 | | <.001 | |
| "NORMAL" (1979-82) | | | | |
| Change/ha/yr | 31 | 99 | 619 | 61 |
| Chi square | 18.35 | | 261.5 | |
| Prob | <.001 | | <.000 | |

Table 20. The ratio of recruits to death rate (B/(1-S) for grazed and ungrazed populations of two species groups at site M21A.

| | GRAZED | | UNGRAZED | |
|---|---|---|---|---|
| | D | U | D | U |
| WET (1973-76) | | | | |
| B/(1-S) | 6292 | 3663 | 12950 | 3510 |
| Chi square | .3571 | | 2.447 | |
| Prob | 0.569 | | 0.128 | |
| DRY (1976-79) | | | | |
| B/(1-S) | 73 | 3 | 419 | 33 |
| Chi square | 25.72 | | 101.3 | |
| Prob | <.001 | | <.000 | |
| "NORMAL" (1979-82) | | | | |
| B/(1-S) | 466 | 1363 | 3744 | 330 |
| Chi square | 7.363 | | 71.32 | |
| Prob | <.005 | | <.000 | |

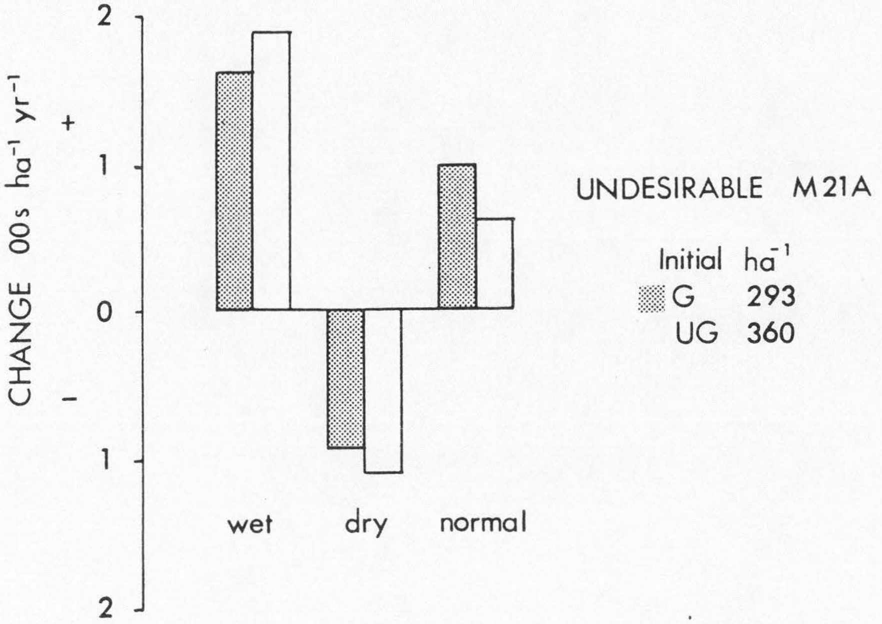

Figure 12. Absolute rate of change in grazed and ungrazed populations of undesirable species growing on site M21A.

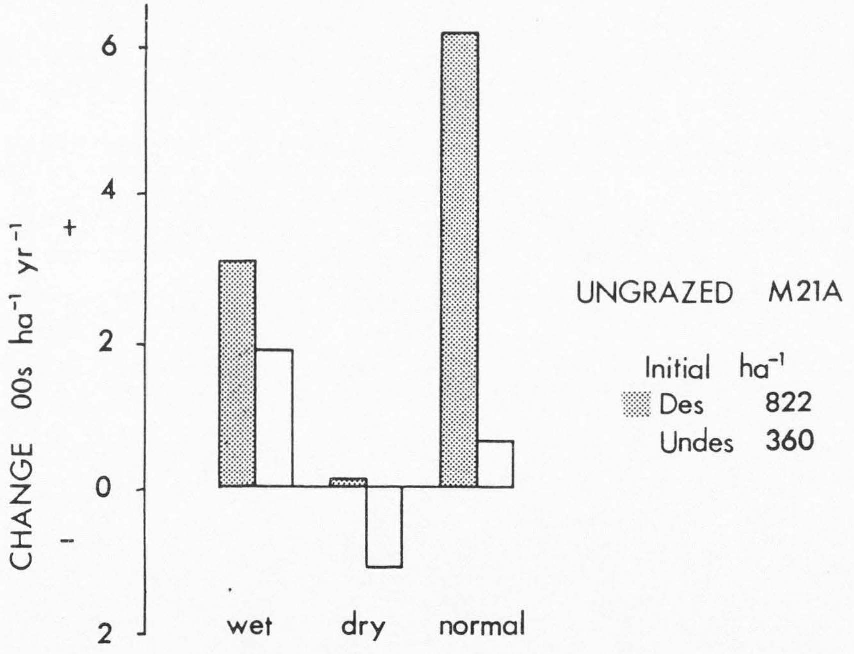

Figure 13. Comparable rates of change in desirable and undesirable species groups growing on protected areas at site M21A.

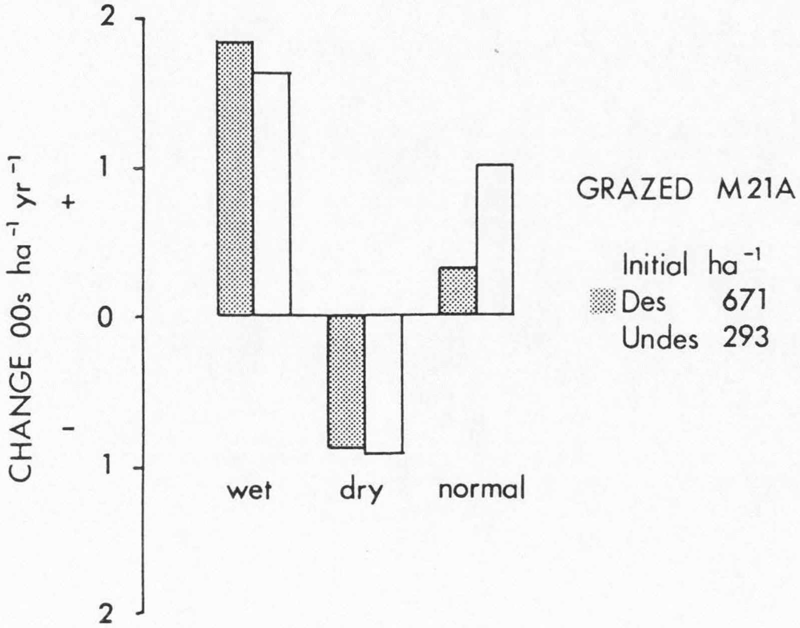

Figure 14. Comparable rates of change in desirable and undesirable species groups growing on grazed areas at site M21A.

## Responses in Species Groups From Four Sites

### Changes in population numbers

All three species groups increased their populations significantly over the period 1973-82 when examined over a range of ecosystems encountered at four paired sites (Table 21). Desirable species increased during wet and more "normal" periods but declined slightly (significantly on grazed areas) during the drought. Undesirable species followed a similar pattern except population declines during the drought were significant on both grazed and ungrazed areas. Intermediate species populations responded positively during wet and dry periods but did not change significantly during the more "normal," post-drought years.

## The effects of treatment

Desirable species did not respond to treatment during either wet or dry periods (Table 22), but their rate of increase was significantly impaired by kangaroo grazing during the more "normal" period. This response was due to significantly reduced mortality and increased recruitment on protected areas (Table 23).

Undesirable species responded significantly to grazing during all periods. This response was positive during both the wet and more "normal" periods and was due to differences in the initial population size during the wet and increased recruitment coupled with the population size difference during the more "normal" period. A significantly greater decline on grazed areas during the drought was attributable to differences in death rates.

Comparison of desirable and undesirable species population responses on areas treated similarly reveals a consistent advantage for desirables on protected areas (Table 23). This advantage was due to greater initial population size coupled with higher recruitment during all periods (Table 24). The death rates of undesirables was greater than desirables during the drought on these protected areas. On grazed areas, undesirable species were favored during wet and more "normal" periods, the advantage being conferred by higher recruitment during the wet period and lower mortality during the more "normal", post-drought period. During the drought, desirable species were favored on these grazed areas as a result of both reduced mortality and increased recruitment.

Table 21. Expected changes in grazed and ungrazed populations of three species groups for three climatically different periods. Species groups were formed by amalgamating data from four paired sites.

| | | DESIRABLE | UNDESIRABLE | INTERMEDIATE |
|---|---|---|---|---|
| | INITIAL #/ha | 574 | 356 | 43 |
| GRAZED | WET (1973-76) | | | |
| | Change/ha/yr | 140 | 294 | 30 |
| | Chi square | 448.5 | 1527 | 147.3 |
| | Probability | <.000 | <.000 | >.000 |
| | DRY (1976-79) | | | |
| | Change/ha/yr | -22 | -186 | 11 |
| | Chi square | 11.07 | 529.4 | 12.09 |
| | Probability | <.005 | <.000 | <.005 |
| | "NORMAL" (1976-79) | | | |
| | Change/ha/yr | 23 | 52 | -1 |
| | Chi square | 10.66 | 66.99 | .1405 |
| | Probability | <.005 | <.001 | 0.723 |
| | INITIAL #/ha | 511 | 182 | 63 |
| UNGRAZED | WET (1973-76) | | | |
| | Change/ha/yr | 146 | 113 | 33 |
| | Chi square | 462.8 | 526.4 | 137.2 |
| | Probability | <.000 | <.000 | <.000 |
| | DRY (1976-79) | | | |
| | Change/ha/yr | -8 | -67 | 9 |
| | Chi square | 1.350 | 168.5 | 7.896 |
| | Probability | 0.247 | <.000 | <.005 |
| | "NORMAL" (1979-82) | | | |
| | Change/ha/yr | 176 | 23 | -1 |
| | Chi square | 446.9 | 25.65 | .1016 |
| | Probability | <.000 | <.001 | 0.751 |

Table 22. Expected changes in populations of three species groups compared across grazed (G) and ungrazed (U) areas for three climatically different periods. The species groups were formed by amalgamation over four sites.

| | DESIRABLE | | UNDESIRABLE | | INTERMEDIATE | |
|---|---|---|---|---|---|---|
| | G | U | G | U | G | U |
| WET (1973-76) | | | | | | |
| Change/ha/yr | 140 | 146 | 294 | 113 | 30 | 33 |
| Chi square | .3794 | | 232.7 | | .1990 | |
| Probability | 0.554 | | <.000 | | 0.681 | |
| DRY (1976-79) | | | | | | |
| Change/ha/yr | -22 | 0 | -185 | -67 | 11 | 9 |
| Chi square | 2.167 | | 196.0 | | .0970 | |
| Probability | 0.149 | | <.000 | | 0.759 | |
| "NORMAL" (1979-82) | | | | | | |
| Change/ha/yr | 23 | 176 | 52 | 23 | -1 | -1 |
| Chi square | 169.2 | | 12.19 | | .0000 | |
| Probability | <.000 | | <.005 | | 1.000 | |

Table 23. The ratio of recruits to death rate (B/(1-S)) for three species groups compared across grazed (G) and ungrazed (U) areas over three climatically different periods. Groups are amalgamated over four sites.

| | DESIRABLE | | UNDESIRABLE | | INTERMEDIATE | |
|---|---|---|---|---|---|---|
| | G | U | G | U | G | U |
| WET (1973-76) | | | | | | |
| B/(1-S) | 6086 | 4477 | 17259 | 8783 | 1638 | 1311 |
| Chi square | 1.849 | | 1.783 | | .0695 | |
| Probability | 0.193 | | 0.200 | | 0.807 | |
| DRY (1976-79) | | | | | | |
| B/(1-S) | 641 | 766 | 129 | 75 | 246 | 249 |
| Chi square | 1.682 | | 6.475 | | .0000 | |
| Probability | 0.218 | | 0.036 | | 1.000 | |
| "NORMAL" (1979-82) | | | | | | |
| B/(1-S) | 1129 | 4827 | 1486 | 699 | 138 | 161 |
| Chi square | 115.7 | | 15.65 | | .2806 | |
| Probability | <.000 | | <.001 | | 0.624 | |

Table 24. Expected changes in desirable (D) and undesirable (U) species groups subjected to similar treatment over three climatically different periods. Species were amalgamated over four sites.

| | GRAZED | | UNGRAZED | |
|---|---|---|---|---|
| | D | U | D | U |
| WET (1973-76) | | | | |
| Change/ha/yr | 140 | 294 | 146 | 113 |
| Chi square | 139.7 | | 18.23 | |
| Probability | <.000 | | <.001 | |
| DRY (1976-79) | | | | |
| Change/ha/yr | -22 | -186 | 0 | -67 |
| Chi square | 281.9 | | 26.80 | |
| Probability | <.000 | | <.001 | |
| "NORMAL" (1979-82) | | | | |
| Change/ha/yr | 23 | 52 | 176 | 23 |
| Chi square | 8.729 | | 218.6 | |
| Probability | <.005 | | <.000 | |

Table 25. The ratio of recruits to death rate (B/(1-S)) for desirable (D) and undesirable (U) species groups subjected to similar treatment over three climatically different periods. Species were amalgamated over four sites.

| | GRAZED | | UNGRAZED | |
|---|---|---|---|---|
| | D | U | D | U |
| WET (1973-76) | | | | |
| B/(1-S) | 6086 | 17259 | 4477 | 8783 |
| Chi square | 12.82 | | 2.900 | |
| Probability | <.005 | | 0.092 | |
| DRY (1976-79) | | | | |
| B/(1-S) | 641 | 129 | 766 | 75 |
| Chi square | 108.4 | | 132.8 | |
| Probability | <.000 | | <.000 | |
| "NORMAL" (1979-82) | | | | |
| B/(1-S) | 1129 | 1486 | 4827 | 699 |
| Chi square | 3.549 | | 96.54 | |
| Probability | 0.063 | | <.000 | |

# Discussion

## Plant Population Numbers

Populations of all three species groups (desirable, undesirable and intermediate) increased significantly during the 10 years following the removal of livestock in 1972. The response was evident at both site M21A and over four separate sites at which paired grazed and ungrazed areas were maintained. The effects of removal of livestock could not be separated from those caused by climatic factors; however, the increases were maintained despite precipitation variation from very wet through very dry to "normal." The investigation has not been conducted for a sufficient length of time or with a design that would enable removal of the effect of initial recording time on the observed changes.

## Effects of Grazing Kangaroos

Plants growing on areas grazed by kangaroos responded differently during the study than did those growing on protected areas. Detailed examination of plant survival in Chapter 4 revealed significant effects of this grazing on a number of important range species, both desirable and undesirable for livestock production. Incorporation of recruitment information in Chapter 5 enabled a more detailed examination of individual species population responses. By considering groups of species of similar importance for the defined goal of recovering these rangelands for livestock production, I have been able to address the problem of prediction of likely community structure in terms of component populations of plants, based on rates of change observed over the study period. Observations involving the total species compliment from one site (M21A) led to similar inference to observations on 18 species amalgamated over four widely spaced sites.

Desirable plant populations observed over four sites increased more rapidly when protected from grazing (322 $ha^{-1}yr^{-1}$ vs 141 $ha^{-1}yr^{-1}$). Overall (1973-1982) there was a significantly greater rate of population increase in undesirable species growing on grazed areas at all four sites (161 $ha^{-1}yr^{-1}$vs 69 $ha^{-1}yr^{-1}$). Responses at site M21A were more dramatic; desirable species increasing more rapidly on protected areas (938 $ha^{-1}yr^{-1}$ vs 123 $ha^{-1}yr^{-1}$), while the advantage for undesirables on grazed areas (167 $ha^{-1}yr^{-1}$ vs 139 $ha^{-1}yr^{-1}$) was less than when the four combined sites were considered. It would seem that the rate of change of plant populations necessary to recover livestock production can only be maximized if grazing by kangaroos is controlled.

## Trend on Yeelirrie Pastures

Despite an increase in the number of perennial plants on all recording sites at Yeelirrie, the trend in the vegetal component of range condition has not been unequivocally upward. While this increase in plant density is likely associated with an increase in soil stability, the effect of destocking on the vegetal component has been variable. Comparison of the relative rates of increase in desirable and undesirable species groups suggests that desirable species have relatively faster rates of increase when protected from grazing by kangaroos. Trend on the protected areas has been unequivocally upward (Humphrey 1949). This type of response appears to support the concepts embodied in the quantitative climax approach to range condition assessment (Dyksterhuis 1949) in that the removal of livestock results in an increase in the proportion of desirable species. The quantitative climax approach used cover rather than plant number but the concept still applies to plant numbers if viewed in the long term.

On grazed areas, while there has been a significant increase in plant density, the proportions of desirable and undesirable species have not changed. Grazing by kangaroos has been sufficient to prevent the improvement predicted by the quantitative climax approach, and I view the observed changes as pasture deferment rather than trend.

It is of interest to consider the interpretation of these changes had we used different initial starting times for the population recordings. If we had commenced in 1976, after a very wet period, an examination of density records would have revealed no significant change. However, comparative rates of population change would have still indicated an upward trend on the protected areas, while trend on the grazed areas would have been less clear, a similar result to that indicated by the longer term data starting in 1973.

The question of responses in different strata did not enter the analysis of trend on site M21A where all but three individuals were located in a single shrub stratum. While different strata were present on the other three paired sites data were only avialable for the shrub and grass stratum. Further data collection and analysis will be necessary to isolate any differential effcts of one stratum on another.

Recent reviews of problems associated with quantifying range trend (Wilson and Tupper 1982, Bermant 1982, and West 1983) reveal that little progress has been made since the inception of the basic idea of using change in range condition as a useful tool in range management (Bailey 1945, and Renner 1948). Wilson and Tupper (1982) only re-emphasized the judgmental nature of trend assessment. West (1983) restated the need for multiple criteria in trend assessment and hinted at possible avenues for advance via the use of multivariate mathematical methods. Bermant (1982) discussed the problems associated with any single measure or index of trend, regardless of its derivation, on the basis of problems associated with differential weightings of components of any index, and the need to be able to account for contradictory and ambiguous data that may arise. The categorical nature of most assessment methods also raises questions about appropriate statistical methods to handle trend data.

To some extent the approach I used permits examination of the dynamics of change rather than the current obsession with the assessment of condition, a static measure of the state of the ecosystem. Stoddart et al. (1975, p. 198) stressed the need not only to observe the state of the range, but also to determine the current dynamics of the vegetation at that point.

Additionally, emphasis placed on the parameters allied to phytomass (e.g., cover) that follows from adoption of quantitative climax concepts (Dyksterhuis 1949), and a perceived need to use phytomass to establish stocking rates, has led to a confounding of short-term site productivity with trend. The potential to produce at some time in the future is really the item of interest in production-oriented trend assessment. If at time T+1 the potential of a site to produce at some arbitrary point in the future is greater than at time T then, and only then, are we justified in claiming there has been an upward trend. The potential of the vegetation at a site to produce phytomass some time in the future is determined not by the current level of phytomass production, but rather by the composition of that vegetation in terms of the number and proportion of each of the component species. This latter state of the vegetation is determined by the relative rates of change of each of the component species populations.

Rate of plant population change provides a more stable indicator of change in the vegetal component of any trend assessment, one that permits the examination of long-term change while allowing a more detailed, causation-oriented, examination of each of its component parameters, recruitment and mortality.

Identifying the differences in rates of population change among species groups and from period to period, and separating the effects of treatment on recruitment and mortality, provides information relevant to understanding why populations behave the way they do, and to developing management strategies designed to reduce detrimental impacts of use on rangeland ecosystems.

## Conclusions

Desirable species, as a group, responded positively to protection from kangaroo grazing, showing greater rates of population increase on protected areas. This was particularly evident on one site where grazing intensity was relatively high. Undesirable species showed no overall (1973-1982) response to grazing versus protection, although they benefited from protection during the drought and from grazing during the initial wet period and more "normal" years following the drought.

Grazing by kangaroos reduced the rate of increase of desirable species populations relative to the rate of increase of undesirable species populations. This response was elicited mainly by reducing recruitment of desirables and increasing recruitment of undesirables, and to a lesser extent by differnetially affecting death rates over these groups of species. Protection of these rangeland plant communities from grazing by both livestock and wildlife increases the rate of recovery of the vegetal component of the ecosystem. Further examination of other management alternatives is needed before any decision about the best method to rehabilitate these areas can be made.

Comparison of absolute rates of change of desirable and undesirable plant species populations provides an estimate of the changes in the potential of rangeland plant communities to produce phytomass at some time in the future. By defining the proposed use (e.g., livestock production), classifying plant species as desirable or undesirable for that use, and observing changes in those defined populations relative to each other, it was possible to determine the effect of different management strategies on the attainment of that goal. Reduced ambiguity associated with initial recording time, coupled with the predictive nature of this methodology, and the facility to use its component parameters (recruitment and mortality) to test specific hypotheses by applying rigorous statistical methods, suggests that the increased effort necessary to collect demographic data may be offset by its greater usefulness in interpreting trend in rangeland ecosystems.

The rigorous analysis of changes in populations of functional groups of species will not replace all other methods of recording change in plant populations but does offer an additional tool for the analysis of trend. Demographic analysis may provide a useful standard for assessing the ability of other measures to detect change, a potential role evidenced by its ability to detect the effects of wildlife herbivory known to be considerably below previous livestock use levels.

# CHAPTER VII

# NEIGHBOR-FREE-SPACE: ITS IMPORTANCE IN THE SURVIVAL OF DESERT SHRUBS.

## Introduction

Plant to plant interactions and the phenomenon of competition between individuals have been cited as organizing factors in semi-arid plant communities (Fonteyn and Mahall 1978, 1981, Yeaton and Cody 1976, Phillips and MacMahon 1981). Attempts to detect this competition in the field have varied from measurements of plant-to-plant distances (Pielou 1962) through nearest neighbor measurements (Phillips and MacMahon 1981) to complex removal experiments (Fonteyn and Mahall 1981), and more recently the use of Thiessen polygons to define space occupied by an individual (Vincent et al. 1976, Bayn 1982).

The relative importance of competition will have a considerable bearing on the development of appropriate management strategies for arid lands. By examining the survival of plants occupying different neighbor-free-space it may be possible to assign likely importance to competition as a factor determing the structure of plant communities in these lands. The development of an algorithm to assign space to each individual (Bayn 1982) provides a method of examining the importance of space on plant survival.

An examination of neighbor-free-space (N-F-S) as defined in Chapter 1 and calculated using program SPACE, and its comparison with the effects of climatic period and grazing by kangaroos on the survival of shrubs inhabiting a halophytic site, is attempted in this chapter.

## Methods

All individual shrubs were located and marked on 1:250 scale aerial photographs of 0.225 ha plots in grazed and ungrazed areas at one site (M21A) on Yeelirrie station (Chapter 4). Maps of the areas were made on four occasions (1973, 1976, 1979, 1982) during a nine year period. Individual plant location and identification were confirmed by on-the-ground verification. All plants were mapped onto a clear acetate film overlay later used for data extraction (Hacker 1978).

Each plant was allocated unique cartesian co-ordinates using an electronic digitizer and the original overlay maps. These co-ordinates were the input data used by program SPACE to calculate space occupied by each individual on the basis of a predetermined allocation rule. For this experiment the allocation rule for space occupied was the polygon area defined by the perpendicular bisector of the distance between individuals (Vincent et al. 1976). This space allocation rule defines neighbors as plants with a common polygon boundary. Adults and juveniles (0 to 3yrs old) were treated separately but no attempt was made to incorporate the number of neighbors, their specific identification or their relative size into the analysis. This would constitute a larger and more complex study worthy of further investigation.

Space occupied was divided into three categories: less than 1.5 $m^2$, 1.5 to 3.0 $m^2$, and greater than 3.0 $m^2$. These divisions provided approximately balanced groups for categorical analysis. Statistical analysis was based on an initial search for a model of best fit, followed by specific hypothesis testing using likelihood ratio and Chi square tests. Likelihood ratio tests provide approximate Chi square test statistics of specific hypotheses defined by a series of nested models in which one component of the model is removed to provide a reduced model which is tested against the unconstrained model of best fit (Fienberg 1980, pp 71-94).

Four categorical factors were included in the analysis:

A--Periods
1. 1973-76 (very wet) * for the adult group only.
2. 1976-79 (severe drought)
3. 1979-82 (more normal precipitation).

The climatic classifications are explained in detail in chapter 4 (Fig 4).

B--Neighbor-Free--Space
1. $< 1.5$ m$^2$
2. 1.5 to 3.0 m$^2$
3. $> 3.0$ m$^2$

C--Treatment
1. grazed
2. ungrazed

D--Survival
1. survived
2. died.

Goodness-of-fit was determined by considering sequentially less complex models until the least complex one with a non-significant Chi square was found. This model was taken to represent the most valid description of the data, and hypotheses about the importance of each component of this model were tested using likelihood ratio tests of nested models.

Individual factor effects were examined using simple Chi square tests of the general hypothesis that there was no effect of the factor.

## Results

### Juveniles

Only two periods of data were available for juveniles (1976-79 & 1979-82) because the first cohort was of mixed age. Goodness-of-Fit tests suggested a complex model involving three, three-way interactions was necessary to adequately describe the data. The model was: Period x N-F-S x Treatment, Period x N-F-S x Survival, N-F-S x Treatment x Survival, and the model was a good fit to the data (Chi square 5.75 (d.f.=3), p=.086). This implies all four factors and their two-way interactions were also significant. Approximate Chi square values from the likelihood ratio tests of the significance of each interaction are presented in Table 26.

Table 26. Approximate Chi square values and their level of significance for each of the important three-way interactions affecting juvenile plants.

| Models and Tests | $G^2$ | df | Chi $^2$ | df | prob. |
|---|---|---|---|---|---|
| General model | 5.579 | 3 | | | |
| Test of (Period x N-F-S x Treatment) | 14.68 | 5 | 9.10 | 2 | 0.011 |
| Test of (Period x N-F-S x Survival) | 12.19 | 5 | 6.61 | 2 | 0.039 |
| Test of (N-F-S x Treatment x Survival) | 16.43 | 5 | 10.85 | 2 | <.005 |

N.B. $G^2$ = 2 (observed x log (observed/expected)) (Fienberg 1980, page 40)

From the test of the interaction (Period x N-F-S x Treatment) it was apparent that the effect of period on N-F-S was significantly affected by treatment. Proportionately more plants on the grazed areas occupied larger N-F-S than on the ungrazed area (Fig 15). This effect was most pronounced in the period 1979-82 when both medium and small N-F-S categories contained significantly more individuals on the ungrazed area than on the grazed area. In 1976-79 only the small N-F-S category had significantly more individuals on ungrazed areas.

The less significant (Period x N-F-S x Survival) interaction indicates that the effect of period on survival is affected by N-F-S, or alternatively the effect of N-F-S on survival is modified by the climatic period. That N-F-S is affected by period is evident from the previous interaction suggesting that N-F-S is affecting survival. Plants with lower N-F-S had lower survival rates during the drought, and survival was higher during the 1979-82 period than during the drought (Fig 16).

The third interaction (N-F-S x Treatment x Survival) is highly significant due to significantly more individuals surviving on the ungrazed areas, and this effect was more significant among the small and medium N-F-S categories than in the large space category. There was no significant difference between the numbers surviving and those dying in any of the N-F-S categories on grazed areas (Fig 17). It should be noted that significantly more individuals were in the small and medium N-F-S categories on ungrazed areas than on grazed areas.

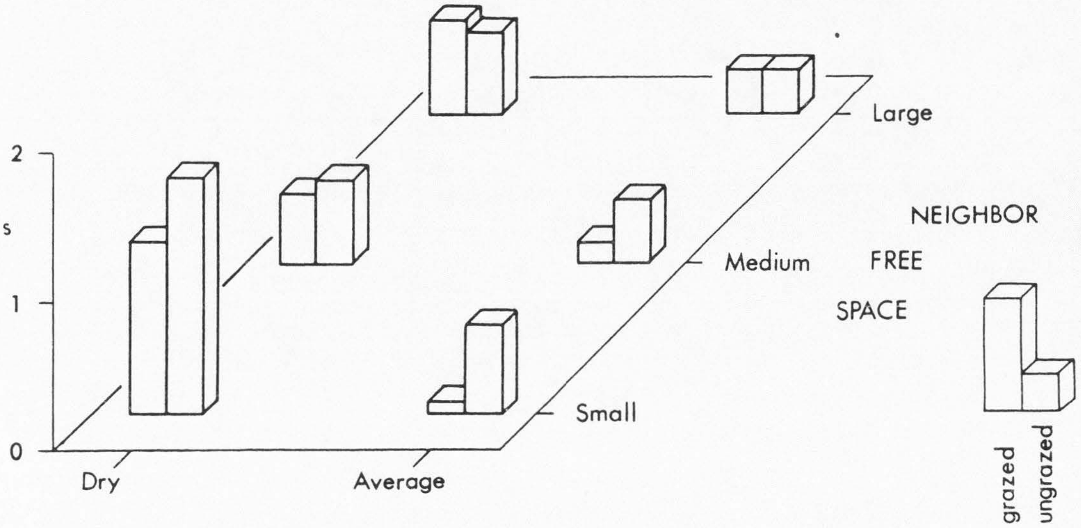

Figure 15. Numbers of juvenile individuals observed on grazed and ungrazed areas during each sampling period for three neighbor-free-space categories.

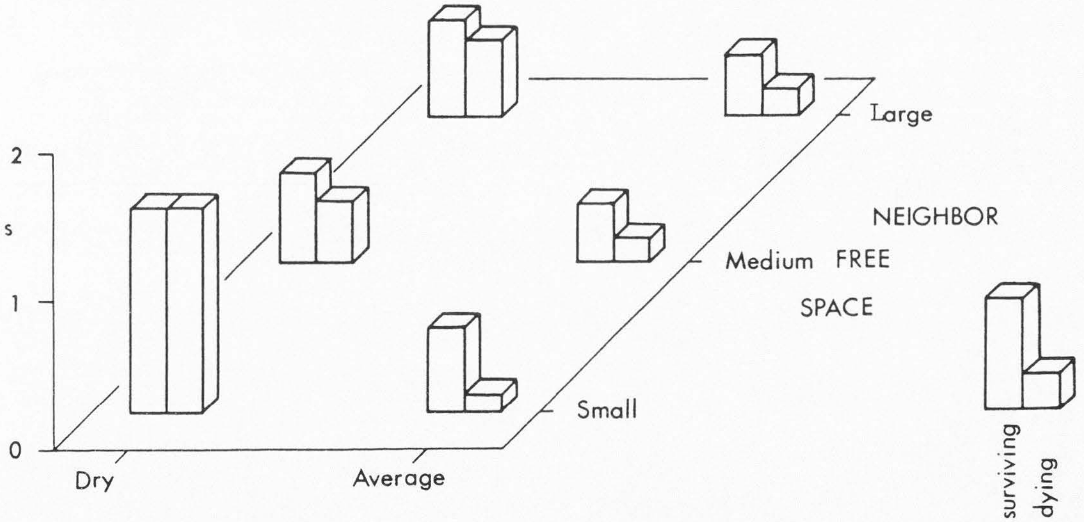

Figure 16. Numbers of juvenile individuals surviving or dying during each sampling priod for three neighbor-free-space categories.

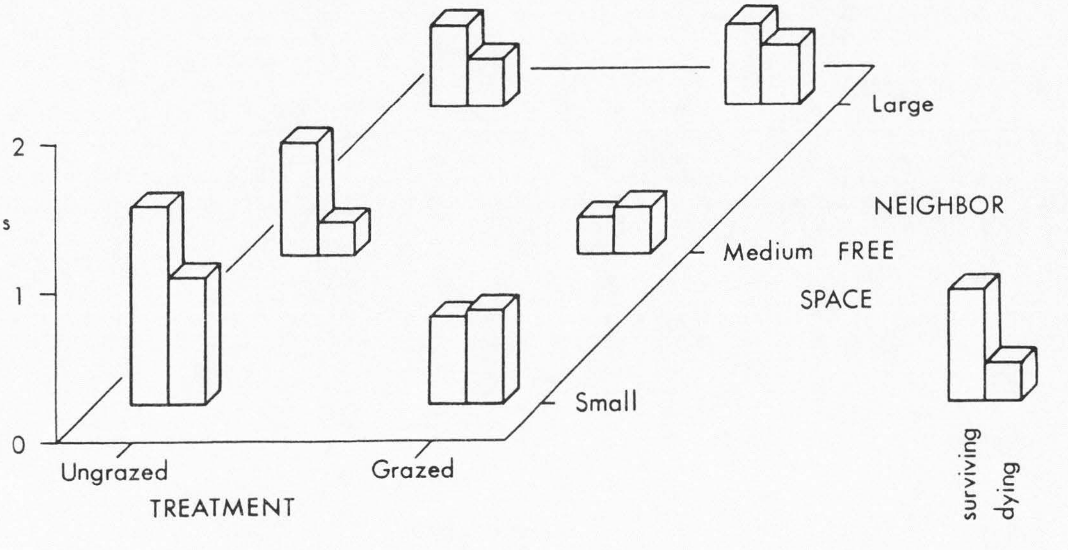

Figure 17. Numbers of juvenile individuals surviving or dying on grazed and ungrazed areas for three neighbor-free-space categories.

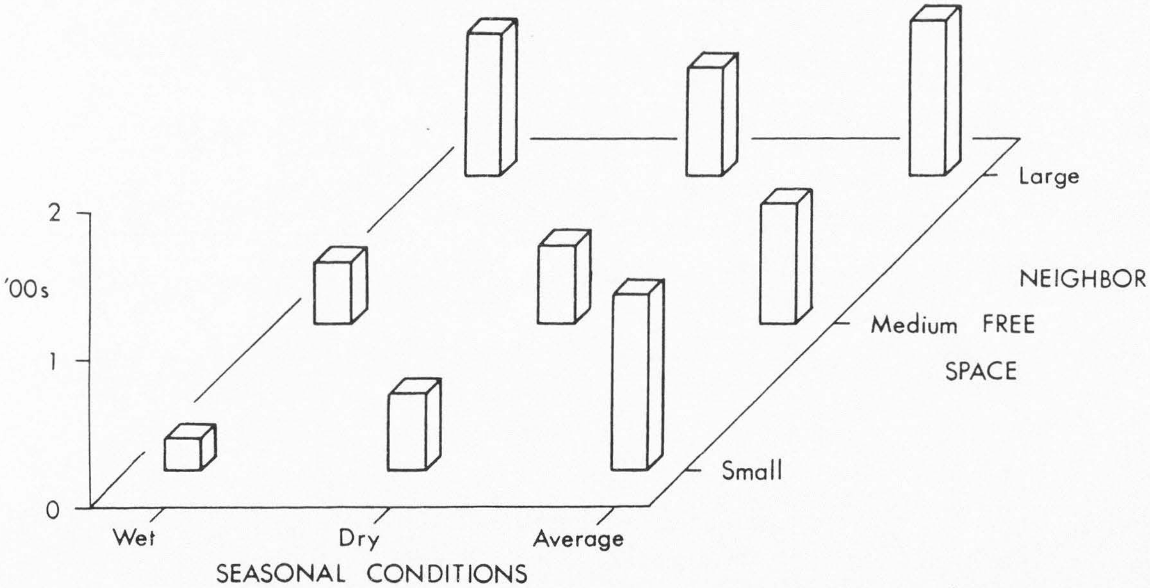

Figure 18. Numbers of adult plants present in each of three neighbor-free-space categories during each of the sampling periods.

Adults

Adult individuals were recorded for three periods (1973-76, 1976-79, and 1979-82) and goodness-of-fit tests indicate a simple model involving three two-way interactions, providing a general model of: Period x N-F-S, Period x Survival, and N-F-S x Treatment, (Chi square = 32.63 with 21 df, p= 0.0511). Results of the likelihood ratio tests of each component of the model are presented in Table 27.

Table 27. Approximate Chi square values and their probabilities for each of the component relationships in the general model for adult individuals.

| Models and Tests | $G^2$ | df | Chi $^2$ | df | prob. |
|---|---|---|---|---|---|
| General model | 29.40 | 21 | | | |
| Test of (Period x N-F-S) | 112.5 | 25 | 83.09 | 4 | <.005 |
| Test of (Period x Survival) | 1107 | 24 | 1078 | 3 | <.000 |
| Test of (N-F-S x Treatment) | 86.73 | 24 | 57.34 | 3 | <.005 |

Neighbor-free-space was significantly affected by period; as population size increased from 1973 to 1982, a greater number of individuals occupied smaller N-F-S (Fig 18). This effect can be seen as a gradual change from 1973 to 1976, when there was no reduction in the number of individuals occupying large N-F-S categories. The survival of adults was significantly lower in post drought years than during the other two periods (Fig 19) but the number of surviving adults increased more than twofold between 1973 and 1982. Treatment significantly affected N-F-S with significantly more ungrazed individuals occupying smaller and medium N-F-S categories. There was

Figure 19. Numbers of adult plants surviving or dying during each of three sampling periods.

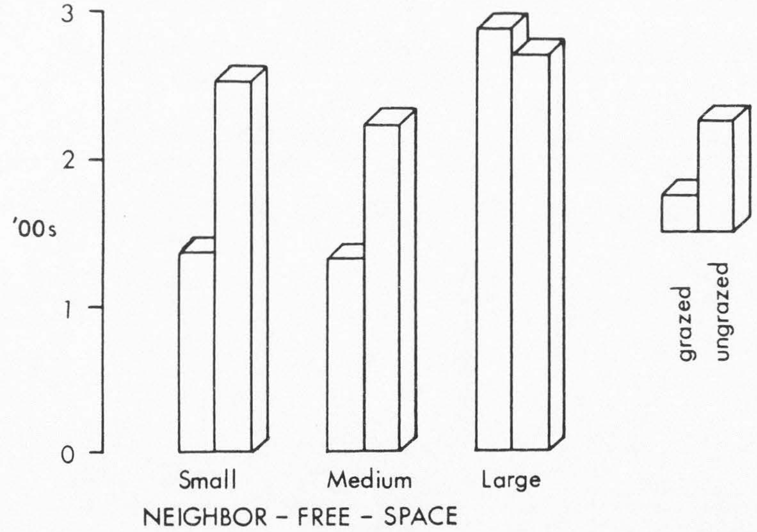

Figure 20. Numbers of adult plants in each of three neighbor-free-space categories on grazed and ungrazed areas.

no significant difference between treatments in the larger N-F-S category (Fig 20).

## Discussion

Of overriding importance for the survival of individual plants in arid ecosystems is the seasonal or climatic pattern as expressed in the precipitation (Austin et al. 1981, Harper 1977, MacMahon 1981). The presence of period in all but two of the significant interactions between the four factors affecting adult and juvenile plants examined on site M21A at Yeelirrie supports this contention. The complexity of the model needed to describe the juvenile plant dynamics reflects the importance of understanding this component of arid plant populations. Juveniles appear to represent the most dynamic segment of the population and perhaps the one most amenable to management (Williams 1978, Harper 1977).

That survival of juveniles was significantly reduced by kangaroo grazing during both periods indicates significant impact by kangaroos on the capacity of these areas to rehabilitate following the removal of livestock. On the other hand, adult plants showed no response to grazing, but did show a significant reduction in survival during post-drought years, a result that supports findings of Chambers (1979) for salt desert shrubs in southwestern Utah.

The results presented here are not sufficient to conclude that competition is an organizing factor in this environment. However, the conservatively defined N-F-S is involved in a significant interaction between period and survival of juvenile individuals, indicating there may be some factor associated with space capture that affects survival. Incorporation of plant size and species identification into the SPACE formula may well have led to more explicit conclusions about the role of space capture in the survival process (Bayn 1982). One of the obvious effects of larger plant populations following destocking is the increase in number of individuals occupying smaller N-F-S categories, increasing the potential for competitive interactions between individuals.

The clumped nature of arid land vegetation (Phillips and MacMahon 1981, Fonteyn and Mahall 1978) may have the effect of exacerbating potentially competitive interactions by concentrating individuals into a relatively small proportion of the total space. Departure from a random distribution in space has been used as a criterion by which to infer competition, environmental variability and plant responses (Pielou 1962, Bayn 1982). By corollary, the use of this approach often requires the assumption of a uniform environment, one that is open to challenge in most natural ecosystems, particularly those in arid and semi-arid environments. Examination of individual plants and their neighbor-free-space may provide a greater opportunity for defining likely competitive interactions, plant resource relationships and their effects on vegetation pattern.

Juvenile plants were significantly affected by seasonal conditions but this was confounded with differences in the intensity of kangaroo grazing, shown elsewhere to be a significant factor affecting the survival of juveniles (Chapter 4). Significantly higher grazing levels were associated with the drought years on this site (Chapter 4, Figs 7 & 8). Further investigation of plant survival responses to drought are necessary to clarify the importance of seasonal conditions and intensity of use.

Another component of N-F-S determination could be environmental heterogeneity (West 1982). These large sample areas, not uncommon in arid zone vegetation studies, undoubtedly included considerable local heterogeneity. The true space captured by each individual may be very different from the simplistic representation used in this study. For this reason these results should be taken to imply that much more detailed studies will be necessary before plant space capture can be considered evidence for competition between individuals.

Reductions in the average space occupied were associated with increased numbers of individuals in small and medium N-F-S classes (particularly adults) but no significant change was apparent in the larger category. This could imply that the added individuals are subdividing already small N-F-S and that larger areas may represent less hospitable habitats. A caution is warranted, however; as the population size increases, the area of unclosed Theissen polygons near the boundary of the plot is likely to decline. The average N-F-S is thus not a linear function of the number of individuals as long as there is uncaptured space about the periphery of the plot. Additionally, the nature of categorization of N-F-S used in this analysis would permit many small spaces to be captured from a single large one without changing its categorization.

## Conclusions

Seasonal conditions affect patterns of survival in halophytic perennial shrubs occupying a site in arid rangelands of Western Australia. The effects of drought were most severe on juvenile individuals; however, adult plants suffered significantly increased mortality during more normal years following the drought while adult survival during the drought was not significantly different from that during very wet years. As population size increased following the removal of livestock the opportunity for competitive interactions likely increased as more individuals occupied smaller neighbor-free-space.

Grazing by kangaroos significantly reduced the survival of juveniles, thus reducing the potential rate of recovery of this site following release from livestock grazing. Adult survival was not affected by kangaroo grazing. Management should carefully examine any recommendation to destock rangelands unless adequate measures are taken to protect juvenile plants from grazing by kangaroos. This may be as simple as ensuring that kangaroo populations do not increase after livestock removal. The importance of the juvenile classes in any recovery process is emphasized by these results.

The use of program SPACE provides a new avenue for examining plant responses to environmental factors and management practices. However, its use in arid vegetation may be limited by the variability of the environment and the size of plots necessary to analyze sparse populations. It should be noted that the two dimensional nature of N-F-S while being a considerable advance over single dimension analyses, still falls short of the four dimensional nature of plant resource capture (volume of resource space x time).

# CHAPTER VIII.

# DYNAMICS OF A PERENNIAL GRASS ON THE RIVERINE PLAIN OF NEW SOUTH WALES: A REANALYSIS

## Introduction

Plant population studies of long-lived perennial plants in arid-zone rangelands are rare; studies on permanent plots in which cohorts of individuals were followed through time are even more scarce. Williams (1955, 1956, 1961, 1968, and 1969) examined one particular ecosystem in his series of studies in the ecology of the riverine plain in southwest New South Wales. His main interest was the dynamics of the dominant grass (Danthonia caespitosa) under various management strategies (grazed at three intensities by merino sheep, and ungrazed). He examined three basic concepts in his analysis of populations of Danthonia caesptosa. First he addressed the hypothesis that grazing had no effect on survival of this grass.

Williams (1969) reported grazing effects in terms of a species response index (ratio of the number of plants per unit area for grazed quadrats / the number for ungrazed quadrats) and a grazing pressure index (ratio of the response index for the high level of grazing / the response index for the lower level of stocking). He assessed any trend in the relative abundance of species by comparison of response indices over seven sampling periods that varied in length from seven to 54 months. Grazing was shown to affect different species in different ways; however, the dominant (Danthonia caespitosa) appeared to be consistently favored by grazing.

Second, Williams (1970), addressed the hypothesis of no difference in survival response between cohorts. His examination of survivorship curves and estimated half-lives revealed that three cohorts responded differently during different climatic periods, but did not respond to different intensities of grazing. He concluded there was a substantial decline in both grazed and ungrazed populations during the study and that grazing at any of the three intensities favored survival in all periods.

Third, Williams (1968) and later with Austin (Austin et al. 1981) addressed the effect of climatic conditions, primarily rainfall, on the survival of *Danthonia caespitosa*. Early conclusions were that the incidence and amount of rain affect recruitment and seedling survival in areas not dominated by large grass tussocks (grazed areas), but in ungrazed areas, where large tussocks were common, rainfall appeared to be more important in determining the dynamics of the established plant population. Austin et al. (1981) concluded that seasonal conditions account for about 17 per cent of the variation in population response, a factor second only to succession in its importance for this plant community. It should be noted their conclusions were based on a total species complement rather than exclusively on *Danthonia caespitosa* and so are not directly comparable to Williams' (1968) earlier conclusions.

This chapter seeks to re-examine these three hypotheses and the published conclusions by subjecting a portion of Williams (1968) data to re-analysis using techniques outlined in earlier chapters. In this sense this is a test of the new methods by application to a larger and more complex data set. Specifically program SURVIV (White 1983) was used to test each of the three hypotheses using survival data, and tests comparing population rates of change (Chapters 3 & 5) were applied to consider effects on both survival and recruitment.

## Methods

Danthonia casepitosa data collected from 1949 to 1965, using chart quadrat methods outlined in Williams (1968) and Austin et al. (1981), were used in this study. The data were truncated by excluding the last three recording dates (1957, 1961 and 1965) because time intervals between recordings were too long to permit realistic, cause-oriented hypotheses to be tested.

Survival of six grazed and six ungrazed cohorts was examined over five recording periods from November 1949 to November 1954. Program SURVIV (White 1983) was used specifically to test the hypotheses :--

a. grazing by merino sheep does not affect survival,

b. adult survival does not vary among cohorts, and

c. adult survival does not vary among recording periods.

The third hypothesis can be interpreted as:-- survival is not affected by different seasonal conditions as definied by amount of precipitation.

Rates of population change were used to examine similar hypotheses using tests outlined in Chapter 3 and applied to arid-zone plant populations in Chapters 5 & 6. For these tests the original population data were reduced to numbers per 126 $m^2$ by reducing the numbers in grazed cohorts by a factor of 126/198, a procedure used by Williams (1969) when he compared grazed and ungrazed population responses.

To achieve a consistent and comparable rate parameter, all survival rates were converted to annual rates. This conversion was necessary because of the variability of intervals between recording dates. Attempts were made to establish functional relationships between survival and precipitaion. Four models were examined in which precipitation was transformed to a ratio of:--

1. The ratio of precipitation recorded during the previous water year (April to March), or part thereof, to the average for that same period was divided by the maximum ratio recorded during the period 1949-54.
2. Index (1) squared.
3. Precipitation recorded during the year prior to recording divided by the maximum annual precipitation recorded during the study.
4. Index (3) squared.

Program SURVIV was used to run the models defined by these functional relationships while incorporating different survival rates for each cohort and constraining survival to zero during periods when no individuals were available to die. Incorporation of slope parameters for grazed and ungrazed populations resulted in a total of 25 estimated parameters in each model.

## Results

### Precipitation

The 1949 to 1954 period was characterized by three above- and three below-average precipitation years (April to March) (Fig 21). In 1950 and 1951 two consecutive below average-years resulted from below-average summer rains, while 1949 had above-average summer rainfall, a pattern repeated in 1954. Rainfall during 1952 and 1953 was about average during both summer and winter periods.

## Survival Rates

Estimated annual survival rates (Tables 28 and 29) were extremely variable; ungrazed juveniles in 1951 survived at a rate of only .002, while adults in ungrazed cohort 2 survived at a rate of 1.00 during the 1953-54 period. Adult survival during any one period was higher than juvenile survival during the same period; however, adult survival varied considerably from period to period within any cohort. Standard error estimates reflect different sample sizes and inference about specific survival rates becomes less precise as each cohort was depleted by plant deaths.

All three specific hypotheses were strongly rejected:--

1. Grazing by Merino sheep did affect survival (Chi square = 1409.7 (d.f=17)) although the effect was not consistently in favor of grazed or ungrazed populations.
2. Adult survival rate was not constant within cohorts (Chi square = 8237.2 (d.f.=15)) with variation from 1.00 to .047 being recorded in ungrazed populations. A range of .747 to .133 was recorded in a mixed-age cohort on grazed areas.
3. Adult survival rate was not constant within years (Chi square = 227.2 (d.f.=15)) with a range of annual mortality rates from .149 to

populations during the same period.

Responses in adult survival within cohorts and within years was more variable on ungrazed sites than on grazed sites where larger population sizes during all periods also reduced the standard errors of survival estimates.

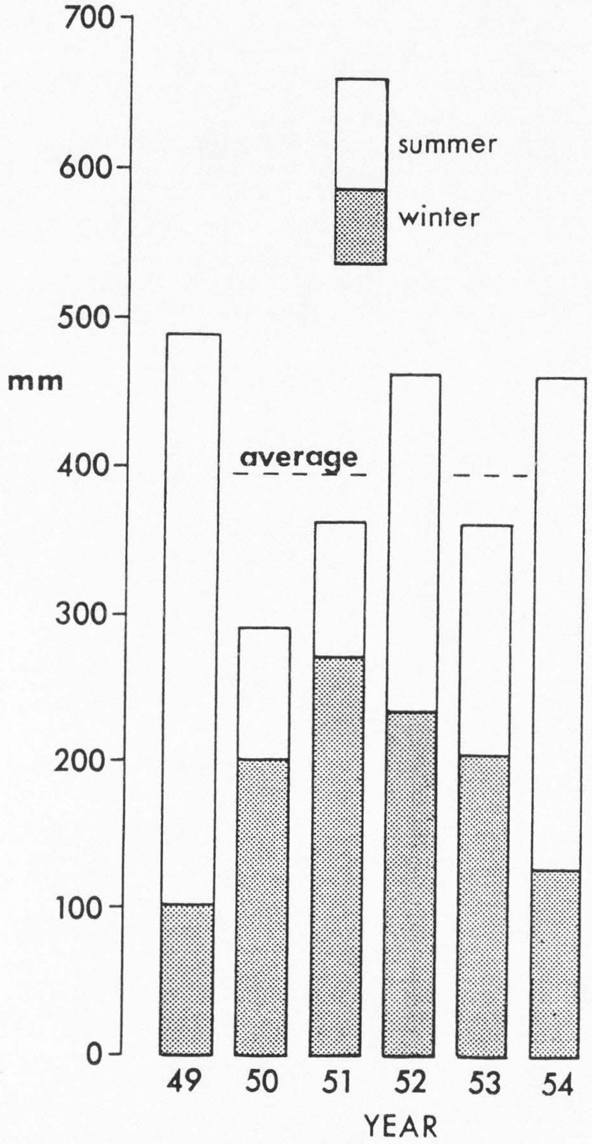

Figure 21. Annual precipitation totals for the Deniliquin study site based on an April to March water year.

Table 28. Annual survival rates estimated by program SURVIV for grazed populations of *Danthonia caespitosa* in six cohorts over five years.

| Cohort | $N_i$ | Period | Survival Rate | s.e. |
|---|---|---|---|---|
| 1 | 6002 | 1949-51 | .747 | .005 |
| | | 1951-51 | .144 | .006 |
| | | 1951-53 | .202 | .011 |
| | | 1953-54 | .455 | .040 |
| | | 1954-54 | .133 | .047 |
| 2 | 8384 | 1949-51 | .194 | .004 |
| | | 1951-51 | .040 | .005 |
| | | 1952-53 | .072 | .025 |
| | | 1953-54 | no survivors | |
| | | 1954-54 | no survivors | |
| 3 | 1139 | 1951-51 | .004 | .001 |
| | | 1951-53 | .376 | .066 |
| | | 1953-54 | .232 | .123 |
| | | 1954-54 | .305 | .369 |
| 4 | 40552 | 1951-53 | .109 | .002 |
| | | 1953-54 | .548 | .011 |
| | | 1954-54 | .112 | .011 |
| 5 | 31379 | 1953-54 | .535 | .003 |
| | | 1954-54 | .132 | .003 |
| 6 | 3801 | 1954-54 | .035 | .002 |
| 7 | 3206 | recruits during 1954-54 period | | |

Table 29. Annual survival rates estimated by program SURVIV for ungrazed populations of *Danthonia caespitosa* in six cohorts over five years.

| Cohort | $N_i$ | Period | Survival Rate | s.e. |
|---|---|---|---|---|
| 1 | 3445 | 1949-51 | .731 | .007 |
| | | 1951-51 | .091 | .006 |
| | | 1951-53 | .149 | .016 |
| | | 1953-54 | .701 | .067 |
| | | 1954-54 | .284 | .101 |
| 2 | 4906 | 1949-51 | .116 | .005 |
| | | 1951-51 | .047 | .010 |
| | | 1951-53 | .449 | .062 |
| | | 1953-54 | 1.000 | n/a |
| | | 1954-54 | .305 | .123 |
| 3 | 346 | 1951-51 | .002 | .001 |
| | | 1951-53 | .697 | .127 |
| | | 1953-54 | .574 | .188 |
| | | 1954-54 | no survivors | |
| 4 | 17353 | 1951-53 | .053 | .002 |
| | | 1953-54 | .699 | .025 |
| | | 1954-54 | .054 | .015 |
| 5 | 10341 | 1953-54 | .633 | .004 |
| | | 1954-54 | .047 | .002 |
| 6 | 1648 | 1954-54 | .001 | .002 |
| 7 | 5144 | recruits during 1954-54 period | | |

Attempts to establish a functional relationship between precipitation and survival failed to produce a model with a reasonable fit to the data. Table 30 summarizes this functional information and presents the results of likelihood ratio tests of the hypothesis that the slope of the precipitation response line is the same between grazed and ungrazed populations. A further investigation of this approach is recommended although not possible in this study.

Table 30. Responses of plant survival in a number of models incorporating functional relationships with precipitation. The precipitation factor is the ratio of precip. received / max precip. (page 149). Degrees of freedom in parentheses.

| Model | Function | G-O-F | Log Like'd | Chi sq. for test of equal precip. resp. on grazed and ungrazed areas. |
|---|---|---|---|---|
| No const's | $S_i=S_o+bP_1$ | .0000 | -4232.76 (18) | .960 (1) p=.327 |
| $b_g = b_{ug}$ | " | .0000 | -4233.24 (19) | |
| No const's | $S_i=S_o+bP_1{}^2$ | .0000 | -4231.61 (18) | .820 (1) p=.365 |
| $b_g = b_{ug}$ | " | .0000 | -4231.02 (19) | |
| No const's | $S_i=S_o+bP_2$ | .0000 | -4155 (18) | 23.96 (1) p<.000 |
| $b_g = b_{ug}$ | " | .0000 | -4167 (19) | |
| No const's | $S_i=S_o+bP_2{}^2$ | .0000 | -3784 (18) | 203.97 (1) p<.000 |
| $b_g = b_{ug}$ | " | .0000 | -3886 (19) | |

$P_1$ = Precip. received during previous portion of water year/max. precip. received during the study.

$P_2$ = Precip. received during 12 months prior to recording/max. annual precip. received during the study.

## Rates of Population Change

Despite an initially (Nov. 1949) larger population and higher recruitment in four of five periods on grazed areas, the two populations converged to a similar size by November 1954. Rates of change in both grazed and ungrazed populations were significantly different from zero during all periods and were negative during all periods except the 1951 seven-month period (Jan. 1951 to Aug. 1951) when massive recruitment occurred on both areas (Table 31 and Fig 22).

Grazed populations increased more rapidly than ungrazed ones during this seven-month period, but declined more rapidly during two of the four remaining periods. All grazed vs ungrazed population rate-of-change comparisons were highly significant (Table 31) as were birth to death rate ratios. More recruits and a lower death rate favored grazed populations during the first period. Greater recruitment during the second period was the major factor favoring grazed areas where the greater increase occurred despite higher death rates. This advantage for grazed populations continued during the third period when recruitment was the major difference. During the fourth period ungrazed populations were favored by lower death rates, which were coupled with a lower population size to produce a lower net decline despite less recruitment. Death rates were higher on ungrazed areas during the fifth period but the smaller population size coupled with a larger recruitment resulted in smaller net decline in these populations than occurred on comparable grazed areas.

Table 31. Rates of change in grazed and ungrazed populations of *Danthonia caespitosa* during five recording periods. Included are test statistics for tests 1, 2 and 3 (p. 43). All Chi square values have one degree of freedom.

| | Grazed | Ungrazed | | |
|---|---|---|---|---|
| Initial #/100 m$^2$ | 7265 | 6628 | G vs UG | Ratio |
| Nov'49-Jan'51 | | | | |
| Change/100 m$^2$ | -4041 | -4240 | | |
| Chi square | 5529 | 6984 | 12.52 | 159.7 |
| Prob | <.000 | <.000 | <.005 | <.000 |
| Jan'51-Aug'51 | | | | |
| Change/100 m$^2$ | 18044 | 11894 | | |
| Chi square | 55836 | 34504 | 1362 | 630.3 |
| Prob | <.000 | <.000 | <.000 | <.000 |
| Aug'51-Jan'53 | | | | |
| Change/100 m$^2$ | -4459 | -5807 | | |
| Chi square | 1274 | 3419 | 91.72 | 14107 |
| Prob | <.000 | <.000 | <.000 | <.000 |
| Jan'53-Apr'54 | | | | |
| Change/100 m$^2$ | -7191 | -2969 | | |
| Chi square | 7720 | 1724 | 2906 | 21.13 |
| Prob | <.000 | <.000 | <.000 | <.001 |
| Apr'54-Nov'54 | | | | |
| Change/100 m$^2$ | -4456 | -1113 | | |
| Chi square | 3745 | 281.0 | 1489 | 184.4 |
| Prob | <.000 | <.000 | <.000 | <.000 |

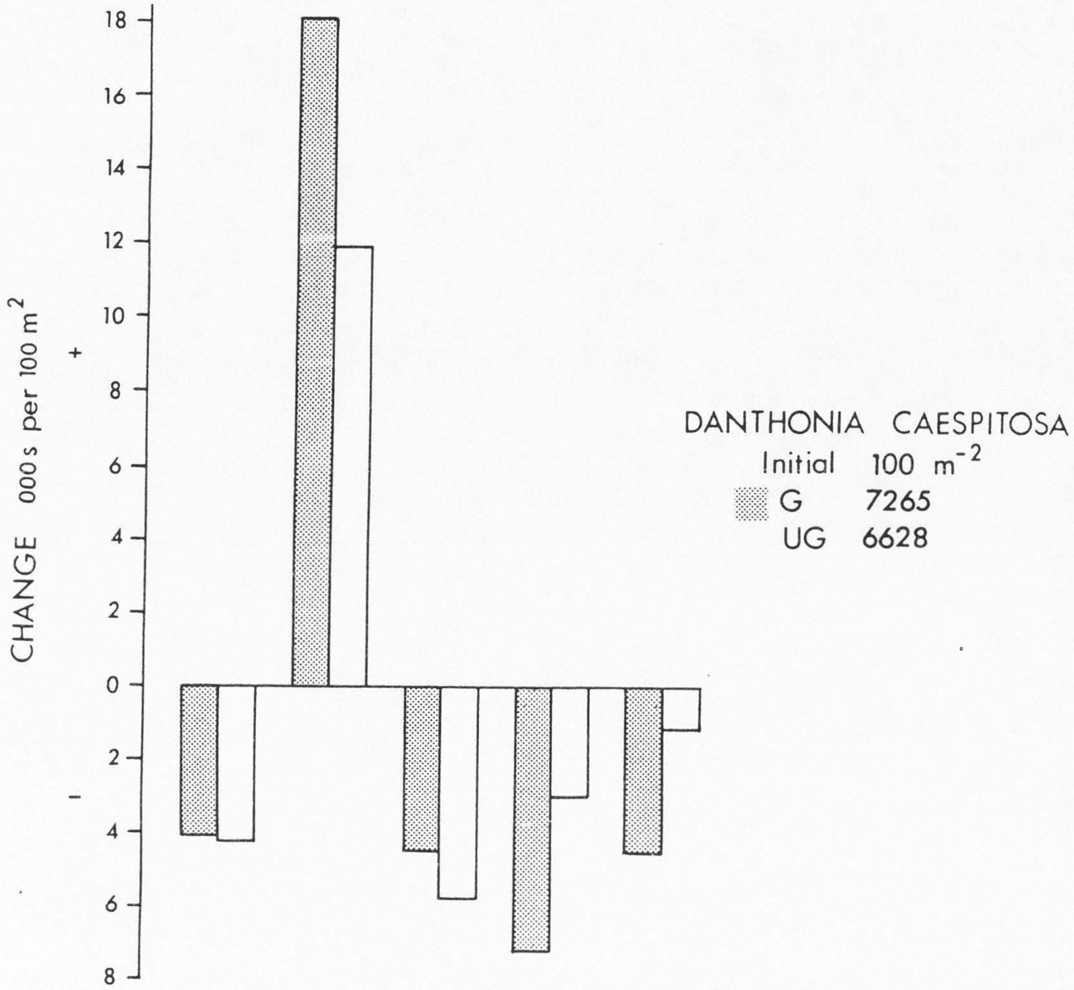

Figure 22. Absolute rates of change of grazed and ungrazed populations of Danthonia caespitosa for five recording periods.

Discussion

Analysis of the first five periods of Williams' (1968) Danthonia caespitosa data using program SURVIV produced inferences similar to his original conclusions. Grazing significantly affected survival of Danthonia caespitosa and this effect was significantly different across cohorts and years. The effects of grazing on survival did not consistently favor one or other treatment, in contrast to Williams' (1969) conclusions. More importantly, population rates of change vary from one period to another.

During early periods of the study grazed populations were favored, suggesting either an effect of exclosure, such as the development of a new microenvironment, or some disturbance factor encouraging increased recruitment on grazed areas. The last two periods examined in this analysis both favored ungrazed populations. The benefits for one or other treatment do not accrue as the result of a consistent recruitment or mortality advantage, but rather these two factors act differently during different periods. On several occasions a disadvantage resulting from increased mortality was overcome by greater recruitment. During the final period this effect was reversed to provide an advantage to ungrazed populations. Pervasive to all periods was the difference in initial population sizes. Accurate comparison of the effects of treatment, climatic, biotic, or management factors may not be possible if population densities are initially very different. In these populations one recruitment event (Jan 1951 to Aug. 1951) exerted a large influence over population behavior by changing relative densities.

The range of overall population response was greater on grazed than on ungrazed areas. While estimates of variance were generally lower for survival on grazed areas this may have been due to initially larger populations. The two major recruitment events (Jan. 1951 - Aug. 1951 and Aug. 1951 - Jan. 1953) led to more recruits on grazed areas, and their effects provided more potential individuals to die during the course of the study than on ungrazed areas. This result is consistent with expected responses of ecosystems to disturbance (Bazzaz 1983). In this instance removing the disturbance factor (by exclosure) changed the population response to environmental factors, a process that could be expected to come to a new equilibrium. Williams' (1968) conclusions citing competition from annuals as a restraining influence in protected populations seem reasonable and supports the idea that control of population change in protected areas may be from mechanisms intrinsic to the developing of a new seral community in equilibrium with a different set of environmental variables. Austin et al. (1981) concluded that succession was the major cause of developing differences between grazed and ungrazed communities, a result supported by changes in response noted from this new analysis.

Application of the methods outlined in Chapter 3 to a more complex data set provided an adequate interpretation while at the same time providing rigorous hypothesis tests not present in the previously published results. The large (>1000) numbers of individuals recorded in Williams' (1968) study lead to such powerful tests that all factors examined were shown to be significant. Results of these analyses confirmed Williams' (1968, 1969) conclusions that these populations respond to season, grazing and cohort; however, the increased rigour of these analyses refuted his claim that grazing favors the populations during all periods.

Attempts to incorporate indices for precipitation into survival estimators were thwarted by the variable nature of the survival response. There were indications, however, from an index based on annual rainfall prior to measurement, of a different response from grazed and ungrazed populations. Annual totals appear to provide a more useful index than do water-year indices but it should be noted that the method of calculating these indices is very crude and not based on the intensity of rainfall events, or rainfall distribution throughout any month. Useful climatic indices are likely to be considerably more complex than a simple aggregate rainfall index.

The difficulty encountered in attempts to relate climatic events to population responses highlights a number of pitfalls of this type of study in arid-land plant communities. For a population as dynamic as Danthonia caespitosa obviously is, recordings should be associated with specific climatic or management events. Meaningful relationships between potential causal agents and population responses can only be established if the recording frequency is related to the dynamics of the population and the frequency of potential causal events, a strong case for conducting these types of investigation under controlled situations. In populations where the response is slower, longevity greater, and the magnitude of change smaller, longer term recordings associated with management scale impacts may be possible (Chapters 4 - 7).

## Conclusions

Analysis of the Danthonia caespitosa data set using program SURVIV and rate of population change tests led to similar conclusions to Williams' earlier analyses. The differences from these earlier conclusions lie mainly in the definition of specific responses. Survival and recruitment are both important in determining population responses although major recruitment events dominate total plant number data. Williams' (1968) conclusion that grazing favored populations of Danthonia caespitosa during all periods was refuted. Protected areas were declining at slower rates than grazed populations during the last two sampling periods. Application of the above tests has added a significant dimension to the interpretation of Williams (1968) data.

Changes in the populations in response to the imposition of the treatment (protection from grazing) suggest grazing by sheep is acting to maintain a plant population behavior different from the ungrazed situation. Successional change may be occurring on the protected sites, governed by a new set of environmental parameters. Differences in disturbance, and/or changes in the competitive relationships between annuals and seedlings, as well as the action of adult grass tussocks on each other, may be acting to provide population control mechanisms different from those acting on grazed populations.

Responses on grazed areas were more extreme than on protected areas suggesting the convergence in numbers in the two populations by 1955 may be fortuitous rather than the result of any prolonged trend toward similarity.

Long-term, widely spaced observations on rapidly changing populations may produce little information useful for managing them. This could lead to ambiguous, potentially damaging results by failing to isolate the potential causes of change, leading to management recommendations based on inappropriate information.

# CHAPTER IX.

# GENERAL CONCLUSIONS

## Methodology

Analysis of the dynamics of plant population parameters (survival and recruitment) using statistical procedures based on a stochastic interpretation of population behavior was applied to arid-land plant populations in an attempt to clarify responses of those populations to environmental and management factors. Few simplifying assumptions about the nature of the two parameters were necessary to derive workable probability density functions suited to testing hypotheses about survival and recruitment responses. Recruitment was considered to be well modeled by the Poisson process and was combined with a model of the death process, assumed to be binomial, to examine rates of population change.

Survival analysis using program SURVIV, a maximum likelihood based estimation and testing program written by White (1983) for animal survival studies, was applied to six perennial plant species populations from a number of sites at Yeelirrie station in the mulga zone of Western Australia. Data collected by Dr. O.B. Williams on grazed and ungrazed populations of *Danthonia caespitosa* on the Riverine plain of southwest New South Wales were similarly analyzed as a means of validating my analytical approach. A BASIC program written by Dr. M.D. Brennan was used to test hypotheses about changes in population number, and to compare the effects of recruitment and mortality on population responses. This program incorporated survival and recruitment information and used numerical methods to derive estimates necessary for constructing likelihod ratio tests.

Three climatically different periods (1973-76 "wet", 1976-79 "dry" and 1979-82 "more normal") were included in the examination of rangeland plant populations at Yeelirrie, where areas of destocked rangeland were protected from, or available for, grazing by large native herbivores principally (kangaroos). Five years, including two above- and three below-average rainfall years, were included in the Danthonia caespitosa experiment.

## Individual Species Responses

Kangaroo grazing affected the survival of three of six species examined at Yeelirrie. Survival of Eragrostis xerophila, a desirable perennial grass, was significantly reduced by grazing. This response was evident during wet, dry, and "more normal" rainfall periods. Two undesirable species (Eremophila spectabilis and Frankenia pauciflora) responded positively to grazing. Adult survival of Eremophila spectabilis was increased by grazing during drought while juvenile survival was reduced by grazing during this period. Its post-drought survival was reduced by grazing. Frankenia pauciflora survival was increased by grazing during the post-drought period.

Rates of population change of all six species were affected by kangaroo activity, at least during one of the three periods of the investigation. The survival responses and effects on recruitment combined to produce a variety of plant population responses. Eragrostis xerophila suffered a severe reduction in its grazed population during the post-drought period when both survival and recruitment were reduced. Maireana glomerifolia, whose survival was not affected by grazing, suffered reduced recruitment on grazed areas during all periods. This response suggests heavy herbivore impact on this desirable shrub during early establishment phases but relative insensitivity to grazing once the plants become established.

A population of the long-lived desirable, perennial shrub (*Eremophila leucophylla*) exhibited a small but significant positive response to grazing during the wet period early in the investigation. This response was recorded at only one site and was due to increased recruitment on the grazed area, where an initially higher population suggests inherent site differences were a significant factor.

*Eremophila spectabilis*, an undesirable shrub, exhibited varied behavior on two sites differing in condition and past use. On a good condition site, responses to grazing were less dramatic than on a poor site, where massive recruitment on grazed areas during the very wet period, coupled with reduced adult mortality, resulted in a large increase in the population on the grazed area. Drought following this major increase resulted in significantly lower adult and higher juvenile mortality on grazed areas. Populations at the poor condition site had reduced stability; increasing and declining more rapidly than on a good condition site. The potential for rapid, large increases in number would enable this species to behave as a woody weed on poor sites. Comparisons between grazed and ungrazed areas at this poor site should be tempered by the knowledge that initial populations differed by an order of magnitude between treatments.

Another undesirable shrub, *Frankenia pauciflora*, responded positively to grazing during the post-drought period. The survival response mentioned above was coupled with increased recruitment during the very wet and post-drought periods. Ptilotus obovatus, an intermediate forage species, exhibited a significant suppression of recruitment during the post-drought years and failed to maintain a population increase during this period.

Over the nine years of the field investigation, all six species increased significantly in number on protected areas. The overall response was due to increases during the very wet and/or "more normal" rainfall periods, and no change or a decline during the intervening drought period. Grazed populations of the five shrubs also increased during the nine years but the grass (Eragrostis xerophila) experienced a decline. Of the five shrubs, two undesirable species increased more rapidly on grazed areas versus ungrazed areas, while the reverse was true for the two desirable species and for Ptilotus obovatus. The effect of drought on grazed areas was to reduce the population size of all species except Ptilotus obovatus.

Five species were present on more than one site and all exhibited signficantly different survival responses depending on site. These differences could not be analyzed in this study and were probably due to a myriad of environmental and historical factors associated with those specific sites. Further, more detailed experiments would be necessary to determine which among these many potential factors are important in determining population response.

Danthonia caespitosa survival was significantly affected by grazing Merino sheep, plant cohort, and seasonal conditions, results similar to those reported by Williams (1968, 1969). Rate of change comparisons using data from grazed and ungrazed populations revealed significant advantages for grazed populations during the three years following the imposition of the treatments. During the last two years ungrazed populations were favored, suggesting a different response in the two populations, perhaps each reacting differently to precipitation; the hypothesis of rainfall influence could not be tested with the data available. Despite the overriding effect of two very large recruitment events during the study, both grazed and ungrazed populations declined during all but one of the recording intervals. Differences in recruitment, mortality and population size were important in determining which population changed at the greatest rate (numbers/period).

Analysis using the methods outlined in this re-examination of Williams' (1968) data permitted a clarification of population responses not afforded by his earlier analyses. In contrast to Williams' (1969) conclusions that grazed populations were favored during all periods, my analysis showed ungrazed populations were favored during the fourth and fifth years of the study. The highly variable behavior of these grass populations, and the long intervals between recording dates, restrict the ability to make inferences about causal relationships. Analyzing very large numbers of individual plant records (up to 40,000 per cohort in this data set) results in such powerful tests that all factors can be shown to be significant. Establishing links between population responses and potential causal agents will require more rigorous experimental design. Recording intervals should be tied to the expected frequency and longevity of impacting factors and to the dynamics of the population under investigation.

## Species Group Responses -- An Approach to Range Trend

Classifying populations of plants as desirable, undesirable or intermediate in value for livestock use, and applying rate-of-change tests to these group provides a convenient approach to examining expected long-term changes from a management point of view. During all three periods investigated at Yeelirrie the desirable species group increased faster, or decreased more slowly, than the undesirable group, when protected from grazing by kangaroos. On areas grazed by kangaroos, undesirable species were favored during the post-drought period. The populations of desirable species protected from grazing increased faster than if grazing of this group were permitted, while undesirables increased faster during high rainfall years in the plots subject to grazing. Drought resulted in smaller population declines for the undesirable species group if it was protected from grazing; however, the net effect was still greater population increase on grazed areas. Kangaroo grazing is differentially affecting the rates of population change, enhancing rates of increase for undesirable species and depressing them for the desirable species group. In the longterm, protection of these plant populations from kangaroo herbivory will result in a more rapid recovery of potential livestock production.

Based on plant population dynamics from 1973 to 1982, at some time in the future there will be a greater proportion of desirable species on areas protected from kangaroo grazing than on adjacent grazed areas. Although the total number (or density) of plants increased on both grazed and ungrazed areas following the removal of livestock, the proportion of undesirable species on grazed areas increased, or at best remained static, a situation that must be considered undesirable relative to responses on protected areas. Grazing by kangaroos is reducing the rate of upward trend in these pastures.

Comparative rate-of-change information has helped to remove ambiguity in trend assessment by placing emphasis on long-term population responses, and has provided a useful method for comparing the relative performance of different management strategies.

## Plant Spatial Arrangements

A preliminary examination of the spatial arrangement of all species at one paired (grazed and ungrazed) site revealed the overriding importance of climatic conditions to the survival of both adult and juvenile individuals. Seasons were featured in all the significant interactions between neighbor-free-space, treatment, and period. The data were not recorded frequently enough to satisfactorily determine the importance of space captured (N-F-S) for the survival of an individual. Average space occupied is a direct function of population size, which my data indicate is more dependent on climate and treatment than on any plant-to-plant interactions. Identifying population organizing agents using this technique may be limited by the spatial variability of arid environments.

## Summary

Application of analyses based on stochastic models of survival and recruitment has proved useful in interpreting population behavior in a number of arid-zone perennial plant species. The effects of management strategies, the importance of different environmental factors and the processes they affect have been successfully examined. Application of these approaches to other populations of rangeland plants is suggested as a potentially profitable avenue by which to improve the understanding, and thus management, of this important natural resource.

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# APPENDICES

# Appendix 1

## An Example of Program SURVIV Output for *Maireana glomerifolia*

Data for Maireana glomerifolia was run on program SURVIV to test a number of hypotheses. The output file is presented in its complete form and represents typical SURVIV output for the simplest case examined in the Yeelirrie data (Chapter 4 and Appendix 2).

Operation of program SURVIV requires the construction of a data file named in the following manner: filename.DAT . The reader should note that all statements in the data file are echoed in the output file and are noted with a corresponding INPUT -- statement. To reconstruct the original input file used for the analysis of Maireana glomerifolia simply arrange the INPUT -- statements in the same order as they appear in the output file that follows. This will give you the necessary form of the input files that must be constructed to run SURVIV. Users are referred to White's (1983) paper for more information on the use of program SURVIV. Details of operational procedures for utilizing the simulation and sample size estimation capabilities are presented with user documentation available with operational copies of the program.

```
Program SURVIV - Survival Rate Estimation with User Specified Cell Probability Functions  27-FEB-84     22:40:39    Page  001
                                                                                Version 1.1(VMS) Apr., 1983
- - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - -

 INPUT --- PROC TITLE MAIREANA GLOMERIFOLIA DATA;

    CPU time in seconds for last procedure was     0.07
 INPUT --- PROC MODEL NPAR=12;

 INPUT ---     COHORT=121/*M21A AND M59A GRAZED*/;
 INPUT ---        2:1.-S(1);
 INPUT ---        3:S(1)*(1.-S(2));
 INPUT ---        3:S(1)*S(2)*(1.-S(3));

 INPUT ---     COHORT=27;
 INPUT ---        13:1.-S(4);
 INPUT ---        2:S(4)*(1.-S(5));

 INPUT ---     COHORT=6;
 INPUT ---        3:1.-S(6);

 INPUT ---     COHORT=127/*M21A UNGRAZED*/;
 INPUT ---        2:1.-S(7);
 INPUT ---        1:S(7)*(1.-S(8));
 INPUT ---        11:S(7)*S(8)*(1.-S(9));

 INPUT ---     COHORT=152;
 INPUT ---        91:1.-S(10);
 INPUT ---        6:S(10)*(1.-S(11));

 INPUT ---     COHORT=113;
 INPUT ---        27:1.-S(12);

 INPUT ---     LABELS;
 INPUT ---        S(1)=SURVIVAL GRAZED COHORT 1 1976 M21A & M59A;
 INPUT ---        S(2)=SURVIVAL GRAZED COHORT 1 1979 M21A & M59A;
 INPUT ---        S(3)=SURVIVAL GRAZED COHORT 1 1982 M21A & M59A;
 INPUT ---        S(4)=SURVIVAL GRAZED COHORT 2 1979 M21A & M59A;
 INPUT ---        S(5)=SURVIVAL GRAZED COHORT 2 1982 M21A & M59A;
 INPUT ---        S(6)=SURVIVAL GRAZED COHORT 3 1982 M21A & M59A;
 INPUT ---        S(7)=SURVIVAL UNGRAZED COHORT 1 1976 M21A ;
 INPUT ---        S(8)=SURVIVAL UNGRAZED COHORT 1 1979 M21A ;
 INPUT ---        S(9)=SURVIVAL UNGRAZED COHORT 1 1982 M21A ;
 INPUT ---        S(10)=SURVIVAL UNGRAZED COHORT 2 1979 M21A ;
 INPUT ---        S(11)=SURVIVAL UNGRAZED COHORT 2 1982 M21A ;
 INPUT ---        S(12)=SURVIVAL UNGRAZED COHORT 3 1982 M21A ;

    CPU time in seconds for last procedure was     7.66
```

```
Program SURVIV - Survival Rate Estimation with User Specified Cell Probability Functions  27-FEB-84      22:40:39     Page  002
MAIREANA GLOMERIFOLIA DATA                                                                Version 1.1(VMS) Apr., 1983
- - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - -

 INPUT --- PROC ESTIMATE NSIG=5 MAXFN=2000 NAME=NOAGE/*adult & juvenile SR equal*/;

 INPUT ---    initial;
 INPUT ---       all=0.5;

 INPUT ---    constraints;
 INPUT ---       S(1)=S(2);
 INPUT ---       S(1)=S(3);
 INPUT ---       S(1)=S(4);
 INPUT ---       S(1)=S(5);
 INPUT ---       S(1)=S(6);
 INPUT ---       S(7)=S(8);
 INPUT ---       S(7)=S(9);
 INPUT ---       S(7)=S(10);
 INPUT ---       S(7)=S(11);
 INPUT ---       S(7)=S(12);

     Number of parameters in model  = 12

     Number of parameters set equal = 10

     Number of parameters fixed     =  0

     Number of parameters estimated =  2



                                Lower    Upper
     I   Parameter    S(I)      Bound    Bound   Label
    ---  ---------   ------     -----    -----   --------------------
     1       1       0.500      0.000    1.000   SURVIVAL GRAZED COHORT 1 1976 M21A & M59A
     2       1       0.500      0.000    1.000   SURVIVAL GRAZED COHORT 1 1979 M21A & M59A
     3       1       0.500      0.000    1.000   SURVIVAL GRAZED COHORT 1 1982 M21A & M59A
     4       1       0.500      0.000    1.000   SURVIVAL GRAZED COHORT 2 1979 M21A & M59A
     5       1       0.500      0.000    1.000   SURVIVAL GRAZED COHORT 2 1982 M21A & M59A
     6       1       0.500      0.000    1.000   SURVIVAL GRAZED COHORT 3 1982 M21A & M59A
     7       2       0.500      0.000    1.000   SURVIVAL UNGRAZED COHORT 1 1976 M21A
     8       2       0.500      0.000    1.000   SURVIVAL UNGRAZED COHORT 1 1979 M21A
     9       2       0.500      0.000    1.000   SURVIVAL UNGRAZED COHORT 1 1982 M21A
    10       2       0.500      0.000    1.000   SURVIVAL UNGRAZED COHORT 2 1979 M21A
    11       2       0.500      0.000    1.000   SURVIVAL UNGRAZED COHORT 2 1982 M21A
    12       2       0.500      0.000    1.000   SURVIVAL UNGRAZED COHORT 3 1982 M21A
    Final function value  444.33413     (Error Return =   0)

    Number of significant digits       9

    Number of function evaluations    52
```

```
Program SURVIV - Survival Rate Estimation with User Specified Cell Probability Functions  27-FEB-84     22:40:39    Page  003
MAIREANA GLOMERIFOLIA DATA                                                              Version 1.1(VMS) Apr., 1983
- - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - -

                                                          95% Confidence Interval
      I    Parameter       S(I)          Standard Error       Lower          Upper
     ---   ---------  --------------    --------------  --------------  --------------
      1        1      0.93548387        0.12310119E-01  0.91135604      0.95961170
      2        1      0.93548387        0.12310119E-01  0.91135604      0.95961170
      3        1      0.93548387        0.12310119E-01  0.91135604      0.95961170
      4        1      0.93548387        0.12310119E-01  0.91135604      0.95961170
      5        1      0.93548387        0.12310119E-01  0.91135604      0.95961170
      6        1      0.93548387        0.12310119E-01  0.91135604      0.95961170
      7        2      0.80341880        0.15041736E-01  0.77393700      0.83290061
      8        2      0.80341880        0.15041736E-01  0.77393700      0.83290061
      9        2      0.80341880        0.15041736E-01  0.77393700      0.83290061
     10        2      0.80341880        0.15041736E-01  0.77393700      0.83290061
     11        2      0.80341880        0.15041736E-01  0.77393700      0.83290061
     12        2      0.80341880        0.15041736E-01  0.77393700      0.83290061


     Variance-Covariance matrix of estimates on diagonal and below,

            Correlation matrix of estimates above diagonal.

   ¶        1              2              3              4              5              6              7              8
   ¶        9             10             11             12
---+--------------------------------------------------------------------------------------------------------------------
   ¶
 1 ¶ 0.15153903E-03  1.0000000      1.0000000      1.0000000      1.0000000      1.0000000      0.00000000E+00 0.00000000E+00
   ¶ 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00
   ¶
 2 ¶ 0.15153903E-03 0.15153903E-03  1.0000000      1.0000000      1.0000000      1.0000000      0.00000000E+00 0.00000000E+00
   ¶ 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00
   ¶
 3 ¶ 0.15153903E-03 0.15153903E-03 0.15153903E-03  1.0000000      1.0000000      1.0000000      0.00000000E+00 0.00000000E+00
   ¶ 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00
   ¶
 4 ¶ 0.15153903E-03 0.15153903E-03 0.15153903E-03 0.15153903E-03  1.0000000      1.0000000      0.00000000E+00 0.00000000E+00
   ¶ 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00
   ¶
 5 ¶ 0.15153903E-03 0.15153903E-03 0.15153903E-03 0.15153903E-03 0.15153903E-03  1.0000000      0.00000000E+00 0.00000000E+00
   ¶ 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00
   ¶
 6 ¶ 0.15153903E-03 0.15153903E-03 0.15153903E-03 0.15153903E-03 0.15153903E-03 0.15153903E-03 0.00000000E+00 0.00000000E+00
   ¶ 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00
   ¶
 7 ¶ 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.22625383E-03  1.0000000
   ¶  1.0000000      1.0000000      1.0000000      1.0000000
   ¶
 8 ¶ 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.22625383E-03 0.22625383E-03
   ¶  1.0000000      1.0000000      1.0000000      1.0000000
   ¶
 9 ¶ 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.22625383E-03 0.22625383E-03
   ¶ 0.22625383E-03  1.0000000      1.0000000      1.0000000
```

```
Program SURVIV - Survival Rate Estimation with User Specified Cell Probability Functions  27-FEB-84      22:40:39    Page  004
MAIREANA GLOMERIFOLIA DATA                                                                  Version 1.1(VMS) Apr., 1983
- - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - -

   ¶
10 ¶ 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.22625383E-03 0.22625383E-03
   ¶ 0.22625383E-03 0.22625383E-03  1.0000000       1.0000000
   ¶
11 ¶ 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.22625383E-03 0.22625383E-03
   ¶ 0.22625383E-03 0.22625383E-03 0.22625383E-03  1.0000000
   ¶
12 ¶ 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.22625383E-03 0.22625383E-03
   ¶ 0.22625383E-03 0.22625383E-03 0.22625383E-03 0.22625383E-03


    Cohort  Cell   Observed  Expected  Chi-square  Note
    ------  ----   --------  --------  ----------  -------------
       1      1          2     7.806       4.319   0 < P < 1
       1      2          3     7.303       2.535   0 < P < 1
       1      3          3     6.832       2.149   0 < P < 1
       1      4        113    99.059       1.962   0 < P < 1
       2      1         13     1.742      72.760   0 < P < 1
       2      2          2     1.630       0.084   0 < P < 1
       2      3         12    23.629       5.723   0 < P < 1
       3      1          3     0.387      17.637   0 < P < 1
       3      2          3     5.613       1.216   0 < P < 1
       4      1          2    24.966      21.126   0 < P < 1
       4      2          1    20.058      18.108   0 < P < 1
       4      3         11    16.115       1.624   0 < P < 1
       4      4        113    65.861      33.739   0 < P < 1
       5      1         91    29.880     125.019   0 < P < 1
       5      2          6    24.006      13.506   0 < P < 1
       5      3         55    98.113      18.945   0 < P < 1
       6      1         27    22.214       1.031   0 < P < 1
       6      2         86    90.786       0.252   0 < P < 1
    -------------------------------------------------------------
    Total (Degrees of freedom =  10)    341.736
    Pr(Larger Chi-square) = 0.0000
    With pooling, Degrees of freedom =   9  Chi-square =     308.999
    Pr(Larger Chi-square) = 0.0000


  . Log-likelihood = -160.08949

      CPU time in seconds for last procedure was    3.88
```

```
Program SURVIV - Survival Rate Estimation with User Specified Cell Probability Functions  27-FEB-84      22:40:39     Page  005
MAIREANA GLOMERIFOLIA DATA                                                                 Version 1.1(VMS) Apr., 1983
- - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - -

 INPUT --- PROC ESTIMATE MAXFN=4000 NAME=NOTRTEFF/*SR set equal across TRTS*/;

 INPUT ---     initial;

 INPUT ---     RETAIN=NOAGE;

 INPUT ---     CONSTRAINTS;
 INPUT ---        S(1)=S(7);
 INPUT ---        S(2)=S(8);
 INPUT ---        S(3)=S(9);
 INPUT ---        S(4)=S(10);
 INPUT ---        S(5)=S(11);
 INPUT ---        S(6)=S(12);

     Number of parameters in model   = 12

     Number of parameters set equal  =  6

     Number of parameters fixed      =  0

     Number of parameters estimated  =  6



                             Lower    Upper
   I    Parameter   S(I)     Bound    Bound   Label
  ---   ---------  ------    -----    -----   --------------------
   1        1      0.935     0.000    1.000   SURVIVAL GRAZED COHORT 1 1976 M21A & M59A
   2        2      0.935     0.000    1.000   SURVIVAL GRAZED COHORT 1 1979 M21A & M59A
   3        3      0.935     0.000    1.000   SURVIVAL GRAZED COHORT 1 1982 M21A & M59A
   4        4      0.935     0.000    1.000   SURVIVAL GRAZED COHORT 2 1979 M21A & M59A
   5        5      0.935     0.000    1.000   SURVIVAL GRAZED COHORT 2 1982 M21A & M59A
   6        6      0.935     0.000    1.000   SURVIVAL GRAZED COHORT 3 1982 M21A & M59A
   7        1      0.935     0.000    1.000   SURVIVAL UNGRAZED COHORT 1 1976 M21A
   8        2      0.935     0.000    1.000   SURVIVAL UNGRAZED COHORT 1 1979 M21A
   9        3      0.935     0.000    1.000   SURVIVAL UNGRAZED COHORT 1 1982 M21A
  10        4      0.935     0.000    1.000   SURVIVAL UNGRAZED COHORT 2 1979 M21A
  11        5      0.935     0.000    1.000   SURVIVAL UNGRAZED COHORT 2 1982 M21A
  12        6      0.935     0.000    1.000   SURVIVAL UNGRAZED COHORT 3 1982 M21A
   Final function value  308.61887      (Error Return =   0)

   Number of significant digits        8

   Number of function evaluations    151
```

```
Program SURVIV - Survival Rate Estimation with User Specified Cell Probability Functions  27-FEB-84      22:40:39    Page  006
MAIREANA GLOMERIFOLIA DATA                                                                      Version 1.1(VMS) Apr., 1983
- - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - -

                                                             95% Confidence Interval
  I   Parameter       S(I)          Standard Error        Lower           Upper
 ---  ---------  --------------     --------------  --------------  --------------
  1       1       0.98387097        0.79992153E-02  0.96819251      0.99954943
  2       2       0.98360656        0.81292574E-02  0.96767321      0.99953990
  3       3       0.94166667        0.15128692E-01  0.91201443      0.97131890
  4       4       0.41899441        0.36878034E-01  0.34671347      0.49127536
  5       5       0.89333333        0.35644334E-01  0.82347044      0.96319623
  6       6       0.74789916        0.39804776E-01  0.66988180      0.82591652
  7       1       0.98387097        0.79992153E-02  0.96819251      0.99954943
  8       2       0.98360656        0.81292574E-02  0.96767321      0.99953990
  9       3       0.94166667        0.15128692E-01  0.91201443      0.97131890
 10       4       0.41899441        0.36878034E-01  0.34671347      0.49127536
 11       5       0.89333333        0.35644334E-01  0.82347044      0.96319623
 12       6       0.74789916        0.39804776E-01  0.66988180      0.82591652


 Variance-Covariance matrix of estimates on diagonal and below,

      Correlation matrix of estimates above diagonal.

   ¶        1              2              3              4              5              6              7              8
   ¶        9             10             11             12
---+-----------------------------------------------------------------------------------------------------------------------
   ¶
 1 ¶ 0.63987445E-04 0.91760135E-15 0.59218744E-14 0.00000000E+00 0.00000000E+00 0.00000000E+00  1.0000000     0.91760135E-15
   ¶ 0.59218744E-14 0.00000000E+00 0.00000000E+00 0.00000000E+00
   ¶
 2 ¶ 0.59669487E-19 0.66084827E-04 0.60202619E-14 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.91760135E-15  1.0000000
   ¶ 0.60202619E-14 0.00000000E+00 0.00000000E+00 0.00000000E+00
   ¶
 3 ¶ 0.71665140E-18 0.74040209E-18 0.22887731E-03 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.54607588     0.58271434E-14
   ¶  1.0000000     0.00000000E+00 0.00000000E+00 0.00000000E+00
   ¶
 4 ¶ 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.13599894E-02-0.53499715E-13 0.00000000E+00 0.24293652E-14 0.24697273E-14
   ¶ 0.00000000E+00  1.0000000    -0.53499715E-13 0.00000000E+00
   ¶
 5 ¶ 0.00000000E+00 0.00000000E+00 0.00000000E+00-0.70324998E-16 0.12705185E-02 0.00000000E+00 0.25967477E-14 0.78988046
   ¶ 0.00000000E+00 0.00000000E+00  1.0000000     0.00000000E+00
   ¶
 6 ¶ 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.15844202E-02 0.71882004     0.00000000E+00
   ¶ 0.00000000E+00 0.00000000E+00 0.00000000E+00  1.0000000
   ¶
 7 ¶ 0.63987445E-04 0.59669487E-19 0.66084827E-04 0.71665140E-18 0.74040209E-18 0.22887731E-03 0.63987445E-04 0.91760135E-15
   ¶ 0.59218744E-14 0.00000000E+00 0.00000000E+00 0.00000000E+00
   ¶
 8 ¶ 0.59669487E-19 0.66084827E-04 0.71665140E-18 0.74040209E-18 0.22887731E-03 0.00000000E+00 0.59669487E-19 0.66084827E-04
   ¶ 0.60202619E-14 0.00000000E+00 0.00000000E+00 0.00000000E+00
   ¶
 9 ¶ 0.71665140E-18 0.74040209E-18 0.22887731E-03 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.71665140E-18 0.74040209E-18
   ¶ 0.22887731E-03 0.00000000E+00 0.00000000E+00 0.00000000E+00
```

```
- - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - -

    ¶
10  ¶ 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.13599894E-02 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00
    ¶ 0.00000000E+00 0.13599894E-02-0.53499715E-13 0.00000000E+00
    ¶
11  ¶ 0.00000000E+00 0.00000000E+00 0.00000000E+00-0.70324998E-16 0.12705185E-02 0.00000000E+00 0.00000000E+00 0.00000000E+00
    ¶ 0.00000000E+00-0.70324998E-16 0.12705185E-02 0.00000000E+00
    ¶
12  ¶ 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.15844202E-02 0.00000000E+00 0.00000000E+00
    ¶ 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.15844202E-02


  Cohort  Cell    Observed  Expected   Chi-square  Note
  ------  ----    --------  --------   ----------  -------------
     1     1          2        1.952      0.001    0 < P < 1
     1     2          3        1.952      0.563    0 < P < 1
     1     3          3        6.831      2.148    0 < P < 1
     1     4        113      110.266      0.068    0 < P < 1
     2     1         13       15.687      0.460    0 < P < 1
     2     2          2        1.207      0.522    0 < P < 1
     2     3         12       10.106      0.355    0 < P < 1
     3     1          3        1.513      1.463    0 < P < 1
     3     2          3        4.487      0.493    0 < P < 1
     4     1          2        2.048      0.001    0 < P < 1
     4     2          1        2.048      0.537    0 < P < 1
     4     3         11        7.169      2.047    0 < P < 1
     4     4        113      115.734      0.065    0 < P < 1
     5     1         91       88.313      0.082    0 < P < 1
     5     2          6        6.793      0.093    0 < P < 1
     5     3         55       56.894      0.063    0 < P < 1
     6     1         27       28.487      0.078    0 < P < 1
     6     2         86       84.513      0.026    0 < P < 1
  -------------------------------------------------------------
  Total (Degrees of freedom =   6)        9.063
  Pr(Larger Chi-square) = 0.1701
  With pooling, Degrees of freedom =   3  Chi-square =       5.997
  Pr(Larger Chi-square) = 0.1118


  Log-likelihood = -24.374226

    CPU time in seconds for last procedure was     5.19
```

```
Program SURVIV - Survival Rate Estimation with User Specified Cell Probability Functions  27-FEB-84      22:40:39     Page  008
MAIREANA GLOMERIFOLIA DATA                                                                   Version 1.1(VMS) Apr., 1983
- - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - -

 INPUT --- PROC ESTIMATE NSIG=5 MAXFN=4000 NAME-NOCONSTRTS/*NO CONSTRAINTS*/;

 INPUT ---    INITIAL;

 INPUT ---    RETAIN=NOTRTEFF;

     Number of parameters in model  = 12

     Number of parameters set equal =  0

     Number of parameters fixed     =  0

     Number of parameters estimated = 12



                                 Lower     Upper
   I   Parameter   S(I)          Bound     Bound  Label
  ---  ---------  ------         -----     -----  --------------------
   1       1       0.984         0.000     1.000  SURVIVAL GRAZED COHORT 1 1976 M21A & M59A
   2       2       0.984         0.000     1.000  SURVIVAL GRAZED COHORT 1 1979 M21A & M59A
   3       3       0.942         0.000     1.000  SURVIVAL GRAZED COHORT 1 1982 M21A & M59A
   4       4       0.419         0.000     1.000  SURVIVAL GRAZED COHORT 2 1979 M21A & M59A
   5       5       0.893         0.000     1.000  SURVIVAL GRAZED COHORT 2 1982 M21A & M59A
   6       6       0.748         0.000     1.000  SURVIVAL GRAZED COHORT 3 1982 M21A & M59A
   7       7       0.984         0.000     1.000  SURVIVAL UNGRAZED COHORT 1 1976 M21A
   8       8       0.984         0.000     1.000  SURVIVAL UNGRAZED COHORT 1 1979 M21A
   9       9       0.942         0.000     1.000  SURVIVAL UNGRAZED COHORT 1 1982 M21A
  10      10       0.419         0.000     1.000  SURVIVAL UNGRAZED COHORT 2 1979 M21A
  11      11       0.893         0.000     1.000  SURVIVAL UNGRAZED COHORT 2 1982 M21A
  12      12       0.748         0.000     1.000  SURVIVAL UNGRAZED COHORT 3 1982 M21A

   Final function value  304.08972      (Error Return =    0)

   Number of significant digits        8

   Number of function evaluations    368
```

```
Program SURVIV - Survival Rate Estimation with User Specified Cell Probability Functions  27-FEB-84      22:40:39     Page  009
MAIREANA GLOMERIFOLIA DATA                                                                     Version 1.1(VMS) Apr., 1983
- - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - -

                                                                95% Confidence Interval
     I    Parameter       S(I)          Standard Error           Lower           Upper
    ---   ---------   --------------    --------------    --------------   --------------
     1        1       0.98347107        0.11590720E-01    0.96075326         1.0061889
     2        2       0.97478992        0.14370411E-01    0.94662391         1.0029559
     3        3       0.97413793        0.14737128E-01    0.94525316         1.0030227
     4        4       0.51851852        0.96159024E-01    0.33004683       0.70699021
     5        5       0.85714286        0.93521953E-01    0.67383983         1.0404459
     6        6       0.50000000        0.20412415        0.99916675E-01   0.90008332
     7        7       0.98425197        0.11047510E-01    0.96259885         1.0059051
     8        8       0.99200000        0.79679358E-02    0.97638285         1.0076172
     9        9       0.91129032        0.25533070E-01    0.86124551       0.96133514
    10       10       0.40131579        0.39757607E-01    0.32339088       0.47924070
    11       11       0.90163934        0.38129597E-01    0.82690533       0.97637335
    12       12       0.76106195        0.40115614E-01    0.68243534       0.83968855


     Variance-Covariance matrix of estimates on diagonal and below,

               Correlation matrix of estimates above diagonal.

   ¶       1              2              3              4
   ¶       9             10             11             12              5              6              7              8
---+------------------------------------------------------------------------------------------------------------------------
   ¶
 1 ¶ 0.13434480E-03 0.20465307E-14 0.25855114E-14 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00
   ¶ 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00
   ¶
 2 ¶ 0.34087714E-18 0.20650870E-03 0.32340193E-14 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00
   ¶ 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00
   ¶
 3 ¶ 0.44164136E-18 0.68489604E-18 0.21718295E-03 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00
   ¶ 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00
   ¶
 4 ¶ 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.92465579E-02 0.27159556E-13 0.00000000E+00 0.00000000E+00 0.00000000E+00
   ¶ 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00
   ¶
 5 ¶ 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.24424534E-15 0.87463557E-02 0.00000000E+00 0.00000000E+00 0.00000000E+00
   ¶ 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00
   ¶
 6 ¶ 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.41666667E-01 0.00000000E+00 0.00000000E+00
   ¶ 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00
   ¶
 7 ¶ 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.12204749E-03 0.27708669E-15
   ¶ 0.27795911E-14 0.00000000E+00 0.00000000E+00 0.00000000E+00
   ¶
 8 ¶ 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.24390792E-19 0.63488000E-04
   ¶ 0.19889826E-14 0.00000000E+00 0.00000000E+00 0.00000000E+00
   ¶
 9 ¶ 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.78405833E-18 0.40465029E-18
   ¶ 0.65193767E-03 0.00000000E+00 0.00000000E+00 0.00000000E+00
```

```
Program SURVIV - Survival Rate Estimation with User Specified Cell Probability Functions  27-FEB-84     22:40:39     Page  010
MAIRLANA GLOMERIFOLIA DATA                                                                 Version 1.1(VMS) Apr., 1983
- - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - -

   ¶
10 ¶ 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00
   ¶ 0.00000000E+00 0.15806673E-02-0.51036298E-13 0.00000000E+00
   ¶
11 ¶ 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00
   ¶ 0.00000000E+00-0.77368044E-16 0.14538662E-02 0.00000000E+00
   ¶
12 ¶ 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00
   ¶ 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.16092625E-02


  Cohort  Cell    Observed  Expected  Chi-square  Note
  ------  ----    --------  --------  ----------  -------------
     1      1         2       2.000      0.000    0 < P < 1
     1      2         3       3.000      0.000    0 < P < 1
     1      3         3       3.000      0.000    0 < P < 1
     1      4       113     113.000      0.000    0 < P < 1
     2      1        13      13.000      0.000    0 < P < 1
     2      2         2       2.000      0.000    0 < P < 1
     2      3        12      12.000      0.000    0 < P < 1
     3      1         3       3.000      0.000    0 < P < 1
     3      2         3       3.000      0.000    0 < P < 1
     4      1         2       2.000      0.000    0 < P < 1
     4      2         1       1.000      0.000    0 < P < 1
     4      3        11      11.000      0.000    0 < P < 1
     4      4       113     113.000      0.000    0 < P < 1
     5      1        91      91.000      0.000    0 < P < 1
     5      2         6       6.000      0.000    0 < P < 1
     5      3        55      55.000      0.000    0 < P < 1
     6      1        27      27.000      0.000    0 < P < 1
     6      2        86      86.000      0.000    0 < P < 1
* *  WARNING  * *    ERROR with chi-square probability.
  ----------------------------------------------------------
  Total (Degrees of freedom =   0)        0.000
  Pr(Larger Chi-square) = ******


  Log-likelihood = -19.845083

     CPU time in seconds for last procedure was   30.94
```

```
Program SURVIV - Survival Rate Estimation with User Specified Cell Probability Functions  27-FEB-84      22:40:39      Page  011
MAIREANA GLOMERIFOLIA DATA                                                                 Version 1.1(VMS) Apr., 1983
- - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - -

 INPUT --- PROC TEST;

    Submodel     Name      Log-likelihood  NDF   G-O-F
    --------  ----------  --------------  ---   ------
        1     NOAGE       -160.08949       10   0.0000
        2     NOTRTEFF    -24.374226        6   0.1118
        3     NOCONSTRTS  -19.845083        0   ******

    NOTRTEFF   VS. NOAGE       Chi-square =   271.431   D.F. =  4  Pr(Larger Chi-square) = 0.0000

* *  WARNING  * *   Sequence of models reinitialized to zero.

    CPU time in seconds for last procedure was   21.09
 INPUT --- PROC STOP;

    CPU time in minutes for this job was    1.15

         E X E C U T I O N   S U C E S S F U L
```

# Appendix 2

# Plant Population Data from Yeelirrie Station

Table 32. Plant population data recorded at Yeelirrie station during the period 1973-82.

SITE M18A Grazed

Erle

| $N_i$ | # Dying | | |
|---|---|---|---|
| 99 | 4 | 0 | 1 |
| 83 | | 27 | 4 |
| 13 | | | 4 |
| 22 | | | |

Ersp

| $N_i$ | # Dying | | |
|---|---|---|---|
| 49 | 2 | 1 | 7 |
| 167 | | 52 | 24 |
| 18 | | | 14 |
| 33 | | | |

Rhsp

| | | | |
|---|---|---|---|
| 1 | 0 | 0 | 0 |
| 11 | | 9 | 1 |
| 0 | | | 0 |
| 4 | | | |

Erxe

| | | | |
|---|---|---|---|
| 67 | 10 | 9 | 25 |
| 104 | | 45 | 37 |
| 29 | | | 19 |
| 9 | | | |

SITE M18A Ungrazed

Erle

| $N_i$ | # Dying | | |
|---|---|---|---|
| 88 | 4 | 0 | 6 |
| 86 | | 24 | 2 |
| 18 | | | 4 |
| 31 | | | |

Ersp

| $N_i$ | # Dying | | |
|---|---|---|---|
| 66 | 3 | 6 | 2 |
| 124 | | 28 | 15 |
| 13 | | | 4 |
| 36 | | | |

Erxe

| | | | |
|---|---|---|---|
| 45 | 2 | 1 | 0 |
| 99 | | 55 | 14 |
| 34 | | | 15 |
| 50 | | | |

SITE M19A Grazed

Erle

| | | | |
|---|---|---|---|
| 170 | 6 | 3 | 6 |
| 56 | | 12 | 4 |
| 17 | | | 4 |
| 17 | | | |

Ersp

| | | | |
|---|---|---|---|
| 13 | 1 | 1 | 1 |
| 29 | | 14 | 1 |
| 5 | | | 1 |
| 6 | | | |

SITE M19A Ungrazed

Erle

| | | | |
|---|---|---|---|
| 74 | 7 | 2 | 3 |
| 22 | | 3 | 1 |
| 11 | | | 0 |
| 7 | | | |

Rhsp

| | | | |
|---|---|---|---|
| 4 | 0 | 0 | 0 |
| 0 | | 0 | 0 |
| 3 | | | 1 |
| 0 | | | |

Ptob

| | | | |
|---|---|---|---|
| 0 | 0 | 0 | 0 |
| 8 | | 0 | 2 |
| 0 | | | 0 |
| 0 | | | |

Sola

| | | | |
|---|---|---|---|
| 23 | 0 | 15 | 4 |
| 5 | | 4 | 0 |
| 1 | | | 0 |
| 4 | | | |

Maco

| | | | |
|---|---|---|---|
| 64 | 29 | 12 | 8 |
| 21 | | 3 | 1 |
| 4 | | | 0 |
| 21 | | | |

Table 32. (Continued)

SITE M20A Grazed

| $N_i$<br>Ersp | | # Dying | |
|---|---|---|---|
| 192 | 10 | 32 | 18 |
| 502 | | 404 | 10 |
| 42 | | | 16 |
| 76 | | | |

| $N_i$<br>Erxe | | # Dying | |
|---|---|---|---|
| 29 | 12 | 3 | 8 |
| 33 | | 22 | 8 |
| 71 | | | 41 |
| 36 | | | |

SITE M20A Ungrazed

| $N_i$<br>Ersp | | # Dying | |
|---|---|---|---|
| 23 | 0 | 11 | 2 |
| 56 | | 37 | 4 |
| 7 | | | 4 |
| 17 | | | |

| $N_i$ | | # Dying | |
|---|---|---|---|

SITE M21A Grazed

Mapy

| | | | |
|---|---|---|---|
| 29 | 1 | 0 | 0 |
| 103 | | 71 | 7 |
| 10 | | | 2 |
| 20 | | | |

Magl

| | | | |
|---|---|---|---|
| 120 | 2 | 3 | 3 |
| 18 | | 7 | 2 |
| 5 | | | 2 |
| 52 | | | |

Mage

| | | | |
|---|---|---|---|
| 2 | 0 | 0 | 0 |
| 4 | | 1 | 0 |
| 7 | | | 0 |
| 0 | | | |

Frpa

| | | | |
|---|---|---|---|
| 64 | 2 | 2 | 1 |
| 110 | | 62 | 5 |
| 1 | | | 0 |
| 123 | | | |

Erlo

| | | | |
|---|---|---|---|
| 0 | 0 | 0 | 0 |
| 1 | | 0 | 0 |
| 0 | | | 0 |
| 0 | | | |

Erla

| | | | |
|---|---|---|---|
| 1 | 0 | 0 | 0 |
| 0 | | 0 | 0 |
| 0 | | | 0 |
| 0 | | | |

Ptob

| | | | |
|---|---|---|---|
| 35 | 1 | 7 | 4 |
| 72 | | 17 | 11 |
| 50 | | | 13 |
| 19 | | | |

Sola

| | | | |
|---|---|---|---|
| 4 | 1 | 0 | 3 |
| 9 | | 4 | 2 |
| 7 | | | 5 |
| 16 | | | |

SITE M21A Ungrazed

Mapy

| | | | |
|---|---|---|---|
| 22 | 0 | 0 | 0 |
| 56 | | 22 | 2 |
| 6 | | | 3 |
| 29 | | | |

Magl

| | | | |
|---|---|---|---|
| 157 | 2 | 1 | 11 |
| 152 | | 91 | 6 |
| 113 | | | 27 |
| 422 | | | |

Mage

| | | | |
|---|---|---|---|
| 3 | 0 | 0 | 0 |
| 2 | | 1 | 0 |
| 3 | | | 1 |
| 15 | | | |

Main

| | | | |
|---|---|---|---|
| 0 | 0 | 0 | 0 |
| 0 | | 0 | 0 |
| 0 | | | 0 |
| 2 | | | |

Frpa

| | | | |
|---|---|---|---|
| 77 | 2 | 7 | 17 |
| 122 | | 80 | 5 |
| 12 | | | 5 |
| 65 | | | |

Erla

| | | | |
|---|---|---|---|
| 1 | 1 | 0 | 0 |
| 7 | | 1 | 0 |
| 0 | | | 0 |
| 3 | | | |

Rhsp

| | | | |
|---|---|---|---|
| 2 | 1 | 0 | 0 |
| 0 | | 0 | 0 |
| 0 | | | 0 |
| 0 | | | |

Ptob

| | | | |
|---|---|---|---|
| 28 | 4 | 3 | 7 |
| 68 | | 10 | 16 |
| 54 | | | 13 |
| 39 | | | |

Table 32. (Continued)

SITE M21A Grazed

| $N_i$ | # Dying | | | $N_i$ | # Dying | | |
|---|---|---|---|---|---|---|---|
| Acan | | | | Hapr | | | |
| 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| 3 | | 0 | 0 | 0 | | 0 | 0 |
| 0 | | | 0 | 0 | | | 0 |
| 0 | | | | 0 | | | |

| Actet | | | |
|---|---|---|---|
| 0 | 0 | 0 | 0 |
| 0 | | 0 | 0 |
| 0 | | | 0 |
| 1 | | | |

SITE M21A Ungrazed

| $N_i$ | # Dying | | | $N_i$ | # Dying | | |
|---|---|---|---|---|---|---|---|
| Sola | | | | Crsu | | | |
| 5 | 0 | 2 | 3 | 3 | 0 | 0 | 0 |
| 11 | | 1 | 5 | 1 | | 0 | 0 |
| 5 | | | 4 | 2 | | | 1 |
| 5 | | | | 1 | | | |

| Acan | | | | Actet | | | |
|---|---|---|---|---|---|---|---|
| 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| 0 | | 0 | 0 | 0 | | 0 | 0 |
| 0 | | | 0 | 1 | | | 0 |
| 0 | | | | 0 | | | |

KEY:--

| | | $N_i$ | # Dying | | |
|---|---|---|---|---|---|
| | | | 73-76 | 76-79 | 79-82 |
| Cohort | 1 | $N_1$ | $D_{11}$ | $D_{12}$ | $D_{13}$ |
| | 2 | $N_2$ | | $D_{22}$ | $D_{23}$ |
| | 3 | $N_3$ | | | $D_{33}$ |
| | 4 | $N_4$ | | | |

Species Codes:--

Erle = Eremophila leucophylla
Ersp = Eremophila spectabilis
Erla = Eremophila lachnocalyx
Erlo = Eremophila longifolia
Sola = Solanum lasiophyllum
Rhsp = Rhagodia spinescens
Acan = Acacia aneura
Actet = Acacia tetragonophylla
Erxe = Eragrostis xerophila

Mapy = Maireana pyramidata
Magl = Maireana glomerifolia
Mage = Maireana georgii
Maco = Maireana convexa
Main = Maireana integra
Ptob = Ptilotus obovatus
Frpa = Frankenia pauciflora
Crsu = Cratystylis subspinescens
Hapr = Hakea preissii

# Appendix 3

# Do Traditional Methods Provide a Reliable Measure of Range Trend?

H.G. Gardiner and B.E Norton

Pages 618-622 in J.F. Bell and T. Atterbury (EDS).
Proceedings of an International Conference on Renewable
Resource Inventories for Monitoring Changes and Trends,
Oregon State University, Corvallis; 1983.

Abstract

Reliable detection of trend in range condition has been hampered by a lack of appropriate statistical treatment and field methodology that generates ambiguous conclusions. Analysis of demographic data offers the most promising avenue for improvement. Mathematical formulation of the basic processes of survival and recruitment and the use of maximum likelihood theory enable a series of progressively more complex models to be tested for goodness of fit to survival data. Those models that are not significantly different from the data can be tested to determine the minimum level of complexity that is necessary to explain the variation in the data. This permits the separation of likely causal factors and treatment comparisons, as is demonstrated using Wilcox bush (Eremophila leucophylla), a semi-arid rangeland shrub from Western Australia.

Keywords -- Rangeland, succession, mathematical analysis, demography, survival, Eremophila leucophylla.

## The Problem

The reliable detection of long-term trend in range condition remains one of the major problems in range management today. The acceptance that trend measurement is dependent on the ability to detect changes in seral stage has been widespread in range literature. Difficulties with this concept are as deep rooted as the basic arguements about the very nature of the successional process. More important for the application of trend measurements to field situations would appear to be the need to separate treatment effects, climatic fluctuation, and intrinsic succession in the vegetation.

The focus of traditional quantitative methods of trend determination has been on detecting change in species composition by comparing samples from the same site at two or more points in time. However, the standard parameters (biomass, cover and frequency) do not provide an unambiguous statement of change, nor do they necessarily provide predictive information to confirm the direction of an apparent trend.

Species composition calculated from biomass values is highly sensitive to climatic fluctuation. There is a tendency for community change to track climatic patterns and generate false impressions of trend, especially when trend determination is derived from samples taken in only two years, each with contrasting precipitation levels and climatic histories. In order to have confidence in trend assessment based on change in proportions of species biomass, one must assume that all species exhibit similar relative growth rates as total precipitation and its temporal distribution, varies. Such an assumption is unsupportable; phenological differences, among others, provide a prima facie case against it.

Composition based on cover data is less likely to produce spurious trend estimates. However, compositional change using cover data emphasizes dominant species in the community, and correspondingly weights the importance of larger and older plants. Cover of a species could significantly increase and appear to be associated with a sucessional trend when actually the change is due to plants growing larger with no alteration, or perhaps even a reduction, in density and frequency. This may have neutral successional value, or even be associated with the process of decline in the species' importance to future community structure: there may be no regeneration and the extant generation may be the last. Likewise, if a few mature plants sampled at the first reading are replaced by a higher density of young at a subsequent sampling, cover alone may indicate no change and yet significant succession may have occurred.

Frequency is a measure of species in a community that ignores both biomass and cover, and is most allied to plant density. Ease of data collection has led to it becoming a popular means of estimating trend. Some procedures manipulate the data on individual species to derive relative frequency as an approximation to plant composition. The pseudo-composition produced by this approach is an artifact of the data analysis and may bear no relation to the biological roles in the true community. To illustrate: a species which in its mature form occurs as very small, widely scattered plants, can show up as the dominant species by frequency criteria when in fact it is ecologically overshadowed by many other species in the community. As the floristic list of a community increases, the relative proportion (and presumably importance) of the dominant species automatically declines because every recorded species is given equal weight regardless of its biomass or cover. Methods that count woody individuals with part of their canopy in, but rooted outside, the frequency quadrat incorporate aspects of both frequency and cover measures, but are readily biassed by subjectivity and difficult to interpret.

Interpretation of individual species frequency data requires caution, particularly at higher frequency values. Changes in frequency can simply reflect changes in dispersion with no change in cover, biomass or density. Frequency changes at the low end of the scale are less ambiguous but should only be interpreted as a change in plant density.

## The Need

Changes in the condition of a rangeland community or ecosystem will be affected by a number of interacting factors (Austin 1981). The challenge to the researcher is to separate the causes of those changes into factors the manager can or cannot control. For example, to be able to separate the effects of grazing, climatic fluctuation and intrinsic succession would provide the manager with information on which to base management decisions.

Detection of detrimental trend is more important than the detection of improvement: a change in management would be more warranted in the face of deterioration of the resource, no matter what the cause, than when improvement is indicated. Not only must a trend measurement be sensitive to his negative change, but it should account for the stochastic nature of the process of change.

The ultimate goal of any method should be to provide a tool that the manager can use to predict the likely effects of any management decision. It should also be flexible enough to permit modification and updating on the basis of new information, and provide, at least in the long-term, a deeper understanding of underlying ecological processes.

## A Solution

Austin (1981) outlined a number of components necessary to constitute a reliable study of vegetation dynamics. He highlighted the need to study populations of individuals located in permanent plots. Beeftink (1979/80) expressed similar views from a purely ecological point of view. To avoid ambiguity successional studies are necessarily long-term and should be based on evidence recorded from permanent plots.

Austin (1981) and Austin et al. (1981) stated that the ideal would be to use data based on records of individual plants, the advantage of which is the ability to examine the basic processes of community change, survival and recruitment. Treatment of this type of data can be simplified if survival is considered as a Bernoulli variable, a plant either dies or survives. For a number of individuals this process is Binomial and when considered as a series of recordings through time, it can be modelled as a Multinomial function. Using this knowledge it is relatively straight-forward to construct tests of a wide range of hypotheses related to the nature of change in plant communities. Further advantages of the individual plant approach are that being recruited or surviving are not derived variables as are other accepted measures. The essential dynamics of the process of change are contained in the data set, unlike density, cover or biomass which are the result of net change over a given temporal or spatial range. Information is not obscured or lost by partial or complete modification to an index, as for frequency. To be able to detect small negative changes in condition and to separate causal factors, it may be necessary to operate at the level of the individual plant.

Plant recruitment and survival within the populations that make up a community are complex functions of a number of environmental variables and inherent species properties. Characterizing the demographic parameters will provide a unique method of describing the dynamics of the vegetation.

Numerous researchers have studied plant survival and a number of different approaches have been adopted to analyze the results. The most widely publicized work has been conducted by John L. Harper and his students. Their main emphasis has been on graphical and tabular representation using survivorship curves and life tables (Harper 1977, Harper and White 1974, Sarukhan and Harper 1973, Law 1981). Their inferences have been based on descriptive comparisons of survivorship with ultimate reference to the archetypal forms reported by Deevey (1947).

Earlier, Tamm (1956) had developed the approach of determining which plants survived, reproduced or died by following individual plants in fixed plots for consecutive years, an approach that was recently applied to semi-arid shrubland by Norton (1978) and re-emphasized by Austin (1981).

The underlying deficiency of perennial plant demographic studies in semi-arid rangelands has been the lack of adequate data sets. Crisp (1978) used data from one 10 meter (m) square quadrat for *Atriplex vesicaria* and and only two sites of similar area of *Maireana sedifolia*. West et al. (1979) used data from only three grazed and six ungrazed 1 m square quadrats in an Idaho sagebrush community; 48 larger plots (100 square feet) were analyzed in a survivorship study in salt desert shrub rangeland (West 1979). The largest data sets (involving thousands of individuals) reported to date are those for perennial grasses in the Australian studies reported by Williams (1970) and Williams and Roe (1975).

Another confounding factor is the erratic nature of the observations in many perennial plant survival data sets. For example, in West's salt desert shrub study cited above, recordings were made at erratic intervals over 35 years. This has the effect of averaging mortality and thus conveying an artificial shape to the survivorship curve. Even more confounding has been the tendency to use average density at different recording times (for example Orr 1980), thus introducing potentially ambiguous results by failing to separate recruitment and mortality.

Few attempts have been made to apply rigorous statistical tests to demographic data sets and those have been confounded by the nature of the data and application of inappropriate tests. West et al. (1979) in their attempt to analyze a small data set used a regression approach that assumes normally distributed data and equality of variance, assumptions that are strongly voilated by survival data. Similarly, the Kolmogorov-Smirnov test applied by West (1979) and West et al. (1979) provides a less than most powerful test of their hypotheses. In a recent publication Austin et al. (1981) applied multivarate statistics to William's data.

## Analysis

Using the previously mentioned Multinomial model of the survival process, it is possible to estimate survival rates under a range of assumptions. The classical method of Maximum Likelihood (Larson 1974) can be used to derive best estimates of the survival rates. On the basis of these estimates it is possible to construct a series of increasingly more complex mathematical expressions or models to explain the variation in the data. For each model, the variance/covariance matrix is easily constructed. Sampling correlation can also be calculated as an added check against the redundancy of variables.

Based on the estimates of the survival rates and their likelihood functions, likelihood ratio tests can be used to compare the different models that provide a good fit to the data. Hypotheses are tested by first formulating the models and then, via the likelihood ratio tests, deciding if the model adds significantly to the understanding of the data. Grazing, climatic, biotic, and environmental factors can thus be tested for their importance as causal factors in the process of change, while at the same time providing a model of that process.

The estimation and testing sequence defined above has been packaged as the computer program SURVIV (White 1983).

## An Example

To demonstrate the power of this approach we will analyze demographic data from one species in semi-arid rangeland of Western Australia. Wilcox bush (Eremopohila leucophylla) is a palatable, drought tolerant shrub regarded as a desirable species by pastoralists. Individual plants were mapped in 150 x 15 m plots using aerial photographs and extensive ground verification. Recordings were made in 1973, 1976, 1979, and 1982. There were sites open to, and protected from grazing by kangaroos. The resulting data matrix (Table 33) hows the numbers of individuals in each of the three cohorts and the number that died during each period of three years.

Table 1. The data matrix for grazed and ungrazed populations of Wilcox bush.

| Treatment | #/cohort (Ni) | # Dying per Period | | |
|---|---|---|---|---|
| | | 1973-76 | 1976-79 | 1979-82 |
| Grazed | 99 | 4 | 0 | 1 |
| | 81 | | 26 | 3 |
| | 13 | | | 4 |
| Ungrazed | 88 | 4 | 0 | 6 |
| | 86 | | 24 | 2 |
| | 18 | | | 4 |

## The Model

Algebraic expressions can be written for each of the data cells and these are used to construct the maximum likelihood estimators of survival (Table 34).

Table 2. Algebraic expressions used to derive values for each data cell in Table 32.

| | Period | | |
|---|---|---|---|
| | 1973-76 | 1976-79 | 1979-82 |
| Cohort 1 | $N_1(1-S(1))$ | $N_1xS(1)(1-S(2))$ | $N_1xS(1)xS(2)(1-S(3))$ |
| Cohort 2 | | $N_2(1-S(4))$ | $N_2xS(4)(1-S(5))$ |
| Cohort 3 | | | $N_3(1-S(6))$ |

The values of S(1) to S(6) in the above matrix are the survival rates that will be estimated in the program SURVIV under a number of different models.

The models considered in this example were:

1. all survival rates equal,
2. adult and juvenile survival rates the same but different from each other,
3. adult survival rates held constant,
4. seasonal survival rates held constant,
5. cohort survival rates held constant,
6. adult survival rates within seasons held constant, and
7 a general model in which all survival rates are different.

Goodness-of-Fit

Of these models only models 2, 3, and 6 provide a good fit to the data, i.e., they are not significantly different from the data at a probability of 0.05.

|  | Model |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|
| Treatment | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
| Grazed | .0000 | .2227[a] | .1137[a] | .0000 | .0001 | .1068[a] | .0489 |
| Ungrazed | .0000 | .1703[a] | .1036[a] | .0000 | .0002 | .3040[a] | .0439 |

[a] Values greater than 0.05 indicate a good fit to the data.

Model Testing

Of the three models (numbers 2, 3, and 6) that provide a good fit to the data, likelihood ratio tests reveal that the best model requires estimates of only two parameters (adult and juvenile survival rates). This model (number 2) provides an adequate description of the data and at the 0.01 level of significance there is no justification for using a more complex model, as can be seen from the probabilities of achieving a higher Chi square value using likelihood ratio tests.

|  | Model Comparisons[a] |  |  |
|---|---|---|---|
| Treatment | 2 x 3 | 2 x 6 | 3 x 6 |
| Grazed | .9237 | .1324 | .0609 |
| Ungrazed | .6153 | .0485 | .0220 |

[a] Since all probabilities are greater than .01, there is no significant advantage to models of greater complexity than number 2.

## Survival Tests Using Model Two

A comparison of the survival rates estimated under model 2 reveals that there are no significant grazing effects on the survival of adult or juvenile plants, although adult and juvenile survival rates are significantly different from one another (Table 35). Confidence intervals overlap when comparing grazed vs ungrazed sites for both adult and juvenile classes, but in both treatments adult survival was significantly higher than juvenile.

Table 3. Adult and juvenile survival rates for grazed and ungrazed treatments.

| Treatment | Class | Survival Rate (95% C.I.) | | |
|---|---|---|---|---|
| Grazed | Adult | .9608 | to | .9926 |
| | Juvenile | .5866 | to | .7751 |
| Ungrazed | Adult | .9413 | to | .9832 |
| | Juvenile | .6455 | to | .8160 |

## Conclusions

Existing methods of trend assessment provide an ambiguous perception of succession. More confidence can be attached to trend derived from demographicinformation but, so far, objective interpretation of survival data has employed inappropriate statistical tests. Application of maximum likelihood inference will enable rigorous analysis of demographic data and reliable description of the extent and probable causes of community change.

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# Appendix 4

# A Photographic Technique for Repeated Mapping of Rangeland Plant Populations in Permanent Plots

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Abstract

A lightweight aluminum photograph stand has been developed to record vegetation in permanent plots. At a camera height of 7 m the plot size is 14 $m^2$ when using a 70 mm camera with an 80 mm lens. Minor degrees of error were detected when testing the accuracy of the stand. This stand will be extremely useful for obtaining a record of permanent plots for many different types of research studies.

## Introduction

Measurements of successional change, or vegetation trend, are difficult to quantify and easy to misinterpret. The usual variables estimated are phytomass, cover or frequency, and gross community changes can occur that might not be reflected by these variables (Gardiner and Norton 1983, West 1983).

Permanent plots were recognized early in the 1900s as providing an extremely valuable source of information for detecting successional trends in vegetation (Cooper 1924). Replacement of one species by another (succession), and the births and deaths of individuals, can easily be detected by sampling permanent plots at regular intervals. With such data, the population dynamics of a species can be estimated, and interpretations of range trends are enhanced. Unfortunately, the two most common techniques available for obtaining such data, the pantograph and chart mapping, are time consuming and often inaccurate. Both techniques require many man-hours. Very few plots are recorded and they are typically only 1 $m^2$ in area. In semiarid rangelands, the small sample size and limited area covered are usually inadequate for reliable records of changes in most species. One notable exception is the data set collected on 9.3 $m^2$ chart-quadrats at the Desert Experimental Range, Utah (Norton 1978). Other techniques for sampling permanent plots are therefore necessary.

Low level aerial photography (Hacker 1978) provides a possible mapping alternative. Many problems, however are associated with small-scale format: different scales due to different aircraft altitudes and uncontrolled distortions caused by aircraft tilt, wind, and site slope.

Maps produced in this manner may not be sufficiently reliable for demographic studies and are generally restricted to low shrublands. Tree canopy cover may obscure essential components of the vegetation, and small individuals, particularly seedlings, are difficult to map accurately. The typical result of sequential recordings of a single plot are assorted photographs of different scales and clarity.

Another possibility is to use a stand to hold a camera for ground-level photography. Cooper (1924) reported devising an oak stand that would hold a 5 X 7 camera six feet above the ground. Unfortunately, the plot accomadated by this stand was only one square meter. Modifications were made throughout subsequent years to either raise or lower the camera height. Camera height has ranged from a low of 1.2 m (Ratliff and Westfall 1973) to a high of 3.5 m (Goodwin and Walker 1972). Corresponding plot sizes ranged from 0.09 $m^2$ to 14 $m^2$, respectively. Only in one photographic method has plot size been sufficiently large to study semiarid vegetation. Goodwin and Walker (1972) developed a photograph stand using a boom rather than the traditional tripod. The camera could be raised to a much greater height, approximately 3.5 m. Using a wide angle lens on a 35 mm camera resulted in a large plot size, but the 35 mm format limits the clarity of the photograph.

Stereographic photograph pairs have commonly been acquired with ground-level stands (Clavern 1966, Pierce and Eddleman 1970, Wells 1971, and Ratliff and Westfall 1973). After taking the first photograph, camera position is changed and a second photograph is taken. Stereo pairs have been used to estimate plant cover on the plot. A single photograph might suffice for recording attributes such as density and plant location necessary for demographic studies.

## The Photograph Stand

Constructed from lightweight box aluminum, a portable stand has been developed for use in semiarid rangelands (Figure 23). Using a boom apparatus rather than a tripod allows the camera height above ground to be increased to as much as 7 m. At the maximum height a 3.5 X 4 m plot is obtained. A plot of this size (14 $m^2$) is adequate for studying most aridland grass and shrub species populations.

In order to consistently re-photograph the same plot, anchor pins were necessary. Three pieces of 1.2 m long 15.8 mm concrete reinforcing bar were driven into the ground at every plot. Guide holes in the frame fit over the anchors so the base position is identical at each sampling time. Slight irregularities of the soil surface seriously affect the repeatability of positioning the camera. Therefore, small leveling legs were installed adjacent to the guide holes so the frame could be leveled before each photograph.

Both a 35 mm and a 70 mm camera were tested with the stand. The 35 mm camera with a 28 mm lens resulted in the largest plot size (6 X 9 m) but the photograph was not sufficiently clear to accurately portray small individuals. Even with a 50 mm lens clarity was not sufficient for accurate, repeatable mapping. The 70 mm camera with a 80 mm lens resulted in a 3.5 X 4 m plot, which was considered large enough and the resolution of the photograph was high. Ektachrome film was used to take advantage of both its rapid development time and the potential for developing the film with a minimum of equipment. Infrared film was also tested but the cold storage and the development requirements were not

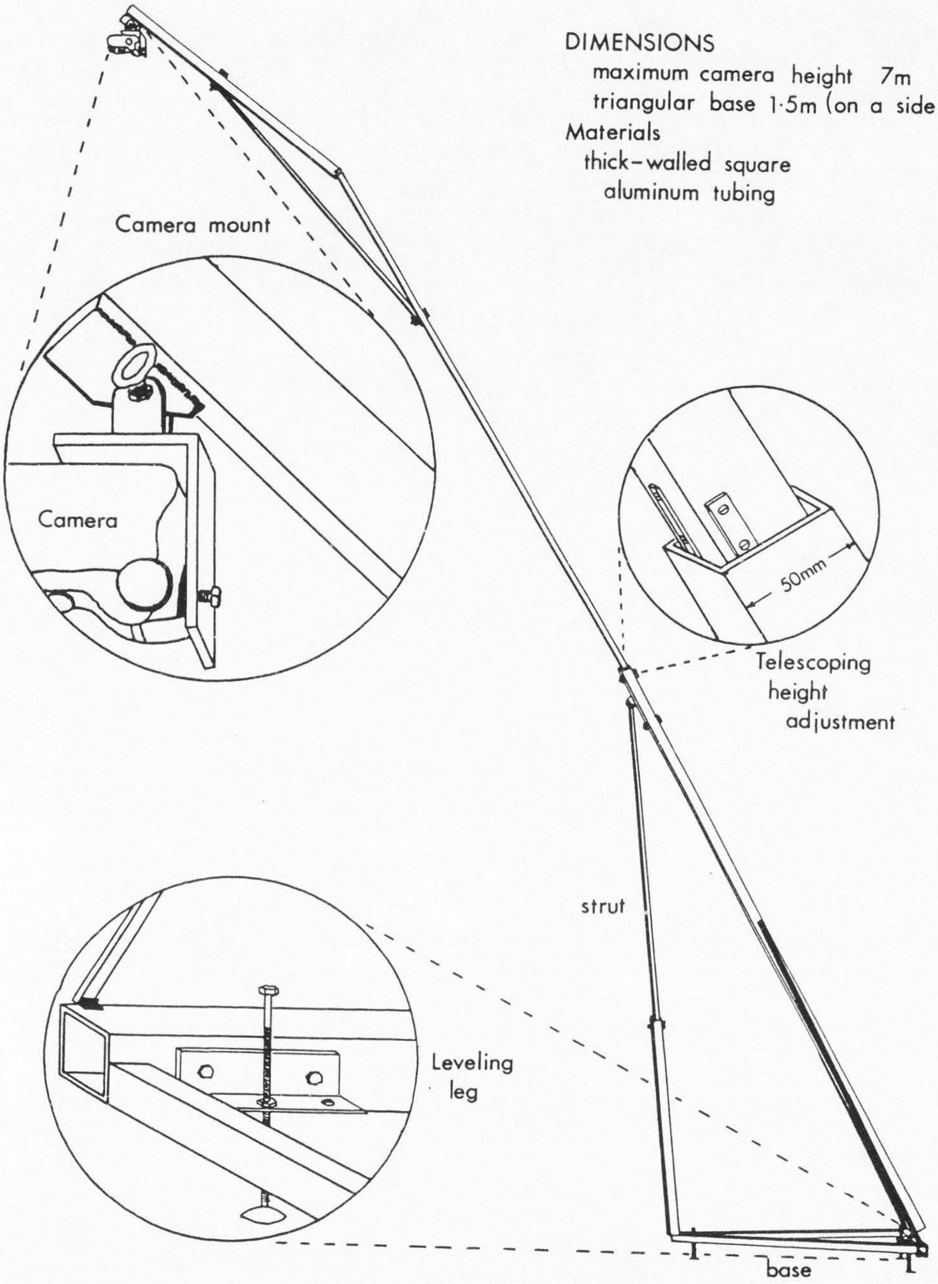

Figure 1. The portable photograph stand used at Tintic Junction, Utah.

conducive to field use.

Color transparencies were developed of each plot photographed. The transparencies were then back-projected onto a piece of glass and the outline of each plant was traced onto a piece of paper. The traced map was then compared to the actual plot for authenticity.

## Results

This stand is currently being used in a plant population study at the Tintic Research Site, Tintic , Utah. During the spring of 1983, seventy plots were photographed, and data were obtained as previously described. A total of 10,256 individual plants were mapped with only minor error.

The most common error was failing to recognize in the photo, and trace on the map, some plants that were in the plot. Approximately 13 percent (1300 individuals) of the total were missed this way. Small plants and new seedlings commonly occurred beneath the canopies of the larger plants. Naturally a vertical photograph could not detect those plants. For this reason, ground verification is essential. Only 15 "plants" (0.01 percent) were traced from the transparency when in fact they were artifacts, either on the film or on the ground.

When the plots were re-visited during the fall of 1983, one hundred percent of the plants mapped during the spring observation could be relocated. In every case either a live plant or a dead stem could be found. Such precision is essential for studying plant population dynamics. In addition, 398 plants, representing a 4 percent error, were mapped for the first time during the fall although they were sufficiently large to have been present at the spring recording time.

Another sampling period (the spring of 1984) is needed before an estimate can be made of the total number of plants being missed in each plot. A removal analysis technique can be used to correct for these errors after the third sampling period.

The amount of time required per plot was highly dependent on the number of plants in the plot (r=0.985). Plot establishment and photographing averaged 45 minutes per plot. Every plot, regardless of the plant density, required this much time. If the plots were already established, photographing time was less than 5 minutes per plot, excluding travel time between plots. Tracing the transparencies onto the map averaged 15 minutes per plot, although variation was high. Ground verification time ranged from 10 minutes for a plot with 119 individuals to 70 minutes for a plot with 666 individuals. Again, the amount of time required was highly dependent on the complexity of the vegetation structure as well as on the number of individuals.

The photo stand was also tested in a grassland community during a grazing behavior study. Plots (2 X 2 m) were photographed and transparencies were again traced to provide a base map of the vegetation. Base maps had previously been established using a chart-mapping technique. The photographs yielded greater accuracy and averaged 66 percent less time per plot (P. Johnson, pers. comm.).

## Conclusions

The use of photographs has been recognized as a viable data collection procedure for a long time; however, problems of small plot size, clarity and repeatability have often presented insurmountable obstacles to using this technique. These problems can be alleviated by increasing plot and film size. By securing a portable aluminum stand to permanent anchors, a plot can be exactly relocated. Such an accurate, repeatable technique will be a valuable tool in grazing behavior research, plant population studies, and in range trend recordings.

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